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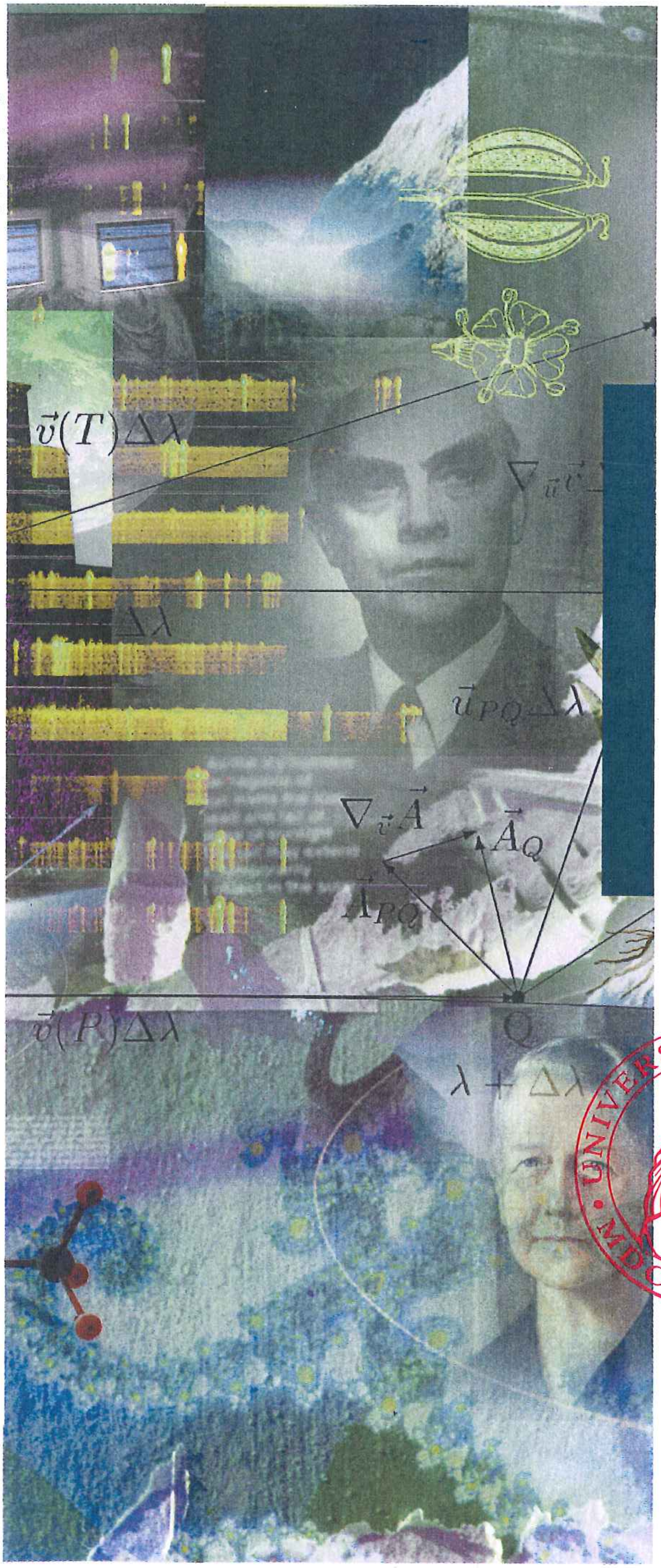
Factors affecting the spatiotemporal distribution of moose, with a special emphasis on supplementary feeding
2010



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Faculty of Mathematics
and Natural Sciences
University of Oslo
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PREFACE

One never works alone, which is especially true for PhD students. I am grateful to my supervisors Atle Mysterud, Leif Egil Loe and Jos Milner. Without you I would not have been anywhere near finishing my PhD project. Atle; your wealth of ecological knowledge and ability to greatly improve (with high speed I should add) my often lengthy and fuzzy manuscript drafts are amazing. Leif Egil; your remarkable talent to explain complex matter in understandable ways has helped me time and time again, especially during my struggles with R. Jos; you opened up your office and house to me and always had time to discuss or answer my far too many ignorant questions. Thanks for being a friend and I look forward to working with you for another year.

In addition, I wish to thank Inger Maren Rivrud for her collaboration and endless discussions regarding the statistics on paper III. Hege Gundersen, Karen Marie Mathisen and Christina Skarpe were of enormous importance to get paper IV published, I truly enjoyed working with you. Most of the data I used would not have been available without the hard and dedicated work of Torstein Storaas, Bent Thorkildsen, Staffan Klasson and Knut B. Nicolaysen. Working with GIS was mostly fun, but when it was not I could always count on the friendly assistance of Barbara Zimmerman. I thank all of my colleagues and friends in Evenstad for the interesting discussions and many hours filled with sports, games and laughs. The support I received from my friends and family in Holland was of enormous value and the many visits gave me a welcome and necessary break from work.

Last of all but certainly the most, I thank my wife Krista Klijzing. I can not write the words to describe how you have helped and encouraged me during my working days but more importantly, how you always have and continue to do in our everyday life. Thank you for believing in me!

Floris M. van Beest

August 2010
Evenstad, Norway

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ABSTRACT

Large herbivores constitute an important natural resource and are actively managed to meet economic, conservation and environmental objectives. To alleviate the potential of resource limitation and damage to commercially important habitats in areas with high population densities, the provisioning of artificial or supplementary forage has become a popular wildlife management intervention throughout Europe and North America. However, the usefulness of supplementary feeding is equivocal and little is known about how it affects spatiotemporal distribution patterns of large herbivores.

The main aim of this thesis is to quantify the effect of supplementary feeding on the spatiotemporal distribution of moose (*Alces alces* L. 1758) living in southern Norway. I used locations of free-ranging GPS (global positioning system) collared moose (N = 26 in summer and N = 32 in winter) with access to supplementary feeding stations to estimate habitat selection and home range size as a function of feeding status (i.e. feeding station users vs. non-users), variation in browse quantity and quality, and also in terms of local climate and individual characteristics. To evaluate fine-scale distribution patterns and foraging decisions around supplementary feeding stations I employed 2 independent datasets (GPS data and browsing estimates) from two study areas (in Telemark and Hedmark counties) that differ in the length of their feeding history. I apply central-place foraging theory to explain the observed patterns.

My results indicate that supplementary feeding affects the spatiotemporal distribution of moose only at intermediate to fine spatial scales during winter, with feeding station users behaving as central-place foragers. However, feeding station users did not differ in their large-scale habitat selection patterns or home range size compared to non-users. Instead, moose habitat selection was driven by a scale-dependent trade-off between browse quantity (landscape-scale) and browse quality (within-home range-scale). Moreover, depletion of high quality browse during winter lead moose to increase selection for lower quality browse within their home range. Variation in home range size was affected by several extrinsic (i.e. climate and natural browse) and intrinsic variables (i.e. individual characteristics) and their effects varied between and within spatiotemporal scales. After 6 years of feeding, moose that used feeding stations selected for commercially valuable browse (i.e. Scots pine) within their home range to the same extent as non-users, which questions the effectiveness of winter feeding in reducing browsing pressure over large spatial scales. In addition, as the time scale of feeding increased from 5-10 to 15-20 years, browsing pressure on commercially valuable browse (i.e. Scots pine and Norway spruce) was amplified at a fine spatial scale. At the same

time, resource depletion in the vicinity of feeding stations lead moose to forage at increasing distances from feeding stations and browsing damage occurred at least up to 1 km from feeding stations. These findings suggest that when supplementary feeding is practised over longer time scales (more than 20 years) there is the potential for a trade off to occur between the energetic cost of returning to the central-place (i.e. feeding station) and the energetic benefits it provides.

Evaluating management actions is important to determine whether the objectives and desired effects are realized. I have shown how supplementary feeding can affect the spatiotemporal distribution of moose and how subsequent browsing pressure around feeding stations can change over time. However, there are a variety of direct and indirect effects that follow the provisioning of supplementary forage that have not yet been adequately assessed. A holistic evaluation of the effectiveness of supplementary feeding as a wildlife management tool is required and needs to consider all the associated benefits and costs, especially considering long-term developments and potential ecosystem-level effects.

LIST OF INDIVIDUAL PAPERS

This thesis is based on 4 papers. They are referred to in the text by their Roman numerals.

I. van Beest, F. M., Loe, L. E., Mysterud, A. & Milner, J. M. (2010) Comparative space use and habitat selection of moose around feeding stations. *Journal of Wildlife Management,* **74**, 219-227.

II. van Beest, F. M., Mysterud, A., Loe, L. E. & Milner, J. M. (2010) Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. *Journal of Animal Ecology,* **79**, 910–922.

III. van Beest, F. M., Rivrud, I.M., Loe, L. E., Milner, J. & Mysterud, A., M. (manuscript) What determines variation in home range size across spatiotemporal scales in a large browsing herbivore?

IV. van Beest, F. M., Gundersen, H., Mathisen, K. M., Milner, J. M. & Skarpe, C. (2010) Long-term browsing impact around diversionary feeding stations for moose in Southern Norway. *Forest Ecology and Management,* **259**, 1900–1911.

INTRODUCTION

In many parts of the world, large herbivores constitute an economically important natural resource, providing income through hunting and tourism, and consequently they are actively managed (Gordon et al. 2004). Populations of large herbivores have been expanding and increasing in density across much of Europe and North America in recent decades (Solberg et al. 1999, Côte et al. 2004, Milner et al. 2006) with various environmental and socio-economic consequences (Côte et al. 2004). Although high herbivore densities may increase economic benefits through increased hunting and tourism opportunities, there are associated costs too, such as an increase in traffic accidents, damage to forestry and agriculture and concern for overgrazing and general ecosystem impacts (Côte et al. 2004, Mysterud 2006). Some high density herbivore populations are now limited by competition for food with consequent negative density-dependent effects on individual quality and performance (Skogland 1983, Kjellander et al. 2006, De Roos et al. 2009). To offset such problems and keep economic revenue high, the provisioning of artificial or supplementary forage has become a popular wildlife management intervention throughout Europe and Northern America. It is especially common in areas where herbivore densities are higher than the natural habitat can maintain (Peek et al. 2002, Putman and Staines 2004). The main goals of supplementary feeding are to increase body weight, survival rate, and/or reproductive performance in order to maintain high population densities (see Putman and Staines 2004 for a detailed review). However, feeding may also be carried out to control or reduce environmental damage, particularly to agriculture, forestry and habitats of high conservation value, or to reduce animal-vehicle collisions. The rationale behind such feeding (diversionary feeding), is to divert animals away from e.g. major traffic arteries, young forest stands or other valuable habitats via the provision of an alternative, strategically placed, food source (Putman and Staines 2004). However, herbivores that use feeding stations will often still consume natural forage which may lead to over-browsing or over-grazing in the vicinity of feeding stations (Schmitz 1990, Doenier et al. 1997, Gundersen et al. 2004, Putman and Staines 2004), though long-term browsing/grazing impacts have rarely been assessed.

Whatever the effectiveness of winter feeding is in achieving its main objectives, there is little understanding about how supplementary winter feeding may affect foraging decisions of large herbivores or how selection criteria for habitat or natural forage resources change relative to the position of feeding stations. Forage variability in general is considered a crucial driver of habitat selection strategies in large herbivores

(Wilmshurst et al. 1999, Apps et al. 2001, Fortin et al. 2003, Hebblewhite et al. 2008). Forage resources required by large herbivores are patchily distributed over space and time, regardless of whether those herbivores are grazers that feed predominantly on graminoids, or browsers that feed on forbs, shrubs or branches of trees (Bailey et al. 1996, Tufto et al. 1996, Fryxell et al. 2004). In addition, a common feature of food resource distribution is that quality and quantity are often inversely correlated (Demment and van Soest 1985, Fryxell 1991), with the most nutritious items tending to be the least common (Hansen et al. 2009). In highly seasonal environments, forage resources are, generally, of lower quality during winter (Shipley et al. 1998) and diminish through the season due to natural browsing, snow cover and lack of new vegetation growth (Edenius 1991). As such, large herbivores should adopt a scale-dependent selection strategy that optimizes access to areas with sufficient abundance of high quality forage. Indeed, scale dependency in habitat selection as a function of forage variability has been observed in many grazing ungulates (Wilmshurst et al. 1999, Apps et al. 2001, Fortin et al. 2003, Anderson et al. 2005), though exceptions do occur (Schaefer and Messier 1995). In contrast, most studies investigating the spatiotemporal relationship between browsing herbivores and their natural food supply have focused on relatively fine spatial scales and/or during one particular season (Tufto et al. 1996, Hobbs 2003, Månsson et al. 2007).

Due to the food limitation affecting many populations of large herbivores, and the important role of forage resources in habitat selection strategies, supplementary feeding is likely to affect distribution patterns of large herbivores. Indeed, there is some indication that feeding stations can serve as attraction points as regular feeding of deer can restrict space use patterns to the vicinity of feeding stations (Guillet et al. 1996, Doenier et al. 1997, Kilpatrick and Stober 2002, Sahlsten et al. 2010). A better understanding of how animals select habitats or resources around supplementary feeding stations may help in the design of more effective feeding programs, especially in areas where both wildlife management and commercial land use practises need to produce benefits at the same spatial scale (Visscher and Merrill 2009).

AIMS AND OBJECTIVES

The Norwegian moose population is a good example of a growing and actively managed ungulate population, as described above. The annual harvest has increased from 7500 individuals in 1960 to over 35000 in 2009 (Statistics Norway; www.ssb.no). The economic importance of the moose population in Norway is substantial with the annual income (incorporating revenue from tourism and hunting) estimated somewhere between 70 – 90 million US dollars in 2000 (Storaas et al. 2001). In contrast, moose-vehicle accidents, browsing damage in young forest stands (mainly of Scots pine [*Pinus sylvestris*]) and management incentives taken to try and reduce these factors may result in annual costs of between 23 - 80 million US dollars (Storaas et al. 2001). Diversionary feeding to reduce forest damage and moose - vehicle collisions is popular in Norway (Gundersen et al. 1998, Andreassen et al. 2005). Supplementary feeding is also increasingly being used as a management practise to increase harvest yield by lowering food limitation. However, relatively little is known about the general impact of supplementary feeding on moose or its habitat.

The main aim of this thesis is to quantify the effect of supplementary feeding on the spatiotemporal distribution of moose in southern Norway.

First, I evaluate the effect of supplementary feeding stations on habitat selection patterns at intermediate spatial scales (i.e. within-home range) during winter in an area with a relatively short feeding history (6 years). I use central-place foraging theory (CPF; described below) as a basis to explain the observed patterns of space use around feeding stations (**paper I**). Furthermore, I evaluate the effectiveness of winter feeding as a management intervention to reduce the use of commercially valuable forest stands (**paper I**). I then continue to quantify space use and habitat selection of moose at multiple spatial and temporal scales. As noted, an important motivation to provide supplementary forage is to offset limitation or depletion of natural forage, in particular during winter when forage re-growth does not occur. In **paper II**, I explore, whether moose change their selection patterns during winter following depletion of natural forage resources, and, for the first time, determine whether the behavioural response to possible depletion of natural forage can be inferred from GPS-based habitat selection patterns. To do so, I assess habitat selection patterns at intermediate to coarse spatial scales during summer and winter seasons in relation to natural forage characteristics (i.e. browse quantity and quality). Supplementary feeding often reduces home range size of large herbivores (Guillet et al. 1996, Cooper et al. 2006). In **paper III,** I tested whether the home range size of moose varied with the intensity of feeding station use but also in terms of quality and density of natural browse, individual characteristics and climatic determinants. Lastly, to enable assessment of more long-term effects of supplementary feeding on moose selection patterns, as well as on the natural vegetation, I quantify how browsing pressure around feeding stations changed over time and space in an area with a feeding history of 15-20 years (**paper IV**).

Clearly, to understand the role of supplementary feeding on the spatiotemporal distribution of moose, I need to put this into a more general ecological framework considering other factors also known to affect distribution patterns. I will therefore first describe such a framework, namely that of habitat selection, central-place foraging theory and the effect of scale on animal space use.

WHAT IS HABITAT SELECTION?

Habitat selection occupies a basic but fundamental place in ecological research (Morris 2003) and is concerned with the "where and how" animals are distributed relative to their environment (Rosenzweig 1981). Understanding this process is imperative because the distribution of individuals not only affects population dynamics (McLoughlin et al. 2006), but also their interactions with other species through competition (Stewart et al. 2002) and predation (Hebblewhite and Merrill 2009) or via cascading trophic effects (Ripple et al. 2001, Suominen et al. 2008). From a conservation perspective, habitat selection studies provide an essential source of information that can aid in the development of effective management strategies (Hobbs 2003, Gordon et al. 2004) and a valuable tool to evaluate species responses to habitat alterations (Saïd and Servanty 2005, Long et al. 2008) or management actions (Bergquist et al. 2009, Månsson et al. 2009).

Despite the widespread use of habitat selection analyses within ecological research, there is an ongoing debate about the most useful, operational definition of habitat selection in the literature. Moreover, the application of interrelated terms such as avoidance, availability, preference, resources, and even habitat is variable and inconsistent (Thomas and Taylor 1990, Morrison and Hall 2002, Thomas and Taylor 2006, Gaillard et al. 2010). Because I use these terms regularly throughout my thesis I find it necessary to present and discuss the definitions that I have used. Hall et al. (1997) defined habitat as "*the resources and conditions present in an area that affect occupancy, including survival and reproduction, by a given organism*." This intuitive description implies that each habitat holds a collection of specific resources that are important for individual survival and population growth (Morris 2003). But what exactly is a resource? Morrison & Hall (2002) defined this as "*any biotic or abiotic factor directly used by an organism, and includes food, nutrients, water, atmospheric gas concentrations, light, soil, weather (i.e., precipitation, temperature, etc.), terrain, and so on*". Prins et al. (2008) argued that this definition is inaccurate because "*….the essence of the concept 'resource' is that organisms can compete for a resource (such as competing for food, nutrients, water, etc.)….*". For example, organisms can not compete for weather (or, in the case of large mammals, for light) which can therefore not be considered a resource. Instead, weather (and, for some species, light) may better represent environmental conditions. Furthermore, Prins et al. (2008) stress that the use of resources may lead to the (temporary) exhaustion of that resource. In other words; resources are depletable.

Because this thesis is about a large forest dwelling species, I will use the term habitat to refer to forest stands (**paper I**). I consider a resource as any biotic, depletable habitat component (mostly browse as in **papers II, III & IV**). Habitat selection, as originally defined by Johnson (1980), is the process by which an animal chooses which habitat or habitat components (i.e. resources) to use. In contrast, a large body of literature treats selection as a pattern, which is the consequence of the process described by Johnson (1980). Habitat selection is then defined as a situation in which habitat or resources therein, are used disproportionately to their availability (sensu Manly et al. 2002). I have used the latter definition as much as possible (**papers I, II & IV**). However, I also regard spatiotemporal scaling of home range size as an indirect means to evaluate habitat selection (e.g. **paper III**), because home ranges are considered a spatial expression of an individual's movement behaviour, driven by a complex interplay between environmental conditions and the internal state and requirements of an individual (Börger et al. 2008, Horne et al. 2008). I define preference as what an animal would prefer to eat in a controlled setting with access to known alternative forage (sensu Thomas and Taylor 2006). I have tried not to use the term avoidance too often, but I define it as lower use of a habitat or resource than would be expected from its availability or, alternatively, when use is low compared to that of another specified habitat or resource (a reference category; **papers I & II**).

Although it would be convenient for ecologists to have one operational definition for habitat selection and interrelated terms, I believe that their meaning and interpretation is, to some extent, a matter of personal taste. To facilitate inter- and intradisciplinary comparisons and to avoid misinterpretation of results one should, therefore, at least provide a species- and study-specific definition of what is meant by habitat selection, something that is often ignored (Hall et al. 1997).

CENTRAL-PLACE FORAGING THEORY

Foraging decisions of large herbivores, such as predicted by optimal foraging theory (OFT; Charnov 1976, Stephens and Krebs 1986), are progressively being incorporated into habitat selection analyses (e.g. Fortin et al. 2003). The OFT focuses on how to maximize energy intake per unit of foraging time under various constraints, and is typically concerned with smaller scales than habitat selection theory. The central-place foraging theory (CPF; Orians and Pearson 1979) is a special case of the OFT and predicts space use and foraging decisions as a function of the distance from a focal point. In the classical case, the focal point is a nest or a den, but any key resource that acts as an attraction point may give rise to a space-use pattern resembling central-place foraging

(Rosenberg and McKelvey 1999). As such, CPF theory may prove useful in predicting habitat/resource selection around feeding stations, although in this case the central-place is a (non-natural) foraging hot-spot and movements are made away from this to meet other needs. Predictions of the CPF theory are largely based on biological mechanisms such as energy efficiency and resource depletion (Rosenberg and McKelvey 1999). Selection for habitat/resources by an individual exhibiting central-place behavior is typically a function of both the habitat's or resource's quality and proximity to the central-place. In this thesis I evaluate if moose that utilize feeding stations use their available space and select for habitat/resources as predicted for a central-place forager. To do so I focus on the following three predictions:

1) Space use should be concentrated around the central-place and decline as distance increases.
2.1) Differences in selection of available habitat (or resources) should be low close to the central-place and increase as distance increases.
2.2) Differences in selection for preferred habitat (or resources) compared to lower ranked habitat should be small in the vicinity of the central-place and increase as distance increases, such that only highly preferred habitats are selected at long distances from the central-place.

I will refer to these predictions again when I present the results and discussion of moose habitat selection during winter (**paper I**) and browsing pressure around long-term supplementary feeding stations (**paper IV**).

THE EFFECT OF SCALE

The effect of scale has been an increasingly important aspect of wildlife studies ever since the proposition that ecological processes are often connected to particular spatial or temporal scales (Johnson 1980, Senft et al. 1987, Wiens 1989, Levin 1992). In fact, the space and time dimensions in habitat selection are closely linked (Wiens 1989). Habitat selection is now widely accepted as being scale-specific and the incorporation of scale may be especially crucial when considering large and mobile species that can cover extensive distances over space and time (Boyce 2006).

Johnson (1980) recognized four main hierarchical spatial levels of selection (Figure 1). Selection decisions at broad spatial scales typically reflect selection for a distribution range (first-order selection) or home range/territory establishment within a landscape (second-order selection). At the within-home range-scale, selection can be separated into selection for a habitat/patch (third-order selection) and selection for a site or food item (fourth-order selection). As such, habitat selection within a population can be described as a hierarchical spatial process with landscape-level home range establishment and the final choice of a dietary item as the endpoints of a selection continuum (Johnson 1980, Morris 1987, Gaillard et al. 2010).

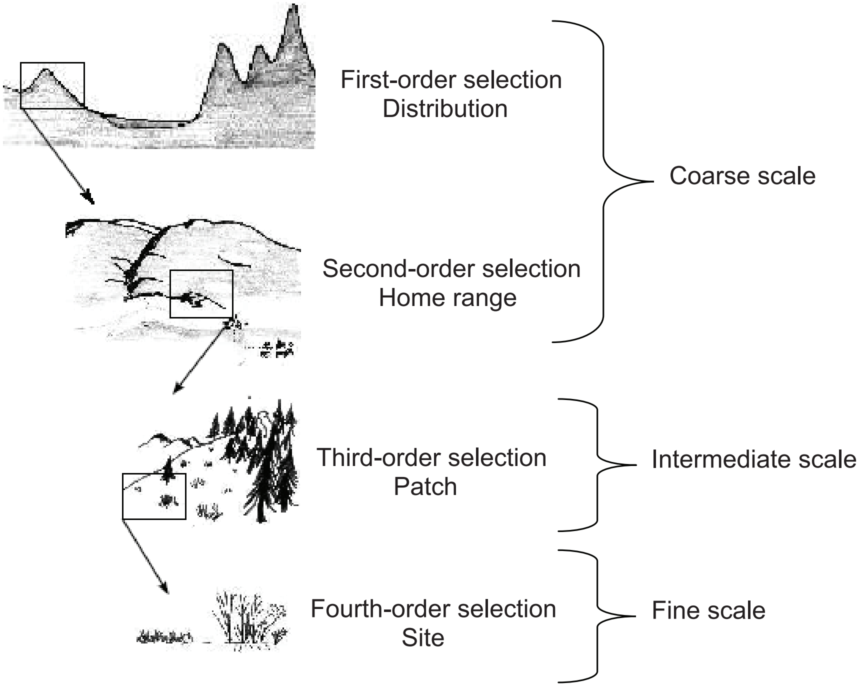

Figure 1: Habitat selection hierarchy. Johnson (1980) distinguished four levels of habitat selection: species distribution, home range, foraging patch and foraging site.

Just like spatial scales, the effect of temporal scale is of crucial significance for habitat selection analysis. For example, habitat selection patterns may vary between years or seasons, as well as within seasons, which requires separate models (or also management strategies) for each timescale or the explicit inclusion of temporal scales in the analyses (Boyce 2006). Furthermore, selection patterns can vary depending on the daily activity cycle of an animal, thereby requiring differentiation between e.g. foraging activities and resting periods.

A thorough understanding of how, and at which spatiotemporal scales, large herbivores respond to their environment is of considerable interest from both scientific and management points of view (Hobbs 2003, Weisberg and Bugmann 2003, Gordon et al. 2004). Besides the importance of availability and quality of natural forage on habitat selection strategies, abiotic factors such as local climate and intrinsic variables such as individual characteristics or current state may also produce scale-dependent spatiotemporal space use patterns (Figure 2). As such, identifying the appropriate scales for the analyses is of prime importance when conducting or interpreting studies of space use and habitat/resource selection. Failing to do so might result in false interpretations of the mechanisms involved (Kie et al. 2002, Börger et al. 2008, McLoughlin et al. 2009).

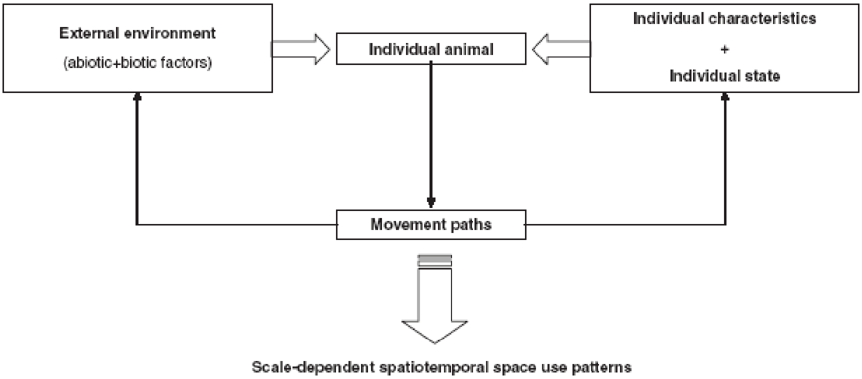

Figure 2: Graphical overview of how space use patterns are influenced by both intrinsic and extrinsic conditions as experienced by an individual (image from Börger et al. 2008).

STUDY SPECIES

The moose is the largest member of the deer family (Cervidae) with males being generally larger than females (Putman 1989, Bubenik 1998). Its distributional range (including all 8 subspecies of which 4 in Eurasia [Baskin & Danell 2003] and 4 in Northern America [Bubenik 1998]) covers most of the circumpolar boreal vegetation zone (Bergstrom and Hjeljord 1987). Adaptations such as large body size, tolerance to low temperatures, substantial flexibility in digestive processes, and long legs are some of the features enabling moose to thrive in areas with strong seasonal variations in temperature and forage quality as well as periods of deep snow cover (Bubenik 1998).

The Eurasian moose evolved some 100 000 – 300 000 years ago (Bubenik 1998) and is currently found throughout Fennoscandia and in parts of Russia, the Baltic states, Belarus, Poland, Ukraine, China and Mongolia (Baskin and Danell 2003, Wilson and Reeder 2005). The Norwegian moose represents the westernmost population within the Eurasian range. Population sizes in Norway, as in the rest of Scandinavia, have grown considerably over the last few decades (since 1970s) and densities in local wintering areas can be extreme (e.g. 5-6 moose/km^2: Lavsund et al. 2003). The decline of natural predators, regulated moose hunting, and decreased competition from free ranging livestock have all contributed to this increase (Cederlund and Markgren 1987). However, an important driving factor behind the increase of moose numbers has been attributed to changes in forest management due to the positive effects of clear cutting on forage availability (Cederlund and Markgren 1987).

The moose is a typical browser (Cederlund et al. 1980, Bergstrom and Hjeljord 1987) and is regarded as an energy maximizer (i.e., the assumed goal of an individual's foraging strategy is to maximize the long-term rate of energy intake; Belovsky 1978, Stephens and Krebs 1986). To meet its nutritional requirements a moose needs approximately 5 kg of food (dry weight) per winter day and ~10 kg of food (dry weight) per summer day (Hjeljord et al. 1982, Persson et al. 2000). During summer, moose typically strip the leaves of deciduous trees and forage on shrubs and herbs. During winter, they feed predominantly on the twigs of deciduous trees and Scots pine (Bergstrom and Hjeljord 1987, Hjeljord et al. 1990)

STUDY AREAS

TELEMARK AREA

The majority of the data used in this thesis (**papers I, II & III**) was collected in southern Norway (Figure 3A) within parts of Telemark, Buskerud and Vestfold counties (referred to in the text as 'Telemark area'). The area (1733 km^2) ranges in altitude from 20 to 800 m with the forest line at approximately 750 m. It is in the boreonemoral zone and is mostly covered by commercially managed coniferous forest (82%). Stands are dominated by Norway spruce (*Picea abies*) and Scots pine but some mixed deciduous stands of birch species (*Betula pubescens* and *B. pendula*), rowan (*Sorbus aucuparia*), willow (*Salix* spp.) and aspen (*Populus tremula*) occur throughout the area. Abundant field layer species include bilberry (*Vaccinium myrtillus* L.), cowberry (*V. vitis-idaea* L.), raspberry (*Rubus idaeus* L.) and, rosebay willowherb or fireweed (*Epilobium angustifolium* L.). The mean monthly temperature during summer (June through September in 2007-08) was 14.5 °C (min: 10.6 °C in September, max: 16.4 °C in July), and during winter (January through April 2007-08) was 1.9 °C (min: -0.6 °C in February, max: 6.6 °C in April) (Siljan weather station at 100 m a.s.l., The Norwegian Meteorological Institute; http://www.met.no). Average (± SE) snow-depths in the centre of the study area (430 m a.s.l) during Jan.-Apr. 2007 and 2008 were 49 ± 2.4 cm and 72 ± 1.5 cm respectively and numbers of days with snow cover were 127 in 2007 and 143 in 2008 (Mykle weather station, The Norwegian Meteorological Institute). Moose densities in the area are estimated at 1.5 individuals per km^2 (Norwegian Directorate for Nature Management; http://www.dirnat.no). Red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.) densities are estimated at 0.5 and 0.2 individuals per km^2 respectively. Large predator species are absent and hunting is the single most important cause of moose mortality in this area.

HEDMARK AREA

I used data collected in a different part of Norway for **paper IV**. This area is located in southeast Norway (Figure 3B), Stor-Elvdal municipality, Hedmark County (referred to in text as Hedmark area) and ranges in elevation from 250 to 1100 m with the forest line at approximately 800-900 m. The area (~1850 km^2) is dominated by low-productivity, commercially managed, boreal forest with pure or mixed stands of Scots pine and

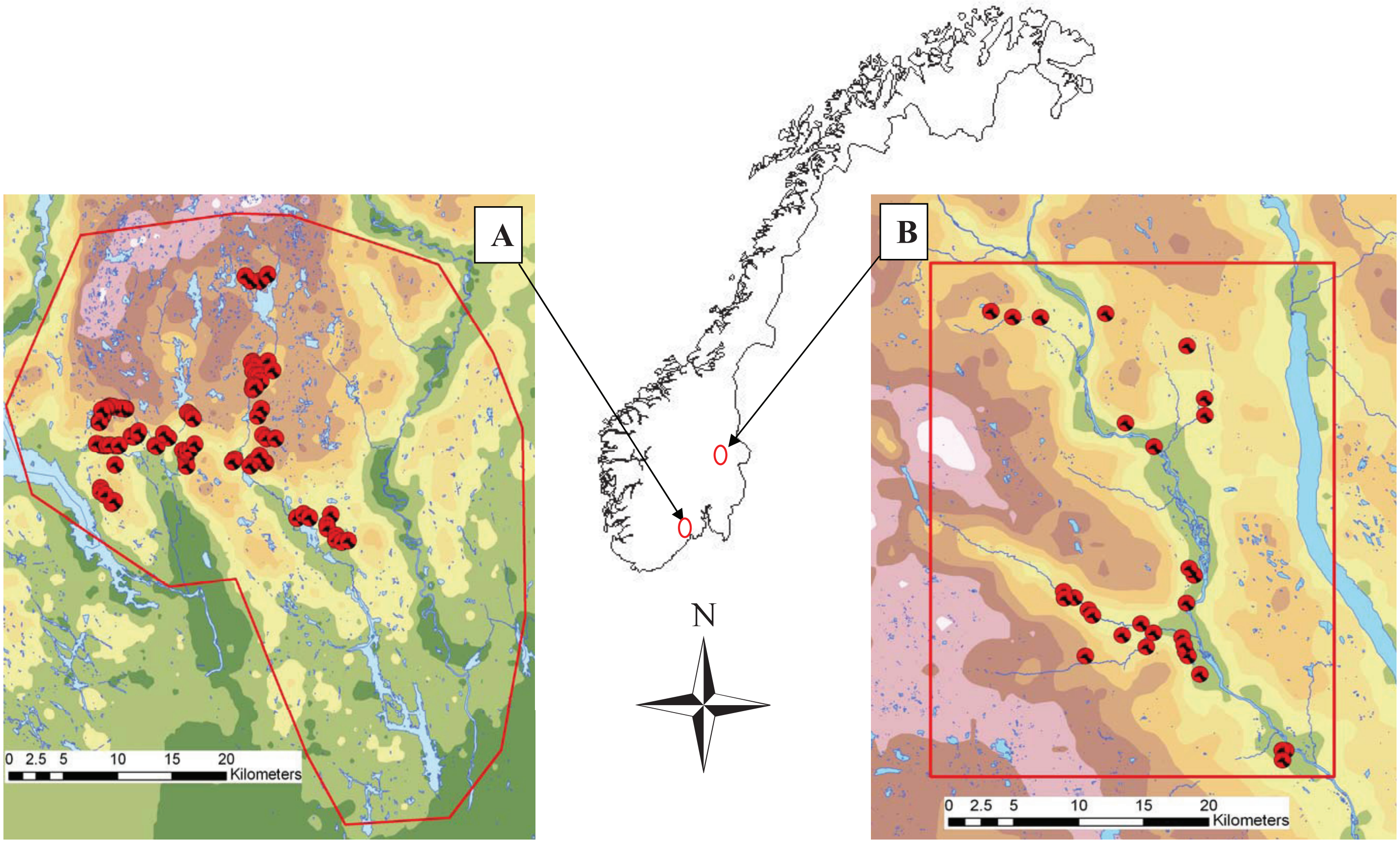

Figure 3: Map of the two study areas in southern Norway. Telemark area on the left (A) and Hedmark area on the right (B). Euclidian distance between the centres of the two areas is 250 km. Supplementary feeding stations used in this thesis are indicated in red.

Norway spruce. In addition, deciduous species such as birch, rowan, willow and aspen occur at low densities throughout the area. The mean monthly temperature during summer (June through September in 2007-08) was 11.9 °C (min: 7.5 °C in September, max: 14.6 °C in July), and during winter (January through April 2007-08) was -2.5 °C (min: -8.3 °C in February, max: 4.4 °C in April) (Haugedalen weather station, Norwegian Meteorological Institute). Numbers of days with snow cover were 154 in 2007 and 182 in 2008. The cervid community in the area is dominated by moose (> 1.1 moose/km2 during winter; Gundersen et al. 2008) with very low densities of roe deer and red deer. Transient individuals of wolf (*Canis lupus*) and brown bear (*Ursus arctos*) are occasionally observed in the area but hunting is the single most important cause of moose mortality in this area.

SUPPLEMENTARY FEEDING PRACTICES

The practice of supplementary feeding wild herbivores varies from place to place in terms of the type, quality and amount of forage offered. In both the study areas considered here, supplementary food is provided by local landowners and consists of baled roughage, predominantly mixed graminoids. One bale of silage weighs ~ 600 kg. Feeding stations are located at fixed (permanent) sites along snow-cleared forest roads with low human activity. The supplementary food is provided *ad libitum* for up to 6 months of the year (i.e., November through April, with starting and ending time dependent on annual snow conditions).

The feeding history in the Telemark area (Figure 3A) is relatively short as supplementary feeding of both moose and red deer was initiated in 2001-02. At present there are a total of 94 permanent feeding stations in the area and the amount of supplementary forage consumed by moose over a 4 month period was 182 ton during winter 2006/07 and 244 ton in 2007/08.

Supplementary feeding of moose and red deer in the Hedmark area (Figure 3B) was initiated in the late 1980s. In this area, the total amount of supplementary food provided at feeding stations has increased greatly over the last years with ~ 150 ton (across 44 feeding stations) during winter 1997-98 and ~ 1700 ton (across 157 feeding stations) during winter 2007-08.

MATERIALS AND METHODS

MOOSE LOCATION DATA & SAMPLE SIZE

Data on animal movement and space use can be collected by various direct and indirect techniques including snow tracking (Mysterud et al. 1999), camera traps (Kuijper et al. 2009), live-trapping (Schradin et al. 2010) and browsing / grazing signs (Månsson et al. 2007). Another method involves the use of animal-borne technology such as radio-telemetry and global positioning system (GPS) devices. The majority of the moose location data used in this thesis was collected via GPS collars (Telemark area; **papers I, II & III**) while browsing signs were also used (Hedmark area; **paper IV**). A total of 34 adult female moose (16 individuals in 2007 and 18 individuals in 2008) were fitted with GPS collars (Tellus Remote GSM, Followit AB, Lindesberg, Sweden) programmed with a 1-h relocation schedule. Collar data were collected from January-November in both years. However, GPS positions taken during spring and autumn were not included in this thesis, partly to avoid the inclusion of long distance movements during the migration period and those associated with the autumn breeding season. Long directional movements, such as during migration periods, can seriously affect home range size (Luccarini et al. 2006) and moreover, habitat use during the migration period may differ from that at other times of the year (Fryxell and Sinclair 1988). In this thesis, snow conditions in the Telemark area were used to define winter length (period with ≥ 30 cm snow depth). As such, winter in 2007 stretched from Jan. 21st until Apr. 8th and in 2008 from Jan. 4th until Apr. 30th. Summer was defined as the period 1st of June till 15th of September for both years.

A recurrent problem in animal tracking studies using GPS technology is collar failure which may result in low sample size (Tomkiewicz et al. 2010). Indeed, my final sample size was reduced to 32 individuals during winter and to 26 individuals during summer because of collar malfunctions ($n = 6$) and the death ($n = 2$) of collared individuals during the study period. Although these numbers are above the mean sample size (18.1 GPS collared animals; min = 4, max = 82) used in 30 recent habitat selection and movement studies as reviewed by Hebblewhite & Haydon (2010), my sample size is likely too small to make strong population-level inference and I therefore caution against generalizing my results over larger spatiotemporal scales than used in my studies.

GPS BIAS

GPS-based telemetry is now one of the most popular and widely used methods in animal tracking studies (Aarts et al. 2008, Tomkiewicz et al. 2010) and allows for frequent, automatic sampling of animal locations over long periods of time which easily leads to the acquisition of large datasets. However, large GPS based datasets bring various complexities and problems that need to be understood and addressed in order to make the data valuable. One important consideration when dealing with animal locations estimated with GPS technology is that they inherently contain errors (Frair et al. 2004, D'Eon and Delparte 2005, Bjørneraas et al. 2010), which may bias habitat selection and home range size analyses when not handled appropriately (Swain et al. 2008, Frair et al. 2010). Two common types of errors in GPS location data are missed locations (or “fixes”) and location errors of successfully acquired fixes (Frair et al. 2004, Lewis et al. 2007). The probability of successfully acquiring a location, as well as the magnitude of the associated location error, may be related to environmental conditions (D'Eon and Delparte 2005, Graves and Waller 2006) and/or behavioural characteristics of the study species (Moen et al. 1996, Bjørneraas et al. 2010). Hence, the first step before analyzing GPS data should be to screen and clean the data by exclusion or correction of location errors and missed fixes in the dataset.

The GPS collars used in this thesis attained an average fix rate (with collars on the moose) of 92 % (range 72-99 %) during winter and 90 % (range 83-97 %) during summer. To correct for possible bias in GPS fix success prior to analyzing habitat selection (**papers I & II**), I employed an iterative simulation approach detailed by Frair et al. (2004). This method is based on a spatially predictive model of the probability of successfully acquiring a fix under certain environmental conditions. Using field tests in the Telemark area during early winter, I estimated how fix rates were biased across forest stands (with varying cutting class and dominant tree species), slopes and sky visibility. Unfortunately I was unable to test for GPS fix rate bias and location error under summer conditions as the collars were on the moose during this period. I therefore used winter conditions throughout my studies when correcting for GPS error. With the final predictive model, I was able to probabilistically fill in all missed locations during the study period (for more detail on this approach see **paper I**).

The GPS location error, estimated during field testing, was calculated as the linear distance between the recorded GPS location and the assumed “true” location (determined from the average of 24 GPS positions) which resulted in a median location error of 16 m with 95 % of the locations within < 75 m ($N_{obs} = 2590$). Because my intention was to link moose locations to environmental data, the location error should, at least, be lower than the resolution e.g. pixel size, of the vegetation map (see section on Forage quantity and quality below). As this was the case (resolution of all underlying environmental maps I have used was ≤ 50x50 m.), I did not correct for location error. However, prior to habitat selection analyses (**papers I & II**), locations where movement between 2 successive GPS locations exceeded 30 km/hr were removed from the dataset and replaced with locations predicted by the iterative simulation approach described above. Moose are known to reach 30 km/h in gallop (Baskin & Danell 2003) but I thought it unlikely that an individual could maintain this speed for more than 1 hr. With this rule I was able to identify and re-position all large locational outliers. Prior to the home range size analyses (**paper III**) I adopted a more detailed technique to detect large locational outliers, based on non-movement characteristics (i.e. using knowledge of how animals do not move) of moose (Bjørneraas et al. 2010). This approach also classifies erroneous fixes based on a speed rule but the threshold is determined and calculated by the mean distance between 21 GPS positions within a moving window. An additional criterion in this method is that the turning angle of the erroneous location should be greater than 166° but less than 194° (i.e. the animal is returning in roughly the same direction it came from; Figure 4).

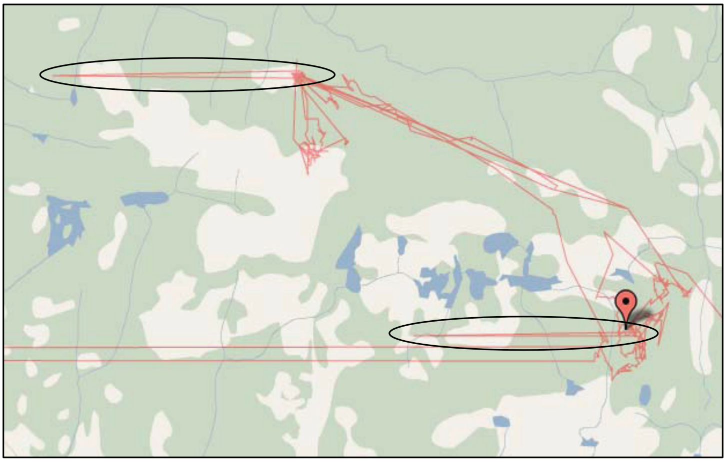

Figure 4: Two erroneous positions identified using non-movement characteristics.

FEEDING STATION USE

To evaluate the effect of supplementary feeding on habitat selection I categorized the GPS-collared moose as feeding station users or non-users (**paper I**). To do so, I calculated the total number of hours spent within a 100 m buffer around feeding stations for each moose separately. I then divided this by the total number of GPS locations obtained during winter for that individual. Because feeding stations are small (< 20 m^2)

and because the location in between the hourly GPS fixes is not known, I assumed that moose located within a 100 m buffer from feeding stations had indeed visited the station. Using this approach I found that, of the 32 collared moose, 10 individuals did not use feeding stations at all, 7 individuals used feeding stations < 1% of the time, 2 individuals between 1 and 2% and 13 individuals used feeding station > 2% during winter. Because the proportion of time spent on feeding stations did not provide an unambiguous division between feeding station users and non users, I also employed an alternative classification method to facilitate the categorization of feeding station use. This method is based on a Euclidean distances analysis (EDA) as proposed by Conner & Plowman (2001). For methodological details of this approach I refer to **paper I**. The results of the EDA analysis established that 15 moose were associated with the position of feeding stations more than expected by chance while the remaining 17 were not. The 15 moose classified as feeding station users with the EDA analysis all used feeding stations > 1% as determined with the first approach and were therefore classified as feeding station users. 'Feeding status' (feeding station users vs. non-users) was subsequently included as a covariate in the habitat selection analysis.

When assessing the effect of supplementary feeding on indirect measures of habitat selection, such as spatiotemporal scaling of home range size (**paper III**), I did not categorize the GPS collared moose into distinct feeding use classes. Instead, I included feeding station use as a continuous variable into the analyses. Again, this was calculated by dividing, for each individual, the number of GPS locations within a 100 m buffer of feeding stations by the total number of locations. However, the number of GPS locations used in this calculation were not taken from the whole winter period but instead extracted from a specific spatiotemporal scale (i.e. from day to month and from total home range size and core home range size).

HOME RANGE ESTIMATION

A popular topic in wildlife tracking studies is assessing home range characteristics and identifying factors that cause home range size to vary between and within species (e.g. McLoughlin and Ferguson 2000, Börger et al. 2006, Saïd et al. 2009). There are numerous methods available to estimate home range size and new techniques are still being developed (Getz and Wilmers 2004, Getz et al. 2007). Over the last few decades there has been considerable debate about which method is most suitable to estimate animal home ranges (Worton 1987, Seaman and Powell 1996). Nevertheless, all available techniques contain unique advantages, disadvantages and assumptions. Deciding which home range estimator to use is mostly related to the question and study species under investigation (Huck et al. 2008).

Throughout this thesis I have used 2 home range estimation techniques: the minimum convex polygon (MCP; Mohr 1947) and the non-parametric local convex hull polygon (LoCoH; Getz and Wilmers 2004, Getz et al. 2007). However, when and how I use a particular technique varies between study objectives as the spatial properties of these methods have important consequences for habitat selection and general space use analyses. For example, I use the MCP in habitat selection analyses (**paper I & II**) as a spatial boundary to sample availability of habitat and resources at the within-home range-scale (see section on resource selection functions below for sampling design). However, MCPs are known to over-estimate home range size as it often includes large unused areas (White and Garrott 1990, Huck et al. 2008) so whenever I use MCP I do not present figures on moose home range size. For this purpose (**paper III**), I employ the LoCoH method. The main advantage of estimating animal home ranges with the LoCoH method is that it allows for holes and hard boundaries in the home range due to inaccessible terrain (e.g. lakes and rocky outcrops) and is therefore less likely to include areas that an individual cannot use compared to other estimators (Getz et al. 2007).

To assess variation in home range size of moose as a function of individual-level characteristics, browse characteristics and local climate patterns (**paper III**); I calculated home range size across multiple spatial and temporal scales for each moose separately. I used days, weeks, biweeks and months within both summer and winter season as time units and total home range area (i.e. 90% isopleths) and core home range area (i.e. 50% isopleths) as spatial units. For methodological details on home range size calculations and assumption of the LoCoH method see **paper III**.

GEOGRAPHIC INFORMATION SYSTEM (GIS) AND FIELD DATA

Map accuracy

Throughout this thesis I used habitat (i.e. forest stand) characteristics derived from 8-year-old GIS maps. Dussault et al. (2001) recommend evaluating the accuracy of important habitat characteristics represented on forest maps via field observations, which may be especially important in habitat selection studies (Frair et al. 2010). For instance, when map misclassification rates exceed 10%, habitat selection coefficients are seriously affected, which might lead to false conclusions (Johnson and Gillingham 2008). To evaluate forest map accuracy I randomly sampled 180 forest stands throughout the Telemark area and found that 94.8 % of the forest stands were correctly classified with regard to cutting class and dominant tree species. The biggest part of the misclassification (2.7 %) was attributed to recent clear cut felling of cutting class 5 in spruce dominated forest stands. Overall, I considered the accuracy of the GIS maps adequate for my purposes.

Browse quantity and quality

An important objective of this thesis is to quantify habitat selection and home range size of moose as a function of changes in spatial (landscape level) and temporal (seasonal level) variability of browse quantity and quality (**papers II & III**). Estimating forage quantity and quality across a forested landscape is not easy and detailed field data on plant distribution, availability and quality has only been collected in a few study sites (Hebblewhite et al. 2008, Zweifel-Schielly et al. 2009). Most studies presume habitat quality and forage availability on the basis of forest stand productivity (Bo and Hjeljord 1991) stand age (Dussault et al. 2005) or stem density (Visscher et al. 2006). The remotely-sensed Normalized Difference Vegetation Index (NDVI) can also be used to link vegetation productivity and phenology with animal movement and space use (Boone et al. 2006, Hansen et al. 2009). Indeed, the NDVI is strongly correlated with above-ground vegetation biomass (Pettorelli et al. 2005), but it remains difficult to determine how much of the vegetation biomass is truly available for herbivores and to accurately assess vegetation quality (Herfindal et al. 2006).

Instead, I developed spatially explicit forage availability maps, based on extensive field data collected in the Telemark area, and for both summer and winter seasons for each of the 6 most common tree species browsed by moose in southern Norway. I included silver birch, downy birch and Scots pine. Rowan, aspen and willow were also included but I combined them into 1 RAW species group. Norway spruce was excluded because of its negligible use as a food item by moose (Cederlund et al. 1980, Hornberg 2001, Kalen and Bergquist 2004) although exceptions do occur (Faber and Pehrson 2000, Gundersen et al. 2004). Species-specific forage availability was measured during summer 2007. To do so I used measurements of tree characteristics, browsing patters as observed for moose in the Telemark area (i.e. site-specific strip length and bite diameter), and sampling of trees in different forest stands across the area to predict and spatially map the availability of species-specific forage quantity (for methodological details see **paper II**).

To express forage quality for moose in terms of single measures of digestibility, nutrient content or secondary compounds is complicated and rarely straightforward when analyzing multiple species (Bergstrom and Danell 1986). Instead, what I refer to as forage quality is based on selection ranks as reported in previous studies of species-specific forage resource selection patterns of moose in the boreonemoral or boreal zone of Scandinavia (results of the literature review are summarized in **Table S1 in paper II**).

I only included studies with a use-availability sampling design to be able to assess if species were actively selected, avoided or used proportional to their availability (Thomas and Taylor 2006). Based on this review, I refer to rowan; aspen and willow (termed RAW species group) as higher quality browse species and silver birch, downy birch and Scots pine as lower quality species during summer. During winter Scots pine is considered to be of higher quality than silver birch and downy birch.

Moose browsing around feeding stations

To quantify changes in the spatial scale of moose winter browsing pressure around supplementary feeding stations over a 20 year time period (**paper IV**), I used field data from 1998 (Gundersen et al. 2004) and 2008, both collected in the Hedmark area. The tree species I considered here (i.e. target species) were the same as for the forage availability maps (given above). In addition, I included Norway spruce because of previously observed leader stem browsing by moose in the vicinity of feeding stations (Gundersen et al., 2004). Moose browsing pressure in 2008 was recorded around the same 30 feeding stations as surveyed in 1998 using sampling plots ($n = 420$) located at 12.5, 25, 50, 100, 200 m from feeding stations (for methodological details see Gundersen et al. 2004). Additional browse surveys were carried out at 500 and 1000 m from feeding stations in 2008 as I expected browsing pressure to have expanded spatially over time. For each target species present in a sampling plot (trees < 0.5 m high were assumed to be unavailable to moose during winter due to snow cover), one tree was selected, based on the average height of that particular species within a plot. For each selected tree I recorded *i*) presence / absence of leader stem browsing during the previous winter, *ii*) the number of lateral twigs available within moose browse height (0.5 - 3 m: Danell et al. 1985), and *iii*) the number of lateral twigs browsed during the previous winter.

STATISTICAL ANALYSES

Resource selection functions

Available methods and statistical models to quantify habitat selection include compositional analysis (Aebischer et al. 1993), K-select analysis (Calenge et al. 2005), habitat suitability models (Dussault et al. 2006), Maxent models (Baasch et al. 2010), and related resource utilization functions (Millspaugh et al. 2006). Perhaps the most popular technique to quantify relative use of habitat resources is the resource selection function (RSF) defined as any function proportional to the probability of use by an organism (Manly et al. 2002). RSFs are typically used to link animal distribution to spatial patterns of habitat or forage resources within an area by contrasting the characteristics of used animal locations with those of a set of randomly drawn locations (Poole and Stuart-Smith 2006, Godvik et al. 2009, Zweifel-Schielly et al. 2009). As such, RSFs are often estimated using logistic regression with used animal locations (response variable coded as ones) and available (or non-use) locations (response variable coded as zeros).

Similarly, I quantify habitat and forage resource selection patterns at different spatiotemporal scales by estimating RSFs based on use-availability designs. I considered GPS locations (**papers I & II**) and browsing signs of moose (**paper IV**) as measures of utilized habitat/forage resources. A more challenging aspect of estimating RSFs at different spatial scales with use-availability designs is the definition of availability. How availability is sampled and the inferred scales of selection are, by default, related. For my purposes, I adopted sampling designs described by Thomas & Tailor (1990, 2006). For coarse-scale habitat selection patterns (second-order of selection; **paper II**) I compared seasonal home range characteristics of individual moose with characteristics of the Telemark area. As such, the total landscape delineated what was considered available to the moose. Availability was sampled by randomly drawing locations at the population level (i.e. design 2; availability is equal for all individuals). For intermediate-scale habitat selection patterns (third-order of selection; **papers I & II**) I compared moose location characteristics in the Telemark area with characteristics of their individual home ranges. In this case, home range delineates availability and was sampled by randomly drawing locations from within seasonal 95% MCP home ranges (i.e. design 3; availability is sampled for each individual separately). For fine-scale habitat selection patterns (fourth-order of selection; **paper IV**) I compared the number of browsed lateral twigs with available twigs at a certain distance from feeding stations. In this case, the utilized (browsed) trees delineate availability which was sampled by counting the number of twigs available (i.e. design 4; availability is sampled around each used site). Leader stem browsing was not quantified with a use-availability but rather with a use-nonuse design. Availability (or non-use) sampled for each use, is what distinguishes design 4 from design 3 (Thomas and Taylor 2006).

Recent advances in mixed-effects models have improved the usefulness of RSFs which have been successfully applied to various species e.g., grey seals (*Halichoerus grypus*; Aarts et al. 2008), wolves (*Canis lupus*; Hebblewhite and Merrill 2008), red deer (Cervus elaphus; Godvik et al. 2009), and woodland caribou (*Rangifer tarandus caribou*; Koper and Manseau 2009). All RSFs estimated here were solved using logistic regressions; either with generalized linear mixed models (GLMM; sensu Gillies et al. (2006); **paper I & II**) or with generalized additive mixed models (GAMM; sensu Wood 2006, Aarts et al. 2008; **paper IV**). Incorporation of a random intercept into RSFs is especially beneficial with unbalanced sampling designs (Gillies et al. 2006) such as in **papers I & II**. To reduce the risk of type I errors as a result of correlated used and availability data, I calculated 95% Highest Posterior Density intervals as they are more conservative compared to standard 95% confidence intervals (Baayen et al. 2008). For methodological details on RSF estimation, confidence intervals and model prediction procedures see methods in **papers I, II & IV**.

Home range size analysis

The issue of spatiotemporal scale in home range size modeling has only been considered in a few, recent studies (Kie et al. 2002, Mitchell and Powell 2004, Börger et al. 2006, Rivrud et al. in press) with Spencer et al. (1990) as an exception. In addition, many studies consider only a single or a few factors to quantify variation in home range size (Cederlund and Sand 1994, Relyea et al. 2000, Kilpatrick and Stober 2002) though animals clearly scale their home range size in response to a variety of intrinsic and extrinsic conditions (Börger et al. 2006, Saïd et al. 2009).

To quantify how moose home range size, and variation therein, changes over space and time I used an established multi-scale approach developed by Börger et al. (2006). As such, I estimated home ranges (LoCoH) of moose using GPS locations collected at successively larger temporal scales (i.e. from daily to monthly scales in both summer and winter seasons) and spatial scales (i.e. from core home range area to total home range area). Home range size at the various spatiotemporal scales was subsequently analysed using linear mixed-effects modeling to decompose the variation of home range size into individual-level, forage and climatic processes (**Table 1 in paper III**).

All statistical analyses used in this thesis were performed in R (R Development Core Team 2008).

RESULTS AND DISCUSSION

HABITAT SELECTION AND SUPPLEMENTARY WINTER FEEDING (PAPER I)

Supplementary winter feeding of cervids as a management tool is increasing, but its effect on space use and habitat/resource selection has rarely been assessed. Here I evaluate whether space use and habitat selection patterns of moose using feeding stations during winter conform to the CPF predictions given in the introduction above.

Firstly, I found that despite the low feeding station usage of the GPS collared moose in the Telemark area (the percentage of time spent at feeding stations during winter was, on average, 5% per feeding station user), the probability of a location being used decreased markedly as distance from feeding stations increased (conforming to CPF prediction 1). For example, the likelihood that a feeding station user selected habitat within 500 m of feeding stations was almost 5 times higher than selecting habitat beyond 1.5 km from feeding stations. This is indicative that feeding stations serve as central attraction points within moose wintering ranges. Secondly, variation in habitat selectivity (as indicated by the red arrows in figure 5) between stands of Scots pine forest of differing age close to feeding stations was low but increased as feeding station users ventured further away (conforming to CPF prediction 2.1). The only notable exception was that recent clear-cut areas (cutting class 1) were selected less compared to older forest stands at all distances from feeding stations, increasing the overall selectivity close to feeding stations. This is to be expected as clear-cut areas mostly contain small trees and shrubs that are unavailable during winter due to snow cover. I did not find any evidence to support CPF prediction 2.2 in the Telemark area. Instead, young Scots pine stands (cutting class 2) were selected most from all available pine habitat at distances of up to 1 km from feeding stations but not thereafter. This inconsistency with CPF theory indicates that intraspecific competition and potential resource depletion close to feeding stations was not of concern to feeding station users in this study area. However, this finding is likely to be related to the low local moose densities around feeding stations arising from the short feeding history in the Telemark area (~6 years at the time of this study). Local animal densities may become increasingly high when winter feeding is practised over longer time frames (Peek et al. 2002). Under such conditions space use patterns and selection decisions in the vicinity of feeding stations may radically change.

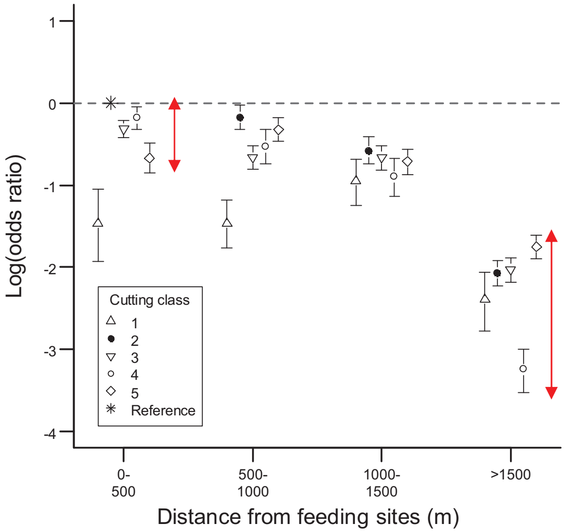

Figure 5: Log(odds ratio) of selecting for available Scots pine stands as a function of distance from feeding station. All estimates are in comparison to the reference category cutting class 2 at 0-500 m from feeding stations. Variation in habitat selectivity is depicted by the red arrows.

When I compared habitat selection estimates of GPS collared feeding station users and non-users at the within-winter home range-scale (**see Figure 1 in paper I**) this revealed that feeding station users continued to select for commercially valuable forest stands (i.e. young Scots pine stands) to the same extent as non-users. Although I did not assess browsing damage in these forest stands, this finding may suggest that pine remained an important part of the diet for moose that used feeding stations. As such, supplementary feeding stations were not successful in diverting moose away from valuable natural browse, at least when evaluated at this temporal scale (~6 years).

LARGE-SCALE HABITAT SELECTION (PAPER II)

An important question for supplementary feeding programmes is whether or not natural browse in wintering areas is limited or depletes over time. Here I evaluated whether moose selection for browse quantity and quality both at the landscape-scale (second-order of selection) and the within-home range-scale (third-order of selection) was scale-dependent and affected by forage depletion (**paper II**).

I found that forage selection patterns by moose in the Telemark area varied across spatial and temporal scales in a manner that suggests a scale-dependent trade-off between available browse biomass (i.e. quantity) and browse quality (**paper II**). Moose actively selected for habitat with a high abundance of lower quality browse species at the landscape-scale. In contrast, at the within-home range-scale moose selection was for high quality browse species, at least during summer and at the beginning of winter (**Figures 2 & 3 in paper II**). Indeed, I found evidence for depletion of high quality browse during winter. The initial positive selection for habitat containing high quality browse biomass in early winter (at the within-home range-scale) decreased as winter progressed (**Figure 3 in paper II**). At the same time, selection for areas with high biomass of lower quality species increased, suggesting depletion of high quality species biomass. Similar changes in selection criteria of moose following reduced availability of high-quality forage have been observed in Sweden (Edenius 1991, Shipley et al. 1998) despite the differences in scale and method of observation from my approach. The forage availability maps I have used were based on forage availability estimates recorded during one time period, giving only a static snap-shot of spatial variation in availability. As such, I cannot provide tangible evidence that resource depletion indeed occurred. However, I also observed low site fidelity during winter months (**see Figure 4 in paper II**) which suggests that resource depletion of quality browse necessitated moose to move more in order to acquire sufficient forage. In contrast, during the growing season when resources are constantly renewed, moose showed high site fidelity and selection for high quality resources remained fairly stable over time. This suggest that temporal changes in browse quality during the growing season did not seriously affect selection decisions made by moose (but see next section for a discussion on changes in browse quality and the effect on home range size).

Although not presented in paper II, I have also assessed whether feeding station users differ in their selection for natural browse compared to non-users. Based on the low feeding station use and similar selection for Scots pine habitat of feeding stations users and non-users described above (**paper I**), I expect similar selectivity of natural browse regardless of feeding status, both at the within-home range-scale (at least for Scots pine browse biomass) and at the landscape-scale, especially during summer. I found no major differences in seasonal selection for natural browse between feeding station users and non-users (**Table 1**). At the within-home range-scale, feeding station users selected less for habitat with high downy birch biomass than non-users but only during winter. The remaining selection estimates for natural browse species, including Scots pine, were not significantly different between feeding station users and non-users (**Table 1**). These results suggest that feeding stations were not successful in reducing the use of commercially valuable natural browse (Scots pine) at the within-home range-scale, supporting the results found in paper I, but also that the effect of feeding stations on the spatiotemporal distribution of moose at the landscape level is low. Moreover, selection patterns during summer were highly comparable between feeding station users and non-users indicative that there were no lagged effects of supplementary feeding.

Table 1: Summary statistics of the landscape-scale and within-home range-scale RSF models for summer and winter, predicting habitat selection for feeding station users (in reference to non-users) as a function of species-specific browse availability. The model includes a random intercept for each individual (moose ID) and selection estimates are presented as log odds ratio ± 95 % HPD intervals. Significant differences between groups (where the HPD interval does not overlap with 0) are indicated in bold.

			HPD interval	
Landscape-scale - winter	***β***	**SE**	**lower**	**upper**
RAW species biomass x feeding status (yes)	0.008	0.009	-0.010	0.026
Scots pine biomass x feeding status (yes)	0.008	0.007	-0.003	0.023
Silver birch biomass x feeding status (yes)	-0.081	0.111	-0.299	0.131
Downy birch biomass x feeding status (yes)	-0.010	0.005	-0.020	0.003
Landscape-scale - summer				
RAW species biomass x feeding status (yes)	0.006	0.008	-0.010	0.022
Scots pine biomass x feeding status (yes)	0.017	0.012	-0.004	0.041
Silver birch biomass x feeding status (yes)	-0.102	0.144	-0.372	0.197
Downy birch biomass x feeding status (yes)	-0.005	0.013	-0.033	0.019
Within-home range-scale - winter				
RAW species biomass x feeding status (yes)	0.003	0.014	-0.026	0.029
Scots pine biomass x feeding status (yes)	0.002	0.008	-0.014	0.018
Silver birch biomass x feeding status (yes)	0.006	0.156	-0.310	0.303
Downy birch biomass x feeding status (yes)	**-0.023**	**0.007**	**-0.037**	**-0.010**
Within-home range-scale - summer				
RAW species biomass x feeding status (yes)	0.012	0.009	-0.006	0.031
Scots pine biomass x feeding status (yes)	0.103	0.146	-0.178	0.391
Silver birch biomass x feeding status (yes)	-0.029	0.010	-0.049	0.009
Downy birch biomass x feeding status (yes)	-0.019	0.013	-0.045	0.007

The spatiotemporal distribution of animals is expected to be driven by attempts to maximize individual fitness through the selective use of forage resources across a range of scales (Senft et al. 1987). Here I have shown how habitat selection of moose as a function of browse availability and quality changed across scales. This agrees with findings from Månsson et al. (2007) who demonstrated that the relationship between moose winter browsing and forage availability (estimated as % cover) is also scale-dependent. It seems that for large herbivores in areas with no direct predation risk, high forage availability is the main determinant for seasonal home range establishment within a landscape (Jiang et al. 2009, Zweifel-Schielly et al. 2009). Elsewhere, habitat selection decisions at large spatial scales may be constrained by avoidance of direct (Frair et al. 2005, Hebblewhite and Merrill 2009) or indirect (perceived) predation risks e.g. proximity to humans (Kittle et al. 2008). Human presence is not considered a major constraint on landscape-scale habitat selection patterns of moose in Scandinavia, due to indirect benefits such as roads and higher forage availability associated with commercial forestry practices (Herfindal et al. 2009).

Overall, I would argue that selection for high abundance of lower quality species at the landscape-scale highlights a habitat selection strategy that allows herbivores (in the absence of predation risk) to compensate for unfavourable temporal variation in resource availability (e.g., depletion of quality resources) at smaller spatial scales. In foraging theory, depletion of resources at fine spatial scales is often the basis for predicting patch departure (Charnov 1976). Predictive models of herbivore patch use and departure in response to resource depletion are typically based on data from small spatial scales using an experimental approach (Kohlmann and Risenhoover 1994). However, more and more emphasize is being placed on predicting patch use based on animal movement occurring at larger scales using GPS data (Fryxell 2008, Owen-Smith et al. 2010). I have demonstrated how the behavioural response to a dynamic process such as resource depletion can be inferred from RSFs using GPS data collected over large spatiotemporal scales.

VARIATION IN HOME RANGE SIZE (PAPER III)

Home range size is expected to be inversely related to forage availability (Tufto et al. 1996, Relyea et al. 2000, Saïd et al. 2009). Indeed, supplementary feeding has earlier been found to reduce home range size in roe deer and red deer (Schmidt 1993, Guillet et al. 1996) and I therefore expect to find similar results for moose. Besides the importance of forage availability, abiotic factors such as local climate can also seriously influence space use patterns and consequently home range size (Börger et al. 2006). However, concurrent analyses of the effect of both intrinsic and extrinsic conditions on home range size are rare and often scale-specific (Börger et al. 2006, Saïd et al. 2009).

I found that the effect and relative importance of various individual-level, forage, and climatic determinants on variation in moose home range size changed depending on the spatiotemporal scale under investigation, suggesting a scale-dependent relationship (**see figure 2 in paper III**). For example, home-range size increased with body weight but only during winter at biweekly scales. Although, an increase in metabolic requirements is known to affect home range size at the interspecific level (Harestad and Bunnell 1979), the scale-specific effect found here supports the idea that body size is not a vital determinant of intraspecific variation in female home range size (Saïd et al. 2005, Saïd et al. 2009), in contrast to findings for males (Relyea et al. 2000). Furthermore, the effects of temperature, precipitation and snow depth varied spatially, being more influential on total home range size than on core area size. Similarly, Börger et al. (2006) found that peripheral home range areas are influenced more strongly by climatic variability than the more heavily used core areas. Nevertheless, some variables such as reproductive status (i.e. calf at heel or not) were consistently important in explaining home range size across scales. I found that the mobility of female moose in the period shortly after parturition was constrained by the presence of a calf (i.e. home range size was smaller for females with a new born calf than those without), but this limitation gradually decreased over time as offspring became more mobile and independent (i.e. similar home range size at the end of summer for both groups; **see Figure 3 in paper III**). The extent to which differences in reproductive status affect the summer habitat selection patterns presented above (i.e. **paper II**) remains to be evaluated.

The proportion of time spent in the vicinity of feeding stations did not affect home range size at any of the spatiotemporal scales I considered, which contrasts with findings for other deer species. This suggests that moose in the Telemark area did not use supplementary feeding stations to a sufficient extent to affect home range size. However, data from the Hedmark area indicate that home range size of moose is hardly affected even when use of feeding stations is as high as 60% (Slangen 2010). In contrast, density of natural browse explained a large part of the observed variation in moose home range size during summer, though the expected negative correlation was only observed at the daily scale (see **Figures S3** in Supporting Information of **paper III**). At longer temporal scales the effect gradually became positive towards the end of summer. Similar results have been found for seasonal home ranges of moose in Canada (Dussault et al. 2005). I expect this result to be a consequence of a decrease in nutritional quality of available forage as it matures over summer. Most of the evidence of seasonal changes in forage nutritional quality is based on grasses (Demment and van Soest 1985) though similar changes can also be expected to occur in browse species (Hjeljord et al. 1990, Bo and Hjeljord 1991). As such, this process may have caused moose to periodically (i.e. over longer time scales than one day) change feeding sites in search of new patches with browse of sufficient high quality in much the same way as is typically observed during periods of forage scarcity (i.e. winter). Indeed, I found a positive effect of browse density on monthly home range size towards the end of winter (see **Figures S4** in Supporting Information of **paper III**).

Local climate influenced home range size of moose mainly at short temporal scales (weekly and daily; **see Figure 2 in paper II**) suggesting that direct effects were more important than indirect effects associated with plant growth. This contrasts with findings for red deer (Rivrud et al. in press). Moose are well adapted to live in cold environments but easily suffer from heat stress, which may seriously constrain their movement (Dussault et al. 2004). Nevertheless, the effects of temperature and precipitation on variation in home range size were not as strong as I initially expected. This may suggest that habitat with good thermal shelter is sufficiently abundant in the Telemark area or, alternatively, that the climatic conditions experienced by the moose during my study period were below the levels at which heat stress becomes a major concern.

Despite the large number of variables included in the analyses, considerable variation in home range size remained unaccounted for. It is plausible that other environmental conditions such as landscape heterogeneity (Kie et al. 2002) or competition (Kjellander et al. 2004) play an important role in scaling of home range size in large herbivores. Clear multiple effects on home range size lead me to conclude that both intrinsic and extrinsic variables are important drivers of scaling of home range size. My results therefore highlight the importance of considering multiple spatial and temporal scales when investigating animal movement and activity (Kie et al. 2002, Börger et al. 2006, Rivrud et al. in press).

LONG-TERM BROWSING PRESSURE AROUND FEEDING STATIONS (PAPER IV)

In the 3 previous sections I have investigated the spatiotemporal distribution of GPS collared moose exposed to supplementary feeding over a relatively short time period (i.e. 6 years). However, for management purposes it is often necessary to evaluate long-term effects, yet this may be difficult to achieve as short-term ecological effects are not always good predictors of effects over the longer term. For example, the increased use of habitat in the vicinity of feeding stations (**paper I**) is likely to increase browsing impact on the natural vegetation. But how does this develop over time? Do the CPF theory predictions given above, still hold for space use patterns and forage resource selection decisions after long-term winter feeding of moose? To assess these questions, I compared pellet group counts and browsing pressure around feeding stations as recorded after 5-10 years of feeding and 15-20 years of feeding (Hedmark area; **paper IV**).

In agreement with the results found in the Telemark area (**paper I**), browsing pressure estimated after 5-10 years of feeding in the Hedmark area largely conformed to my CPF predictions 1 and 2.1. Browsing pressure declined with distance from feeding stations and variation in browsing pressure between species was low close to feeding stations but increased with distance (as indicated by the red arrows in **figure 6**). Again, I found no support for CPF prediction 2.2 as browsing pressure on preferred forage species (i.e. rowan, aspen and willow) was not highest at the greatest distance from feeding stations (200 m). After 10 years of additional winter feeding (i.e. 15-20 years of feeding), I found 2-3 fold higher faecal pellet group numbers in the vicinity of feeding stations (**see Figure 2 in paper IV**), which suggests an increase in local moose densities or an overall increase in use of feeding stations. Concurrently, browsing pressure on leader stems at the same spatial scale was no longer negatively correlated with distance from feeding station (up to 200 m) and variation in browsing pressure did not amplify with distance (**see Figure 4, paper IV**). These results therefore do not fit well with CPF predictions 1 and 2.1.

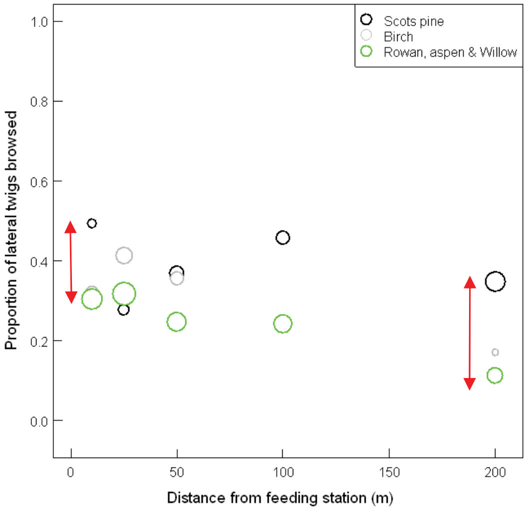

Figure 6: Proportion of lateral twigs browsed after 5-10 years of winter feeding as a function of distance from feeding station. Variation in habitat selectivity is depicted by the red arrows.

However, in contrast to the results from the Telemark area and the Hedmark area after 5-10 years of feeding, when assessing selection decisions at a slightly larger spatial scale (up to 1 km) I did find evidence to support CPF prediction 2.2. Browsing pressure on preferred species (rowan aspen and willow) was highest at 1 km from feeding stations, lower for medium preference species (Scots pine) and completely absent for the least preferred Norway spruce (**see Figure 5 in paper IV**).

I found little support for the effectiveness of supplementary feeding as a tool to reduce or control habitat damage, at least on a fine spatial scale. I observed a spatial shift in peak browsing pressure on commercially valuable trees (i.e. Scots pine) when the timeframe of feeding was increased from 5-10 to 15-20 years of feeding (**see Figure 6 in paper IV**). I would argue that this is a direct result of intense browsing over a long time period (15-20 years) causing fine-scale depletion of this forage resource, or at least reducing its availability below acceptable levels for moose. Depletion of available resources around a central-place is often reported (Fryxell 1992, Elliott et al. 2009). In addition, browsing pressure on Norway spruce, a species normally avoided by moose but of considerable economic value, increased markedly over time and space. Browsing pressure on Scots pine leader stems were of such levels that economic losses could be expected up to at least 1 km from feeding stations (Ward et al. 2004).

Although providing supplementary food may reduce intake of natural vegetation to nearly zero in some species (Putman and Staines 2004 and references therein), browsing herbivores typically continue to forage on natural vegetation. This is likely to be related to a shortage of essential nutrients or fibre in the supplied forage (Schwartz and Hundertmark 1993). However, as I have shown here, over the short-term, moose concentrate their space use and foraging activity to the vicinity of feeding stations as predicted by CPF theory, and browsing damage to forest stands will therefore be restricted to a fine spatial scale. However, when winter feeding is continued over extended time periods (20 years or more) and in permanent locations there is serious potential for resource depletion at increasingly larger spatial scales. At some point in time this may result in a situation where the energetic cost of returning to the central-place (i.e. feeding station) will outweigh the energetic benefits it provides. Such a trade-off could result in the abandonment of feeding stations and central-place foraging behaviour. This will subsequently lead to an increase of browsing damage at the landscape-scale and completely undermine the initial purpose of diversionary feeding. A potentially valuable approach that deserves further attention is to provide supplementary food within a spatial rotation scheme. Such an approach would allow certain areas to recuperate until sufficient re-growth is available to withstand browsing pressure for a new period of time. An alternative approach is to supply browsing herbivores with the harvest residue that remains after tree logging, which has been shown to substantially increase the availability of natural winter browse for moose (Månsson et al. 2010). Although more evidence is required, this could be a potentially useful approach to control browsing pressure because the location of such sources of natural forage will frequently change over space and time and, as such, lowers the risk of fine-scale resource depletion and severe browsing damage to surrounding forest stands.

CONCLUSIONS AND FUTURE PERSPECTIVES

My results clearly indicate that supplementary feeding affects the spatiotemporal distribution of moose at intermediate to fine spatial scales during winter, with feeding station users concentrating their space use around feeding stations and behaving as central-place foragers (**papers I & IV**). By contrast, supplementary feeding had no effect on habitat selection at intermediate to coarse spatial scales (**paper II**) or on home range size (**paper III**). Nor were there any lagged effects of supplementary feeding during the summer season. Instead, availability and quality of natural browse and, to a lesser extent, local climate and individual characteristics appeared important in habitat selection and scaling of home range size across a range of spatiotemporal scales. Additional evidence from regions with longer feeding traditions is needed to assess whether these findings are typical or whether habitat selection patterns evolve over time and change with winter severity and intensity of feed use. Nevertheless, my results demonstrate how, after relatively few years of feeding, feeding station users continued to select for commercially valuable browse (i.e. Scots pine) to the same extent as non-users (**paper I & table 1**) which raises a serious concern about the effectiveness of winter feeding in reducing browsing pressure over large spatial scales. Although a more definite conclusion in this respect would benefit from a comparison of browsing pressure at the landscape-scale before and after the inception of feeding programmes, this may be difficult to achieve as baseline data is rarely collected. At least at a fine spatial scale, I demonstrated a considerable increase in browsing pressure on the natural vegetation associated with long-term supplementary feeding (**paper IV**). Resource depletion close to long-term feeding stations lead to higher browsing pressure at distances further away. In addition, browsing pressure on commercially valuable species such as Scots pine but also Norway spruce, which is normally avoided by moose, increased considerably. Overall, supplementary feeding as a diversionary tactic to reduce moose browsing on commercially valuable species was therefore not supported.

In my studies I have focussed on assessing the role of supplementary feeding and other factors on the spatiotemporal distribution of moose. Although such assessments are important to understand how animals perceive and exploit their available forage resources across scales, there is a growing need to translate and couple an individual’s space use and habitat selection strategies to fitness indices (Gaillard et al. 2010). For management purposes, a logical next step is therefore to assess the effect of supplementary feeding on e.g. body weight, survival and reproduction. This is crucial as more and more property managers are investing substantial resources into winter supplementary feeding programs without adequate knowledge of the consequences. In contrast to birds (Robb et al. 2008) and large carnivores (Lopez-Bao et al. 2009), there is little consensus about the general impact of supplementary feeding on fitness or nutritional status of grazing herbivores (Putman and Staines 2004) and very little is known about the long-term physiological and life-history consequences of such feeding on browsing herbivores. Many questions are still unanswered. Are central-place foraging moose gaining more or less body mass than those feeding solely on the natural vegetation? Are parasite or disease transmission exacerbated? How do such patterns change over time and with feeding intensity? What is the effect of the supplied forage on physiological condition? There is concern that supplying browser herbivores with silage might increase tooth wear (Kaiser et al. 2009), which could subsequently reduce longevity. Furthermore, long-term supplementary feeding can affect the spatial genetic structure of large herbivores (Blanchong et al. 2006), and may reduce natural selection (Schmidt and Hoi 2002) and social learning (Mysterud 2010). A holistic evaluation of the effectiveness of supplementary feeding as a wildlife management tool is required and needs to consider all the associated benefits and costs, especially considering developments on the long-term. High moose densities, such as those occurring around long-term feeding stations, can seriously alter ecosystem properties with knock-on effects for other trophic levels. For example, severe moose browsing over extended time negatively affects tree productivity (Persson et al. 2005) and can change the vegetation composition of the field layer (Mathisen et al. 2010). These processes have already been shown to impact the abundance and composition of invertebrates (Suominen et al. 2008) and subsequently the breeding success of insectivorous birds around feeding stations (Pedersen et al. 2007). Managing moose is about managing ecosystems. Therefore, supplementary feeding of moose, or any other large herbivore, should be viewed in this wider perspective. Much exciting research remains to be done before this can be achieved on a firm scientific platform.

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INDIVIDUAL PAPERS

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Management and Conservation Article

Comparative Space Use and Habitat Selection of Moose Around Feeding Stations

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ABSTRACT The practice of feeding cervids in winter, either as a supplement to enhance nutritional status or to divert animals away from roads, railways, or vulnerable habitats, is rising noticeably. Moose (*Alces alces*) densities in Scandinavia are currently at historically high levels, resulting in amplified damage to economically important young Scots pine (*Pinus sylvestris*) forest stands. Nevertheless, there is limited information as to how diversionary feeding affects herbivore space use and habitat selection. We followed 32 female moose marked with Global Positioning System collars to evaluate 1) if feeding stations serve as attraction points to the extent that habitat-selection patterns resemble those of central-place foragers (i.e., high usage and more uniform selection close to the attraction point), and 2) if moose using feeding sites select young pine stands less than those not using feeding sites. Moose that used diversionary forage concentrated their space use around feeding stations and selected habitats as predicted for a central-place forager with a decreasing probability of using areas away from feeding sites and a low degree of habitat selectivity close to feeding sites. However, moose that used feeding sites continued to select young pine stands to the same extent as moose that did not use feeding sites. Feeding sites were, therefore, not successful in diverting moose away from valuable natural browse, so we recommend wildlife managers establish feeding sites in sacrifice areas where moose browsing is permissible and, if possible, >1 km from young pine plantations.

KEY WORDS *Alces alces*, central-place foraging, deer, diversionary winter feeding, habitat use, mixed-effect logistic regression, resource selection function, southern Norway.

The supplementary winter feeding of large herbivores is a widespread, yet controversial, wildlife management practice (Boyce 1989, Smith 2001, Putman and Staines 2004). During the past decade, this practice has increased noticeably throughout Europe and North America. Although there are many reasons for diversionary feeding (reviewed by Putman and Staines 2004), an important goal is the prevention of environmental damage, particularly to agriculture and forests of commercial or conservation value (Smith 2001, Peek et al. 2002, Gundersen et al. 2004, Putman and Staines 2004). The rationale behind such feeding is either to reduce the amount of natural forage required by wintering herbivores via the provision of alternative forage or to redirect animals toward less-vulnerable habitats. However, ungulates will often still consume natural forage, and evidence of the effectiveness of winter feeding as a diversionary tactic is equivocal (Schmitz 1990, Doenier et al. 1997, Gundersen et al. 2004, Putman and Staines 2004).

Central-place foraging theory predicts space use and foraging decisions as a function of the distance from a focal point (Orians and Pearson 1979). In the classical case, the focal point is typically a nest or a den, but any key resource that acts as an attraction point may give rise to a space-use pattern resembling central-place foraging (Rosenberg and McKelvey 1999). The central-place foraging theory, a special case of the wider optimal-foraging theory, is, therefore, likely to be useful for predicting ungulates' habitat-selection patterns if artificial feeding sites can be assumed to serve as attraction points. A typical feature of central-place foraging is a declining probability of use of locations with increasing distance from the focal point (Rosenberg and McKelvey 1999). Also, central-place foragers are expected to show both lower selection for preferred resources and a lower overall variation in selection of resources close to the focal point (Schoener 1979). There is limited information as to whether feeding stations restrict space use of individual ungulates and how that, in turn, affects habitat-selection patterns. For ungulates that use feeding stations, habitat selection may vary with distance to feeding site because of locally high densities and amplified competition for assumed high-quality habitat types close to feeding sites. Studies on smaller cervids have shown that providing artificial winter feed can change migratory movement for white-tailed deer (*Odocoileus virginianus*; Lewis and Rongstad 1998) and restrict natural space-use patterns to the vicinity of feeding stations for roe deer (*Capreolus capreolus*; Guillet et al. 1996) and white-tailed deer (Kilpatrick and Stober 2002). For managers, it is important to know the spatial scale at which winter feeding affects space use and habitat selection so that effective winter feeding programs can be designed for various goals.

Moose (*Alces alces*) populations in Norway, as in the rest of Fennoscandia, have grown considerably during the past

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decades, and densities in local wintering areas can be extreme (e.g., 5–6 moose/km^2; Lavsund et al. 2003). A concurrent problem with high moose densities is the excessive winter browsing in regenerating, young Scots pine (*Pinus sylvestris*) stands, resulting in substantial economic losses to forestry (Andren and Angelstam 1993, Ball and Dahlgren 2002). Gundersen et al. (2004) demonstrated how winter feeding of moose in Norway may reduce browsing damage to forestry interests at a local scale (up to 5 km) but may lead to serious habitat damage at a forest-stand scale (e.g., severe browsing and bark-stripping $\leq$200 m).

Our objectives were to quantify how the provisioning of winter forage affects space-use and habitat-selection patterns of moose. When additional feed at least partly compensates for intake of natural preferred browse, we predicted that (P$_1$) artificial forage would reduce the selection for commercially valuable young pine stands among moose that used feeding stations, because time spent in pine stands would likely decrease. If moose experience feeding sites as attraction points in their seasonal home range, we predicted (P$_2$) that space use would be concentrated in the vicinity of feeding stations and (P$_3$) low habitat selectivity in the vicinity of feeding stations with selectivity increasing with distance.

STUDY AREA

The study area (1,733 km^2) was located in southern Norway within parts of Telemark, Buskerud, and Vestfold counties in the boreonemoral zone (Fig. 1). The area was mostly covered by commercially managed, coniferous forest (82%), dominated by Norway spruce (*Picea abies*; 72%) and, in the drier and poorer locations, by Scots pine (17%). In addition, a few mixed deciduous stands (6%) of birch (*Betula* spp.), mountain ash (*Sorbus aucuparia*), willow (*Salix* spp.), and aspen (*Populus tremula*) occurred throughout the area. The topography was rugged with steep slopes, and the altitude ranged from sea level to 800 m. Monthly normal temperatures during January and April were -5° C and 4.3° C, respectively (Norwegian Meteorological Institute 2008). Average ($\pm$SE) snow depths in the center of the study area during January–April 2007 and 2008 were 49 ± 2.4 cm and 72 ± 1.5 cm, respectively, with deeper accumulation at higher elevations (Norwegian Meteorological Institute 2008). Large predator species were absent, and hunting was the most important cause of moose mortality in this area.

Local landowners have been feeding moose and red deer (*Cervus elaphus*) ad libitum with ensilaged bales of mixed graminoids for $\leq$6 winters. There were 94 permanent feeding stations, and during the 4-month winter, moose consumed 182 tonnes of forage in 2006–2007 and 244 tonnes in 2007–2008.

METHODS

Moose Telemetry Data and Habitat Maps

We fitted 32 adult female moose with Global Positioning System (GPS) collars, programmed with a 1-hour relocation schedule during 2 winters. We tranquilized moose by dart gun from a helicopter, using established techniques (Arnemo et al. 2003). We used annual snow conditions to define winter length (>30-cm snow depth), which corresponded with the period that artificial forage was supplied. In 2007, winter was from 21 January to 8 April, and in 2008, it was from 4 January to 30 April. We excluded all GPS locations collected within 24 hours of marking a moose.

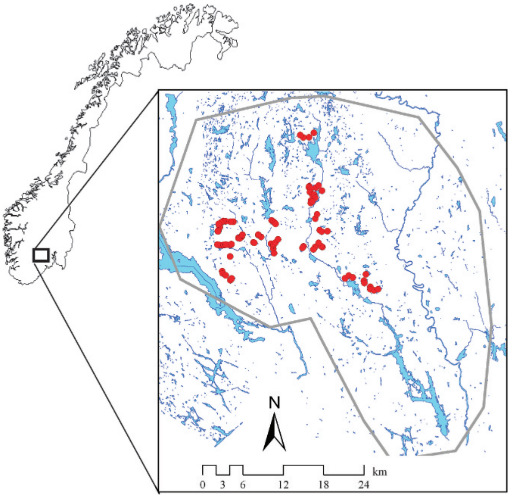

Figure 1. Map of the study area in southern Norway (part of Telemark, Buskerud, and Vestfold counties). The map shows the spatial distribution of permanent moose feeding stations (n = 94) during the winters of 2007 and 2008, the lakes, rivers, and boundary of the study area.

We used forest-stand indices from 6-year-old Geographic Information System (GIS) maps. Dussault et al. (2001) recommend evaluating the accuracy of important habitat characteristics represented on forest maps via field observations, which is especially important for fine-scale habitat-selection studies. To assess the forest-stand classification accuracy of our GIS maps, we randomly sampled 180 forest stands throughout the study area and determined whether the forest stands were correctly classified with regard to cutting class and dominant tree species. We partitioned cutting classes (cc) by tree height: cc.1 = stands with trees <1 m; cc.2 = stands with trees of 1–7 m tall; cc.3 = 8–14 m tall; cc.4 = 15–20 m tall, and cc.5 = trees $\geq$20 m in height.

Correcting for GPS Bias

A recurring problem in studies reliant on data obtained with GPS technology is variable fix rates in location accuracy (D'Eon and Delparte 2005, Graves and Waller 2006). Because the average GPS-collar fix rate during our study was 91.9% (range among collars: 72–99%), we investigated whether fix rates were biased across habitat types and corrected for it in the habitat-selection analysis. We placed collars 1.5 m above the ground for 24 hours with the antenna pointed directly upwards, during early winter (Nov 2007). We made positioning attempts each hour. We repeated trials 4 times for each combination of habitat variables (see below), a total of 120 trial sites. We selected trial sites by stratified random sampling across 3 habitat characteristics that we suspected could affect the GPS fix rate: 1) dominant tree species (Scots pine vs. Norway spruce; we did not include mixed deciduous stands because they comprise a minor habitat type [6% of all stands]); 2) slope (flat, <4°; moderate, 4–8°; steep, >8°); and 3) cutting class. Furthermore, we determined sky visibility, defined as the percentage of sky obstructed by terrain features for each trial location. We calculated sky visibility in ArcView GIS 3.2 (script developed by D. O. Wallin, Department of Environmental Science, Western Washington University, Bellingham, WA), and we derived slope from a Triangulated Irregular Network grid (50-m cell size) in ArcMAP 9.2.

We defined and calculated location accuracy as the linear distance between the recorded GPS location and the assumed true location (i.e., the average of 24 GPS positions). The median location error at trial sites was 16 m with 95% of the locations within <75 m. These results are considered acceptable (Hebblewhite and Merrill 2008) and similar to the spatial resolution of our GIS habitat variables.

To test and account for habitat-specific bias in GPS fix rate, we did the following: at each trial site, we knew the number of successes and failures of GPS positioning attempts (average fix success, 96.9%; range, 87.8–100%) and the combination of habitat characteristics. From these data, we built a mixed-effect logistic regression model with success (1) or failure (0) for each location attempt as the response variable, with habitat characteristics as fixed-effect predictor variables, and collar identity as a random intercept (to account for systematic differences in collar quality). Our results indicated that the odds ratio of acquiring a GPS fix were lowest in the spruce-dominated forest of cc.3, compared with the open pine stands of cc.1. The odds of a GPS collar successfully acquiring a location were positive for increased sky visibility and negative for increased slope and cutting class. From this model, we predicted the probability of attaining a fix for all combinations of habitat characteristics. Habitat variables were available as layers in GIS maps, and we could, therefore, use the model to predict the probability of obtaining a GPS fix at every location in the study area (i.e., a probability value for every pixel of a GIS raster map). Pixels of mixed deciduous stands received the same probability as pine-dominated stands (i.e., the reference category). To correct for GPS bias, we used an iterative simulation method (Frair et al. 2004). For each missing location in the moose GPS data set, we randomly selected a location and a randomly drawn probability value of a uniform distribution within a rectangle defined by the previous and next known locations. We compared the predicted value of acquiring a fix for that location (found on the GIS probability map) to the randomly drawn probability value. If the random value was greater than the predicted value, we retained the random location; otherwise we selected a new random location and probability value. Therefore, we retained locations with the lowest predicted probability of obtaining a fix, and thus the higher probability of being a missed location, more often. In this manner, we filled in 2,483 missed locations with 60.5% assigned to spruce-dominated forest (26.4% within cc.3). Pine and mixed deciduous forest received 37.5% and 2% of the filled in locations, respectively.

Feeding Site Use

To categorize individual moose as feeding-site users or nonusers, we used the Euclidean distances analysis (EDA) proposed by Conner and Plowman (2001): $d_i = u_i/r_i$. Here, u_i represents a vector of distances from feeding stations to used positions within the wintering home range, and r_i is a vector of distances from the feeding stations to randomly selected points within the winter home range. When the ratio is $d_i < 1.0$, the animal is associated with the feeding stations more than is expected by chance (Conner and Plowman 2001). We used 95% minimum convex polygons (MCPs) to delineate moose wintering home ranges (Mohr 1947). For moose with a range overlapping ≥1 feeding station, we randomly selected 2,000 points with replacement from the MCP (i.e., Design III sampling; Boyce et al. 2002, Manly et al. 2002, Thomas and Taylor 2006). The number of random points we chose was comparable with the average number of used locations per individual moose. We excluded individuals without feeding stations in their seasonal home range from the EDA. We calculated distances to the closest feeding station for u_i and r_i using Spatial Analyst in ArcMAP 9.2. We used a bootstrap procedure to calculate d_i 10,000 times and classified an individual as a feeding-site user when the upper limit of the 95% confidence interval did not overlap with 1, where 1 = no selection of feeding sites. We subsequently included feeding status (i.e., feeding-site user vs. nonuser) as a covariate in the habitat-selection analysis.

Dussault et al. (2005) demonstrate that results from distance-based analyses do not disclose habitat preference and, moreover, do not necessarily quantify actual habitat use. We, therefore, determined the proportion of time spent within 100 m of feeding stations to quantify feeding site use for each individual separately and to confirm our EDA results with an alternative classification method. We considered that moose located within a 100 m buffer from feeding sites had visited the station because feeding stations were small (<20 m^2) and because the location in between the hourly fixes is not known. As such, we calculated the number of hours spent within a 100-m buffer around feeding stations for each moose separately (each unique location represented a visit of 1 hr because we used a 1-hr GPS relocation schedule) and divided that by the number of GPS locations obtained during winter for that individual.

We used independent sample *t*-tests to estimate differences in forest road density, proximity to human settlement, proximity to cc.2 of Scots pine stands, and proximity to tractor roads between used and unused feeding stations. We also used independent sample *t*-tests to test for differences in home range size (95% MCPs) between feeding-site users and nonusers. All variables fulfilled the assumptions of normality and homogeneity of variance between groups. Moreover, we evaluated whether feeding stations within Norway spruce–dominated forests were used to the same extent as feeding stations within Scots pine–dominated forests with Fisher's Exact Test.

Habitat Selection

We assessed habitat selection by modeling resource selection functions (RSF), defined as any function proportional to the probability of use of a habitat by an animal (Manly et al. 2002). We employed mixed-effect logistic regression models and adopted the extension of the fixed-effect, exponential RSF by Manly et al. (2002), as proposed by Gillies et al. (2006): $w(x) = \exp(\beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} +, \ldots, + \beta_n x_{nij} + \gamma_{0j})$. Here x_n are covariates with fixed regression coefficients β_n, the β_0 is the mean intercept, and γ_{0j} is the random intercept, which is the difference between the mean intercept β_0 for all groups and the intercept for group j (Skrondal and Rabe-Hesketh 2004, Gillies et al. 2006). Incorporation of a random intercept into RSFs is especially beneficial with unbalanced sampling designs because it adjusts the overall average probability of use, which depends on an arbitrary number of randomly sampled points (both used and available) for each individual (Gillies et al. 2006, Godvik et al. 2009). Based on parsimony, the final mixed-effect RSF models contained only a random intercept for moose identification (because the inclusion of a second random intercept for year did not improve model fit (Δlog-likelihood, <3.84; Hilborn and Mangel 1997, Gillies et al. 2006).

We estimated habitat availability by drawing a random sample of points from within each individual's wintering home range (i.e., the third-order scale of selection; Johnson 1980). The number of available points selected equaled the number of points used by each individual. Thus the response (dependent) variable in our RSF models consisted of used (1) and available (0) locations. We selected the independent variables included in the RSF models a priori to answer our predictions. Variables were 1) dominant tree species (a 3-level factor: Norway spruce, Scots pine, and mixed deciduous), 2) cutting class (as described above), and 3) feeding-status (feeding-site user vs. nonuser). To quantify differences in selection between feeding-site users and nonusers for the various habitat types (P_1), we included them as second-order interactions. We did not include the interaction between dominant tree species and cutting class because of some missing category combinations within the study area.

To analyze selection patterns of feeding-site users (P_2 and P_3), we excluded all nonusers from the analysis. Moreover, because we used distance from feeding stations as an explanatory variable, we excluded all simulated positions associated with unsuccessful fixes to ensure that no bias toward distance from feeding stations entered the analysis. We categorized distance from feeding stations for all used and available locations into 4 classes of 500-m intervals.

We developed mixed-effect RSF models using R version 2.7.0 (R Foundation for Statistical Computing, Vienna, Austria). The outcome of all these models is the log odds of using a pixel in the map; therefore, we could not derive absolute probabilities of selection. However, calculation of log-odds ratios relative to a reference category consisting of a chosen combination of levels of the categorical independent variables is informative and reliable (Godvik et al. 2009). We set the reference category in our mixed-effect RSF models to pine-dominated stands of cc.2 because differences in selection for this habitat type were our primary interest. To evaluate the properties of the individual coefficients in the mixed-effect models, we used 10,000 Markov Chain Monte Carlo samples and 95% Highest Posterior Density (HPD) intervals. The use of Bayesian HPD confidence intervals is preferred when analyzing large, unbalanced data sets with mixed-effect models because the resulting inferences are more conservative compared with standard 95% confidence intervals (Baayen et al. 2008). For example, the 95% HPD interval for parameter t is the shortest interval where the posterior probability that t lies within the interval is 0.95. We used HPD intervals to evaluate whether selection estimates were significantly different from zero and plotted parameter estimates to assess biological importance (Baayen et al. 2008).

RESULTS

Feeding Site Use

No moose or collars were lost during the study period, but the malfunction of one collar resulted in fewer data points for one individual during winter 2007. After we corrected for GPS bias, the average (±SE) number of GPS locations used per moose ($n = 32$) and year ($n = 2$) were 2,022 ± 93 and 32,354 ± 1,984, respectively.

Of the 32 collared adult female moose, we classified 15 individuals (47%) as feeding-site users, and 17 animals as nonusers, including 8 individuals (25%) that did not have feeding stations within their wintering range (Fig. 2). All feeding-site users spent ≥ 35 hours each at feeding stations within the 3-month study, whereas all nonusers were far below that threshold (max. 12 hr). The mean proportion of time (±SE) spent within 100 m of feeding stations for feeding-site users was 4.85 ± 0.98% (i.e., 92 ± 17.3 hr), and for nonusers with feeding stations in their wintering range, it was 0.19 ± 0.06% (i.e., 3.8 ± 1.29 hr). Of the 61 feeding stations located in wintering home ranges of the feeding-site users, we recorded that 31 (51%) were never used by the collared moose (i.e., no locations within 100-m circular buffer). Feeding site users had a mean of 12 feeding stations available within the winter home range (min. = 1, max. = 24), with a mean of 3 feeding stations used per individual (min. = 1, max. = 6). Feeding stations used by the GPS-collared moose were located in areas with higher forest road density (1.37 ± 0.08 km^2) than feeding stations not used by collared moose (1.14 ± 0.07 km^2, $t_{58} = 2.019$, $P = 0.042$). We found no difference between used and unused feeding stations in relation to proximity to human settlement ($t_{58} = 1.579$, $P = 0.119$), proximity to cc.2 of Scots pine stands ($t_{58} = 0.432$, $P = 0.667$), or proximity to tractor roads ($t_{58} = 0.828$, $P = 0.411$). Furthermore, we

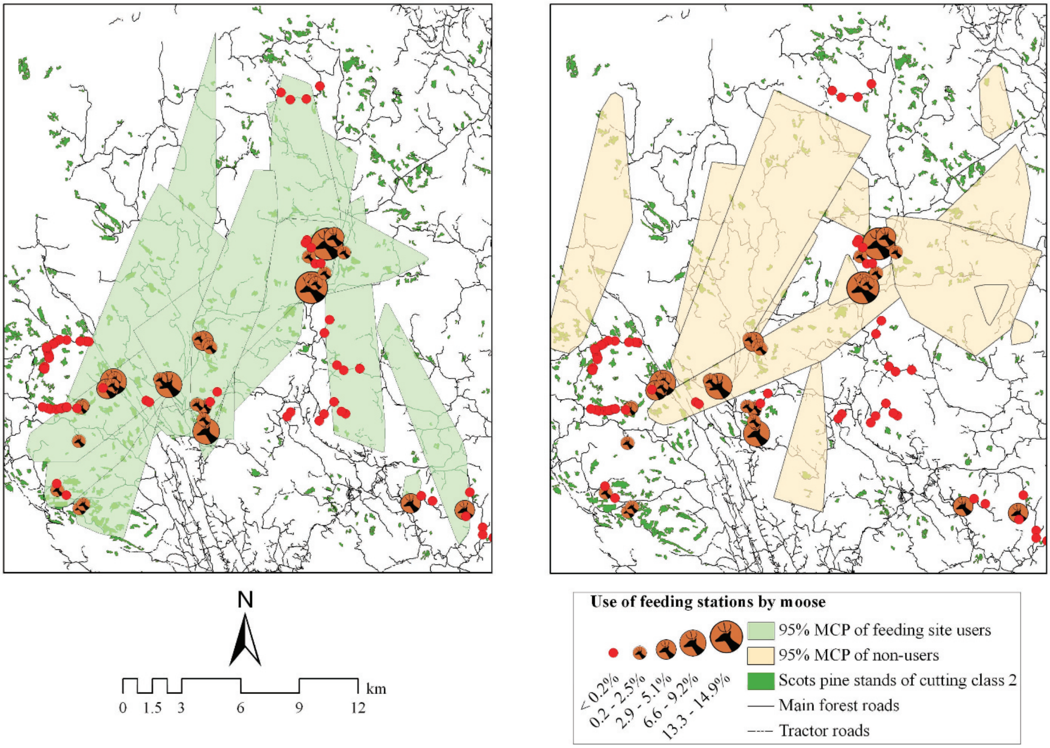

Figure 2. Map showing winter home ranges (95% minimum convex polygons [MCP]) of moose using feeding stations (feeding-site users, *n* = 15) and those not using feeding stations (nonusers, *n* = 17) in southern Norway during the winters of 2007 and 2008. The spatial distribution of all cutting class 2 Scots pine stands and the proportional use of feeding stations by the collared moose are also shown. We calculated the proportional use of a feeding station as the percentage of moose–hours spent within 100 m of a particular feeding station divided by the number of hours spent at all feeding stations.

found no difference in home-range size between feeding-site users (mean ± SE; 34.5 ± 5.4 km^2) and nonusers (27.8 ± 4.2 km^2; $t_{30} = -1.227$, $P = 0.229$). The odds of using a feeding station in Norway spruce–dominated habitat were 2.8 times higher than in Scots pine, but this was not significantly different (Fisher's Exact Test, $P = 0.142$).

Habitat Selection

In our assessment of forest-stand classification accuracy, we found that 94.8% of the forest stands were correctly classified with regard to cutting class and dominant tree species. A substantial part of the misclassification (2.7%) was attributed to recent clear-cut felling of cc.5 in Norway spruce–dominated forest stands. We considered the accuracy of the GIS layers adequate for our purposes.

Among moose that did not use feeding stations, selection was highest for young Scots pine stands (cc.2), indicated by HPD intervals of other cutting classes below zero and not overlapping with the reference category for this group (Fig. 3). Among moose using feeding sites, selection was higher for older pine-dominated stands (cc.2–cc.5) than it was for nonusers (P_1) and lower for spruce and deciduous stands (Table 1; Fig. 3). However, estimates of selection for the critical habitat type cc.2 within pine stands was not statistically different between feeding-site users and nonusers, with HPD intervals between groups overlapping (Fig. 3).

For feeding-site users, the likelihood of using a location was highest close to feeding stations and decreased markedly with distance from feeding station, as expected from central-place foraging theory (P_2; Table 2; Fig. 4). This pattern was not a result of confounding spatial elements (such as other types of attraction points systematically located close to feeding stations) because overall space use by nonusers with feeding stations available in their home range ($n = 10$) was unrelated to distance from feeding sites (Table 2; Fig. 4). Also as predicted (P_3), variation in selection for the different pine cutting classes (with the exception of recently felled areas of cc.1) was relatively small in the vicinity of feeding stations (HPD intervals overlap the most ≤ 1.5 km), but increased at locations >1.5 km from feeding stations (Table 3; Fig. 5). Moreover, as distance from feeding stations increased, the use of mixed deciduous forest and Norway spruce stands by feeding-site users increased (Table 3).

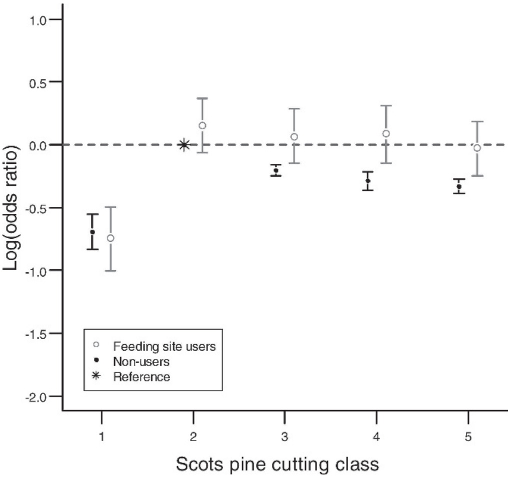

Figure 3. Selection estimates (log odds ratio ± 95% Highest Posterior Density [HPD] intervals) for cutting class within Scots pine–dominated forest stands by moose using feeding stations (feeding-site users, $n = 15$) and those not using feeding stations (nonusers, $n = 17$) in southern Norway during the winters of 2007 and 2008. All estimates are in comparison with the reference category: cutting class 2 for nonusers; HPD intervals >0 indicate selection and <0 indicate avoidance of habitat compared with the reference category. Habitat categories with HPD intervals overlapping with the reference category are used at a similar rate.

Table 1. Selection estimates (log odds ratio ± 95% Highest Posterior Density [HPD] intervals) of mixed-effects, logistic-regression model predicting selection for habitat (i.e., cutting class, dominant tree species) by moose using feeding stations (feeding-site users, $n = 15$) and those not using feeding stations (nonusers, $n = 17$) in southern Norway during the winters of 2007 and 2008 (Fig. 3). All estimates are in comparison to the reference category.[a–c] The model includes a random intercept for each individual (moose identification; SD = 0.275 [HPD interval 0.221–0.380]).

Variable	β	SE	HPD interval Lower	HPD interval Upper
Intercept	0.699	0.071	0.546	0.844
Dominant tree species[a]				
Mixed deciduous	−0.492	0.070	−0.626	−0.354
Norway spruce	−0.956	0.022	−1.000	−0.913
Cutting class (cc.)[b]				
cc.1	−0.693	0.074	−0.836	−0.551
cc.3	−0.204	0.023	−0.249	−0.159
cc.4	−0.288	0.037	−0.361	−0.216
cc.5	−0.331	0.029	−0.390	−0.277
Feeding status[c]				
Feeding-site user	0.151	0.103	−0.064	0.370
Dominant tree species × feeding status				
Mixed deciduous × feeding-site user	−0.577	0.099	−0.781	−0.389
Norway spruce × feeding-site user	−0.115	0.031	−0.175	−0.056
Cutting class × feeding status				
cc.1 × feeding-site user	−0.203	0.104	−0.405	−0.003
cc.3 × feeding-site user	0.119	0.032	0.053	0.180
cc.4 × feeding-site user	0.224	0.052	0.121	0.324
cc.5 × feeding-site user	0.151	0.040	0.073	0.229

[a] Reference category = Scots pine.
[b] Reference category = cc.2.
[c] Reference category = nonuser.

DISCUSSION

Although feeding was initiated with the aim of reducing browsing damage to the commercially important young Scots pine, we found that moose using feeding sites selected these stands to the same extent as moose not using feeding sites (rejecting P_1). Unfortunately, we had no control over the spatial positioning of the feeding stations, so, as with any correlational study, there is the potential for confounding factors. However, the observed patterns emerged despite most feeding sites used by the collared moose being located within spruce-dominated, rather than pine-dominated, habitat. This could be attributed to the availability of shelter habitat and abundant forage within close range of the feeding stations.

In the classical case of central-place foraging theory, an animal's foraging trip starts at a central place (e.g., a nest or den) and continues until the animal captures a prey, after which, the animal returns to the central place (Orians and Pearson 1979). The application of distance-based models is preferred when analyzing habitat selection for animals for which a central place can be identified (but see Dussault et al. 2005) because they incorporate potential spatial clustering of habitats surrounding the central place and, thus, account for potential bias in selection estimates (Rosenberg and McKelvey 1999). An artificial feeding site can be regarded as an additional component in the habitat selection of ungulates using such sites, and we argue that a feeding site resembles a central-place attraction point. How to analyze this specific case has not been addressed before.

Consistent with our predictions, the relative probability of a location being used decreased significantly as distance from feeding sites increased (supporting P_2). In addition, the variation in selection for pine-dominated habitat increased with distance from feeding stations (as expected by P_3). Several observational studies report that herbivores developed an increased reliance on artificial feed and reduced natural forage intake to near zero (Putman and Staines 2004). Nonetheless, persistent use of natural forage has been observed in white-tailed deer (Schmitz 1990, Doenier et al. 1997) and moose (Gundersen et al. 2004) while being offered supplementary forage. This behavior may be related to a shortage of essential nutrients or fiber in the supplied forage (e.g., hay is not considered high-quality forage for moose; Schwartz and Hundertmark 1993).

Feeding sites attracted approximately half of the individual moose marked in our study area: 25% did not have feeding sites within their home range, and 28% had feeding stations available in their winter home range but did not use them. This may be due to several factors, such as individual variation in vigilance (White et al. 2001), migration status (Luccarini et al. 2006), or social rank (Schmidt and Hoi 1999). Also, severity of winter conditions (e.g., increasing snow depth) is an important factor influencing the use of

Table 2. Estimates (log odds ratio ± 95% Highest Posterior Density [HPD] intervals) of mixed-effects logistic-regression model predicting space-use patterns for 25 Global Positioning System–collared moose in relation to distance from feeding stations in southern Norway during the winters of 2007 and 2008 (Fig. 4). The model includes moose using feeding stations (feeding-site users, n = 15) and those not using feeding stations that were available within their wintering range (nonusers, n = 10). All estimates are in comparison to the reference category.[a,b] The model includes a random intercept for each individual (moose identification; SD = 0.530 [HPD interval 0.417–0.763]).

Variable	β	SE	HPD interval	
			Lower	Upper
Intercept	−0.835	0.148	−1.154	−0.516
Distance class (m)[a]				
d1	1.517	0.031	1.457	1.577
d2	1.449	0.029	1.390	1.504
d3	1.154	0.032	1.091	1.214
Feeding status[b]				
Nonuser	0.742	0.214	0.277	1.198
Distance class × feeding status				
d1 × nonuser	−1.700	0.050	−1.798	−1.602
d2 × nonuser	−1.572	0.045	−1.665	−1.490
d3 × nonuser	−1.982	0.050	−2.083	−1.891

[a] Reference category = d4 (>1,500 m).

[b] Reference category = feeding-site user.

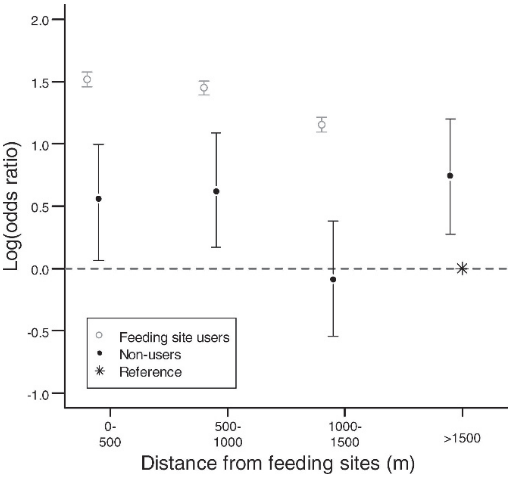

Figure 4. Space-use estimates (log odds ratio ± 95% Highest Posterior Density [HPD] intervals) for distance from feeding stations by moose using feeding stations (feeding-site users, n = 15) and those not using feeding stations that were available within their wintering range (nonusers, n = 10) in southern Norway during winters 2007 and 2008. All estimates are in comparison with the reference category: >1,500 m from feeding stations for feeding-site users; HPD intervals >0 indicate selection and <0 indicate avoidance of distance classes compared with the reference category.

Table 3. Selection estimates (log odds ratio ± 95% Highest Posterior Density [HPD] intervals) of mixed-effects logistic regression model predicting selection for habitat by moose using feeding stations (feeding-site users, n = 15) in southern Norway during the winters of 2007 and 2008 (Fig. 5). All estimates are in comparison to the reference category.[a–c] The model includes a random intercept for each individual (moose identification; SD = 0.346 [HPD interval 0.249–0.569]).

Variable	β	SE	HPD interval	
			Lower	Upper
Intercept	1.581	0.112	1.326	1.823
Dominant tree species[a]				
Mixed deciduous	−1.486	0.200	−1.880	−1.108
Norway spruce	−1.183	0.051	−1.286	−1.083
Cutting class (cc.)[b]				
cc.1	−1.471	0.222	−1.926	−1.049
cc.3	−0.315	0.054	−0.423	−0.212
cc.4	−0.183	0.072	−0.325	−0.042
cc.5	−0.672	0.095	−0.854	−0.482
Distance class (m)[c]				
d2	−0.178	0.075	−0.323	−0.024
d3	−0.588	0.086	−0.746	−0.409
d4	−2.067	0.077	−2.221	−1.917
Dominant tree species × distance class				
Mixed deciduous × d2	0.842	0.237	0.385	1.307
Norway spruce × d2	0.180	0.069	0.047	0.317
Mixed deciduous × d3	−0.698	0.298	−1.301	−0.140
Norway spruce × d3	0.259	0.075	0.115	0.409
Mixed deciduous × d4	1.183	0.254	0.669	1.670
Norway spruce × d4	0.653	0.069	0.518	0.787
Cutting class × distance class				
cc.1 × d2	0.178	0.264	−0.341	0.699
cc.3 × d2	−0.172	0.073	−0.315	−0.028
cc.4 × d2	−0.171	0.111	−0.387	0.043
cc.5 × d2	0.526	0.113	0.308	0.742
cc.1 × d3	1.108	0.261	0.613	1.636
cc.3 × d3	0.240	0.083	0.079	0.401
cc.4 × d3	−0.128	0.126	−0.374	0.124
cc.5 × d3	0.548	0.118	0.311	0.773
cc.1 × d4	1.142	0.283	0.585	1.698
cc.3 × d4	0.357	0.073	0.212	0.497
cc.4 × d4	−0.992	0.139	−1.257	−0.713
cc.5 × d4	0.992	0.108	0.786	1.208

[a] Reference category = Scots pine.

[b] Reference category = cc.2.

[c] Reference category = d1 (0–500 m).

supplementary feed by cervids (Doenier et al. 1997). Snow conditions may have been sufficiently mild for moose not to need the feeding stations during the winters studied. Moreover, feeding history in this area is relatively short (6 yr). It is, therefore, possible that some individuals with feeding stations in their wintering range have not discovered them simply because they have not visited all parts of the area we define as their winter range (95% MCP area) or have not yet learned to feed on the supplied forage. Although the proportion of time spent on feeding stations during winter was, on average, only 5% per individual, diversionary winter feeding as a management intervention has nonetheless altered space-use and habitat-selection patterns of moose, even throughout this relatively short period. Changes in behavior patterns can be expected to be even stronger in situations where animals use feeding stations more intensively.

Local densities around feeding stations can become exceedingly high (≤80% of a local population; Peek et al. 2002 and references therein). In agreement, we found that the likelihood that habitat selected by a feeding-site user within 500 m from feeding sites was almost 5 times higher

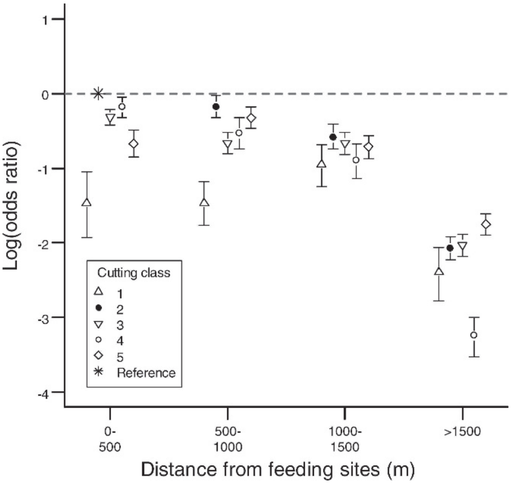

Figure 5. Selection estimates (log odds ratio ± 95% Highest Posterior Density [HPD] intervals) for cutting class within Scots pine–dominated forest stands by moose using feeding stations (feeding-site users, $n = 15$) in southern Norway during winters 2007 and 2008, in relation to distance from feeding stations. All estimates are in comparison with the reference category: cutting class 2 at 0–500 m from feeding stations; HPD intervals >0 indicate selection and <0 indicate avoidance of habitat compared with the reference category.

than selecting locations beyond 1.5 km from the feeding sites. However, we did not observe an increase in selection of assumed high-quality habitat types with increasing distance from feeding sites, which is inconsistent with predictions from central-place foraging theory. Instead, selection for assumed high-quality winter foraging habitat (i.e., pine stands of cc.2) by moose was highest closer to feeding stations (<1 km) and decreased as distance from feeding stations increased. This suggests that intraspecific resource competition, potentially leading to resource depletion near feeding stations, was not a major factor influencing habitat selection of feeding-site users. Moreover, our results indicate that selection for older pine stands and spruce-dominated forest increased with distance from feeding stations. These habitat types are generally characterized by reduced snow cover, which facilitates traveling, provides shelter (Dussault et al. 2006), and holds important forage resources, such as dwarf shrubs (Heikkila et al. 1996).

MANAGEMENT IMPLICATIONS

Diversionary winter feeding as a management intervention can greatly alter space-use and habitat-selection patterns. However, it may not be effective in protecting valuable stands if the valued species (in our case, Scots pine) remains an important part of the diet of individuals using feeding stations. Because feeding-site users concentrated their movements around feeding stations, we recommend establishing feeding sites in sacrifice areas where browsing is permissible and, if possible, >1 km from valuable stands. Future assessment of the effectiveness of diversionary feeding as a tool to reduce browsing damage would benefit from a detailed analysis of the cost of supplying additional feed and the benefits it may generate in reduced forestry losses. Additional evidence from regions with longer feeding traditions is needed to assess how space-use and habitat-selection patterns evolve over time and change with winter severity and intensity of feed use.

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II

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Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore

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Summary

1. Mechanisms that affect the spatial distribution of animals are typically scale-dependent and may involve forage distribution. Forage quality and quantity are often inversely correlated and a much discussed trade-off is whether or not to select for high-quality forage at the expense of forage abundance. This discussion has rarely involved scale-dependence or been applied to Northern browsing herbivores. At small spatial scales, browsers are assumed to select for the best quality forage. But, as high-quality forage resources are often scarce and may become depleted, coarse-scale habitat selection is assumed to be driven by forage availability.

2. To evaluate if moose selection for forage quantity and quality is scale-dependent we modelled summer and winter habitat selection of 32 GPS-marked female moose (*Alces alces*) at two spatial scales (landscape-scale vs. within-home range-scale). We used mixed-effects resource selection functions (RSFs) and landscape-scale forage availability models of six tree species of varying quality for moose. We considered silver birch (*Betula pendula*), downy birch (*Betula pubescens*.), Scots pine (*Pinus sylvestris*) as low quality browse species and rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), willow (*Salix* spp.) as high-quality species.

3. As expected, the overall selection patterns for available browse biomass and quality varied across spatiotemporal scales. At the landscape-scale, moose selected for habitat with high available browse biomass of low quality species while at the within-home range-scale moose selected for sites with the highest quality browse species available. Furthermore, selection patterns during summer remained fairly stable, while during winter, selection at the within-home range-scale switched from sites with high quality to sites with lower quality browse species which suggests depletion of high-quality species. Consistent with expectations from seasonal resource depletion, site fidelity (bimonthly home range overlap) was much lower in winter than in summer.

4. Coarse-scale habitat selection by moose as a function of forage variability revealed a scale-dependent trade-off between available browse quantity and browse quality. Moreover, resource depletion changed the winter selection criteria of free-ranging moose and we demonstrate how the behavioural response to such a dynamic process can be inferred from RSFs.

Key-words: *Alces alces,* deer, grazing, global positioning system, mixed models, patch quality, resource selection function, site fidelity

Introduction

Resource variability over time and space and its effect on the spatial distribution of animals has been the focus of much recent work (Bergman *et al.* 2001; Fortin *et al.* 2003; Fryxell, Wilmshurst & Sinclair 2004; Boone, Thirgood & Hopcraft 2006). A common feature of food resource distribution is that quality and quantity are often inversely correlated (Demment & van Soest 1985; Fryxell 1991), with the most nutritious tending to be the least common (Hansen *et al.* 2009). A much discussed trade-off faced by large ruminants is the selection of high-quality forage at the expense of forage abundance. Indeed, at the patch scale grazing herbivores typically select for higher quality species instead of highly available forage

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(Langvatn & Hanley 1993; Wilmshurst, Fryxell & Hudson 1995), although exceptions have been reported at high latitudes (Van der Wal *et al.* 2000).

Considerably less effort has been devoted to assessing whether such trade-offs are scale-dependent (Johnson 1980; Senft *et al.* 1987; Wiens 1989; Levin 1992). At fine spatial scales, resource selection by wildebeest (*Connochaetus taurines*) is for grass quality rather than biomass. However, seasonal rainfall patterns affecting grass growth (i.e. forage biomass in savanna ecosystems) is regarded as a main driver of the mass migration of several grazing ungulate species at coarser spatial scales (Wilmshurst *et al.* 1999; Fryxell *et al.* 2005). This provides evidence for scale-dependence in selection for forage resources and suggests that large-scale selection patterns may constrain the options available at smaller spatial scales (Wilmshurst *et al.* 1999). Much of the evidence of trade-offs between food quantity and quality comes from studies on either grazers or mixed feeders (Fritz & de Garine Wichatitsky 1996; Bergman *et al.* 2001; Fortin *et al.* 2003; Fryxell, Wilmshurst & Sinclair 2004; Boone, Thirgood & Hopcraft 2006). At northern latitudes, the spatial relationship between browsing herbivores and their food supply has predominantly focused on relatively fine spatial scales such as habitat patches or single trees (see Hobbs 2003 and references therein) or through indirect evidence of space use patterns via pellet group counts (Månsson *et al.* 2007a). Much less is known about how the distribution of browse of varying quality affects habitat selection at intermediate to coarse spatial and temporal scales based on individually marked animals. This is partly due to the logistical difficulties of sampling animal locations and estimating mixed-plant community biomass and quality at large spatial scales in heterogeneous environments (Fryxell *et al.* 2005; Pettorelli *et al.* 2006; Hebblewhite, Merrill & McDermid 2008).

Habitat conditions at northern latitudes are strongly seasonal (Dussault *et al.* 2005a). During winter, forage resources for large herbivores are, generally, of low quality (Shipley, Blomquist & Danell 1998) and diminish through the season due to natural browsing, snow cover and lack of new vegetation growth (Edenius 1991). Loss of high-quality forage can be expected to change habitat selection patterns and to lower within-season site fidelity (Wittmer, McLellan & Hovey 2006). For example, if herbivores intensively select for plant species with high quality and low abundance, these food items may be depleted forcing an individual to increase selection for habitat that contains abundant forage of lower quality. The incorporation of such insights to RSFs (Manly *et al.* 2002) using global positioning system (GPS) technology has currently not been attempted.

The moose (*Alces alces* L.) is a typical browser (Cederlund *et al.* 1980; Bergstrom & Hjeljord 1987) and is regarded as an energy maximizer (i.e. the assumed goal of an individuals' foraging strategy is to maximize the long-term rate of energy intake; Belovsky 1978; Stephens & Krebs 1986). Summer dietary nitrogen greatly affects moose body mass (Hjeljord & Histol 1999; McArt *et al.* 2009) and highlights the importance of summer habitat selection strategies. Nevertheless, the majority of studies exploring resource selection and foraging strategies of moose have been biased towards winter behaviour (Vivas & Saether 1987; Danell, Edenius & Lundberg 1991; Andersen & Saether 1992; Shipley, Blomquist & Danell 1998; Poole & Stuart-Smith 2006). Previous findings of Månsson *et al.* (2007a) showed that the relation between moose browsing and forage availability of the most abundant browse species changed from use lower than expected from availability at small spatial scales (i.e. habitat patch scale) to proportional use at larger scales (i.e. landscape-scale). This suggests that a multi-scale approach is appropriate when studying moose-resource relationships (Poole & Stuart-Smith 2006; Månsson *et al.* 2007a).

Here we estimated habitat selection of moose across two spatiotemporal scales; (i) seasonal selection at the landscape-scale (the second order of Johnson 1980) and (ii) intra-seasonal selection at the within-home range-scale (the third order of Johnson 1980). The objective of our study was to determine whether habitat selection by moose as a function of available browse biomass (i.e. forage quantity) and quality is scale-dependent. If habitat selection is not scale-dependent, we predicted that moose would select for areas with high biomass of high-quality browse regardless of temporal and spatial scale (P_1). However, if selection patterns at coarse spatial scales are constrained by forage quantity-quality decisions, we predicted that at the landscape-scale moose would select for sites containing browse species of high abundance (following Månsson *et al.* 2007a) and lower quality ($P_{2.1}$), but focus selection on higher quality browse at the within-home range-scale ($P_{2.2}$). Moreover, as high-quality forage is constantly renewed during summer, we expected selection patterns to remain stable throughout the season ($P_{3.1}$) and the degree of site fidelity to be high (i.e. large overlap between monthly home ranges; $P_{3.2}$). Contrastingly in winter, we predicted a decline in selection for higher quality browse species at the within-home range-scale due to resource depletion ($P_{4.1}$; Edenius 1991; Shipley, Blomquist & Danell 1998) and the degree of site fidelity to be low (i.e. small overlap between monthly home ranges; $P_{4.2}$). To compensate for depleted high-quality resources we expected moose to increase selection for habitat with lower quality species as winter progressed ($P_{4.3}$).

Materials and methods

STUDY AREA

The study area (1733 km^2) is located in southern Norway within parts of Telemark, Buskerud and Vestfold counties (Fig. 1). The area is in the boreonemoral zone and is mostly covered by commercially managed coniferous forest (82%). Stands are dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) but some mixed deciduous stands of birch species (*Betula pubescens* and *B. pendula*), rowan (*Sorbus aucuparia*), willow (*Salix* spp.) and aspen (*Populus tremula*) occur throughout the area. Abundant field layer species include bilberry (*Vaccinium myrtillus* L.), cowberry (*V. vitis-idaea* L.), raspberry (*Rubus idaeus* L.) and, fireweed (*Epilobium angustifolium* L.). The mean monthly temperatures in June and September (i.e.

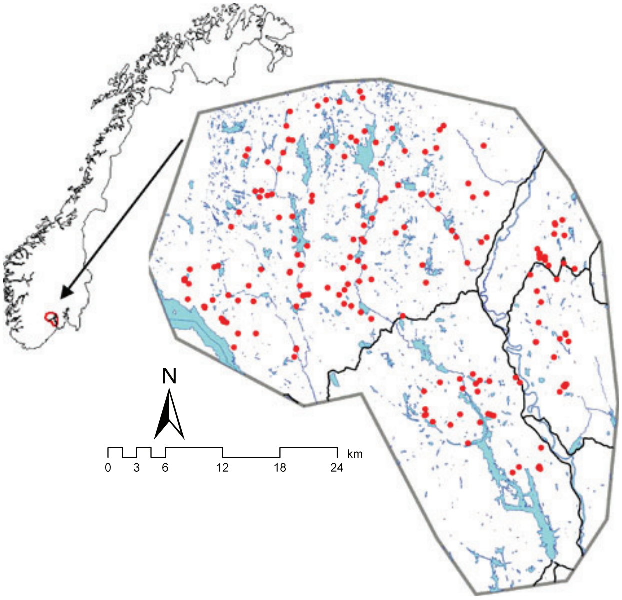

Fig. 1. Map of the study area in southern Norway (part of Telemark, Buskerud and Vestfold counties). The map shows the spatial distribution of forest stands sampled for browse biomass availability (n = 189), lakes, rivers, major roads and boundary of the study area.

summer period) are 15·4 and 10·6 °C, and in January and April (i.e. winter period) are – 5 and 4·3 °C respectively (Siljan weather station at 100 m a.s.l., The Norwegian Meteorological Institute; http://www.met.no). Average (± SE) snow-depths in the centre of the study area (430 m a.s.l) during January–April 2007 and 2008 were 49 ± 2·4 cm and 72 ± 1·5 cm (Mykle weather station, The Norwegian Meteorological Institute). Moose densities in the area are estimated at 1·5 individuals per km^2 (Norwegian Institute for Nature Management; http://www.dirnat.no). Red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.) densities are 0·5 and 0·2 individuals per km^2, respectively. Large predator species are absent and hunting is the single most important cause of moose mortality in this area.

FORAGE QUALITY AND QUANTITY

During summer moose strip the leaves of deciduous trees and forage on a wide range of shrubs and herbs. During winter, they predominantly feed on twigs of deciduous trees and Scots pine (Bergstrom & Hjeljord 1987; Hjeljord, Hovik & Pedersen 1990). For this study we considered six tree species (i.e. target species) that occur throughout the study area and are reported to be frequently browsed by moose in Scandinavia, but that are likely of variable quality to moose. To express forage quality for moose in terms of single measures of digestibility, nutrient content or secondary compounds is complicated and rarely straightforward when analysing multiple species (Bergstrom & Danell 1986). For example, Shipley, Blomquist & Danell (1998) concluded that broad categories of chemicals for our six target species were not reliable indicators of forage quality for moose as they poorly predicted diet selection. Therefore, what we refer to as forage quality is rather based on selection ranks as reported in previous studies of species-specific forage selection patterns of moose in the boreonemoral or boreal zone of Scandinavia (results of the literature review are summarized in Table S1, Supporting Information). We assume that such a ranking of selection at a fine scale reflects moose preference, i.e. what they would prefer to eat in a controlled setting with access to known alternative forage (Thomas & Taylor 2006). We only included studies with a use-availability sampling design to assess if species were actively selected, avoided or used proportional to their availability (Thomas & Taylor 2006). Based on this review, we refer to rowan, aspen and willow as higher quality browse species and silver birch, downy birch and Scots pine as lower quality species during summer. During winter Scots pine is considered to be of higher quality than silver birch and downy birch. Norway spruce was excluded from this study because of its negligible use as a food item by moose (Cederlund *et al.* 1980). At the onset of the study we also included various field layer species (e.g. % cover of bilberry, other berries, herbs and grasses). However, due to a high correlation between browse biomass and cover of the field layer (Table S2; Supporting Information) we restricted the mixed-effect RSFs (described below) to the six tree species as logistic regression is sensitive to collinearity between explanatory variables (Nielsen *et al.* 2002). Collinearity between available browse biomass for the six target species was sufficiently low (all values were Pearson $r < 0·35$) to include them in one RSF model. To quantify and predict seasonal variation in species-specific forage availability throughout the study area our approach consisted of several parts.

The first phase involved the modelling of available browse biomass for the six target species as a function of tree characteristics. After the peak of the growing season when maximum biomass is attained (first 2 weeks of August 2007), we sampled 50 unbrowsed trees per target species with available shoots evenly distributed across the height interval 0–3·0 m, as this interval offered the largest amount of available browse per tree for moose (Danell, Huss-Danell & Bergstrom 1985). Trees were sampled at locations distributed widely across the study area to minimize the impact of individual site influences and ensure the available biomass models would be general for the area. For each tree we measured height (cm), an index of canopy volume

(m^3: two perpendicular measurements of canopy diameter (cm) × the difference between tree height and the height (cm) at the bottom of the canopy) and stem diameter (mm; mean of two perpendicular measurements, 20 cm above-ground). To estimate available summer biomass (i.e. leaf biomass) we stripped all leaves from shoots at the mean strip length measured for that species in the study area (Table S3, Supporting Information). To estimate winter biomass (i.e. twig biomass) we clipped living shoots > 50 cm above-ground (mean annual snow depth) at the mean bite diameter measured for that species in the study area (Table S3, Supporting Information) and discarded the leaves. All samples were dried at 80 °C to constant mass and weighed to the nearest 0·1 g. We used multiple regression models to predict available browse biomass (for leaf and twig biomass separately) per target species with tree height, canopy volume and stem diameter as predictors. The response variable was log-transformed to fulfil the assumptions of normality. To find the most parsimonious model predicting leaf and twig biomass (Table 1) we used backwards selection with F tests (Crawley 2007; Murtaugh 2009) using P = 0·05 as the threshold for inclusion or exclusion of predictor variables. Model selection using F tests is a more conservative method than AIC or BIC based model selection procedures (Murtaugh 2009). Analyses were performed using the statistical software R version 2.8.0 (R Development Core Team 2008) throughout.

The second phase involved sampling target species within various forest stand types throughout the study area, in order to calculate species-specific seasonal forage biomass spatially using the predictive leaf and twig biomass equations (Table 1). We sampled 189 forest stands (Fig. 1) during June and July 2008 using a random stratified sampling design. Stands were selected from 7-year-old GIS-based forest maps with good identification accuracy of the main habitat characteristics (see van Beest *et al.* 2010 for more details on map accuracy). Selection was based on cutting class (5 class factor; based on standard national forest evaluation of Norway), dominant tree species (3 class factor; Scots pine, Norway spruce or mixed deciduous) and aspect (4 class factor constituting the four cardinal directions). We sampled each habitat factor combination (n = 60) at least three times, using five 50 m^2 circular plots per forest stand (i.e. total of 945 plots over 189 forest stands). The plots were placed in the four cardinal directions with one in the centre, at least 25 m apart and > 15 m from forest stand edges. Within each plot we recorded the abundance of all tree species > 20 cm tall and for the target species we measured the variables that best predicted leaf and twig biomass below 3 m height for a particular species (Table 1). We were then able to estimate total available summer biomass for each target species in every plot by calculating leaf biomass. For the winter biomass calculations we calculated twig biomass assuming a 50 cm deep snow layer and considered all biomass below this threshold unavailable.

The final part of our forage availability assessment was to link the ground-based vegetation measurement with GIS-based covariates to spatially predict and map the species-specific variation in forage biomass availability for summer and winter. We used generalized linear mixed models (GLMM) to predict the amount of forage biomass within forest stands for each species separately. Spatial covariates included cutting class, dominant tree species, stand productivity (2 class factor; high and low), altitude (m), slope (°), aspect, hill shade (index of solar incidence), and sky view (percentage sky not obstructed by terrain features). Covariates were screened for collinearity using r < 0·5. Species biomass was transformed using the log-link function and forest stand ID was included as a random factor to account for dependence between plots within forest stands. To find the most parsimonious model predicting biomass availability across the study area, we used backward selection with F tests (Murtaugh 2009) as described above. Before model development, we randomly withheld 20% of the data for model cross-validation (Johnson *et al.* 2006; Hebblewhite, Merrill & McDermid 2008) to compare observed with predicted biomass values using Pearson r (all models > 0·35) and R^2_{adj} (all models > 0·31). Due to low predictive power and similar quality of the rowan, aspen and willow models we pooled these species together and created one model (RAW species group), as is typical in moose browse surveys (Solbraa 2003). The final forage availability models are presented in Table 2 for summer and Table 3 for winter. Following Hebblewhite, Merrill & McDermid (2008), we used the fixed effects estimates of the forage availability models to map species-specific biomass (g/50m^2) throughout the study area using RASTER calculator in ArcGIS v.9.2 (2006 ESRI, Redlands, CA, USA).

MOOSE DATA

A total of 34 adult female moose were tranquilized by dart gun from a helicopter, using established techniques (Arnemo, Kreeger & Soveri 2003). We fitted the moose with GPS collars (Tellus Remote GSM, Followit AB, Lindesberg, Sweden) programmed with a 1-h relocation schedule. Collars were equipped with dual-axis motion sensors which record vertical and lateral head and neck movements. During each location attempt the total number of movements (range = 0–250) was stored in the collar memory. Collar data were collected from January to November 2007 (n = 16) and 2008 (n = 18) but the sample size was reduced to 32 individuals during winter and to 26 individuals during summer due to collar malfunctions. All GPS locations collected within 24 h of marking

Table 1. Variables that best predict species-specific forage biomass availability for moose during winter and summer

Season	Species	Intercept	Log(canopy volume) in m^3	Mean stem diameter (cm)	R^2_{adj}	F	d.f.	P
Summer	Rowan	3·40	0·54	–	0·68	102·0	1,48	< 0·0001
	Aspen	2·63	0·30	0·25	0·63	28·9	2, 47	< 0·0001
	Willow species	1·97	0·16	0·45	0·64	39·3	2, 47	< 0·0001
	Silver birch	3·18	0·58	–	0·79	166·4	1,48	< 0·0001
	Downy birch	3·25	0·62	–	0·70	155·3	1,48	< 0·0001
Winter	Rowan	1·89	0·42	0·42	0·63	39·3	2, 47	< 0·0001
	Aspen	2·44	0·34	0·26	0·64	42·2	2, 47	< 0·0001
	Willow species	2·02	0·32	0·21	0·66	46·2	2, 47	< 0·0001
	Silver birch	2·28	0·39	0·31	0·72	78·9	2, 47	< 0·0001
	Downy birch	2·34	0·40	0·33	0·75	71·8	2, 47	< 0·0001
	Scots pine	4·34	0·48	0·24	0·92	327·8	2, 47	< 0·0001

Table 2. Summary of the mixed-effects regression models and model evaluation (Pearson r and R^2_{adj}) predicting summer forage availability across the study area for each target species. Scots pine biomass during summer was considered to be similar to winter biomass availability (Table 3). All estimates are made in comparison to the reference categories

Summer	Downy birch		Silver birch		RAW species	
Fixed effects	β	SE	β	SE	β	SE
(Intercept)	−0·756	0·488	−1·663	0·868	2·515	0·355
Cutting class[a]						
2	1·188	0·526	0·262	0·136	−0·315	0·364
3	−0·576	0·526	−0·128	0·135	−0·908	0·359
4	−1·252	0·555	−0·174	0·137	−0·042	0·365
5	−2·292	0·574	−0·29	0·136	−0·747	0·362
Dominant tree species[b]						
Scots pine	–	–	−0·15	0·113	−2·018	0·306
Norway spruce	–	–	−0·294	0·113	−0·993	0·277
Productivity[c]						
Low	1·669	0·42	–	–	1·048	0·289
Altitude (m)	–	–	−0·001	< 0·001	–	–
Skyview	–	–	0·027	0·01	–	–
Random effect	SD		SD		SD	
Forest stand ID	2·186		0·995		1·537	
Model evaluation						
r (Pearson)	0·410		0·445		0·520	
R^2_{adj}	0·309		0·314		0·372	

[a] Reference = cutting class 1.
[b] Reference = deciduous stands.
[c] Reference = high productivity.

Table 3. Summary of the mixed-effects regression models and model evaluation (Pearson r and R^2_{adj}) predicting winter forage availability across the study area for each target species. All estimates are made in comparison to the reference categories

Winter	Downy birch		Silver birch		RAW spp		Scots pine	
Fixed effects	β	SE	β	SE	β	SE	β	SE
(Intercept)	−1·182	0·661	−1·465	0·827	2·425	0·421	−3·867	0·916
Cutting class[a]								
2	2·244	0·538	0·207	0·13	−0·313	0·433	0·689	0·69
3	0·386	0·538	−0·142	0·128	−1·05	0·429	−1·694	0·756
4	−0·417	0·569	−0·117	0·13	−0·307	0·436	−1·456	0·789
5	−1·075	0·59	−0·254	0·13	−0·994	0·433	−1·899	0·805
Dominant tree species[b]								
Scots pine	–	–	−0·274	0·105	−2·52	0·364	3·846	0·624
Norway spruce	–	–	−0·373	0·099	−1·831	0·33	−0·364	0·71
Productivity[c]								
Low	1·787	0·438	–	–	0·707	0·343	1·931	0·81
Aspect[d]								
North	−0·998	0·509	–	–	–	–	–	–
South	−0·831	0·493	–	–	–	–	–	–
West	0·173	0·485	–	–	–	–	–	–
Slope (°)	−0·043	0·022	–	–	–	–	–	–
Skyview	–	–	0·023	0·01	–	–	–	–
Random effect	SD	–	SD	–	SD	–	SD	–
Forest stand ID	2·137	–	0·893	–	1·798	–	2·547	–
Model evaluation								
r (Pearson)	0·351	–	0·431	–	0·589	–	0·593	–
R^2_{adj}	0·358	–	0·405	–	0·335	–	0·439	–

[a] Reference = cutting class 1.
[b] Reference = deciduous stands.
[c] Reference = high productivity.
[d] Reference = East facing slopes.

were excluded. Annual snow conditions in the study area were used to define winter length (time with ≥30 cm snow depth). As such winter in 2007 stretched from 21 January until 8 April and in 2008 from 4 January until 30 April. Summer was arbitrarily defined as the period 1 June till 15 September for both years. Spring and autumn were not included in this study.

In this study, the average GPS-collar fix rate was 96% (range 87–99%) during winter and 90% (range 83–97%) during summer. We used an iterative simulation method (Frair *et al.* 2004) to correct for possible bias in GPS fix success prior to analysing habitat selection (van Beest *et al.* 2010).

MOOSE ACTIVITY AND HABITAT SELECTION ANALYSIS

We estimated habitat selection patterns by moose as a function of species-specific forage availability using RSFs, defined as any function proportional to the probability of use of a resource by an animal (Manly *et al.* 2002). Resource selection functions reflect habitat use and not foraging activity as such. To focus our habitat selection analyses on foraging behaviour, we used GPS-based motion sensor data (described above) to estimate moose activity as a function of species-specific forage availability. Large herbivores spend the majority of their active time feeding (Mysterud 1998). It is therefore reasonable to assume that high movement counts in the collar reflect foraging bouts while low movement counts mirror ruminating or bedding (Moen, Poster & Cohen 1996b; Dussault *et al.* 2004). Using activity as a proxy for foraging behaviour we expected moose activity to increase with available forage biomass and quality (i.e. good foraging habitat). We used mixed-effects logistic regression with moose ID as a random intercept to estimate the probability of moose being active (response variable) as a function of species-specific forage availability (predictor variables). GPS positions were classified into inactive (i.e. locations with < 10 movement counts/unit time) or active (i.e. ≥ 10 movement counts/unit time). The cut-off value of 10 movement counts/unit time was subjectively chosen to minimize the potential of small head or neck movements while lying down, to be included as active (foraging) locations. The results indicated that moose activity was positively related to forage availability and quality as expected (Fig. S1 Table S4; Supporting Information). To remove potential bias of inactive (resting) positions to the habitat selection analyses we restricted the RSF models to active positions only (64·9% of all used locations). After this procedure the average (±SE) number of (GPS) locations used per moose during summer and winter were 1005 ± 159 and 917 ± 109, respectively.

RSFs were estimated with use–availability logistic regression (design III data; Thomas & Taylor 2006) with random intercepts for each individual to account for unbalanced sampling design (Gillies *et al.* 2006; Hebblewhite & Merrill 2008; Godvik *et al.* 2009; van Beest *et al.* 2010). Based on parsimony, the mixed-effect RSF models contained only a random intercept for moose ID because the inclusion of a second random intercept for year did not improve model fit based on AIC (Burnham & Andersen 1998). Mixed-effect RSFs were fitted using the library 'lme4' (Bates 2007) implemented in R (R Development Core Team 2008).

Habitat availability at the within-home range-scale was estimated by drawing a random sample of points from within each individuals' wintering and summer home range (delineated by a 95% Minimum Convex Polygon; MCP). The number of available points selected equalled the number of active points used by each individual. Habitat availability at the landscape-scale was estimated similarly but random points were sampled from within the study area boundaries and used points were considered what was available at the within-home range-scale (Aebischer, Robertson & Kenward 1993).

To test our predictions we developed four mixed-effects RSF models; one for each combination of season and spatial scale. At the within-home range-scale the fixed effects included: browse biomass for all target species (three species and one species group in summer and winter), month (4-class factor) and their interaction to assess intra-seasonal changes in selection. At the landscape-scale the mixed-effects RSF models contained only browse biomass of all target species as covariates, as we did not expect large differences in monthly selection estimates at this spatial scale. This was supported by a model selection procedure based on Δ AIC\ (Burnham & Andersen 1998) which also confirmed that the use of a random intercept (moose ID) increased model fit across all spatiotemporal scales (Table S5; Supporting Information).

The outcome of all our final mixed-effect RSF models (i.e. selection estimates) is the log odds of moose using a pixel in the study area maps (resolution of 50 × 50 m) as a function of the predictor variables. Because of the arbitrary number of randomly sampled points (both used and available) in our RSF models (as is typical in design III data sampling) we can not derive absolute probabilities of selection. Instead we calculated log odds ratios relative to a reference category which is informative and reliable (Godvik *et al.* 2009; van Beest *et al.* 2010). To visualize moose selection patterns we set the reference point to the mean available biomass value for each target species depending on the spatiotemporal scale in question (e.g. summer, winter, landscape or home range-scale). This will give a clear indication if moose use areas that contain more (i.e. selection), the same (i.e. proportional use) or less (i.e. avoidance) available biomass then the scale-dependent mean. Thus, a regression line with a slope of 0 indicates a proportional relationship (i.e. random use). To evaluate whether selection estimates were significantly different from 0 (i.e. reference point) we used 10 000 Markov Chain Monte Carlo (MCMC) samples and 95% Highest Posterior Density intervals (HPD intervals) using the library 'coda' (Plummer *et al.* 2008) implemented in R (R Development Core Team 2008). The use of Bayesian HPD confidence intervals is preferred when analysing large, unbalanced data sets with mixed-effect models because any uncertainty in both fixed- and random-effect parameters is taken into account (Bolker *et al.* 2009), leading to more conservative inference compared to standard 95% confidence intervals (Baayen, Davidson & Bates 2008). To assess the predictive performance of our RSF models we calculated the area under the ROC (Receiver Operating Characteristic) curve, which varies between 0·5 (no predictive power) and 1 (perfect predictive power; Boyce *et al.* 2002).

QUANTIFYING SITE FIDELITY

Site fidelity can be defined as the tendency of an animal to remain within the same area for an extended period of time (White & Garrott 1990) and is typically quantified by the degree of overlap between consecutive home ranges (Doncaster & Macdonald 1991; Kernohan, Gitzen & Millspaugh 2001; Edwards, Nagy & Derocher 2009). We calculated the proportion of bimonthly home range overlap using 95% MCPs within each season and for each individual moose. Because the use of MCP as a home range estimator has been questioned (Kernohan, Gitzen & Millspaugh 2001) we additionally calculated and report bimonthly home range overlap using the volume of intersection of the 95% kernel utilization distributions (kernel UDs; Millspaugh *et al.* 2004). Home range overlap was calculated using the library 'adehabitat' (Calenge 2006) implemented in R (R Development Core Team 2008).

Results

LANDSCAPE-SCALE SELECTION

In general, habitat selection by moose at the landscape-scale increased with biomass of the lower quality species (Fig. 2; Table S6 in Supporting Information), suggesting that the availability of high-quality species at coarse spatial scales was not sufficiently high to affect selection (as expected by $P_{2\cdot1}$). During summer, selection for higher quality species biomass, represented by the RAW species group and silver birch (Fig. 2; Table S6 in Supporting Information), did not differ significantly from proportional use as HPD intervals overlapped with 0 (Fig. 2a). Selection for the lower quality downy birch increased with available biomass, as expected ($P_{2\cdot1}$) but decreased with biomass of Scots pine (Fig. 2a). In contrast, during winter we found negative selection estimates for increasing biomass of high-quality RAW species and lower quality silver birch, and positive selection estimates for the low quality downy birch and Scots pine (Fig. 2b). The areas under the ROC curve for the landscape-scale RSF models were 0·717 and 0·751 for summer and winter respectively.

HOME RANGE-SCALE SELECTION

At the within-summer home range-scale, moose selection increased with biomass of the higher quality RAW species (as expected by $P_{2\cdot2}$ and $P_{3\cdot1}$) but also with biomass of the lower

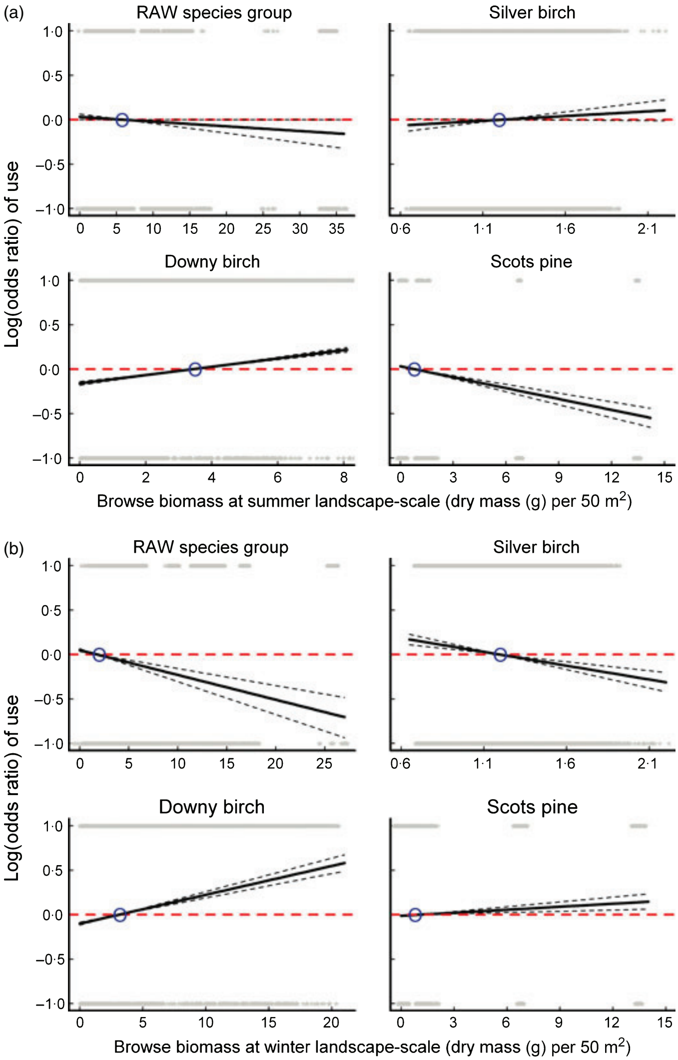

Fig. 2. Selection estimates (log odds ratio of use ± 95% highest posterior density intervals) for available browse biomass for each target species at the (a) summer and (b) winter landscape-scale, where the log odds ratios are calculated relative to the average available browse biomass for that target species (reference circle). Selection estimates above 0 (reference level) indicate higher selection relative to the reference, whereas values below 0 indicate lower selection. Grey stars in the plots represent the raw data of used points (upper) and available points (lower) over the range of species-specific available forage biomass.

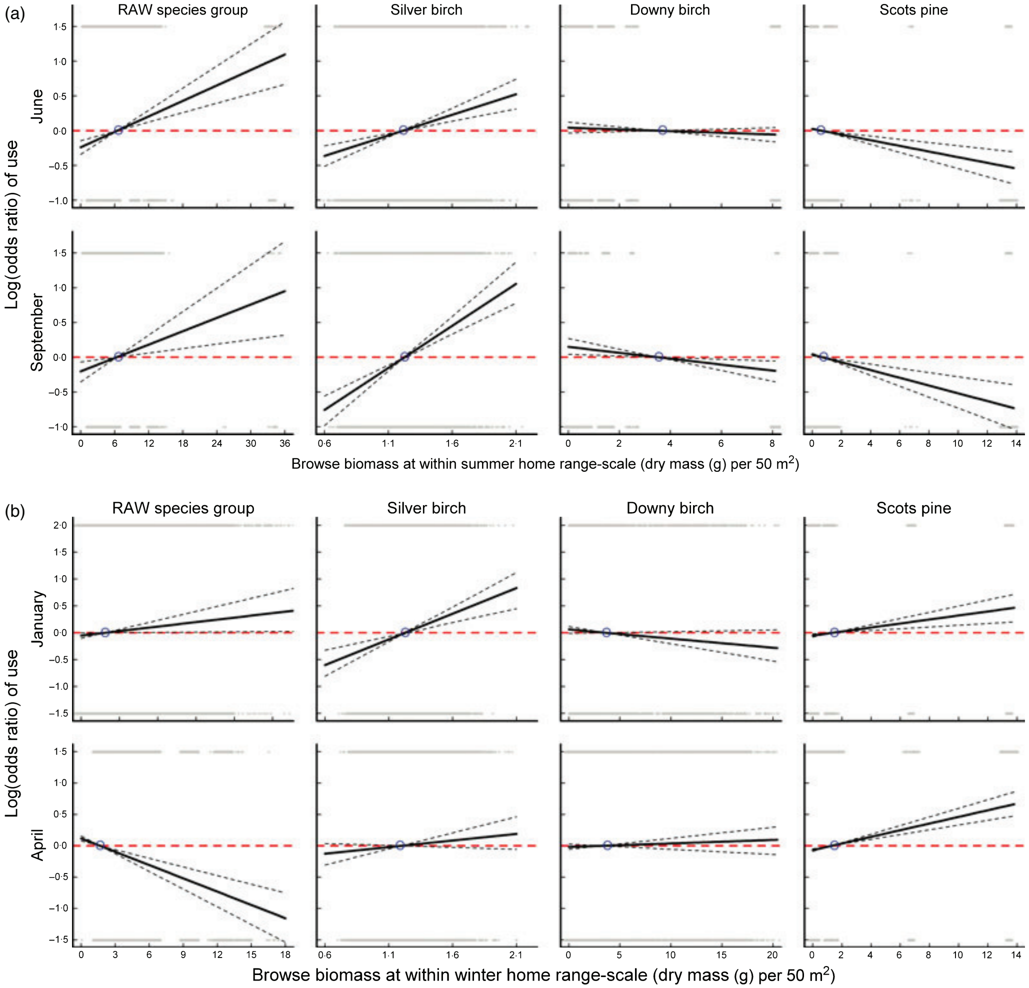

Fig. 3. Selection estimates (log odds ratio of use ± 95% highest posterior density intervals) for available browse biomass for each target species at the (a) within-summer, and (b) within-winter home range-scale, where the log odds ratios are calculated relative to the average available browse biomass for a target species (reference circle). The figure shows the first and last month of each season (see Fig. S3 for selection estimates across all months during summer and winter). Only locations where moose were active were included in the models. Selection estimates above 0 (reference level) indicate higher selection relative to the reference, whereas values below 0 indicate lower selection. Grey stars in the plots represent the raw data of used points (upper) and available points (lower) over the range of species-specific available forage biomass.

quality silver birch (Fig. 3a; Table S7 in Supporting Information). Selection for low quality downy birch biomass changed slightly from proportional use in early summer (June) to negative selection in late summer (September; Fig. 3a). Selection for available Scots pine biomass remained negative throughout summer. The mean proportion of bimonthly home range overlap using 95% MCPs was 0·78 (CI: 0·71–0·86, $n = 66$) and 0·7 (CI: 0·63–0·78, $n = 26$) for the 95% kernel UDs (Fig. 4a). Overall, within-summer site fidelity was rather high and the selection patterns remained fairly constant (as expected by $P_{3·1}$ and $P_{3·2}$) suggesting that the renewal of resources throughout the growing season allowed moose to adopt a stable selection strategy (see Fig. S2a in Supporting Information for complete selection patterns during summer).

This was not the case during winter. In early winter (January) moose selection increased with biomass of the high-quality RAW species but as expected ($P_{3·2}$) this pattern was negative in late winter (April; Fig. 3b). Selection for lower quality silver birch biomass also decreased over winter from positive in January to proportional in April (HPD intervals overlap with 0). The reversed was observed for downy birch

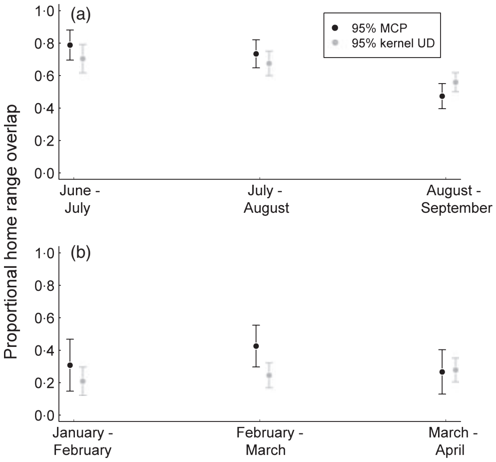

Fig. 4. Mean (and 95% confidence intervals) proportion of bimonthly home range overlap within-summer (a) and winter (b) using 95% MCP and 95% kernel UD. Sample size (n = total number of monthly home ranges for all moose) = 66 and 92 for summer and winter, respectively.

with negative selection for high biomass habitat in early winter (January) to proportional in late winter (April; Fig. 3b). Selection for Scots pine available biomass was positive throughout winter, with a peak during mid-winter (Fig. S2b in Supporting Information). The mean proportion of bimonthly home range overlap using 95% MCP was 0·33 (CI: 0·19–0·48, $n = 32$) and 0·25 (CI: 0·17–0·33, $n = 92$) for the 95% kernel UDs (Fig. 4b). Overall, within-winter site fidelity was lower than in summer and selection for high-quality species declined markedly over time (as expected by $P_{4\cdot 1}$ and $P_{4\cdot 2}$) suggesting that depletion of higher quality food resources forced moose to change their selection strategy by increasingly selecting for lower quality species as winter progressed ($P_{4\cdot 3}$; see Fig. S2b in Supporting Information for complete selection patterns during winter). The areas under the ROC curve for the within-home range-scale RSF models were 0·719 and 0·766 for summer and winter respectively.

Discussion

Habitat selection can be envisaged as a hierarchical spatial process with landscape-level home range establishment and the final choice of a dietary item as the endpoints of a selection continuum (Morris 1987; Senft *et al.* 1987). Our study of spatiotemporal habitat selection as a function of forage variability in a large browser, the moose, shows that selection criteria are affected by a scale-dependent trade-off between forage quality and quantity (rejecting P_1, supporting $P_{2\cdot 1}$ and $P_{2\cdot 2}$). We found that the pattern of habitat selection within-home ranges changed during winter but remained stable during summer (supporting $P_{3\cdot 1}$ and $P_{4\cdot 1}$). Furthermore, bimonthly home range overlap within seasons (an index for site fidelity) was high in summer and low in winter (supporting $P_{3\cdot 2}$ and $P_{4\cdot 2}$). We interpret these results as direct effects of the depletion of higher quality food resources during winter. The initial positive selection for habitat containing higher quality browse biomass switched to avoidance as winter progressed while selection for areas with high biomass of lower quality species increased (supporting $P_{4\cdot 3}$). To our knowledge this study is the first to demonstrate how a behavioural response to depleted resources can be inferred from RSFs using GPS data.

SCALE-DEPENDENT TRADE-OFFS IN FORAGE QUALITY-QUANTITY

Scale dependency in habitat selection as a function of forage variability is increasingly reported, especially in grazing ungulates (Wilmshurst *et al.* 1999; Apps *et al.* 2001; Fortin *et al.* 2003; Anderson *et al.* 2005), although exceptions do occur. For example, muskoxen (*Ovibos moschatus*) selected for the same food resource (*Carex aquatilis*) across several spatial scales (Schaefer & Messier 1995). However, this generalization could be an effect of the hierarchical levels being chosen from within one scaling domain (Wiens 1989; Schaefer & Messier 1995) or due to an absence of trade-offs, as observed in domestic sheep (*Ovis aries*) (Mysterud *et al.* 1999). Scale dependency for moose-resource relationships has previously been highlighted by Månsson *et al.* (2007a) who showed that forage availability (using % cover as an index) influenced winter browsing patterns across multiple spatial scales.

Selection decisions for forage quantity (expressed as available forage biomass) and quality by moose (a large browser) were also scale-dependent in our case. Moose selected for higher quality browse at the within-home range-scale, at least during summer. However, because these resources are relatively scarce and widely dispersed across the study area, the energetic costs associated with movement and searching seem to constrain selection for higher quality food resources at the landscape-scale. Instead, moose selected for high abundance of lower quality browse species that could still serve as adequate bulk feed. As such, we argue that coarse-scale habitat selection by moose as a function of forage variability can be explained by a scale-dependent trade-off between available browse biomass (i.e. quantity) and browse quality.

Selection patterns for the lower quality species also varied across spatial and temporal scales. For example, selection for habitat with a high availability of Scots pine biomass was high during winter, at both spatial scales, but low during summer. This is what we would expect from the literature as Scots pine is considered an important component of the moose winter diet (Kalen & Bergquist 2004; Månsson *et al.* 2007b) and is typically avoided as a food item during summer, although exceptions have been reported (Faber & Lavsund 1999). Selection for silver birch and downy birch biomass also varied and changed across scales which may be explained by differences in quality and growth rate between the two birch species (Danell, Huss-Danell & Bergstrom 1985). Silver birch, which represents only a small proportion of the available biomass in our study area, was highly selected at the within-home range-scale in a similar way to the high-quality RAW species group. In contrast, the abundant but lower quality downy birch was highly selected at the landscape-scale only. Irrespective of season, moose in southern Norway typically choose to feed on the fast growing and higher quality silver birch (Danell & Ericson 1986; Shipley, Blomquist & Danell 1998) and selection for this species should, therefore, be higher at smaller spatial scales as explained above. The predictive performance of our RSF models, evaluated with the area under the ROC curve, was acceptable (Dussault *et al.* 2004). Nevertheless, some variability in selection for forage quantity and quality was not accounted for by the models, especially during summer. Moose are known to forage on a wide variety of species found in the field layer (Hjeljord, Hovik & Pedersen 1990; Bo & Hjeljord 1991; Heikkila *et al.* 1996) and the absence of field layer vegetation in our analyses may have contributed to the unexplained variation in the summer habitat selection models. Future studies assessing moose-resource relationships would benefit from incorporating the field layer vegetation into RSF analyses to get a more complete understanding of scale-dependent habitat selection strategies and foraging behaviour. However, this is not a trivial task due to collinearity between field layer vegetation and available browse biomass as observed in this study.

Constraints in habitat use and trade-offs associated with non-dietary goals such as human disturbance (Hebblewhite & Merrill 2008), predator avoidance (Frair *et al.* 2005) and, or shelter (Mysterud *et al.* 1999; Choquenot & Ruscoe 2003) are well known and may cause habitat selection to vary across scales (Boyce 2006). It is plausible that selection for higher quality browse by moose regardless of temporal and spatial scale (P_1) was constrained due to factors such as topography (Kittle *et al.* 2008) or snow cover (Dussault *et al.* 2005b; Månsson 2009). Identifying the appropriate spatial scales of analysis for RSFs for a given biological question is critical, due to the effect that environmental heterogeneity and other large-scale processes have on a species' habitat selection patterns across multiple scales (Boyce 2006), and will facilitate more biologically relevant interpretations of the mechanisms involved. Furthermore, as individual-based data sets that contain both life-history and GPS-based animal movement data are increasingly available, an important area for future research is to address fitness consequences (e.g. survival and reproduction rate; Moen *et al.* 1996a) associated with individual variation in habitat selection strategies and their links to scale (Bowyer & Kie 2006).

DEPLETION AND RENEWAL OF FORAGE RESOURCES

In foraging theory, depletion of resources at fine spatial scales is the basis for predicting patch departure (Charnov 1976) and giving-up-densities (Brown 1988). Documentation on forage depletion and the behavioural response by browsing herbivores is mostly based on fine scale experimental studies. For example, white-tailed deer (*Odocoileus virginianus*) altered foraging behaviour and diet selection as a result of forage depletion (Kohlmann & Risenhoover 1994) at the patch level. However, predicting patch use through forage biomass alone appeared difficult and patch quality was proposed as an important additional predictor. Edenius (1991) showed that, during winter, moose initially selected for higher quality aspen trees and when available biomass was depleted moose steadily increased selection for lower quality and more abundant Scots pine trees. Similarly, Shipley, Blomquist & Danell (1998) observed an increase of low quality species in the moose winter diet when plant abundance of high-quality species declined. These results are highly comparable to our findings of habitat selection patterns by free-ranging moose at the within-winter home range-scale, despite our very different methodological approach and scale of observation. It seems that selection decisions at the landscape-scale for high abundance of lower quality species, as observed in our study, allow herbivores to compensate for unfavourable temporal variation in resource availability (e.g. due to depletion of quality resources) at smaller spatial scales (Fryxell *et al.* 2005).

Because forage is constantly renewed during summer we expected that selection for higher quality habitat would remain stable throughout the growing season. However, the within-summer home range-scale RSF model that best fitted the data included an interaction between month and available forage biomass indicating some monthly variation in habitat selection patterns. This result is probably related to temporal variation in forage quality as forage matures over summer (Hjeljord, Hovik & Pedersen 1990; Hebblewhite, Merrill & McDermid 2008; McArt *et al.* 2009). Nevertheless, the monthly variation in habitat selection was minor (Fig. 3a) and did not include qualitative changes (e.g. from selection to avoidance) compared to during winter following resource depletion (Fig. 3b). The absence of such a change in selection suggests that the seasonal variation in the relative quality of the target species was sufficiently low not to be of major concern to the moose. Moreover, we observed large overlap in bimonthly home ranges during summer (> 50% for both MCP and kernel UD techniques), suggesting that the constant and high availability of high-quality browse allowed moose to adopt a space use pattern with a high degree of site fidelity. This result is to be expected as fidelity to high-quality habitat can increase individual fitness (Edwards, Nagy & Derocher 2009). During winter, when high-quality browse was depleted, we observed low site fidelity (< 50% for both MCP and kernel UD techniques) which suggests that moose shifted their monthly winter ranges in order to acquire high-quality browse or alternative forage elsewhere. Similar changes in within seasonal space use patterns have been observed in other ungulate species. For example, Wittmer, McLellan & Hovey (2006) attributed the low fidelity of woodland caribou (*Rangifer tarandus caribou*) in winter to increased search effort for diminishing high-quality forage such as arboreal lichen.

Conclusion

Large herbivores are typically confronted with spatial and temporal variation in the quality and quantity of available forage resources. These resource attributes are key to the reproductive success and survival of moose (Moen, Pastor & Cohen 1997) and other ungulates (White 1983; Pettorelli *et al*. 2005; McLoughlin *et al*. 2006). Our approach, using mixed-effect RSFs (Gillies *et al*. 2006) and spatially explicit forage availability models incorporated both quality and quantity of browse and yielded novel insight into moose habitat selection strategies over multiple spatiotemporal scales. The scale-dependent trade-off linked to habitat selection presented here, driven by landscape-level variation in forage quantity, quality and depletion will enable more accurate predictions of the spatial distribution of herbivores over time, even at within-season scales.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Results of the literature review to estimate and rank forage quality of the six target species.

Table S2. Pearson correlation coefficient between available forage biomass of the target species (dry mass (g) per 50 m^2) and field layer vegetation (% cover/50 m^2).

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Figure S1. Activity estimates (probability of being active ± 95% highest posterior density intervals) of moose as a function of available browse biomass for each target species at the (a) summer and (b) winter home range-scale.

Figure S2. Selection estimates (log odds ratio of use ± 95% highest posterior density intervals) for available browse biomass for each target species at the (a) within-summer and (b) within-winter home range-scale where the log odds ratios are calculated relative to the average available browse biomass for a target species (reference circle).

Supporting Information – Paper II

Table S1. Results of the literature review to estimate and rank forage quality of the 6 target species. Species specific forage quality was determined by moose selection ranks as reported in previous studies conducted in the boreonemoral or boreal zone of Scandinavia.

Season	Study region	Selection rank of species *	Reference
Winter	Örebro County, south-central Sweden	R > W > A > Sb > Db	Bergstrom & Danell 1986
Winter	Västerbotten County, northern Sweden	R > W > A >Sb > Sp > Db	Shipley, Blomquist & Danell 1998
Winter	Västerbotten County, northern Sweden	Sb > Db	Danell, Huss-Danell & Bergstrom 1985
Winter	northern Sweden	Sb > Db	Danell & Ericson 1986
Winter	south-west Sweden	R > A > Sp > W > B	Cassing, Greenberg & Mikusinski 2006
Winter	Örebro County, south-central Sweden	RAW > Sb > Sp, Db	Månsson et al. 2007
Winter	Hedmark County, south-east Norway	RAW > Sp > B	Gangsei 2004
Winter	Aust- and Vest-Agder Counties, southern Norway	RAW> Sp >B	Greibesland 2006
Winter	Akershus County, south-east Norway	Sp > RAW > B	Gangsei 2003
Winter	Buskerud County, south ernNorway	RAW > Sp > B	Hovde 2009

Summer	Østfold County, southern Norway	W > A > R > B	Hjeljord, Hovik & Pedersen 1990
Summer	Västerbotten County, northern Sweden	A > R > W > Sb > Db	Edenius, Ericsson & Naslund 2002
Summer	Agder and Telemark County, southern Norway	RAW > B > Sp	Gotehus & Hellerslien 2004
Summer	Oppland County, south-east Norway	RAW > B	Wam, Hjeljord & Solberg 2008
Summer	Telemark County, southern Norway	RAW > B > Sp	Gangsei 2008

* Species abbreviations; R = Rowan, A = Aspen, W = Willow species, Sb = Silver birch, Db = Downy birch, B = Birch species combined, Sp = Scots pine, RAW = Rowan, Aspen and Willow species combined.

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Table S2. Pearson correlation coefficient between available forage biomass of the target species (dry mass (g) per 50 m^2) and field layer vegetation (% cover / 50 m^2).

	Billberry cover	Grass cover	Herb cover	Other berry cover
RAW species biomass	0.351	0.599	-0.485	0.066
Silver birch biomass	0.168	0.525	-0.111	0.718
Downy birch biomass	0.683	0.587	-0.178	0.648
Scots pine biomass	0.179	-0.305	-0.663	0.763

Table S3.

Mean (SD) strip length (cm) and bite diameter (mm) by moose for 6 target species as observed in the study area. We sampled 100 trees per species per variable with a total of 1100 trees sampled because Scots pine was never stripped.

Species	**Strip length (cm)**	**Bite diameter (mm)**
Rowan	19.6 (11.3)	4.7 (1.1)
Aspen	23.7 (11.6)	4.5 (1.5)
Willow species	26.5 (11.7)	3.7 (1.3)
Silver birch	28.9 (9.7)	3.6 (1.3)
Downy birch	28.4 (9.5)	3.5 (1.3)
Scots pine	--	7.2 (1.9)

Table S4. Summary of the mixed-effects logistic regression model predicting moose activity during summer and winter as a function of species-specific forage availability in Southern Norway. The model includes a random intercept for each individual (moose ID) and estimates are presented as log odds ratio ± 95 % HPD intervals. Model output forms the analytical basis for Fig. S1.

Summer					**Winter**				
			HPD interval					**HPD interval**	
Fixed effects	***β***	**SE**	**Lower**	**Upper**	***Fixed effects***	***β***	**SE**	**Lower**	**Upper**
(Intercept)	-0.039	0.211	-0.512	0.459	(Intercept)	-0.260	0.139	-0.541	0.024
RAW species biomass	0.031	0.004	0.023	0.039	RAW species biomass	0.018	0.006	0.006	0.031
Silver birch biomass	0.216	0.072	0.072	0.356	Silver birch biomass	0.003	0.074	-0.142	0.145
Downy birch biomass	-0.040	0.006	-0.053	-0.028	Downy birch biomass	0.002	0.003	-0.004	0.008
Scots pine biomass	-0.042	0.005	-0.053	-0.031	Scots pine biomass	0.031	0.003	0.025	0.037
Random effects	**SD**		**Lower**	**Upper**	***Random effects***	**SD**		**Lower**	**Upper**
***(*Intercept)**					***(*Intercept)**				
moose ID (*N* = 26)	1.001		0.882	1.560	moose ID (*N* = 31)	0.636		0.507	0.863

Figure S1. Activity estimates (probability of being active ± 95 % highest posterior density intervals) of moose as a function of available browse biomass for each target species at the (a) summer and (b) winter home range-scale. Stars in the plots represent the raw data of active points (1) and inactive points (0) over the range of species-specific available forage biomass.

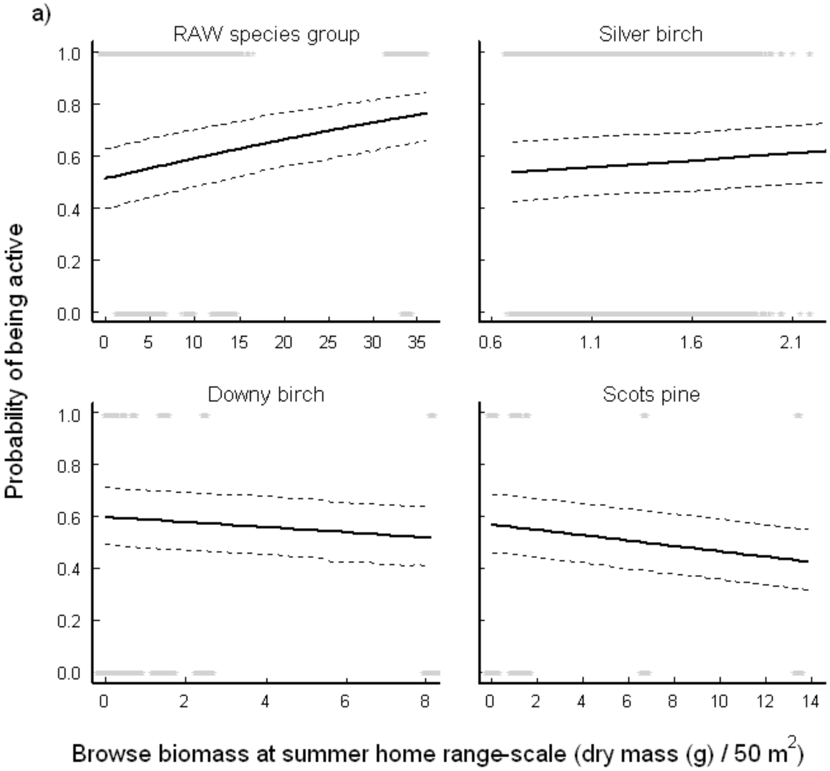


Figure S1 (cont.)

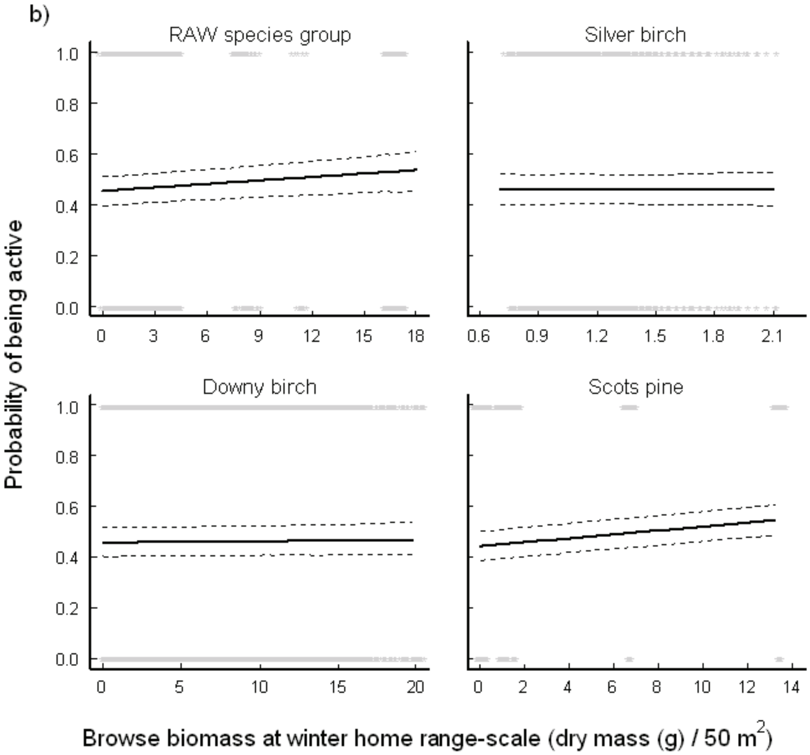


Table S5. Results of model selection for summer and winter RSF models for moose at the home range-scale and landscape-scale. The top model per spatiotemporal scale is indicated in bold and was selected based on Δ AIC.

Season	**Spatial scale**	**RSF-analysis**	**Variables in RSF-model**	**Δ AIC**
Summer	Home range	Logistic	Species specific biomass	174
Summer	Home range	Logistic	Species specific biomass x month	105
Summer	Home range	Logistic with random intercept	Species specific biomass	47
Summer	Home range	Logistic with random intercept	Species specific biomass x month	**0**
Winter	Home range	Logistic	Species specific biomass	611
Winter	Home range	Logistic	Species specific biomass x month	545
Winter	Home range	Logistic with random intercept	Species specific biomass	218
Winter	Home range	Logistic with random intercept	Species specific biomass x month	**0**
Summer	Landscape	Logistic	Species specific biomass	489
Summer	Landscape	Logistic	Species specific biomass x month	495
Summer	Landscape	Logistic with random intercept	Species specific biomass	**0**
Summer	Landscape	Logistic with random intercept	Species specific biomass x month	25
Winter	Landscape	Logistic	Species specific biomass	643
Winter	Landscape	Logistic	Species specific biomass x month	644
Winter	Landscape	Logistic with random intercept	Species specific biomass	**0**
Winter	Landscape	Logistic with random intercept	Species specific biomass x month	18

Table S6. Summary of the landscape-scale mixed-effects RSF models for summer and winter, predicting moose habitat selection as a function of species-specific forage availability in Southern Norway. The model includes a random intercept for each individual (moose ID) and selection estimates are presented as log odds ratio ± 95 % HPD intervals. Model output forms the analytical basis for Fig. 2 and Fig. S2.

Landscape-scale RSF model summer					**Landscape-scale RSF model winter**				
			HPD interval					**HPD interval**	
Fixed effects	β	**SE**	**Lower**	**Upper**	***Fixed effects***	β	**SE**	**Lower**	**Upper**
(Intercept)	0.137	0.225	-0.347	0.606	(Intercept)	0.723	0.186	0.304	1.122
RAW species biomass	-0.005	0.003	-0.011	< 0.001	RAW species biomass	-0.028	0.005	-0.037	-0.019
Silver birch biomass	0.107	0.060	-0.012	0.226	Silver birch biomass	-0.311	0.055	-0.418	-0.202
Downy birch biomass	0.047	0.003	0.041	0.052	Downy birch biomass	0.032	0.003	0.027	0.038
Scots pine biomass	-0.041	0.004	-0.049	-0.033	Scots pine biomass	0.011	0.003	0.005	0.018
***Random effects* (Intercept)**	**SD**		**Lower**	**Upper**	***Random effects* (Intercept)**	**SD**		**Lower**	**Upper**
moose ID ($N = 26$)	1.121		0.850	1.636	moose ID ($N = 31$)	1.000		0.846	1.512

Table S7. Summary of the within home range-scale mixed-effects RSF models for summer and winter, predicting moose habitat selection as a function of species-specific forage availability in Southern Norway. Selection estimates (log odds ratio ± 95 % HPD intervals) are in comparison to the reference category ^{a} (summer RSF) or ^{b} (winter RSF). The model includes a random intercept for each individual (moose ID) and forms the analytical basis for Fig. 3 and Fig. S3.

Within home range-scale RSF model summer					**Within home range-scale RSF model winter**				
			HPD interval					**HPD interval**	
Fixed effects	***β***	**SE**	**Lower**	**Upper**	***Fixed effects***	***β***	**SE**	**Lower**	**Upper**
(Intercept)	-0.577	0.143	-0.866	-0.298	(Intercept)	-1.155	0.252	-1.612	-0.700
RAW species biomass	0.037	0.008	0.023	0.053	RAW species biomass	0.017	0.011	-0.026	0.044
Silver birch biomass	0.591	0.123	0.355	0.836	Silver birch biomass	0.956	0.202	0.515	1.287
Downy birch biomass	-0.012	0.011	-0.035	0.009	Downy birch biomass	-0.017	0.009	-0.032	0.003
Scots pine biomass	-0.041	0.009	-0.058	-0.023	Scots pine biomass	0.037	0.010	0.016	0.058
Season ^{a}					Season ^{b}				
July	-0.592	0.183	-0.944	-0.225	February	0.238	0.259	-0.339	0.662
August	-0.394	0.190	-0.756	0.002	March	0.499	0.258	-0.116	0.888
September	-0.554	0.231	-1.012	-0.115	April	0.909	0.260	0.311	1.325
RAW species biomass x July	-0.013	0.010	-0.034	0.007	RAW species biomass x February	-0.042	0.020	-0.098	-0.019
RAW species biomass x August	0.020	0.012	-0.004	0.042	RAW species biomass x March	-0.104	0.022	-0.163	-0.076
RAW species biomass x September	-0.005	0.014	-0.031	0.025	RAW species biomass x April	-0.070	0.021	-0.122	-0.042

Silver birch biomass x July	0.605	0.169	0.263	0.922	Silver birch biomass x February	-0.285	0.249	-0.688	0.287
Silver birch biomass x August	0.390	0.172	0.031	0.709	Silver birch biomass x March	-0.383	0.247	-0.712	0.253
Silver birch biomass x September	0.617	0.209	0.219	1.027	Silver birch biomass x April	-0.747	0.250	-1.161	-0.192
Downy birch biomass x July	-0.018	0.015	-0.048	0.013	Downy birch biomass x February	0.002	0.011	-0.021	0.023
Downy birch biomass x August	-0.035	0.016	-0.066	-0.001	Downy birch biomass x March	0.016	0.011	-0.009	0.034
Downy birch biomass x September	-0.030	0.020	-0.072	0.007	Downy birch biomass x April	0.023	0.011	-0.002	0.042
Scots pine biomass x July	-0.044	0.013	-0.068	-0.018	Scots pine biomass x February	0.035	0.013	0.010	0.059
Scots pine biomass x August	0.004	0.013	-0.020	0.029	Scots pine biomass x March	0.041	0.013	0.016	0.064
Scots pine biomass x September	-0.015	0.015	-0.045	0.015	Scots pine biomass x April	0.016	0.013	-0.008	0.043
***Random effects* (Intercept)**	**SD**		**Lower**	**Upper**	***Random effects* (Intercept)**	**SD**		**Lower**	**Upper**
moose ID ($N = 26$)	0.259		0.199	0.366	moose ID ($N = 31$)	0.749		0.463	0.779

[a] Reference = June

[b] Reference = January

Figure S2. Selection estimates (log odds ratio of use ± 95 % highest posterior density intervals) for available browse biomass for each target species at the (a) within-summer and (b) within-winter home range-scale where the log odds ratios are calculated relative to the average available browse biomass for a target species (reference circle). Selection estimates above 0 (reference level) indicate higher selection relative to the reference, whereas values below 0 indicate lower selection. Stars in the plots represent the raw data of used points (upper) and available points (lower) over the range of species-specific available forage biomass. Only locations where moose were active were included into the models.

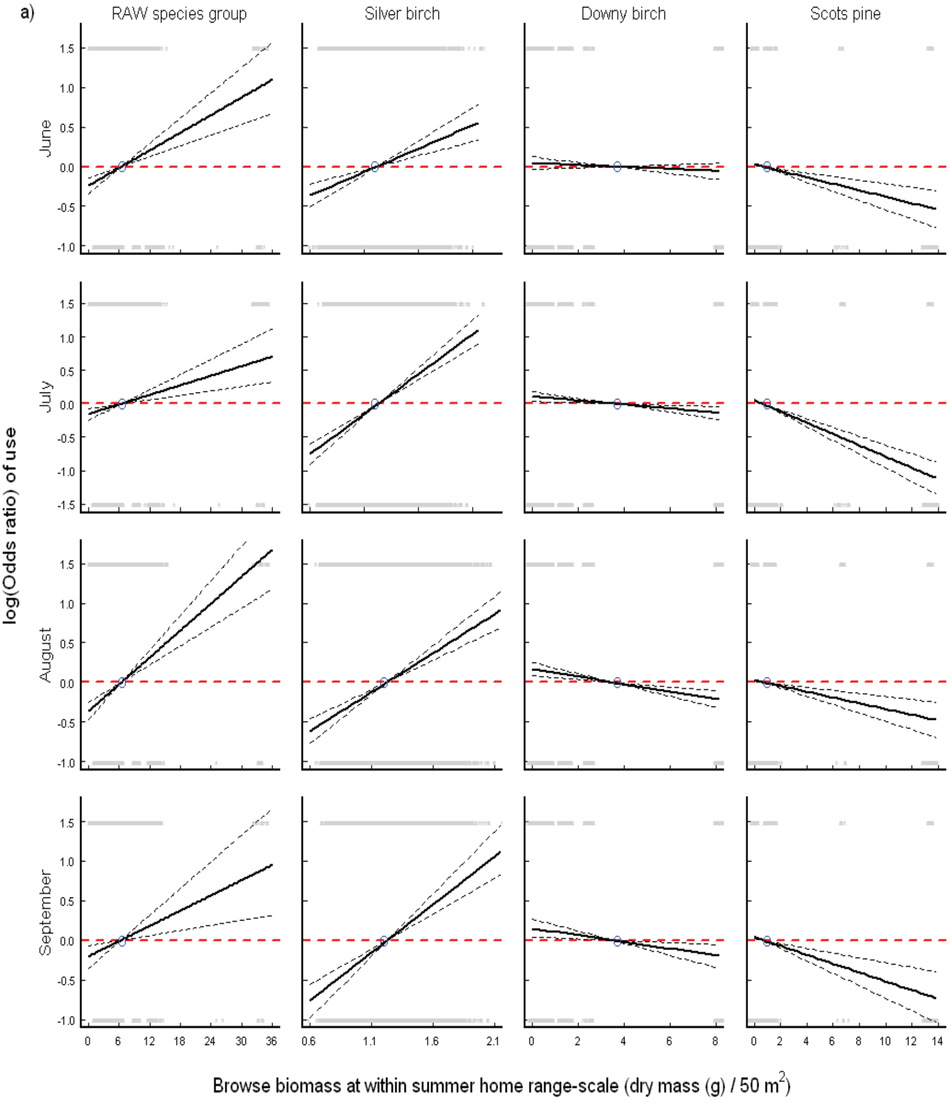
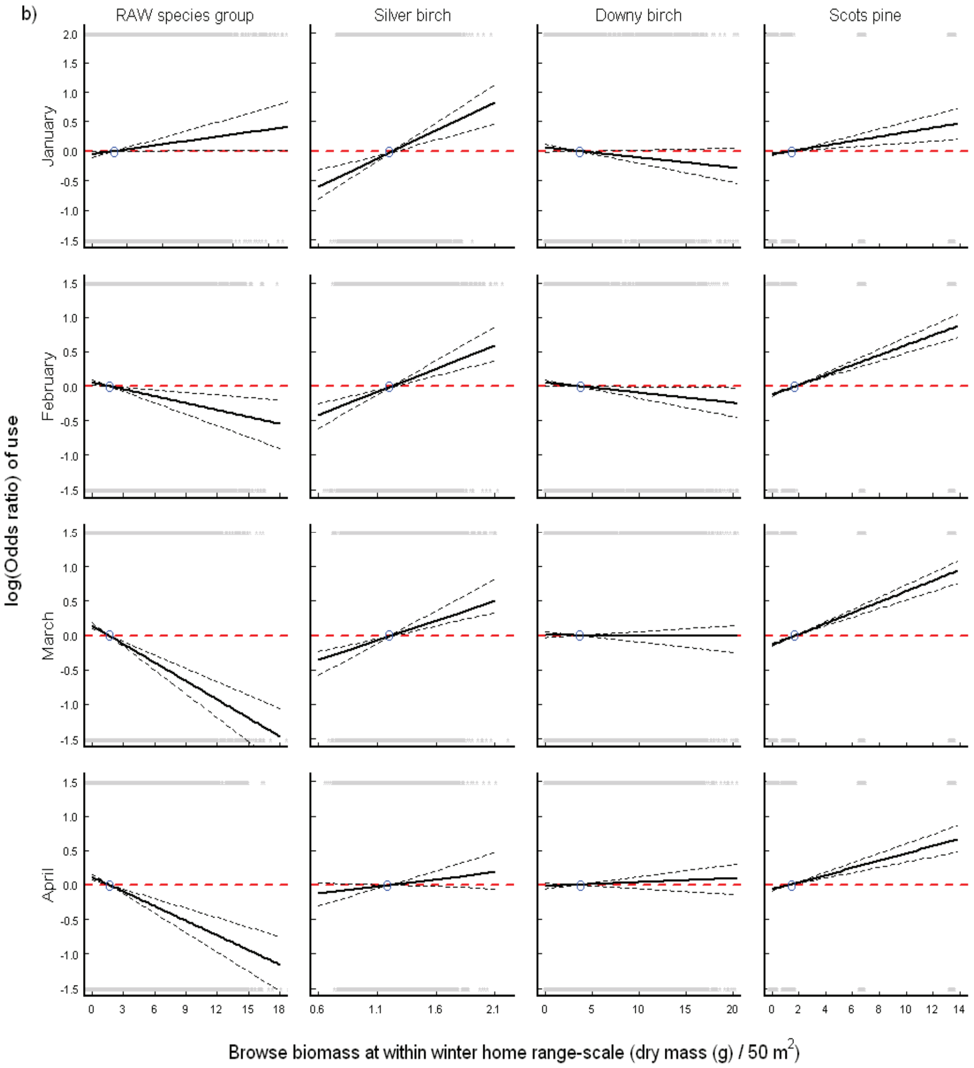

a)
RAW species group
Silver birch
Downy birch
Scots pine
June
July
August
September
log(Odds ratio) of use
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
0
6
12
18
24
30
36
0.6
1.1
1.6
2.1
0
2
4
6
8
0
2
4
6
8
10
12
14
Browse biomass at within summer home range-scale (dry mass (g) / 50 m^2)

Figure S2 (cont.) .



What determines variation in home range size across spatiotemporal scales in a large browsing herbivore?

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RH: Variability in home range size

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Summary

1. Most studies on intraspecific home range size variation have investigated only a single or a few factors and often at one spatial or temporal scale. However, considering multiple spatial and temporal scales when defining a home range is of crucial importance as mechanisms that affect variation home range size may differ depending on the scale under investigation.

2. We aim to quantify the relative effect of various individual-level, forage and climatic determinants on variation in home range size across multiple spatiotemporal scales of a large browsing herbivore, moose (*Alces alces*), living in southern Norway.

3. Total home range size and core home range areas were estimated for daily to monthly scales within both summer and winter season (16 spatiotemporal scales), using the local convex-hull (LoCoH) home range method. Variation in home range size was analyzed using linear mixed effects models for repeated measurements.

4. Reproductive status was the most influential individual-level factor explaining variation in moose home range size, with females accompanied by a calf having smaller ranges across all scales. Climate affected total home range size more than core areas but the overall effect was lower than expected. Temperature and snow depth affected home range size directly at short temporal scales while the effect of precipitation varied with temporal scale during summer and was absent in winter. Home range size decreased with increasing browse density at daily scales but increased over time within monthly scales during both summer and winter. In contrast, browse quality was consistently negatively correlated with home range size but explained only a minor part of the variation at short temporal scales.

5. The relative effects of intrinsic and extrinsic determinants on variation in home range size differed with spatiotemporal scale, providing clear evidence that home range size is scale dependent in this large browsing herbivore. As such, we recommend studying animal movement or activity across a range of spatiotemporal scales, especially when investigating the effect of only a few determinants.

Key-words

Alces alces, climate, forage variability, linear mixed models, local convex hull home range estimator, scale-dependence

Introduction

Movements of individual animals are often restricted to a specific area, defined as a home range, likely due to increased benefits of familiarity with that area (Stamps 1995; van Moorter *et al.* 2009). Understanding why home range size varies between and within species remains a fundamental issue in ecological research (McLoughlin & Ferguson 2000; Börger, Dalziel & Fryxell 2008). Interspecific variation in home range size is largely driven by body-size-dependent metabolic requirements (McNab 1963; Harestad & Bunnell 1979; Lindstedt, Miller & Buskirk 1986; Carbone *et al.* 2005). Intraspecific variation in home range size may be caused by a range of intrinsic and extrinsic factors (Table 1). In most studies, only a single or a few factors have been used to describe intraspecific variation in home range size and often at one specific spatial or temporal scale (e.g. Table 1).

Scale dependence forms an important part of ecological theory (Wiens 1989; Levin 1992). Clearly, the mechanisms underlying intraspecific variation in home range size also involve scale dependence (Kie *et al.* 2002; Rivrud, Loe & Mysterud in press). For example, Börger *et al.* (2006b) showed how the effects of local climate on home range size of roe deer (*Capreolus capreolus*) differed between total home range area and the core home range area. Similarly, the effect of home range determinants can change across temporal scales. Spencer, Cameron & Swihart (1990) found a significant relationship between weekly home range size and body mass of cotton rats (*Sigmodon hispidus*) but the effect was absent at shorter (daily) time scales.

The overall objective of this study is to examine how individual-level, forage and climatic determinants influence variation in home range size of a large browser, the moose (*Alces alces*) in Southern Norway, across multiple spatial (core area to total home range area) and temporal (daily to monthly) scales. Moose are an appropriate model species to investigate what determines intraspecific variation in home range size as home range size is highly variable between individuals and over time (Stenhouse *et al.* 1995; Dussault *et al.* 2005a). Based on previous findings in cervid home range size (Table 1), we will test the following predictions:

Individual level determinants: We expect large individual variation in home range size across all scales (P. 1.1). Variation in body mass and age are typically poor predictors of within species home range size (especially for female moose, Table 1) and we therefore expect to find no effects of body weight or age on home range size over space and time (P. 1.2 and P. 1.3 respectively). In contrast, the effects of reproductive status on herbivore space use are typically larger (Table 1). We expect females that are accompanied by a calf to have larger summer ranges than females without offspring due to increased energetic requirements (P. 1.4).

Forage characteristics: Forage variability is considered a primary factor in herbivore space use (Tufto, Andersen & Linnell 1996; McLoughlin & Ferguson 2000). We therefore expect overall density of browse and the proportion of high quality browse to have a marked negative effect on moose home range size across all temporal scales (P. 2.1 and P. 2.2 respectively). The presence of supplementary feeding stations may also affect animal movement and habitat selection patterns within seasonal home ranges (Guillet, Bergstrom & Cederlund 1996; Sahlsten *et al.* 2010; van Beest *et al.* 2010a). We expect winter home range size to decrease as the time spent at supplementary feeding stations increases (P. 2.3).

Climatic determinants: Recently the effect of climatic determinants on home range size has received increased attention because of climate-change issues (McCarty 2001; Walther *et al.* 2002). Mechanisms might include both direct effects on short temporal scales, associated with thermoregulation or increased costs of moving in deep snow, as well as indirect effects operating through plant growth, typically at longer temporal scales (Rivrud *et al.* in press). Moose are adapted to cold environments but may suffer from heat stress at warm ambient temperatures in all seasons (Dussault *et al.* 2004). We therefore expect moose home range size to be negatively correlated with temperature across all spatiotemporal scales, but most clearly at short temporal scales (P. 3.1). Similarly, we expect winter home range size to decrease with increasing snow depth across all scales (P. 3.2). Although contrasting results have been found for the effect of precipitation on home range size (Table 1), precipitation is known to increase heat loss in ungulates (Parker 1988). We therefore expect precipitation to negatively affect moose home range size with the effect to be most pronounced at short temporal scales (P. 3.3). Finally, the effect of day length is known to be a key determinant of activity and home range size of roe deer (Börger *et al.* 2006b). We expect the effect of hours of daylight on moose home range size to be more influential during winter (positive relationship) than summer (negative relationship) (P. 3.4).

Materials and Methods

STUDY AREA

The study area (1 733 km^2) is located in southern Norway within parts of Telemark, Buskerud and Vestfold counties (59° 21' N, 9° 38' E). The area is in the boreonemoral zone and is mostly covered by commercially managed coniferous forest (82%). Stands are dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) but some mixed deciduous stands occur throughout the area. The mean monthly temperatures in June and September (i.e, summer period) are 15.4 and 10.6°C, and in January and April (i.e., winter period) are - 5 and 4.3°C respectively. Average (± SE) snow-depths in the centre of the study area (430 m.a.s.l) during Jan.-Apr. 2007 and 2008 were 49 ± 2.4 cm and 72 ± 1.5 cm respectively (The Norwegian Meteorological Institute http://eklima.met.no). Moose densities in the area are estimated at 1.5 individuals per km^2 (Norwegian Institute for Nature Management; http://www.dirnat.no). Red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.) densities are 0.5 and 0.2 individuals per km^2 respectively. Large predator species are absent and hunting is the single most important cause of moose mortality in this area.

MOOSE AND GLOBAL POSITIONING SYSTEM (GPS) DATA

A total of 34 adult female moose accompanied by a calf were tranquilized by dart gun from a helicopter, using established techniques (Arnemo, Kreeger & Soveri 2003), during January 2007 and January 2008. Body mass was recorded by weighing the restrained moose from the helicopter (body mass range: 235 – 430 kg). We then fitted the moose with GPS collars with a vhf radio transmitter (Tellus Remote GSM, Followit AB, Lindesberg, Sweden), programmed with a 1-h relocation schedule. GPS location data was collected each year from January-November (N = 16 in 2007 and N = 18 in 2008). All but 9 of the marked individuals were harvested during the regular hunting season as part of the annual quota set by the local wildlife board. Age of the marked individuals (range: 2 -14 yr) was determined by counting tooth annuli (Rolandsen *et al.* 2008). Missing data on age estimation reduced the total sample size to 24 individuals (N = 10 in 2007 and N = 14 in 2008). All marked adult females were located and approached carefully on foot in early June to determine the presence of a new-born calf. If no calf was observed, we relocated the female a few days later. The procedure was repeated until we were confident of calving status. Fourteen adult females were observed with a calf during summer (58%) and none of the females were accompanied by twins.

All GPS locations collected within 24 h of initial marking were excluded. The GPS data were screened for positional outliers using an established technique based on moose movement characteristics (Bjørneraas *et al.* 2010). With this approach we removed 498 erroneous locations (< 0.5% of the full GPS dataset). During this study, the average GPS-collar fix rate was 93 % (range: 83 – 99 %) and the mean location error in the GPS collars was 29.9 m (range: 8 – 49 m). We judged the potential bias of these factors on home range size estimation to be low, so we did not correct for location error during the analyses as the error was smaller than the resolution of our forage availability maps (see section on forage variability in Materials and Methods). Long directional movements, such as during migration periods, can seriously affect home range size (Luccarini *et al.* 2006) and habitat use during the migration period may differ from that observed during more stationary periods of the year (Fryxell & Sinclair 1988). To avoid potential bias we removed all GPS locations during each individual's migration period, as is typically done in home range size analyses

(Ramanzin, Sturaro & Zanon 2007; Rivrud *et al.* in press). In order to classify individuals as migratory or resident, we used the first GPS location of each individual (i.e. reference point) and calculated the net displacement distance (using Euclidean distances in meters) between each subsequent location and the reference point. For individuals displaying a distinct migratory pattern (N = 22 out of 24) we identified the start and end dates of migration using piecewise regression in the library "segmented" (Muggeo 2008) implemented in the statistical software R (R Development Core Team 2008). With this approach we removed 10 029 locations (5.9% of the full GPS dataset).

FORAGE VARIABILITY AND LOCAL WEATHER DATA

Large herbivores are often confronted with spatial and temporal variation in the quality and quantity of their food resources. For this study we used spatially explicit forage availability maps for both summer and winter seasons based on the 6 most common browse species available to moose in southern Norway; full details are given in van Beest *et al.* (2010b). Based on a review of available literature (see van Beest *et al.* 2010b), we considered silver birch (*Betula pendula*), downy birch (*Betula pubescens*) and Scots pine (*Pinus sylvestris*) as low quality browse species and rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and willow (*Salix* spp.) as high quality species. Species specific forage availability was measured during summer 2007. We used a random stratified sampling design (n = 945 plots over 189 forest stands) to estimate forage availability (dry mass g/50m^2) across forest stand characteristics (cutting class, productivity, dominant tree species) and topography (slope, aspect, altitude, sky view). Summer forage was estimated from leaf biomass and winter forage from twig biomass. Seasonal forage biomass was spatially mapped at a 50m^2

pixel resolution using ArcGIS (2006 ESRI, USA) following the best predictive generalized linear mixed models (GLMM) of spatial covariates as analysed in R (R Development Core Team 2008). We extracted the total amount of forage biomass in both summer and winter season for each moose home range (see below) from the forage availability maps, using SPATIAL ANALYST in ArcGIS (2006 ESRI, USA). We divided the total amount of forage biomass by home range size (ha) to obtain a measure of forage density (dry mass g/ha). The proportion of high quality browse within each home range was calculated by dividing the amount of quality browse biomass by the total amount of forage biomass. On some occasions the marked individuals ventured completely or partly outside the area for which we had forage availability data. We therefore excluded individuals with < 95% home range overlap with the forage availability maps at each spatiotemporal scale. To quantify feeding site use for each individual separately and at each spatiotemporal scale we determined the proportion of time spent within 100 m of feeding stations (sensu van Beest *et al.* 2010a). We did so by calculating the number of GPS locations within a 100 m buffer around feeding stations and divided this by the total number of GPS locations obtained during winter for that individual at a specific spatiotemporal scale. Because feeding stations were small (< 20 m^2) and because the location in between the hourly fixes is not known, we assumed that moose located within a 100 m buffer from feeding sites had indeed visited the station.

To assess the effect of climate on moose home range size in our study area we obtained data on daily temperature, rainfall and snow depth from the nearest available meteorological weather station. Data on mean daily temperatures (°C) during 2007 and 2008 were taken from a weather station located 18 km east of the centre of our study area (100 m above sea level). Data on daily rainfall (mm) and snow depth (cm) were obtained from a different weather station located 15 km south of the centre of our study area (450 m above sea level; The Norwegian Meteorological Institute http://eklima.met.no). We regressed daily temperature, rainfall and snow depth against Julian day using generalized additive models (GAM) in the library "mgcv" (Wood 2006) implemented in R (R Development Core Team 2008) and used the residuals of each covariate as fixed effects to analyse variation in home range size. This approach removes the seasonal pattern from the weather data and retains the unpredictable climatic variability over time. Day length (hours of daylight) in the southern part of Norway during our study period were obtained from the U.S. Naval Observatory (http://aa.usno.navy.mil).

SPATIOTEMPORAL SCALES AND HOME RANGE SIZE ESTIMATION

We considered 4 temporal scales: daily, weekly, biweekly and monthly scales, which are known to be appropriate timeframes to assess variation in home range size as a function of food and climate (Rivrud *et al.* in press). We also considered 2 spatial scales, delimited by the core area (50% isopleths) and total home range area (90% isopleths). All scales were analysed separately for both summer and winter, giving a total of 16 spatiotemporal scales. We used 90% isopleths rather than the more commonly reported 95% isopleths as these produce total home range estimates that are less biased by sample size (Börger *et al.* 2006a). Annual snow conditions in the study area were used to define winter length (period with ≥ 30 cm snow depth). As such, winter in 2007 stretched from Jan. 21st until Apr. 8th and in 2008 from Jan. 4th until Apr. 30th. Summer was defined as the period 1st of June till 15th of September for both years. Spring and autumn were not included in this study, partly to avoid the inclusion of long distance movements during migration and those associated with the autumn breeding season, but also because we do not have forage availability maps for these periods.

Home range sizes (ha) of female moose were estimated using the non-parametric Local Convex Hull (LoCoH) method (Getz & Wilmers 2004; Getz *et al.* 2007) using the library "adehabitat" (Calenge 2006) implemented in R (R Development Core Team 2008). The main advantage of estimating animal home ranges with the LoCoH method is that it allows for holes and hard boundaries in the home range due to inaccessible terrain (e.g. lakes and rocky outcrops) and is therefore less likely to include areas that an individual cannot use compared to parametric kernels (Getz *et al.* 2007). For comparative purposes, home ranges were estimated using two LoCoH methods: *a*-LoCoH (or the adaptive sphere-of-influence method in which home ranges are constructed from all points *a* within a radius determined by the maximal distance between any two positions in the GPS dataset) and *k*-LoCoH (or fixed number of points method in which home ranges are constructed from $k = \sqrt{n}$ where *n* is the mean number of locations per marked individual in the GPS dataset). Because the number of individuals and the number of home range estimates per individual varied between spatiotemporal scales, due to insufficient overlap with the forage availability maps, we used scale- and individual-dependent values for *a* and *k*.

MODEL DEVELOPMENT AND STATISTICAL ANALYSES

To examine variation in moose home range size across spatiotemporal scales we used an established multi-scale approach (Börger *et al.* 2006b), which is based on linear mixed models in the "nlme" library (Pinheiro *et al.* 2005) implemented in R (R Development Core Team 2008). Log-transformed home range size (ha) was fitted as the response variable in all models. Depending on the season, we included the following fixed effects in the models; age, body mass, calf at heel (yes or no; summer models only), proportion of time spent at feeding stations (winter models only), browse density, proportion of high quality browse; the residuals of temperature, precipitation, and snow depth (winter models only) and hours of daylight (see Table 2 for more details). To allow the effect of each home range size determinant to change over time (i.e. within seasons) we also fitted an interaction between each covariate and hours of daylight in all full models. Collinearity between covariates was checked using Pearson *r* (all values < 0.3) and in addition with the variance inflation factor (VIF). All VIF values were below 2 which is indicative that collinearity was not a concern (Zuur, Ieno & Elphick 2010). We fitted separate models for summer and winter (16 models in total; including 4 temporal scales and 2 spatial scales for each season) and all individuals had ≥ 2 repeated home range estimates at each temporal scale.

Moose ID and year were fitted as random intercepts in the full models. Random effects model any remaining patterns in the residuals of the fixed effects that may occur when modelling, for example, repeated observations of the same individual (Pinheiro & Bates 2000; Börger *et al.* 2006b). We used the Akaike Information Criterion (AIC) to evaluate if the inclusion of random effects were necessary compared to more parsimonious models without random terms (Pinheiro & Bates 2000). As year was never retained, the final models included moose ID as the only random intercept (Table S1 in Supporting Information).

Any residual dependence among observations that was not accounted for by the fixed or random effects was modelled using correlation structures for the within group errors (Pinheiro & Bates 2000; Börger *et al.* 2006b; Rivrud *et al.* in press). We fitted either spatial or temporal correlation structures as it is (currently) not possible to fit both in the same model. We evaluated which correlation structure best fitted the data using AIC (Börger *et al.* 2006b; Rivrud *et al.* in press). Spatial correlation between home ranges was modelled using the mean coordinates of the home ranges, and temporal correlation was modelled by numbering consecutive home range estimates for each individual separately starting from the first home range estimate. We always used the exponential correlation structure as this method provided the best fit based on AIC. Last, the models were checked for unequal variance structures (heteroscedasticity) of the within-group errors. We evaluated the fit of several available variance functions (Pinheiro *et al.* 2005). In all cases where a variance function improved the model the power function provided the best fit based on AIC.

Once the distributional assumptions of the mixed model structure were fulfilled (Table S1; Supporting Information), model selection of the fixed effects was conducted by backwards selection from the full model with F tests using $P = 0.05$ as the threshold for inclusion or exclusion of predictor variables and interactions (Murtaugh 2009). During model selection, we used maximum likelihood estimation for parameter values while the final model was fitted using restricted maximum likelihood estimation (Pinheiro & Bates 2000). To assess the amount of variation in the data explained by the final models we used a generalized R^2, which is calculated as the square of the correlation between the fitted values of the model and the observed values in the data(Zheng & Agresti 2000). We report the generalized R^2 values for the final models and for the random effects (Pinheiro & Bates 2000; Börger *et al.* 2006b). We also calculated the generalized R^2 for each explanatory variable retained in the final models. We did this by manually excluding a covariate (and the interaction term if included) from the final model and calculating the difference in generalised R^2 of the final model and the reduced model (Schradin *et al.* 2010).

Results

We estimated a total of 6 161 home ranges (3 383 within summer and 2 778 within winter) using GPS relocation data of 24 adult female moose. We found no distinct differences in the final models between the two LoCoH home range estimation methods (i.e. similar home range sizes and slopes of explanatory variables retained in the models). We report results based on the *k*-LoCoH method as the final models were generally more parsimonious (data not shown). Home range size varied greatly across spatiotemporal scales and was consistently larger during summer than winter (Fig. 1; Table S2; Supporting Information). Summary statistics of the final mixed-effects models predicting monthly, biweekly, weekly and daily home range size of moose are given in the Supporting Information as tables S3, S4, S5 and S6 respectively. The proportion of variation explained by the final models (i.e. generalized R^2) ranged between 0.41 and 0.79 across scales (Table 3).

INDIVIDUAL-LEVEL DETERMINANTS

As expected (P 1.1), we observed large individual variation in home range size (an order of magnitude or more) across all spatiotemporal scales (Fig. 2). The proportion of variation explained by moose ID (i.e. generalized R^2 of random effect) ranged between 0.10 and 0.35 across scales (Table 3), explaining more variation during summer than during winter and more variation in total home range area (90% isopleth) than in core area (50% isopleth).

Body mass (log transformed) was of relatively minor importance to home range size across spatiotemporal scales (as expected by P. 1.2) (Fig. 2) with two exceptions: core home range size during winter at biweekly and weekly scales (Table 4B; Fig. S1 in Supporting Information). Core home range size increased significantly with body mass at the weekly scale throughout winter ($\beta = 1.209$, SE = 0.63, $F_{1,21} = 7.70$; $R^2 = 0.03$) but, at the biweekly scale, the effect changed over time (interaction between body mass and daylight during winter: $\beta = 0.877$, SE = 0.54, $F_{1,21} = 4.8$; $R^2 = 0.11$) with heavier females increasing their core area towards the end of winter (i.e. April; Fig. S1 in Supporting Information).

As expected (P. 1.3), age did not appear to be an important variable affecting home range size. It was retained at only one spatiotemporal scale (i.e. 90% isopleth at biweekly scale model during summer; Table 4A) where home range size decreased with increasing age but only at the end of summer (i.e. September; Fig. S2 in Supporting Information). The effect accounted for the least amount of variation in home range size at this scale ($R^2 = 0.03$; Table 3; Fig. 2A).

Reproductive status (P. 1.4) appeared to be one of the most influential variables determining home range size during summer. It was retained in all final models (Table 4A) and explained a substantial amount of the variation in the data (R^2 range: 0.04 – 0.49 across all scales; Table 3A; Fig. 2A). However, in contrast to our expectation, females with a calf at heel had smaller summer ranges than females without, a pattern that was consistent across scales. Differences in home range size between females with and without a calf decreased over the course of summer (i.e. interaction between calf at heel and daylight) with similar range sizes between groups in September (Fig. 3).

FORAGE CHARACTERISTICS

Overall browse density (P. 2.1) explained a substantial amount of variation in total home range size (90% isopleth) during summer ($R^2 \geq 0.10$ across scales; Fig. 2A). However, the expected decrease in home range size with increasing browse density

(P. 2.1) was only observed at the daily scale (Table 4A; Fig. S3 in Supporting Information). At longer temporal scales the effect changed over time. For example, in the beginning of summer (i.e. June) browse density did not affect total home range size. In contrast, home range size increased with browse density towards the end of summer (i.e. September). During winter, overall browse density affected home range size at both daily and monthly scales but browse density was not included in the best models at intermediate temporal scales (Table 4B). As expected, home ranges generally decreased with increasing browse density (both total home range and core area) except at the end of winter at the monthly scale where home ranges increased with browse density (Fig. S4 in Supporting Information).

The proportion of high quality browse (P. 2.2) was negatively correlated with home range size as expected (Table 4; Figs. S5 & S6 in Supporting Information) and affected home range size mainly at intermediate to short temporal scales (Fig 2). However, browse quality explained a relatively minor part of the total observed variation in home range size (range of R^2: 0.02 – 0.10; Table 3; Fig. 2) but appeared to be more important during winter (range of R^2: 0.05 – 0.10) than summer (R^2 = 0.02).

Contrary to expectation (P. 2.3), the proportion of time spent at feeding stations during winter did not influence winter home range size at any spatiotemporal scale.

CLIMATIC DETERMINANTS

The effect of temperature (P. 3.1) on moose home range size varied across scales and within seasons (Table 4) and appeared to be slightly more important during winter than summer (R^2summer < R^2winter; Fig. 2) and more important for total home range size than core area size (R^2 90% isopleth < R^2 50% isopleth; Table 3). Daily home range size during summer (both 90% and 50% isopleths) did not decrease with temperature as expected, but instead remained unaffected in the beginning of summer and increased with temperature in September (Fig. S7 in Supporting Information). During winter, daily core areas decreased with temperature as expected, but only in January. In contrast, at the end of winter (April) daily ranges increased with temperature (Fig. S8 in Supporting Information). The opposite pattern was found for biweekly winter ranges, which increased with temperature at the beginning of winter and decreased in April.

Snow depth (P.3.2) negatively affected home range size as expected (Table 4B; Fig. S9 in Supporting Information), although this relationship was only significant in the daily and weekly models. Snow depth explained more variation in total home range size (i.e. 90% isopleth; range of $R^2 = 0.08 – 0.19$) than in core area size (i.e. 50% isopleth; $R^2 = 0.09$; Fig. 2).

Precipitation (P. 3.3) affected home range size during summer at the daily and monthly scales (Table 4A) but explained only a minor part of the total variation ($R^2 = 0.01 – 0.05$; Fig. 2A). During summer the effect changed over time (interaction with hours of daylight) and varied between temporal scales (Fig. S10 in Supporting Information). In the beginning of summer, daily ranges (both total and core area) increased with precipitation while at the end of summer daily ranges decreased. At the monthly scale the inverse pattern was observed with total home range size (i.e. 90% isopleth) decreasing in early summer and increasing in late summer. Precipitation during winter (i.e. snow fall) was not retained in any of the final models.

Hours of daylight (P. 3.4) was a consistently important variable across scales and explained more variation in home range size than any of the climate variables

(Fig. 2). Home range size increased with hours of daylight during winter (smallest and largest home ranges in January and April respectively) and decreased with decreasing daylight during summer (smallest and largest home ranges during September and June respectively).

Discussion

Most temperate ungulates are frequently confronted with climatic stochasticity (Saether 1997; Mysterud *et al.* 2001) as well as spatiotemporal fluctuations in the availability and quality of food (Tufto *et al.* 1996; Anderson *et al.* 2005; McArt *et al.* 2009). However, concurrent analyses of the scale-dependent effect of both bottom up processes and variability in local weather patterns on animal space use are rare (Börger *et al.* 2006b). Bottom up processes affect herbivores directly (Vucetich & Peterson 2004; Winnie, Cross & Getz 2008) and the way they exploit the variability of forage resources over time and space can have important effects on their Darwinian fitness (McLoughlin *et al.* 2007). Simultaneously, variability in local weather patterns may affect species either directly (Coulson *et al.* 2001; Hallett *et al.* 2004), indirectly through trophic interactions among species (Krebs & Berteaux 2006; Mysterud *et al.* 2008) or both (Rivrud *et al.* in press). In addition, the behavioural response to climate and forage variability may vary considerably among individuals of the same species (Nicholson, Bowyer & Kie 1997; Dussault *et al.* 2005a; Börger *et al.* 2006b).

This study is one of the first to assess the relative effects of multiple individual-level, forage and climatic determinants on spatial and temporal variation in home range size for a large browsing herbivore. Our results indicate that the amount of variation in home range size explained by these determinants varies depending on the scale under investigation (i.e. home range size of moose is scale dependent). This makes it difficult to conclude whether intrinsic or extrinsic variables are the most important drivers in scaling of home range size. Instead, this study supports the notion that there is no single or most appropriate scale at which to study animal movement or activity (Börger *et al.* 2006b; Rivrud *et al.* in press). Nevertheless, several important consistencies were evident across all spatiotemporal scales. For example, we observed great individual variation in home range size of moose irrespective of scale which is in agreement with previous findings (Stenhouse *et al.* 1995; Dussault *et al.* 2005a). In addition, the presence of a calf and hours of daylight appeared major determinants of home range size. In contrast, the effect of browse variability and climate on home range size appeared to be most pronounced at intermediate to short spatiotemporal scales which partly contrasts with findings for mixed feeders such as red deer (Rivrud *et al.* in press).

INDIVIDUAL LEVEL DETERMINANTS

Differences between individuals (modelled by the random term moose ID; P. 1.1) explained more of the variation in home range size than individual-level attributes such as age and body mass (as expected from P. 1.2 and P. 1.3). This is in agreement with results found for roe deer (Tufto *et al.* 1996; Saïd *et al.* 2005; Börger *et al.* 2006b) and highlights the fact that individual variation in home range size is not fully captured by the factors age, body mass and reproductive status at the intra-specific level (but see Saïd *et al.* 2009 for an effect of age). This contrasts with findings from inter-specific studies, typically spanning a wider range of body mass, in which body size is a major factor determining home range size (e.g. Lindstedt *et al.* 1986; Carbone *et al.* 2005). Reproductive status (summer models; P. 1.4) nonetheless appeared to be a key individual- level factor explaining home range size in moose. Based on energetic requirements, we would expect lactating females to have larger home ranges than barren females, while predation arguments would suggest reduced movements due to vulnerable offspring. Contrasting empirical evidence of the effect of reproductive status on female space use has indeed been found. Females accompanied by offspring either enlarged their summer home range during weaning (e.g. roe deer: Tufto *et al.* 1996; Saïd *et al.* 2005), reduced it (e.g. white-tailed deer (*Odocoileus virginianus*): Schwede, Hendrichs & McShea 1993; Alpine ibex (*Capra ibex ibex*); Grignolio *et al.* 2007) or showed no change (e.g. moose; Cederlund & Sand 1994). In this study, female moose without a calf had larger home ranges than females with a calf at heel, a result that was evident across all spatiotemporal scales (in contrast to P. 1.4). However the observed differences declined as summer progressed with similar range sizes at the end of summer for both groups (Fig. 3). This suggests that the mobility of female moose in the period shortly after parturition is limited by the presence of a calf, but this constraint gradually decreases over time as offspring becomes more mobile and independent (Grignolio *et al.* 2007)..

FORAGE CHARACTERISTICS

Given the importance of forage variability in the distribution and dynamics of herbivore populations (Tufto *et al.* 1996; McLoughlin & Ferguson 2000; Relyea, Lawrence & Demarais 2000; Anderson *et al.* 2005), it is not surprising that variation in quality and quantity of browse determines the location and size of moose home ranges within a forested landscape (Dussault *et al.* 2005a; Månsson *et al.* 2007; Herfindal *et al.* 2009; van Beest *et al.* 2010b).

In agreement, overall browse density explained a large part of the observed variation in home range size, being most pronounced at relatively short temporal scales (i.e. weekly and biweekly scales; Fig. 2). However, during summer the expected decrease in home range size with increasing browse density (P. 2.1) was only observed at the daily scale (Fig S3 in Supporting Information). At longer temporal scales the effect gradually became positive towards the end of summer (i.e. September). Dussault *et al.* (2005a) found identical results for moose living in Quebec and argued that forage density may not be the most critical factor influencing home range size during summer when forage is abundant and instead is more related to the distribution of protective cover and human presence. Another explanation may be the temporal variation in nutritional quality of available forage as it matures over summer, as proposed by the forage maturation hypothesis (Hebblewhite, Merrill & McDermid 2008). As forage abundance and density increases over summer, the nutritional quality decreases as fibres and tannins accumulate (Demment & van Soest 1985). Much of the evidence supporting the forage maturation hypothesis comes from studies on grass quality and the movement of grazing herbivores (Fryxell & Sinclair 1988; Wilmshurst *et al.* 1999; Hebblewhite *et al.* 2008), but there is some indication that similar processes affect the quality of browse available to moose over summer (Hjeljord, Hovik & Pedersen 1990; Bo & Hjeljord 1991). In fact, summer dietary nitrogen availability has been proposed to act as a nutritional constraint on moose in Alaska (McArt *et al.* 2009). Although we have no data to test this hypothesis, changes in the nutritional value of the available browse may have caused the moose in our study area to periodically (i.e. over longer time scales than one day) change feeding sites in search of new patches with browse of sufficient high quality in much the same way as is typically observed during periods of forage scarcity (e.g. during winter: Edenius 1991; van Beest *et al.* 2010b). Indeed, we found a positive effect of browse density on monthly home range size towards the end of winter (April; Fig S4 Supporting Information). Depletion of high quality browse during winter may cause moose to increase their movement in order to select for more abundant but lower quality browse species (Edenius 1991) which results in reduced overlap between monthly home ranges (van Beest *et al.* 2010b). The proportion of high quality browse species within home ranges appeared to be negatively correlated with home range size across all scales as expected (P. 2.2) and appeared most important during winter at short to intermediate temporal scales when browse density did not affect home range size (Fig. 2).

We have previously shown that the use of supplementary feeding stations by moose can change foraging behaviour during winter (van Beest *et al.* 2010a). However, the proportion of time spent in the vicinity of feeding stations was not retained in any of the final models, suggesting that the moose did not use supplementary feeding stations to a sufficient extent to affect home range size. The absence of such an effect may be related to the short (~ 6 yr) feeding history in our study area (Sahlsten *et al.* 2010; van Beest *et al.* 2010a).

CLIMATIC DETERMINANTS

The focus on climatic effects on demography and population dynamics has augmented dramatically over recent years (Stenseth *et al.* 2002; Parmesan 2006; Grotan *et al.* 2009). Vucetich & Peterson (2004) showed that the moose population of Isle Royale is not only regulated by bottom up processes but also, to a large extent, by abiotic factors such as winter precipitation (the North Atlantic Oscillation (NAO) index) and summer temperature. Recruitment rates of moose populations across Norway have also been linked to different climate variables although opposite effects may occur between geographical areas (Grotan *et al.* 2009). By comparison, studies of behavioural responses to climate in herbivores have lagged behind, and the few existing studies are focussed on intermediate feeders and grazers, such as red deer (Rivrud *et al.* in press) and reindeer (*Rangifer tarandus plathyrynchus*: Stien *et al.* 2010).

In this first study of climate effects on home range size of a large browsing herbivore, the effects of temperature and precipitation on variation in home range size were not as notable as initially expected (P. 3.1 and P. 3.2. respectively). Local climate affected moose home range size mainly at intermediate to short temporal scales (i.e. biweekly to daily scales; Fig. 2) suggesting that direct effects were more important than indirect effects. This contrasts with findings for red deer (Rivrud *et al.* in press). Indirect effects of climate on herbivore space use operate largely through plant growth and quality (Rivrud *et al.* in press). Grass species are likely to respond to climatic fluctuations faster and more strongly than browse species (as discussed above) which may explain why indirect effects of climate on space use of intermediate feeders and grazers are more evident than for browsing herbivores. Temperature, snow depth and precipitation affected the total home range size more, although only slightly, than core home range size which agrees with the concept that peripheral home range areas are influenced more by climatic variability than the heavily used core areas (Börger *et al.* 2006b).

We expected moose home range size to be negatively correlated with temperature across all scales (P. 3.1) but this was clearly not the case (Figs S7 & S8 in Supporting Information). Daily ranges decreased in January but increased with temperature in April while at the monthly scale the opposite pattern was observed. Indeed, the interpretation of direct effects of temperature on animal space use during a season is complicated by changes in pelage insulation and snow depth (Rivrud *et al.* in press). The fact that moose did not reduce their home range as temperature increased may indicate that the current range of temperatures experienced by the moose in our study area fall largely below their upper critical threshold (Dussault *et al.* 2004). Alternatively, sufficient habitat with good thermal shelter may be available for temperature and the potential risk of heat stress to not be a major concern to the moose during our study period.

Movement in deep snow is known to increase energy expenditure (Parker, Robbins & Hanley 1984) and reduced activity when snow depth exceeds acceptable levels is commonly reported for a range of species (Schmidt 1993; Grignolio *et al.* 2004; Dussault *et al.* 2005b; Luccarini *et al.* 2006; Rivrud *et al.* in press). Indeed, snow depth was negatively correlated with moose home range size as expected (P. 3.3) but only at short temporal scales (weekly and daily; Fig. S9, Supporting Information). In contrast, Rivrud *et al.* (in press) reported that home range size of red deer was strongly affected by snow depth across all spatial temporal scales (from monthly to daily scales). Differences in body size between moose and red deer and the fact that moose are better adapted to walking in deep snow may explain why moose respond less strongly to snow depth over longer spatial scales. Furthermore, intermediate feeders and grazers may be more heavily affected by snow than browsers as a significant part of their available forage is covered by snow.

Hours of daylight appeared an important factor across all spatiotemporal scales as it explained the most variation in home range size of any variable considered (Fig. 2). However this is likely an overestimation as daylight was included in all interactions, so increasing its R2. Nevertheless, we demonstrate that by including hours of daylight as an interaction in the models we can reveal how behavioural responses to local climate and forage variability may change within seasons.

CONCLUSION

Using an established statistical approach (Börger *et al.* 2006b; Rivrud *et al.* in press), we provide clear evidence that variation in home range size of a large browsing herbivore is scale dependent and results from the effect of several intrinsic and extrinsic determinants. Home range size varied most in response to changes in daylight within seasons, reproductive status and individual differences other than age and body mass. Forage variability (density and quality of browse) and climate (temperature, precipitation and snow depth) influenced moose range size especially at short temporal scales. Such insight into the behavioural responses to climatic stochasticity and forage variability may facilitate conservation and management of populations which is especially important for large herbivores due to their significant impact on forestry, agriculture and natural ecosystems (Côte *et al.* 2004).

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Table 1: Summary of a literature review on the effect of various individual, forage and climatic determinants on home range size of cervids. For more details on the predictions see text at Introduction. For each study reviewed we state the spatial and temporal scales under investigation, home range size (HR) estimator used (minimum convex polygon is abbreviated as MCP) and the cervid species under investigation. Note that the literature review was restricted to variables available in this study.

Factor & predictions	**Temporal scale**	**Spatial scale and HR estimator**	**Effect on home range size**	**Species**	**Reference**
Intrinsic					
Individual variation (P. 1.1)	Seasonal	100% MCP	Large	Moose	Stenhouse *et al.* (1995)
	Seasonal	60 & 95% MCP	Large	Moose	Dussault et al. (2005)
	Seasonal	95% MCP & fixed kernel	Large	Mule deer	Nicholson *et al.* (1997)
	Multiple	50-90% fixed & adaptive kernel	Large	Roe deer	Börger *et al.* (2006)
Body mass (P. 1.2)	Annual	95% harmonic mean	+ (males only)	Mule deer	Relyea *et al.* (2000)
	Summer	50 & 95% fixed kernel	no effect	Roe deer	Saïd *et al.* (2005)
	Seasonal	95% fixed kernel	no effect	Roe deer	Saïd *et al.* (2009)
Age (P. 1.3)	Annual	90% MCP	no effect (females), + (males)	Moose	Cederlund & Sand (1994)
	Seasonal	95% fixed kernel	-	Roe deer	Saïd *et al.* (2009)
	Seasonal	95 & 50% fixed kernel	no effect	Roe deer	Saïd *et al.* (2005)
Reproductive status (P. 1.4)	Annual	90% MCP	calf > no calf (autumn only)	Moose	Cederlund & Sand (1994)
	Summer	90% adaptive kernel	calf > no calf	Roe deer	Tufto *et al.* (1996)
	Summer	50 & 95% fixed kernel	calf > no calf	Roe deer	Saïd *et al.* (2005)
Extrinsic (Forage related)					
Browse density (P. 2.1)	Seasonal	60 & 95% MCP	- (winter) + (summer)	Moose	Dussault *et al.* (2005)
	Seasonal	95% fixed kernel	-	Red deer	Anderson *et al.* (2005)
	Seasonal	95% fixed kernel	-	Roe deer	Saïd *et al.* (2009)

Browse quality	Summer	50 & 95% fixed kernel	-	Roe deer	Saïd *et al.* (2005)
(P. 2.2)	Seasonal	95% fixed kernel	-	Roe deer	Saïd *et al.* (2009)
Use of feeding stations	Winter	95 & 50% MCP & harmonic mean	-	Roe deer	Guillet *et al*. (1996)
(P. 2.3)	Winter	95% adaptive kernel	-	White-tailed deer	Kilpatrick & Stober (2002)
Extrinsic (climate related)					
Temperature (P. 3.1)	Multiple	50-90% fixed & adaptive kernel	-	Roe deer	Börger *et al.* (2006)
	Daily	100% MCP	-	Red deer	Kamler *et al.* (2007)
	Multiple	50-90% MCP & fixed kernel	- (summer),+ (winter)	Red deer	Rivrud *et al.* (2010)
Snow depth (P. 3.2)	Winter	60 & 95% MCP	-	Moose	Dussault *et al.* (2005)
	Winter	95% MCP & fixed kernel	-	Red deer	Luccarini et al. (2006
	Winter	50-90% MCP & fixed kernel	-	Red deer	Rivrud *et al.* (in press)
Rainfall (P. 3.3)	Multiple	50-90% fixed & adaptive kernel	-	Roe deer	Börger *et al.* (2006)
	Daily	100% MCP	no effect	Red deer	Kamler *et al.* (2007)
	Multiple	50-90% MCP & fixed kernel	+	Red deer	Rivrud et al . (in press)
Daylight	Multiple	50-90% fixed & adaptive kernel 50-	- (summer), + (winter)	Roe deer	Börger *et al.* (2006)
(P. 3.4)	Multiple	90% MCP & fixed kernel	- (daily scale)	Red deer	Rivrud *et al.* (2010)

Table 2: Description of the covariates fitted as fixed effects in the linear mixed-effects models to explain variation in moose (N= 24) home range size. See Material and Methods for more details on data collection for each covariate.

Parameter	**Description**
Age	The age (yr) of each individual moose as determined by tooth annuli.
Body mass	The January live mass (kg) of each individual moose as recorded during collaring. Note that age and body mass of adult females were not correlated.
Calf at heel	Two-level factor indicating whether a female moose was accompanied by a calf (yes / no). Note that this covariate was included in the summer models only as all but one female moose was not accompanied by a calf during winter.
Feeding station use	The proportion of time spent within 100 m of a artificial feeding station during each temporal scale (winter models only). Calculated by dividing the number of GPS locations (hourly positions) within 100 m of a feeding station during a specific temporal scale by the total number of GPS locations during a specific temporal scale.
Browse density	The density of available moose browse (dry mass in kg / ha) in each home range. The six most abundant browse species in the study area were included in the calculations. Note that ground layer vegetation is not included.
Browse quality	The proportion of high quality moose browse available in each home range. Browse density was divided by the density of high quality species (*Sorbus aucuparia, Populus tremula, Salix* spp.).
Temperature, rainfall and snow	We used the residuals of a regression (GAM) against Julian day for each variable and season separately.

depth	These covariates therefore account for the effect of climatic variability over a season. Note that the residuals of these three covariates were not correlated between each other. Snow depth was included in the winter models only.
Daylight	Mean number of daylight hours per temporal scale. Note that daylight was included in all 2-way interactions to allow the effect to change over time (during seasons).
Summer season	Defined as the period 1 June till 15 September in both 2007 and 2008.
Winter season	Definition was based on snow depth (period with >30 cm). As such winter in 2007 was the period 21 January till 8 April and in 2008 as 4 January till 30 April.

Table 3: Generalized R^2 values at the population level (i.e. for the final models including all fixed effects), the random effects and for each fixed effect separately retained in the final model across spatiotemporal scales during summer (A) and winter (B).

A	**Summer**	
Timescale & fixed effects	**90%**	**50%**
Month		
Browse density	0.19	NR
Precipitation	0.05	NR
Calf at heel	0.17	0.49
Daylight	0.21	NR
R^2 moose ID (random term)	0.35	0.32
R^2 final model (all fixed effects)	0.75	0.53
Biweek		
Browse density	0.10	NR
Temperature	0.08	NR
Calf at heel	0.22	0.19
Daylight	0.15	0.25
R^2 moose ID (random term)	0.26	0.24
R^2 final model (all fixed effects)	0.63	0.49
Week		
Browse density	0.24	0.11
Browse quality	NR	0.02
Calf at heel	0.18	0.13
Daylight	0.08	0.20
Age	0.03	NR
R^2 moose ID (random term)	0.22	0.19
R^2 final model (all fixed effects)	0.58	0.51
Day		
Browse density	0.25	0.23
Browse quality	0.02	0.02
Temperature	0.03	0.02
Precipitation	0.01	0.01
Calf at heel	0.04	0.04
Daylight	0.12	0.11
R^2 moose ID (random term)	0.17	0.15

R^2 final model (all fixed effects)	0.51	0.46

B	**Winter**	
Timescale & fixed effects	**90%**	**50%**
Month		
Browse density	0.37	0.36
Daylight	0.33	0.34
R^2 moose ID (random term)	0.19	0.14
R^2 final model (all fixed effects)	0.79	0.73
Biweek		
Browse quality	0.10	0.05
Temperature	0.06	0.03
Daylight	0.23	0.27
Body mass	NR	0.11
R^2 moose ID (random term)	0.29	0.12
R^2 final model (all fixed effects)	0.44	0.41
Week		
Browse quality	0.09	0.07
Temperature	NR	0.02
Snow depth	0.19	0.09
Daylight	0.20	0.21
Body mass	NR	0.03
R^2 moose ID (random term)	0.25	0.18
R^2 final model (all fixed effects)	0.52	0.41
Day		
Browse density	0.23	0.21
Browse quality	0.05	0.07
Temperature	0.02	0.02
Snow depth	0.08	0.09
Daylight	0.13	0.11
R^2 moose ID (random term)	0.15	0.10
R^2 final model (all fixed effects)	0.53	0.51

Table 4: Overview of the *F* values, and the direction of the relation (+ for positive relations and – for negative relations) with home range size, of the fixed effects in the most parsimonious models determining moose home range size (ha) across spatiotemporal scales during summer (A) and winter (B) seasons. *F* values in bold indicate $p < 0.05$. NR = Not retained in final model.

A	**Summer**			
Timescale & fixed effects	**90%**		**50%**	
Monthly scale				
Browse density	0.37	+	NR	
Precipitation	2.28	+	NR	
Calf at heel (yes)[a]	**8.39**	-	**18.61**	-
Daylight	0.69	-	NR	
Browse density * Daylight	**10.23**	-	NR	
Precipitation * Daylight	**7.18**	-	NR	
Calf at heel * Daylight	**9.91**	-	NR	
Biweekly scale				
Browse density	**7.76**	+	NR	
Calf at heel (yes)[a]	**6.97**	-	**12.68**	-
Daylight	3.20	+	3.06	+
Calf at heel * Daylight	**5.83**	-	**5.70**	-
Weekly scale				
Browse density	**5.48**	+	**10.52**	+
Browse quality	NR		**6.89**	-
Calf at heel (yes)[a]	**6.62**	-	**9.46**	-
Daylight	1.45	+	1.33	+
Age	0.66	-	NR	
Browse density * Daylight	**6.09**	-	**5.86**	-
Calf at heel * Daylight	NR		**6.68**	-
Age * Daylight	**6.41**	+	NR	
Daily scale				
Browse density	**70.43**	-	**683.40**	-
Browse quality	**7.53**	-	**65.81**	-
Temperature	**4.55**	+	**2.06**	-

Precipitation	1.40	+	3.55	+
Calf at heel (yes)[a]	3.89	-	**5.19**	-
Daylight	**17.65**	+	**13.23**	+
Temperature * Daylight	**4.19**	-	**6.57**	-
Precipitation * Daylight	**4.76**	+	**8.32**	+
Calf at heel * Daylight	**8.33**	-	**6.94**	-

[a] = in reference to no calf at heel

B	**Winter**			
Timescale & fixed effects	**90%**		**50%**	
Monthly scale				
Browse density	1.29	-	0.81	+
Daylight	1.84	+	0.75	+
Browse density * Daylight	**8.05**	+	**5.05**	+
Biweekly scale				
Browse quality	**20.87**	-	**17.27**	-
Temperature	**10.28**	-	**21.55**	-
Daylight	2.86	+	0.01	-
Body mass	NR		**4.80**	+
Temperature * Daylight	**4.64**	-	**5.06**	-
Body mass * Daylight	NR		**8.00**	+
Weekly scale				
Browse quality	**5.84**	-	**8.52**	-
Temperature	NR		**7.40**	+
Snow depth	**11.35**	-	**5.71**	-
Daylight	**23.93**	+	**14.61**	+
Body mass	NR		**7.70**	+
Daily scale				
Browse density	**115.91**	-	**423.89**	-
Browse quality	**36.34**	-	**44.39**	-
Temperature	NR	+	**4.68**	+
Snow depth	**5.72**	-	**7.91**	-
Daylight	**38.97**	+	**7.46**	+

Browse quality * Daylight	**7.48**	**-**	**4.68**	**-**
Temperature * Daylight	NR		**11.41**	+

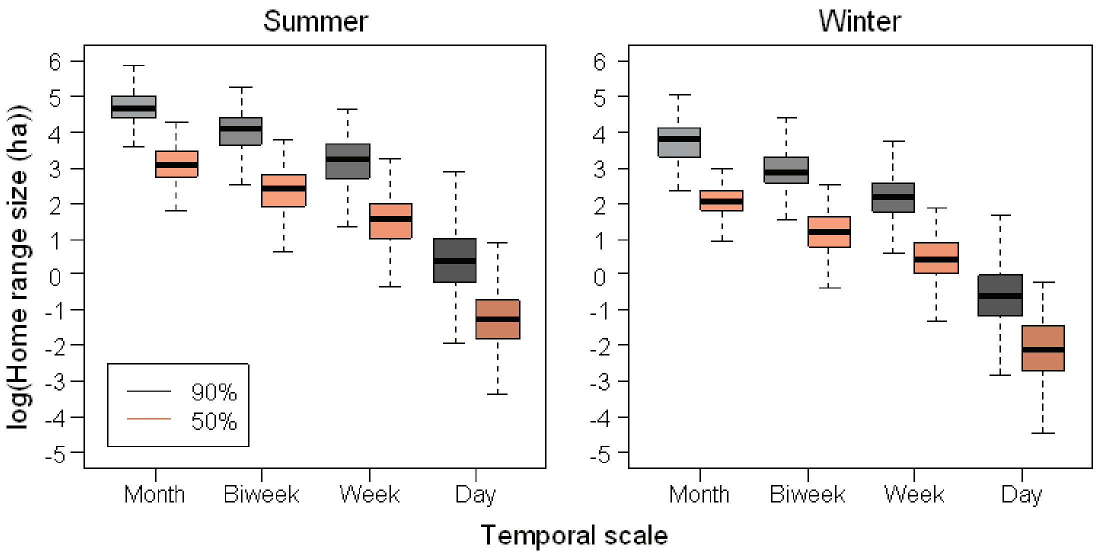

Summer
Winter
log(Home range size (ha))
6
5
4
3
2
1
0
-1
-2
-3
-4
-5
90%
50%
Month
Biweek
Week
Day
Temporal scale

Fig. 1

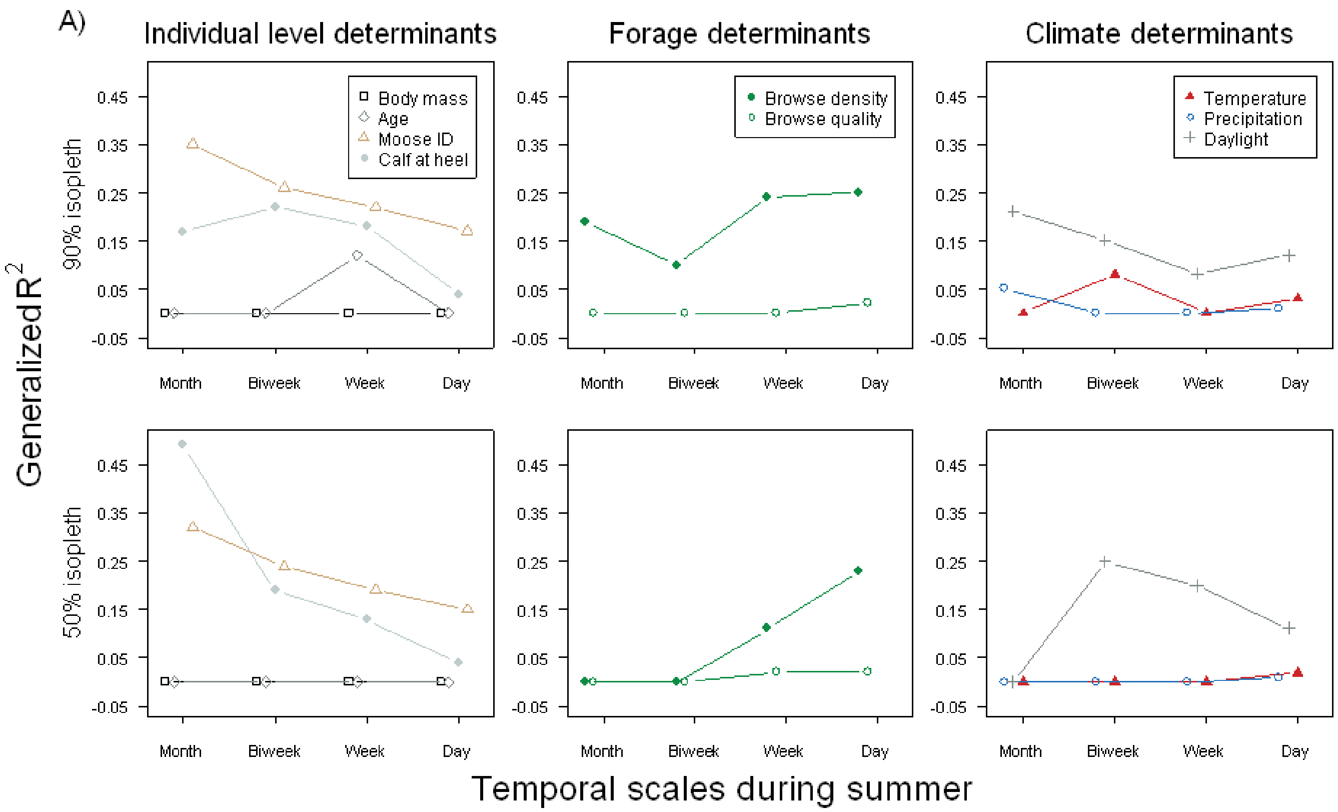

A)
Individual level determinants
Forage determinants
Climate determinants
Generalized R2
90% isopleth
50% isopleth
0.45
0.35
0.25
0.15
0.05
-0.05
Body mass
Age
Moose ID
Calf at heel
Browse density
Browse quality
Temperature
Precipitation
Daylight
Month
Biweek
Week
Day
Temporal scales during summer

Fig. 2(A)

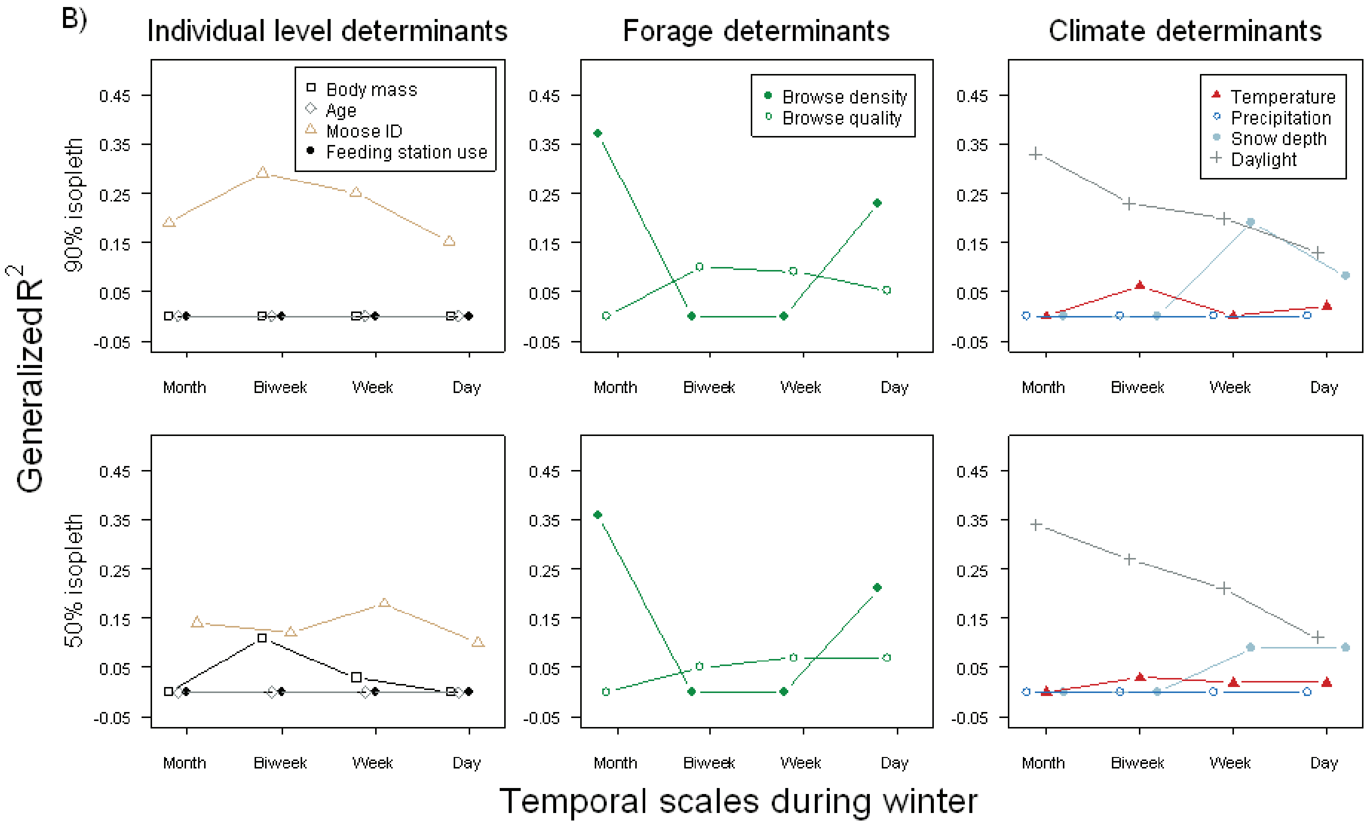
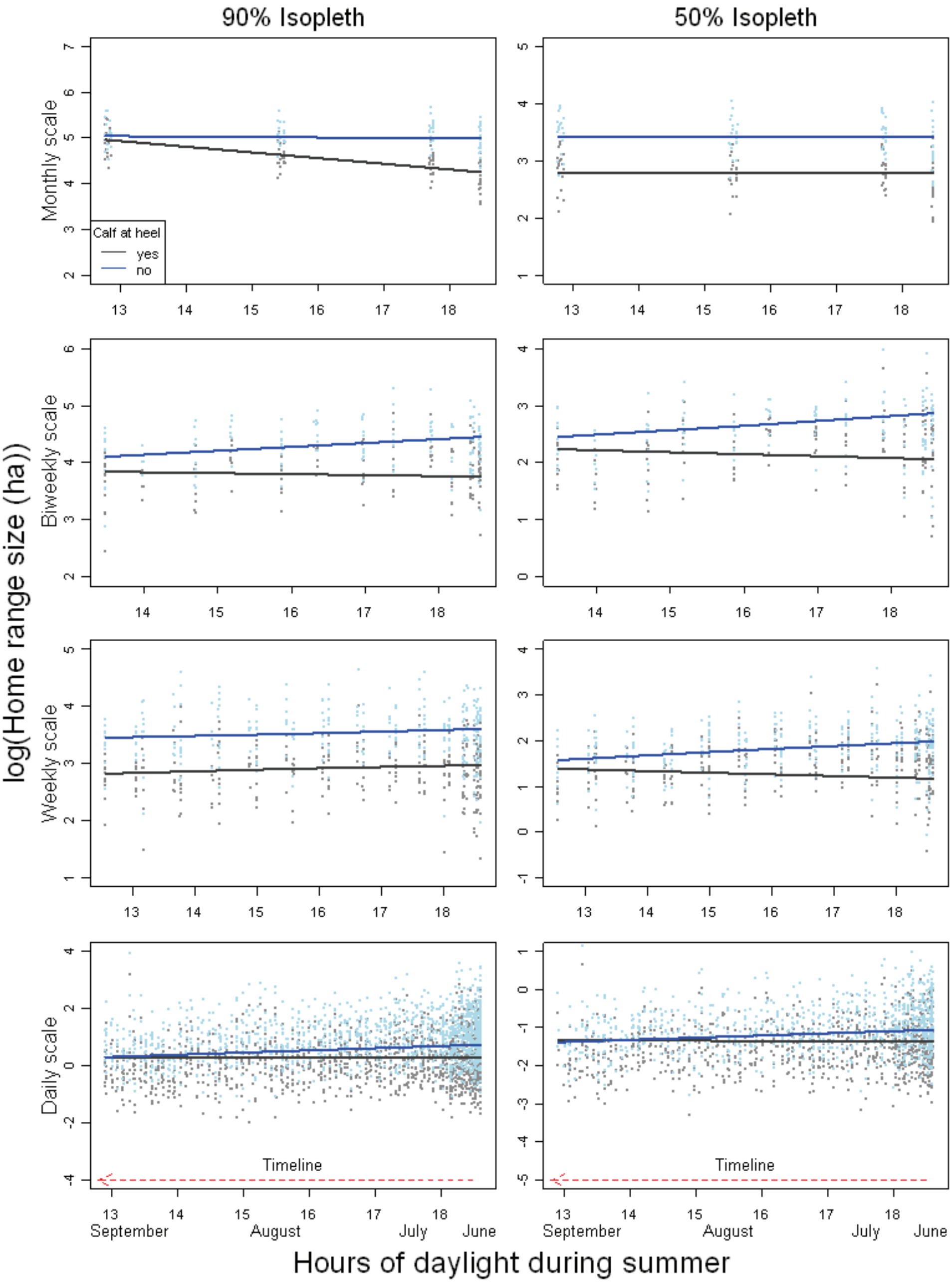

B)
Individual level determinants
Forage determinants
Climate determinants
Generalized R^2
90% isopleth
50% isopleth
0.45
0.35
0.25
0.15
0.05
-0.05
Body mass
Age
Moose ID
Feeding station use
Browse density
Browse quality
Temperature
Precipitation
Snow depth
Daylight
Month
Biweek
Week
Day
Temporal scales during winter

Fig. 2 (B)

Fig. 3


90% Isopleth
50% Isopleth
log(Home range size (ha))
Monthly scale
Biweekly scale
Weekly scale
Daily scale
Calf at heel
yes
no
2
3
4
5
6
7
1
0
-1
-2
-3
-4
-5
13
14
15
16
17
18
Timeline
September
August
July
June
Hours of daylight during summer

Supporting Information – Paper III

Table S1: Overview of the mixed-model structure for each spatiotemporal scale. Moose ID and Year show the standard deviation (SD) of the random intercept in the most parsimonious mixed-effects model. Spatial correlation indicates the range of the spatial autocorrelation in the models (by using the harmonic mean center of the home ranges in meters). Temporal correlation shows the range of the temporal autocorrelation in the models (integer valued continuous-time measures starting from the first home range estimates taken). Variance function used was always the power of covariate variance structure with the fitted values of the model as variance covariate. NR = not retained in final model.

	Summer		**Winter**	
Timescale and model structure	**90%**	**50%**	**90%**	**50%**
Month				
Moose ID	0.33	0.28	0.41	0.37
Year	NR	NR	NR	NR
Temporal correlation	NR	NR	NR	NR
Spatial correlation	322 m	NR	NR	NR
Variance	NR	NR	NR	NR
Biweek				
Moose ID	0.46	0.34	0.28	0.17
Year	NR	NR	NR	NR
Temporal correlation	NR	NR	NR	NR
Spatial correlation	NR	NR	167 m	130 m
Variance	NR	-0.58	NR	NR
Week				
Moose ID	0.48	0.42	0.45	0.30
Year	NR	NR	NR	NR
Temporal correlation	ρ = 0.40	ρ = 0.29	NR	ρ = 0.35
Spatial correlation	NR	NR	39 m	NR
Variance	-0.22	-0.30	NR	NR
Day				

Moose ID	0.38	0.17	0.25	0.16
Year	NR	NR	NR	NR
Temporal correlation	ρ = 0.11	ρ = 0.11	ρ = 0.34	NR
Spatial correlation	NR	NR	NR	NR
Variance function	NR	-0.18	NR	NR

Table S2: Summary statistics of adult female moose home range size (ha) across spatiotemporal scales. N = number of moose included in home range calculation, n = mean number of home range estimates per moose ID. *k*= the mean number of nearest neighbor points from which home ranges were constructed (k-local hull convex method).

	Summer		**Winter**	
Timescale	**90%**	**50%**	**90%**	**50%**
Month				
Mean	126.8	25.4	51.3	8.4
Min - Max	22.69 - 351.6	6.1 - 73.9	10.9 - 156.1	1.5 - 19.8
N	22	22	20	20
n	3.7	3.6	2.1	2.3
k	26	26	22	22
Biweek				
Mean	69.27	13.38	22.38	3.92
Min - Max	9.89 - 192.13	1.59 - 44.14	1.76 - 80.66	0.49 - 12.51
N	22	22	21	21
n	6.0	6.4	4.5	4.6
k	17	17	13	13
Week				
Mean	31.8	6.1	10.9	1.9
Min - Max	2.78 - 105.3	0.6 - 26.7	0.6 - 57.9	0.2 - 6.6
N	22	24	23	23
n	13.4	12.9	10.0	9.9
k	8	8	6	6
Day				
Mean	2.40	0.42	0.88	0.18
Min - Max	0.1 -27.9	0.01 - 3.74	0.05 - 27.4	0.006 - 1.53
N	24	24	24	24
n	57.4	58.2	41.2	43.4
k	4	4	3	3

Table S3: Summary of the mixed-effects models predicting monthly home range size (log(ha)) in both summer (A) and winter (B) of female moose in Telemark County, southern Norway. The models include a random intercept for individual moose (see Table S1) and the number of moose included in the models varied across scales (see Table S2).

A	**Summer**			
Home range isopleth and model parameters	**Estimate**	**SE**	**df**	***F*-value**
90%				
(Intercept)	4.997	0.132	1, 52	**283.52**
Browse density	0.068	0.043	1, 52	0.37
Precipitation	0.046	0.027	1, 52	2.28
Calf at heel (yes)[a]	-0.471	0.178	1, 20	**8.39**
Daylight	-0.009	0.024	1, 52	0.69
Browse density * Daylight	-0.046	0.010	1, 52	**10.23**
Precipitation * Daylight	-0.054	0.024	1, 52	**7.18**
Calf at heel * Daylight	-0.110	0.035	1, 52	**9.91**
50%				
(Intercept)	3.399	0.108	1, 59	**178.85**
Calf at heel (yes)[a]	-0.633	0.147	1, 21	**18.61**

[a] = in reference to no calf at heel

B	**Winter**			
Home range isopleth and model parameters	**Estimate**	**SE**	**df**	***F*-value**
90%				
(Intercept)	3.844	0.117	1, 19	**107.30**
Browse density	-0.207	0.174	1, 13	1.29
Daylight	0.078	0.039	1, 13	1.84
Browse density * Daylight	0.196	0.069	1, 13	**8.05**

50%				
(Intercept)	2.042	0.112	1, 19	**32.33**
Browse density	0.054	0.146	1, 13	0.81
Daylight	0.057	0.039	1, 13	0.75
Browse density * Daylight	0.138	0.062	1, 13	**5.05**

Table S4: Summary of the mixed-effects models predicting biweekly home range size (log(ha)) in both summer (A) and winter (B) of female moose in Telemark County, southern Norway. The models include a random intercept for individual moose (see Table S1) and the number of moose included in the models varied across scales (see Table S2).

A	**Summer**			
Home range isopleth and model parameters	**Estimate**	**SE**	**df**	***F*-value**
90%				
(Intercept)	4.331	0.153	1, 109	**143.37**
Browse density	0.095	0.047	1, 109	**7.76**
Calf at heel (yes)[a]	-0.553	0.214	1, 20	**6.97**
Daylight	0.071	0.027	1, 109	3.20
Calf at heel * Daylight	-0.088	0.045	1, 109	**5.83**
50%				
(Intercept)	2.710	0.121	1, 117	**188.99**
Calf at heel (yes)[a]	-0.600	0.173	1, 20	**12.68**
Daylight	0.082	0.029	1, 117	3.06
Calf at heel * Daylight	-0.119	0.050	1, 117	**5.70**

[a] = in reference to no calf at heel

B	**Winter**			
Home range isopleth and model parameters	**Estimate**	**SE**	**df**	***F*-value**

90%				
(Intercept)	2.856	0.098	1, 68	**110.05**
Browse quality	-2.315	0.542	1, 68	**20.87**
Temperature	-0.042	0.025	1, 68	**10.28**
Daylight	0.016	0.031	1, 68	2.86
Temperature * Daylight	-0.031	0.013	1, 68	**4.64**
50%				
(Intercept)	1.104	0.082	1, 70	**294.68**
Browse quality	-1.536	0.413	1, 70	**17.27**
Temperature	-0.097	0.027	1, 70	**21.55**
Daylight	-0.029	0.031	1, 70	0.01
Body mass	0.877	0.535	1, 19	**4.80**
Temperature * Daylight	-0.030	0.013	1, 70	**5.06**
Body mass * Daylight	0.562	0.199	1, 70	**8.00**

Table S5: Summary of the mixed-effects models predicting weekly home range size (log(ha)) in both summer (A) and winter (B) of female moose in Telemark County, southern Norway. The models include a random intercept for individual moose (see Table S1) and the number of moose included in the models varied across scales (see Table S2).

A	**Summer**			
Home range isopleth and model parameters	**Estimate**	**SE**	**df**	***F*-value**
90%				
(Intercept)	3.556	0.165	1, 268	**840.90**
Browse density	0.046	0.031	1, 268	**5.48**
Calf at heel (yes)[a]	-0.625	0.231	1, 19	**6.62**
Daylight	0.023	0.020	1, 268	1.45
Age	-0.024	0.031	1, 19	0.66
Browse density * Daylight	-0.029	0.014	1, 268	**6.09**

Age * Daylight	0.013	0.005	1, 268	**6.41**
50%				
(Intercept)	1.852	0.145	1, 281	**249.61**
Browse density	0.106	0.051	1, 281	**10.52**
Browse quality	-0.617	0.299	1, 281	**6.89**
Calf at heel (yes)[a]	-0.604	0.196	1, 22	**9.46**
Daylight	0.069	0.027	1, 281	1.33
Browse density * Daylight	-0.047	0.025	1, 281	**5.86**
Calf at heel * Daylight	-0.106	0.041	1, 281	**6.68**

[a] = in reference to no calf at heel

B	**Winter**			
Home range isopleth and model parameters	**Estimate**	**SE**	**df**	***F*-value**
90%				
(Intercept)	2.164	0.104	1, 203	**444.37**
Browse quality	-0.562	0.333	1, 203	**5.84**
Snow depth	-0.008	0.002	1, 203	**11.35**
Daylight	0.075	0.015	1, 203	**23.93**
50%				
(Intercept)	0.420	0.084	1, 200	**27.29**
Browse quality	-0.814	0.283	1, 200	**8.52**
Temperature	0.039	0.013	1, 200	**7.40**
Snow depth	-0.004	0.002	1, 200	**5.71**
Daylight	0.073	0.020	1, 200	**14.61**
Body mass	1.209	0.629	1, 21	**7.70**

Table S6: Summary of the mixed-effects models predicting daily home range size (log(ha)) in both summer (A) and winter (B) of female moose in Telemark County, southern Norway. The models include a random intercept for individual moose (see Table S1) and the number of moose included in the models varied across scales (see Table S2).

A	**Summer**			
Home range isopleth and model parameters	**Estimate**	**SE**	**df**	***F*-value**
90%				
(Intercept)	0.614	0.126	1, 1394	**24.44**
Browse density	-0.234	0.026	1, 1394	**70.43**
Browse quality	-0.412	0.150	1, 1394	**7.53**
Temperature	0.021	0.008	1, 1394	**4.55**
Precipitation	0.002	0.003	1, 1394	1.40
Calf at heel (yes)[a]	-0.321	0.167	1, 22	3.89
Daylight	0.078	0.020	1, 1394	**17.65**
Temperature * Daylight	-0.012	0.005	1, 1394	**4.19**
Precipitation * Daylight	0.004	0.002	1, 1394	**4.76**
Calf at heel * Daylight	-0.078	0.027	1, 1394	**8.33**
50%				
(Intercept)	-1.153	0.064	1, 883	**1142.18**
Browse density	-0.632	0.023	1, 883	**683.40**
Browse quality	-0.951	0.129	1, 883	**65.81**
Temperature	-0.001	0.008	1, 883	**2.06**
Precipitation	0.004	0.003	1, 883	3.55
Calf at heel (yes)[a]	-0.196	0.087	1, 22	**5.19**
Daylight	0.061	0.019	1, 883	**13.23**
Temperature * Daylight	-0.013	0.005	1, 883	**6.57**
Precipitation * Daylight	0.004	0.001	1, 883	**8.32**
Calf at heel * Daylight	-0.065	0.025	1, 883	**6.94**

[a] = in reference to no calf at heel

B	**Winter**			
Home range isopleth and model parameters	**Estimate**	**SE**	**df**	***F*-value**
90%				
(Intercept)	-0.553	0.060	1, 960	**72.25**
Browse density	-0.336	0.028	1, 960	**115.91**
Browse quality	-1.165	0.185	1, 960	**36.34**
Snow depth	-0.003	0.001	1, 960	**5.72**
Daylight	0.072	0.011	1, 960	**38.97**
Browse quality * Daylight	-0.172	0.063	1, 960	**7.48**
50%				
(Intercept)	-2.099	0.046	1, 412	**337.33**
Browse density	-0.588	0.028	1, 412	**423.89**
Browse quality	-1.515	0.212	1, 412	**44.39**
Temperature	0.024	0.009	1, 412	**4.68**
Snow depth	-0.003	0.001	1, 412	**7.91**
Daylight	0.029	0.012	1, 412	**7.46**
Browse quality * Daylight	-0.169	0.070	1, 412	**4.68**
Temperature * Daylight	0.011	0.003	1, 412	**11.41**

Figure S1: Plot of predicted log-transformed home range sizes (ha) in relation to log-transformed body mass (kg) of moose in southern Norway. Estimates are given for the biweekly and weekly scale during winter, and for the minimum, mean and maximum value of daylight, corresponding to January, February/March and April respectively. Predictions for body mass were made while keeping other variables retained in the model constant at their mean value. Lines show predicted values for 90% and 50% isopleths and points in corresponding colours are raw residuals. NR = not retained in final models.

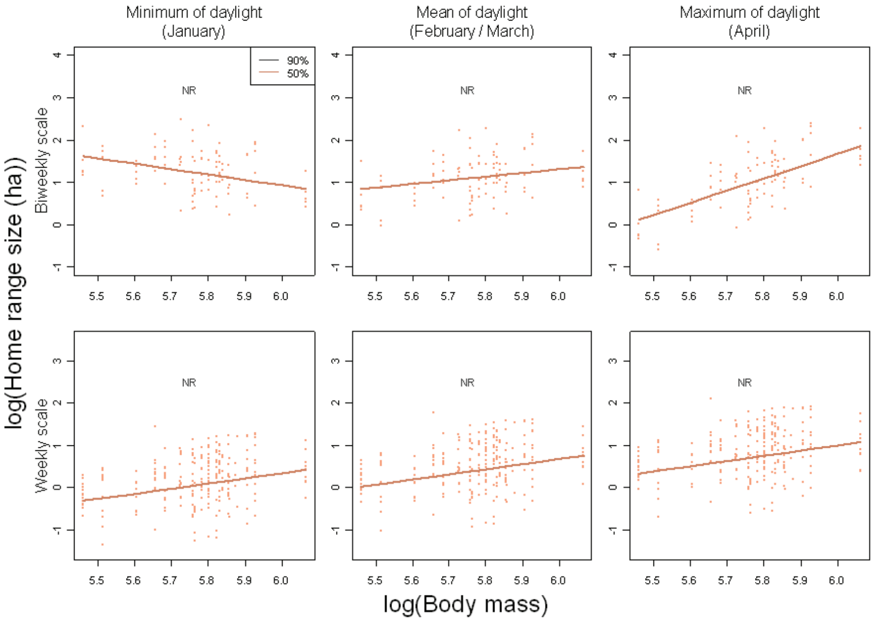


Figure S2: Plot of predicted log-transformed home range sizes (ha) in relation to age (yr) of moose in southern Norway. Estimates are given for the weekly scale during summer, and for the minimum, mean and maximum value of daylight, corresponding to September, July/August and June respectively. Predictions for age were made while keeping other variables retained in the model constant at their mean value. Lines show predicted values for 90% and 50% isopleths and points in corresponding colours are raw residuals. NR = not retained in final models.

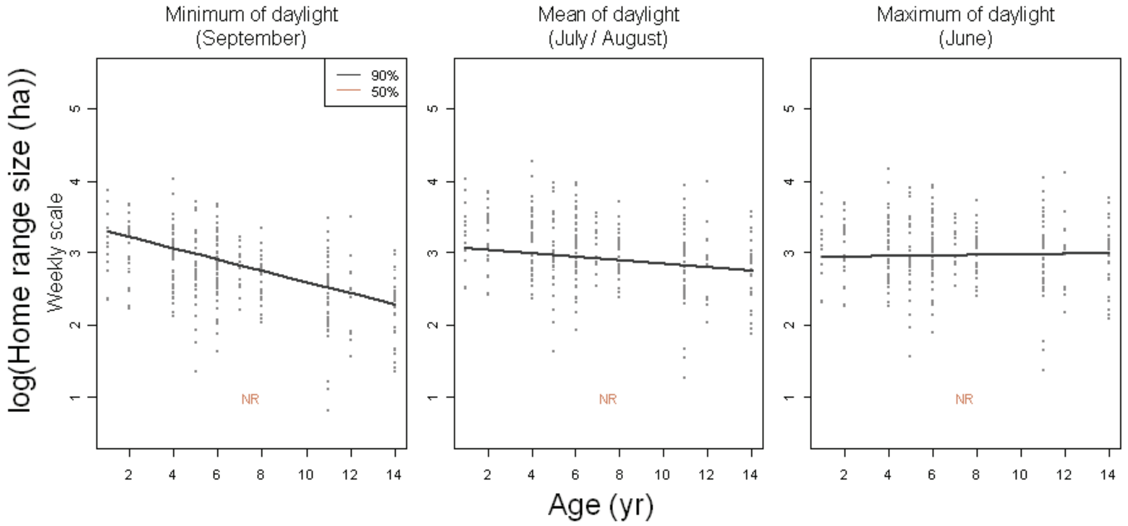


Figure S3: Plot of predicted log-transformed home range sizes (ha) in relation to log-transformed browse density of moose in southern Norway. Estimates are given for all temporal scales during summer, and for the minimum, mean and maximum value of daylight, corresponding to September, July/August and June respectively. Predictions for overall browse density were made while keeping other variables retained in the model constant at their mean value. Lines show predicted values for 90% and 50% isopleths and points in corresponding colours are raw residuals. NR = not retained in final models.

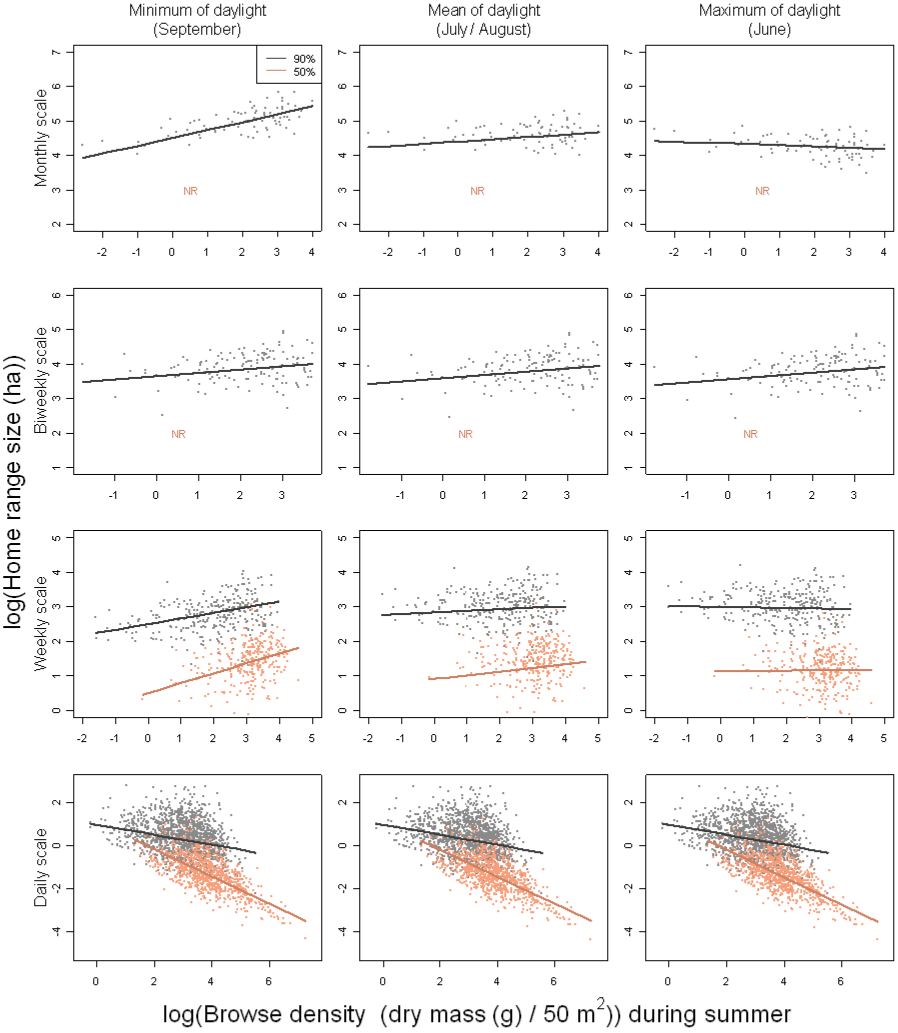


Figure S4: Plot of predicted log-transformed home range sizes (ha) in relation to log-transformed browse density of moose in southern Norway. Estimates are given for monthly and daily scales during winter, and for the minimum, mean and maximum value of daylight, corresponding to January, February/March and April respectively. Predictions for overall browse density were made while keeping other variables retained in the model constant at their mean value. Lines show predicted values for 90% and 50% isopleths and points in corresponding colours are raw residuals.

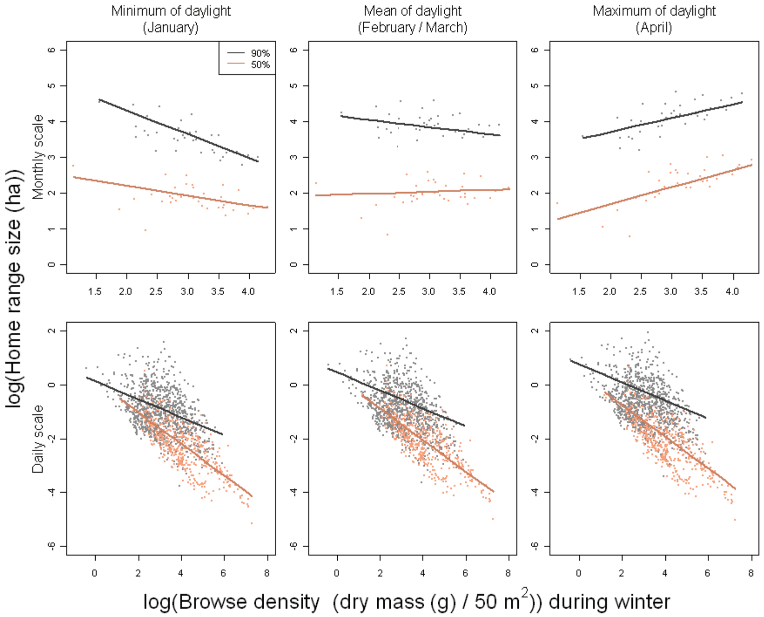


Figure S5: Plot of predicted log-transformed home range sizes (ha) in relation to proportion of browse quality of moose in southern Norway. Estimates are given for weekly and daily scales during summer, and for the minimum, mean and maximum value of daylight, corresponding to September, July/August and June respectively. Predictions for the proportion of browse quality were made while keeping other variables retained in the model constant at their mean value. Lines show predicted values for 90% and 50% isopleths and points in corresponding colours are raw residuals. NR = not retained in final models.

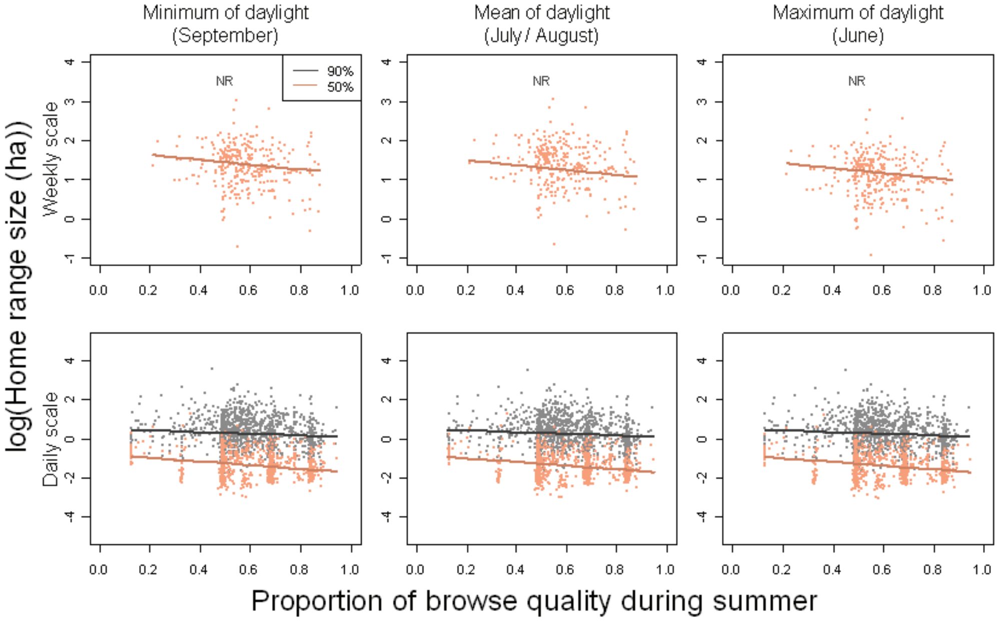


Figure S6: Plot of predicted log-transformed home range sizes (ha) in relation to the proportion of browse quality of moose in southern Norway. Estimates are given for biweekly, weekly and daily scales during winter, and for the minimum, mean and maximum value of daylight, corresponding to January, February/March and April respectively. Predictions for the proportion of browse quality were made while keeping other variables retained in the model constant at their mean value. Lines show predicted values for 90% and 50% isopleths and points in corresponding colours are raw residuals.

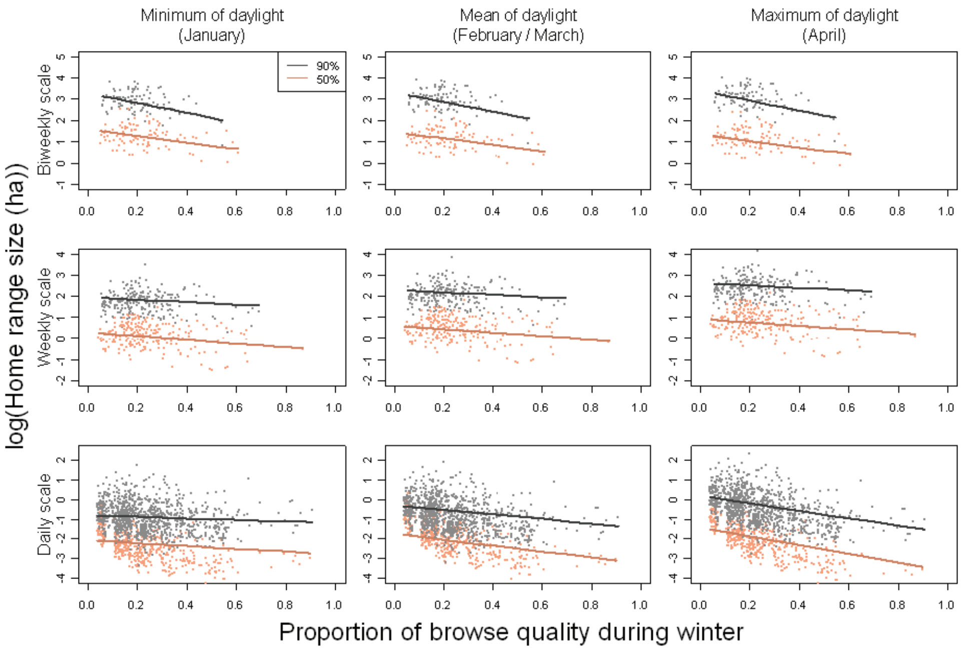


Figure S7: Plot of predicted log-transformed home range sizes (ha) in relation to temperature (residuals of a regression against Julian day) of moose in southern Norway. Estimates are given for daily scales during summer, and for the minimum, mean and maximum value of daylight, corresponding to September, July/August and June respectively. Predictions for temperature were made while keeping other variables retained in the model constant at their mean value. Lines show predicted values for 90% and 50% isopleths and points in corresponding colours are raw residuals.

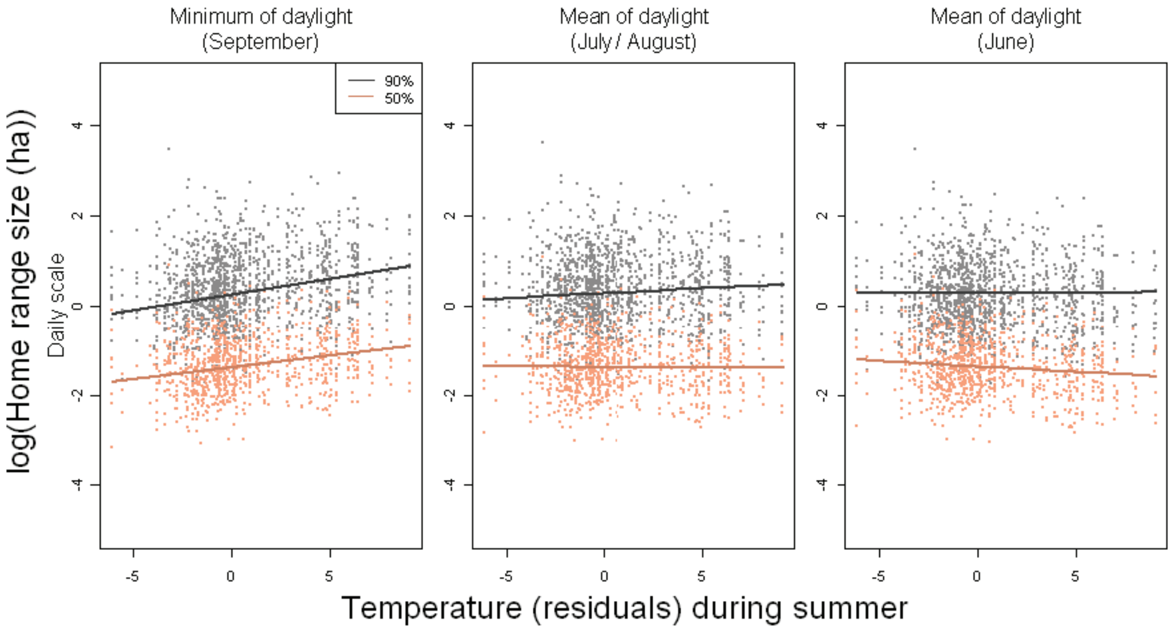


Figure S8: Plot of predicted log-transformed home range sizes (ha) in relation to temperature (residuals of a regression against Julian day) of moose in southern Norway. Estimates are given for biweekly, weekly and daily scales during winter, and for the minimum, mean and maximum value of daylight, corresponding to January, February/March and April respectively. Predictions for temperature were made while keeping other variables retained in the model constant at their mean value. Lines show predicted values for 90% and 50% isopleths and points in corresponding colours are raw residuals. NR = not retained in final models.

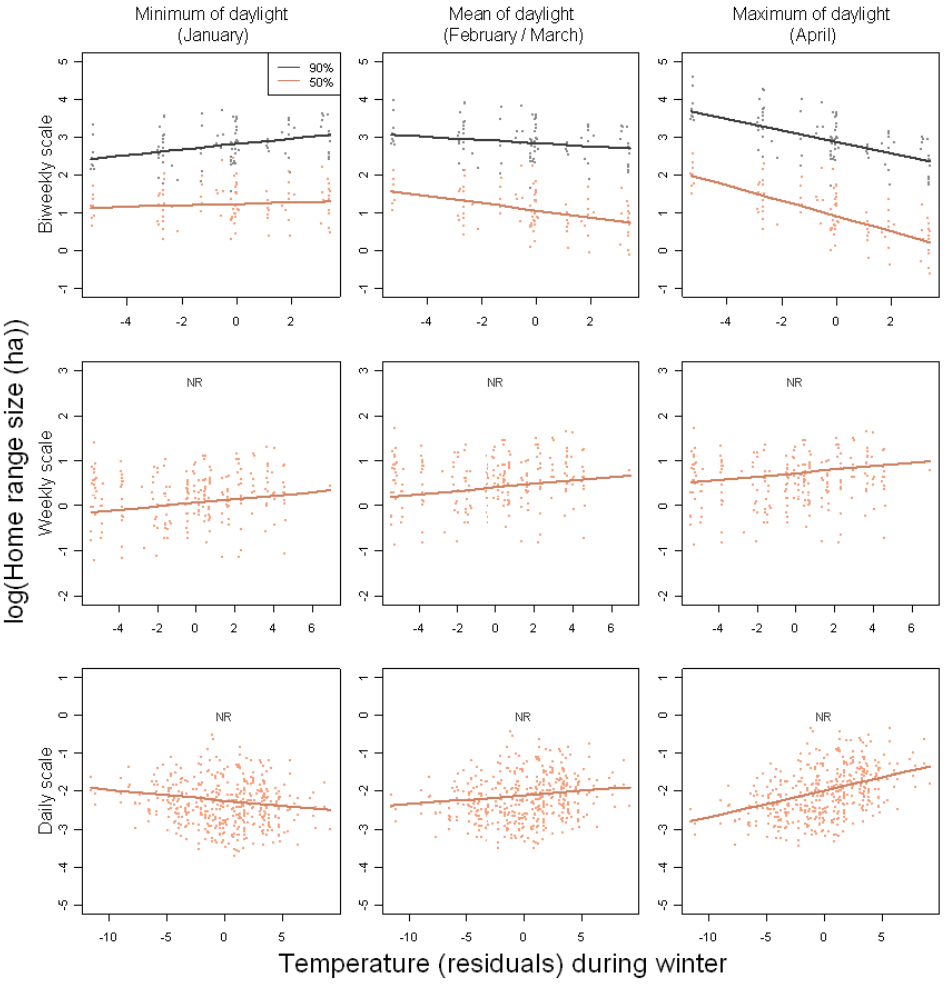


Figure S9: Plot of predicted log-transformed home range sizes (ha) in relation to snow depth (residuals of a regression against Julian day) of moose in southern Norway. Estimates (mean values) are given for all temporal scales during winter. Lines show predicted values for 90% and 50% isopleths and points in corresponding colours are raw residuals. Predictions for snow depth were made while keeping other variables retained in the model constant at their mean value. NR = not retained in final models.

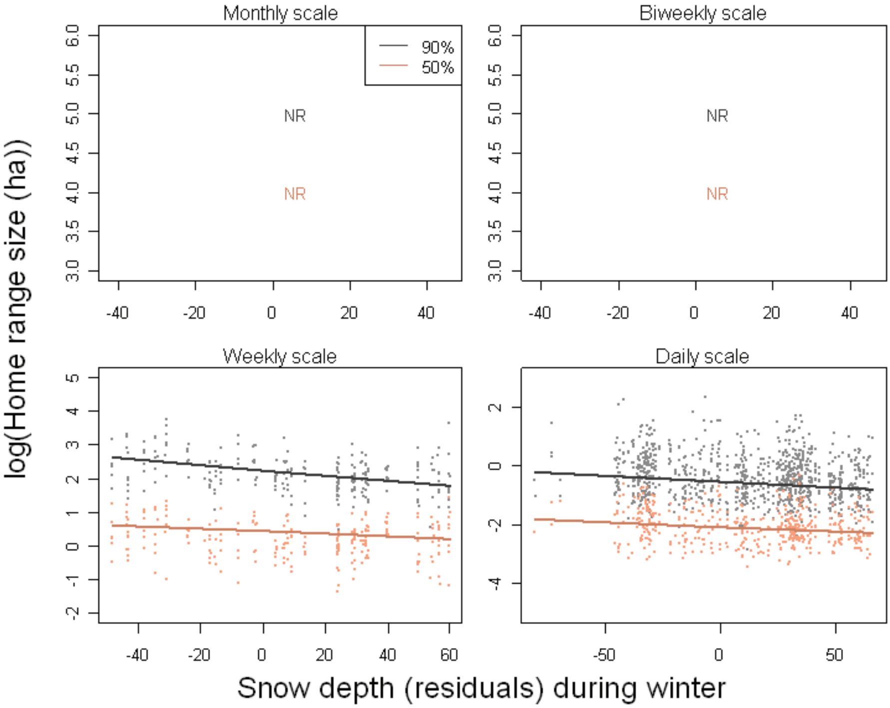
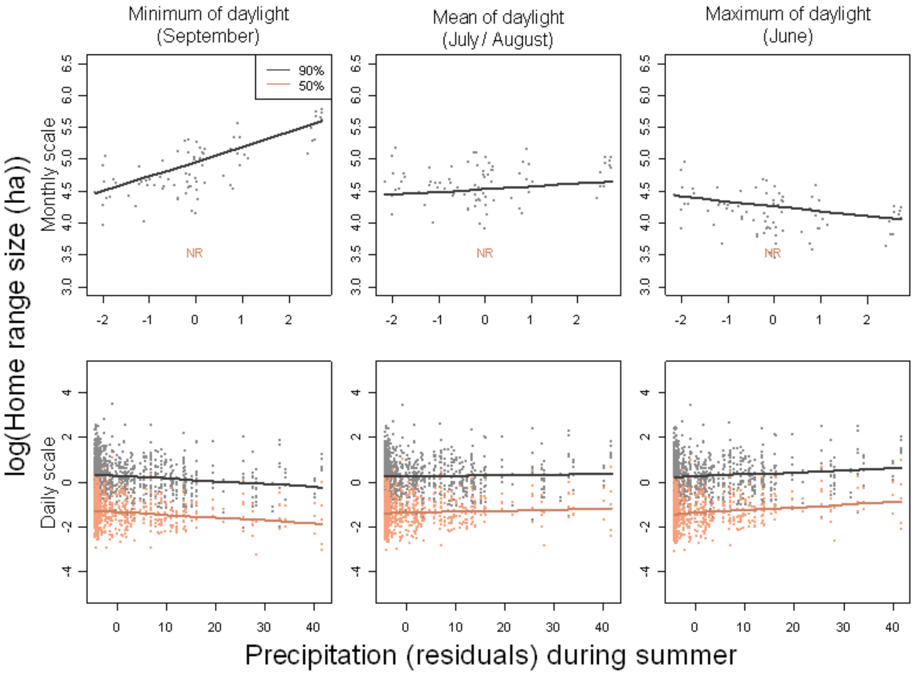


Figure S10: Plot of predicted log-transformed home range sizes (ha) in relation to precipitation (residuals of a regression against Julian day) of moose in southern Norway. Estimates are given for monthly and daily scales during summer, and for the minimum, mean and maximum value of daylight, corresponding to September, July/August and June respectively. Predictions for precipitation were made while keeping other variables retained in the model constant at their mean value. Lines show predicted values for 90% and 50% isopleths and points in corresponding colours are raw residuals. NR = not retained in final models.



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Long-term browsing impact around diversionary feeding stations for moose in Southern Norway

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ABSTRACT

Diversionary winter feeding of browsing ungulates is an increasingly common management practice although evidence for its efficacy to reduce excessive browsing remains ambiguous. Moreover, comparative estimates on changes in browsing pressure (proportion of available shoots browsed) following long-term winter feeding are currently lacking. We quantified spatiotemporal changes in browsing pressure of moose (*Alces alces* L.) on commercial and non-commercial tree species around 30 feeding stations after 15–20 years of winter feeding. The results were compared with browsing pressure indices recorded at the same feeding stations 10 years previously. We expected leader stem and lateral twig browsing to have increased over time at a fine spatial scale ($\leq$200 m from feeding station) and to have increased in spatial extent away from feeding stations. Furthermore, we tested whether moose browsing patterns conformed to central-place foraging theory. Despite 2–3-fold higher faecal pellet group numbers in the vicinity of feeding stations, leader stem browsing increased only on the commercially valuable Norway spruce (*Picea abies* (L.) Karst), a species normally avoided by moose. Lateral twig browsing largely decreased within 200 m of feeding stations while at a broader scale ($\leq$1 km from feeding stations), leader stem browsing was high on most tree species (ca. 60% of available stems browsed) as expected, Peak browsing on lateral twigs of Scots pine (*Pinus sylvestris* L.) occurred further from feeding stations after 15–20 years of winter feeding than 10 years earlier. Browsing pressure on active feeding stations ($n = 18$) was comparable to that on inactive feeding stations ($n = 12$), suggesting the occurrence of rebrowsing. The ability of central-place foraging theory to explain fine-scale browsing patterns around feeding stations decreased as diversionary feeding continued over time. Long-term diversionary winter feeding of moose in unproductive boreal forests has serious implications for the intensity of fine-scale browsing pressure, which may lead to resource depletion close to feeding stations followed by high browsing pressure at distances further away from feeding stations. Our study emphasizes the importance of considering the longevity of a winter feeding programme at its inception.

1. Introduction

Populations of browsing herbivores, including moose (*Alces alces*), have been expanding and increasing in density across Europe and North America in recent decades (Solberg et al., 1999; Côte et al., 2004; Milner et al., 2006), with consequences for forest ecosystems (Motta, 1996; Hornberg, 2001; Rooney, 2001). Intense browsing by deer is widely regarded as a problem in forest regeneration (Reimoser and Gossow, 1996; Bergqvist et al., 2003) as it impedes tree growth and survival (Welch et al., 1992; Vila et al., 2003; Persson et al., 2005) and lowers timber quality (e.g. leader stem browsing; Gill, 1992; Bergqvist et al., 2001). Throughout Scandinavia, the main conflict between forestry interests and moose concerns recurrent browsing on commercially valuable young Scots pine (*Pinus sylvestris*) stands during winter (Danell et al., 1991b; Edenius, 1993; Ball and Dahlgren, 2002; Bergqvist et al., 2003; Kalen and Bergquist, 2004). The impact on young trees can be severe where local moose densities are high (Lavsund, 1987; Andren and Angelstam, 1993). Attempts have been made to control excessive forest browsing by reducing moose densities locally (Lavsund et al., 2003) but the effects of culling have been controversial (Côte et al., 2004).

An alternative and increasingly common wildlife management practice is to provide supplementary food for game animals (Smith,

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2001; Peek et al., 2002; Putman and Staines, 2004). The main goals of supplementary feeding are to increase body weight, survival rate, and reproductive performance in order to maintain high population densities (see Putman and Staines, 2004 for a detailed review). However, feeding may also be carried out to control or reduce environmental damage, particularly to agriculture, forestry and habitats of high conservation value, or to reduce animal–vehicle collisions. The rationale behind such feeding (diversionary feeding), is to divert animals away from, e.g. major traffic arteries, young forest stands or other valuable habitats via the provision of an alternative strategically placed food source (Putman and Staines, 2004; van Beest et al., 2010). Various studies have shown that feeding stations can serve as attraction points and that regular feeding of cervids may restrict space use to the vicinity of feeding stations (e.g. roe deer (*Capreolus capreolus*): Guillet et al., 1996; white-tailed deer (*Odocoileus virginianus*): Doenier et al., 1997; Kilpatrick and Stober, 2002). van Beest et al. (2010) showed how moose that used diversionary forage in a commercial forest in southern Norway concentrated their movements within 1 km of feeding stations, with a decreasing probability of using habitat further away, as expected from central-place foraging theory (Orians and Pearson, 1979). In contrast, moose that did not use feeding stations were most likely to select areas at distances >1500 m from feeding stations.

Diversionary feeding has the potential to reduce cervid–vehicle collisions (Wood and Wolfe, 1988; Gundersen et al., 1998; Andreassen et al., 2005), however, its efficacy in decreasing forest damage remains equivocal and appears to depend, among other things, on the animal species and the spatial and temporal scales under investigation (Sullivan and Klenner, 1993; Gundersen et al., 2004; Ziegltrum, 2004; van Beest et al., 2010). Browsing ungulates that receive supplementary forage frequently continue to forage on natural vegetation, which can cause excessive browsing, especially in the vicinity of feeding stations (Schmitz, 1990; Doenier et al., 1997; Gundersen et al., 2004; Putman and Staines, 2004; Cooper et al., 2006). Although the extent of such heavily utilized browsing zones (i.e. sacrifice areas that are of reduced economical value to commercial timber production) has been documented in the past (Doenier et al., 1997; Gundersen et al., 2004), their dynamics over time as diversionary feeding continues is not known.

The aim of this study is to assess moose browsing pressure, quantified by the proportion of available leader stems and lateral twigs browsed around winter feeding stations, after 15–20 years of use and to compare the intensity and scale of browsing with that observed 10 years earlier (Gundersen et al., 2004). If long-term diversionary feeding has no effect on fine-scale movement and foraging behavior of moose then browsing pressure around feeding

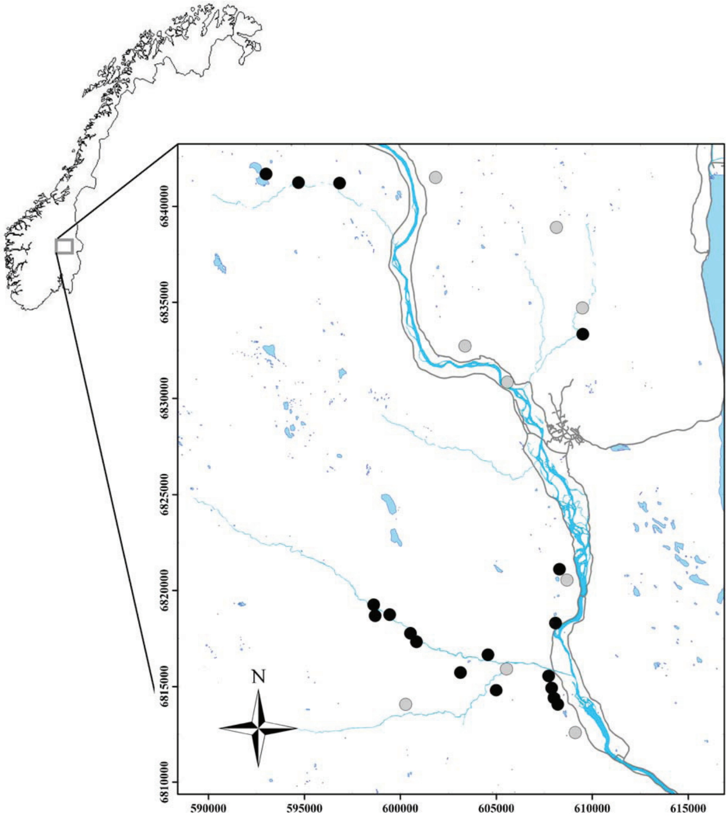

Fig. 1. Map of the study area in southeast Norway with *x*- and *y*-coordinates given every 5 km using the Universal Transverse Mercator (UTM) coordinate system (UTM zone 32N). The map shows the spatial distribution of feeding stations ($n = 30$), lakes, rivers and major roads. Circles indicate feeding stations that were active ($n = 18$, black) or inactive ($n = 12$, grey) during winter 2007–2008.

Table 1
Species-specific overview of (A) the mean number of all trees above 0.5 m present within sampling plots (50 m^2), and (B) the mean height of all trees sampled (within the height range 0.5–3 m) per distance from feeding station in 1998 and 2008 in Stor-Elvdal, Norway.

Variable	Distance from feeding station (m)	RAW species group		Birch species		Scots pine		Norway spruce	
		1998	2008	1998	2008	1998	2008	1998	2008
(A) Number of trees present	12.5	6.3	6.7	11.0	10.2	2.4	4.7	5.8	6.1
	25	6.9	5.5	14.5	7.1	3.1	5.3	4.8	6.6
	50	8.9	9.3	10.5	8.4	1.3	9.2	4.2	5.6
	100	12.3	5.0	6.1	6.7	1.8	4.8	3.7	8.4
	200	7.0	5.1	8.9	10.6	2.3	3.4	3.8	5.9
	500	–	1.5	–	6.5	–	4.5	–	7.2
	1000	–	2.7	–	5.9	–	5.0	–	7.6
(B) Height (m) of sampled trees	12.5	1.20	0.86	1.36	1.19	1.27	0.74	1.23	1.20
	25	1.35	0.83	1.53	1.73	0.97	0.83	1.74	1.34
	50	1.12	1.17	1.76	1.22	1.34	0.94	1.79	1.53
	100	1.12	0.93	1.55	1.58	1.33	0.85	1.94	1.81
	200	1.01	1.23	1.41	1.34	1.37	1.09	1.91	1.65
	500	–	1.05	–	1.59	–	1.22	–	2.06
	1000	–	0.79	–	1.60	–	1.32	–	2.07

stations should remain constant across spatiotemporal scales (H_0). Alternatively, if feeding stations act as focal attraction points (van Beest et al., 2010) which may intensify the use of habitat close to feeding stations (Peek et al., 2002; Cooper et al., 2006; Luccarini et al., 2006) then fine-scale browsing pressure should increase across spatial and temporal scales (H_{A1}). Moreover, browsing patterns should conform to central-place foraging theory, with a declining probability of use of locations with increasing distance from the focal point (Schoener, 1979; Rosenberg and McKelvey, 1999), in this case a feeding station (H_{A2}). To test hypothesis H_{A1} we predict (P_1): the intensity of moose browsing around feeding stations to have increased over time (higher proportion of browsed leader stems and lateral twigs ≤200 m from feeding stations than 10 years earlier) and (P_2): a high occurrence of intense moose browsing beyond 200 m from the feeding stations. To test hypothesis H_{A2} we predict (P_3): browsing pressure to decline with distance from feeding station (decreasing proportion of lateral twigs and leader stems browsed with increasing distance from feeding stations).

2. Methods

2.1. Study area and diversionary feeding

The study area is located in Stor-Elvdal municipality, Hedmark County, southeast Norway (Fig. 1) and ranges in elevation from 250 to 1100 m with the forest line at approximately 800–900 m. The area is dominated by a low-productive, commercially managed, boreal forest with pure or mixed stands of Scots pine and Norway spruce (*Picea abies*). In addition, deciduous species such as birch (*Betula pubescens* Ehrh. and *B. pendula* Roth.), rowan (*Sorbus aucuparia* L.), willow (*Salix* spp.) and aspen (*Populus tremula* L.) occur at low densities throughout the area. Mean temperature and snow-depth at 240 m during November–April 1997–1998 were −3.2 °C and 30.2 cm, respectively, and −2.5 °C and 52.7 cm during November–April 2007–2008 (Haugedalen weather station in the same coniferous forest approximately 35 km south of the study area; Norwegian Meteorological Institute; http://www.eklima.met.no). The cervid community in the municipality is dominated by moose (>1.1 moose/km^2 during winter; Gundersen et al., 2008) with very low densities of roe deer (*Capreolus capreolus* L.) and red deer (*Cervus elaphus* L.).

Diversionary feeding of moose was initiated in the late 1980s by local landowners with the aim of reducing moose-vehicle collisions (Andreassen et al., 2005). The supplemental food consists of baled roughage, predominantly mixed graminoids, and one bale of silage weighs ~600 kg. Feeding stations are located at fixed (permanent) sites along forest roads with low human activity. The supplemental food is provided *ad libitum* for up to 6 months of the year (i.e. November through April, with starting and ending time depending on annual snow conditions). The total amount of supplemental food provided at feeding stations increased greatly over the last decade with ~150 ton (across 44 feeding stations) during winter 1997–1998 and ~1700 ton (across 157 feeding stations) during winter 2007–2008.

2.2. Quantifying browsing pressure

In Scandinavia, the winter diet of moose is typically composed of twigs of Scots pine and various deciduous tree species (Hornberg, 2001; Månsson et al., 2007). The tree species considered in this study (i.e. target species) were: rowan, aspen, several willow species, silver birch, downy birch and the

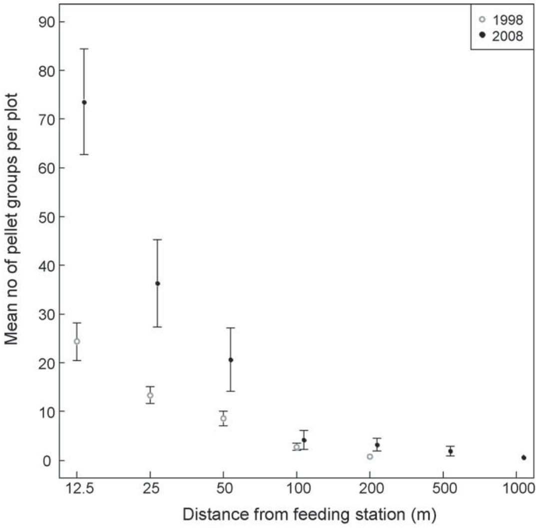

Fig. 2. Mean (and 95% CI) number of moose pellet groups per plot (50 m^2) at increasing distance from feeding stations after winter 1997–1998 (open grey circles) and 2007–2008 (black circles). In 1998 pellet groups were only counted up to 200 m.

commercially harvested species Scots pine and Norway spruce. Although Norway spruce is not a preferred forage species of moose (Cederlund et al., 1980; Hornberg, 2001; Kalen and Bergquist, 2004) it was included because of previously observed leader stem browsing in the vicinity of feeding stations (Gundersen et al., 2004).

Gundersen et al. (2004) quantified moose browsing pressure on Scots pine and Norway spruce around 30 feeding stations during spring 1998 using circular sampling plots of 50 m^2 located at 12.5, 25, 50, 100, 200 m from feeding stations (for methodological details see Gundersen et al., 2004). To evaluate temporal changes in browsing pressure (P_1), we recorded browsing pressure around the same feeding stations at the same distances during spring 2008. Furthermore, as browsing is expected to have expanded spatially over time (P_2), additional browse surveys were carried out at 500 and 1000 m from feeding stations. Sampling plots were established along 2 transects radiating out from the center of each feeding station in a random direction at a minimum of 25° from each other. With this design 14 plots were established around each station with a total of 420 plots sampled across the study area. Use of habitat by moose was estimated by counting faecal pellet groups (Ball and Dahlgren, 2002; Palmer and Truscott, 2003). Pellet groups from the previous winter were distinguished from older pellets by color, texture and position relative to litter and old vegetation (Neff, 1968). Furthermore, we recorded the total number of alive trees of all species present ($\geq$0.5 m high) within each plot. Trees <0.5 m high were assumed to be unavailable to moose during winter due to snow cover. An overview of tree numbers and average height of target species per sampling plot and distance are given in Table 1. For each target species present in a plot, one tree was selected, based on the average height of that particular species within a plot, and we recorded: (i) presence/absence of leader stem browsing during previous winter, (ii) the number of lateral twigs available within moose browse height (0.5–3 m: Danell et al., 1985), and (iii) the number of lateral twigs browsed during the previous winter. The same measurements were taken in 1998, except that presence/absence of leader stem browsing was only recorded for Scots pine and Norway spruce (Gundersen et al., 2004). Last winter's browsing was separated from earlier browsing by color and moisture on the bitten edge of the twigs.

2.3. Statistical analysis

Species-specific browsing pressure around feeding stations was modeled with generalized additive mixed models (GAMMs) using the library mgcv (Wood, 2006) implemented in R (R Development Core Team, 2008). GAMMs provide a flexible framework to model species-habitat relationships (Aarts et al., 2008). Explanatory variables, with expected non-linear effects, can be fitted as parametric or non-parametric smoothing terms and moreover, variables can be modeled as random effects (see Augustin et al., 2007; Musio et al., 2007 for applications in forestry).

Leader stem and lateral twig browsing around feeding stations were modeled separately for each target species using a logistic

Table 2

Parameter estimates of species-specific GAMM models predicting leader stem browsing by moose up to 200 m from feeding stations in 1998 and 2008 in Stor-Elvdal, Norway. The models include a random intercept for transect ID within feeding station ID. The models form the analytical basis for Fig. 3. Sample size (no. of trees) for Scots pine = 167, Norway spruce = 331; RAW species group = 53; and Birch species = 158.

Model species	Parametric coefficients	Estimate	S.E.	*t*-value	*p*-value
Scots pine	Intercept	0.269	0.431	0.625	0.533
	Year (2008)	−0.379	0.362	−1.049	0.296
	Active (Yes)	0.651	0.541	1.204	0.231
	Smooth terms	edf	Est. rank	*F*-value	*p*-value
	s(Distance = 1998)	1	1	8.49	0.004
	s(Distance = 2008)	1	1	0.56	0.461
		N	Std. Dev.	Residual	
	Random intercept	83	<0.001	0.931	
Norway spruce	Intercept	−4.584	0.669	−6.852	<0.001
	Year (2008)	2.832	0.58	4.879	<0.001
	Active (Yes)	1.292	0.439	2.941	0.003
	Smooth terms	edf	Est. rank	*F*-value	*p*-value
	s(Distance = 1998)	1	1	9.61	0.002
	s(Distance = 2008)	1	1	3.44	0.064
		N	Std. Dev.	Residual	
	Random intercept	150	0.214	0.881	
RAW species	Intercept	1.542	0.680	2.27	0.027
	Year (2008)	–	–	–	–
	Active (Yes)	0.392	0.859	0.46	0.650
	Smooth terms	edf	Est. rank	*F*-value	*p*-value
	s(Distance = 1998)	–	–	–	–
	s(Distance = 2008)	1	1	1.53	0.221
		N	Std. Dev.	Residual	
	Random intercept	26	<0.001	1.009	
Birch species	Intercept	0.426	0.433	0.99	0.326
	Year (2008)	–	–	–	–
	Active (Yes)	0.752	0.530	1.42	0.158
	Smooth terms	edf	Est. rank	*F*-value	*p*-value
	s(Distance = 1998)	–	–	–	–
	s(Distance = 2008)	1	1	0.03	0.855
		N	Std. Dev.	Residual	
	Random intercept	79	0.859	0.920	

link function and binomial error distribution. Due to low sample size for rowan, aspen and willow species we pooled these and created one model (RAW species group), as is typical in Scandinavian moose browse surveys (Solbraa, 2003). For the same reason, silver birch was grouped together with downy birch (Birch species). The response variable in all models was 'browsed' (1 = yes, 0 = no) and the following predictor variables were fitted: 'year' (2 class factor; 1998–2008) and 'active' (2 class factor; feeding station (FS) used in winter 2007–2008 (active; $n = 18$) – FS not used in winter 2007–2008 (inactive; $n = 12$)) which incorporates potential differences in browsing pressure between feeding stations that were used by moose during winter 1997–1998 but were not operational during winter 2007–2008 and those that were operational throughout the period. 'Distance from feeding station' was included as a smoothing function with the optimal smooth curve estimated by the generalized cross-validation procedure (Wood, 2006) with an upper bound set at 4 knots (3 df). The smoothing function was included for each year separately to allow browsing estimates to vary non-linearly over time and space. To test P_1, all sampling plots from 1998 and those up to 200 m from feeding stations in 2008 were included in the analyses, so quantifying temporal differences in browsing pressure explicitly. To test P_2, all sampling plots (up to 1000 m from feeding stations) from 2008 only were analyzed. We used $\alpha = 0.05$ to evaluate significant relations between the dependent and independent variables throughout. To control for potential dependencies at higher levels than the plot level and to account for unbalanced sampling design within transects across feeding stations (Gillies et al., 2006; Aarts et al., 2008) we included transect ID nested within feeding station ID as a random intercept for the leader stem browsing analyses. Lateral twig browsing was analyzed with plot ID nested within transect ID within feeding station ID. Models that did not converge using a random intercept were analyzed using GAM (i.e. lateral twig browsing Norway spruce).

3. Results

3.1. Moose utilization of sites around feeding stations

The mean number of moose pellet groups per sampling plot (50 m^2) in the vicinity of feeding stations ($\leq$50 m distance) was considerably higher in 2008 compared to 1998 (Fig. 2), with a 3-fold increase at 12.5 and 25 m from feeding stations and a 2-fold increase at 50 m from feeding stations. At distances more than 50 m from feeding stations the mean number of pellet groups per plot remained similar between years (overlap between 95% confidence intervals) with few pellet groups observed at 500 m and 1000 m distances in 2008.

3.2. Temporal changes in browsing pressure

The proportion of Scots pine leader stems browsed up to 200 m from feeding stations did not differ between years ($p = 0.296$) but decreased with increasing distance from feeding stations only in 1998 ($p = 0.004$: Table 2; Fig. 3). Norway spruce leader stem browsing decreased with increasing distance from feeding stations in both years (non-significant trend in 2008: $p = 0.064$) but

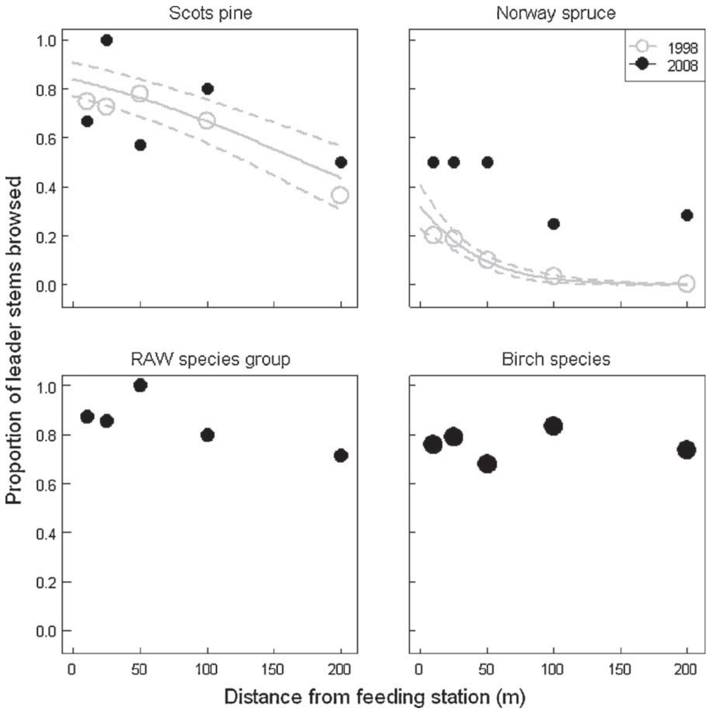

Fig. 3. Proportion of leader stems browsed for each target species up to 200 m from active feeding stations in 1998 (grey lines and circles) and 2008 (black lines and circles). The plotted raw data points are the mean proportion of leader stems browsed in five distance classes (12.5, 25, 50, 100, and 200 m). The area of the circles is proportional to the amount of data in each distance class. Solid lines represent the mean predicted values and dashed lines the 95% confidence limits (see model estimates in Table 2). Leader stem browsing on RAW species and birch species was not recorded in 1998.

browsing pressure was significantly higher in 2008 compared to 1998 ($p < 0.001$). Leader stem browsing on RAW species and birch species was not recorded in 1998, while in 2008 the proportion of leader stems browsed on both deciduous species groups was consistently high (>60%) regardless of distance from feeding station (Table 2; Fig. 3).

The proportion of lateral twigs browsed up to 200 m from feeding stations was significantly lower in 2008 than in 1998, across all species except Norway spruce (Table 3; Fig. 4). Lateral twig browsing on Norway spruce was absent in 1998, while approximately 10% of the available twigs were browsed at 50 m from feeding stations in 2008 (Fig. 4). Lateral twig browsing was significantly higher at active than inactive feeding stations on Norway spruce and birch species ($p < 0.001$) but not on Scots pine ($p = 0.089$) or RAW species ($p = 0.685$: Table 3). The proportion of Scots pine lateral twigs browsed within 200 m of feeding stations decreased with distance from feeding station in 1998 ($p < 0.001$) and varied non-linearly in 2008 ($p = 0.035$). Lateral twig browsing on the RAW species group decreased with increasing distance from feeding station in 1998 ($p = 0.011$) but not in 2008 ($p = 0.312$). The proportion of birch species lateral twigs browsed decreased with distance from feeding station in both years (Table 3; Fig. 4).

3.3. Spatial development of browsing pressure

The proportion of Scots pine leader stems browsed during winter 2007–2008 did not decrease significantly as distance from feeding stations increased ($p = 0.571$; Table 4), and remained at ~60% up to 1000 m from feeding stations. However, there was considerable between-station variation within 200 m of feeding stations (Fig. 5). Furthermore, Scots pine leader stem browsing did not differ between active and inactive feeding stations ($p = 0.176$; Table 4). A similar pattern of leader stem browsing as a function of distance from feeding station was observed for the RAW species group ($p = 0.422$; ~90% browsed up to 1000 m) and birch species ($p = 0.225$: ~70% browsed up to 1000 m). Leader stem browsing on the deciduous species did not differ significantly between active and inactive feeding stations ($p = 0.778$ and $p = 0.139$ for RAW species group and birch, respectively; Table 4). Contrastingly, leader stem browsing on Norway spruce trees decreased with distance from feeding stations ($p = 0.001$: ~50% browsed at 50 m and 0% browsed at 1000 m) and was significantly higher at active feeding stations compared to inactive stations ($p = 0.023$: Table 4; Fig. 5).

Browsing pressure on lateral Scots pine twigs during winter 2007–2008 varied non-linearly with distance from feeding station ($p < 0.001$: Table 5) with peak browsing pressure at 600 m from feeding stations (Fig. 6). Lateral twig browsing on Norway spruce trees decreased with increasing distance from feeding stations but remained below 10% throughout. Browsing on RAW species lateral twigs did not decrease with distance from feeding stations ($p = 0.122$) in contrast to birch species twigs ($p < 0.001$). Browsing pressure on lateral twigs of Norway spruce and birch trees was higher around feeding stations that were actively used during winter 2007–2008 compared to inactive feeding station ($p < 0.001$ and $p = 0.002$, respectively), but this was not the case for browsing on Scots pine twigs and the RAW species group (Table 5; Fig. 6).

Table 3
Parameter estimates of species-specific GAMM models predicting lateral twig browsing by moose up to 200 m from feeding stations in 1998 and 2008 in Stor-Elvdal, Norway. The models include a random intercept for plot ID within transect ID within feeding station ID. The models form the analytical basis for Fig. 4. Sample size (no. of twigs) for Scots pine = 4419, Norway spruce = 64793; RAW species group = 1602; and Birch species = 17793.

Model species	Parametric coefficients	Estimate	S.E.	*t*-Value	*p*-Value
Scots pine	Intercept	−1.654	0.316	−5.231	<0.001
	Year (2008)	−1.675	0.403	−4.149	<0.001
	Active (yes)	0.669	0.394	1.701	0.089
	Smooth terms	edf	Est. rank	*F*-value	*p*-Value
	s(Distance = 1998)	1	1	14.88	<0.001
	s(Distance = 2008)	1.614	3	2.854	0.035
		N	Std. dev.	Residual	
	Random intercept	151	0.724	0.899	
Norway spruce	Intercept	−9.057	0.323	−28.08	<0.001
	Year (2008)	–	–	–	–
	Active (yes)	4.974	0.3196	15.56	<0.001
	Smooth terms	edf	Est. rank	χ^2	*p*-Value
	s(Distance = 1998)	–	–	–	–
	s(Distance = 2008)	2.994	3	565.3	<0.001
RAW species	Intercept	−0.956	0.386	−2.48	0.013
	Year (2008)	−0.794	0.228	−3.48	<0.001
	Active (yes)	−0.179	0.443	0.405	0.685
	Smooth terms	edf	Est. rank	*F*-value	*p*-Value
	s(Distance = 1998)	1	1	6.43	0.011
	s(Distance = 2008)	1.34	3	1.19	0.312
		N	Std. dev.	Residual	
	Random intercept	131	0.559	0.907	
Birch species	Intercept	−2.595	0.251	−10.353	<0.001
	Year (2008)	−0.462	0.171	−2.712	0.006
	Active (yes)	1.165	0.293	3.971	<0.001
	Smooth terms	edf	Est. rank	*F*-value	*p*-Value
	s(Distance = 1998)	1	1	45.37	<0.001
	s(Distance = 2008)	1.9	3	6.72	<0.001
		N	Std. dev.	Residual	
	Random intercept	453	1.022	0.901	

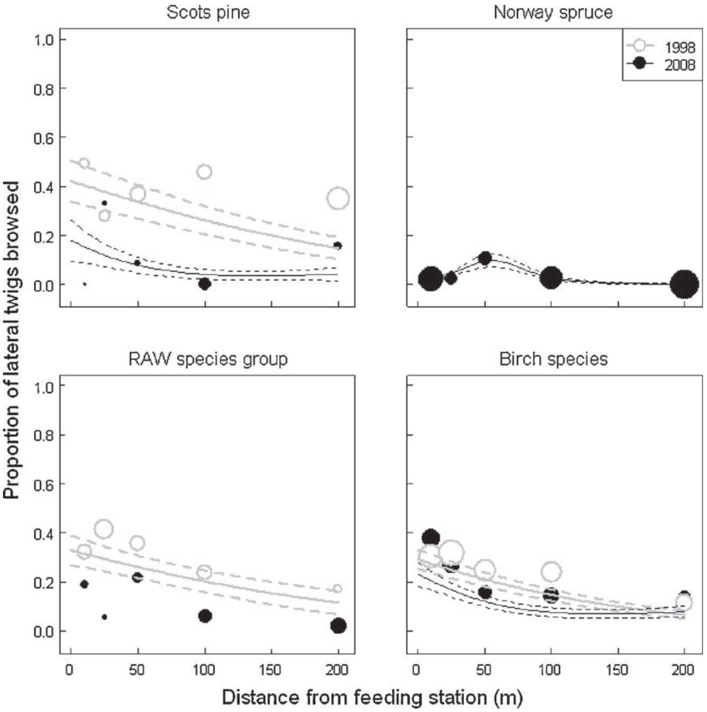

Fig. 4. Proportion of lateral twigs browsed for each target species up to 200 m from active feeding stations in 1998 (grey lines and circles) and 2008 (black lines and circles). The plotted raw data points are the mean proportion of lateral twigs browsed in five distance classes (12.5, 25, 50, 100, and 200 m). The area of the circles is proportional to the amount of data in each distance class. Solid lines represent the mean predicted values and dotted lines the 95% confidence limits (see model estimates in Table 3). Lateral twig browsing on Norway spruce trees was absent in 1998.

4. Discussion

The results presented here indicate that providing large herbivores with additional winter food on a long-term basis may have serious implications for the intensity of fine-scale browsing pressure and the spatial extent of forest damage. We found browsing pressure around diversionary feeding stations to increase across spatiotemporal scales (rejecting H_0). Moose used sites around feeding stations more heavily after 15–20 years of feeding than after 5–10 years, fulfilling our key assumption, yet the expected increase in browsing pressure in the vicinity ($\leq$200 m) of feeding stations (P_1), was only observed in Norway spruce, a species generally not eaten by moose (Bergstrom and Hjeljord, 1987; Hornberg, 2001; Kalen and Bergquist, 2004). At a broader spatial scale, we found high browsing pressure on both leader stems and lateral twigs for most target species, as expected (P_2). Browsing pressure on all target species decreased with increasing distance from feeding stations in 1998 as expected from central-place foraging theory. However, after 10 years of additional winter feeding (2008) the relationship between browsing pressure and distance from feeding stations was more complex (non-linear) and the expected decrease in browsing pressure was absent for palatable species (P_3).

4.1. Temporal changes in browsing pressure

Contrary to our expectation (P_1) we found no difference in leader stem browsing for Scots pine at distances $\leq$200 m from feeding stations when the time frame of diversionary feeding increased from 5–10 years to 15–20 years. This result may be influenced by the already high browsing incidence, ca. 70%, at 5–10 years after feeding stations were established, perhaps approaching the proportion of leader stems that are easily available and attractive to the moose. By contrast, and in accordance with P_1, leader stem browsing of Norway spruce did increase over time. Previous reports of moose browsing on Norway spruce in northern Europe are few and generally illustrate a sudden increase in localized bark stripping and browsing of lateral twigs (Randveer and Heikkila, 1996; Faber and Pehrson, 2000). These studies proposed that high moose densities coinciding with a reduced availability of more preferred browse species are important causes for moose to include the least preferred but abundant Norway spruce into their diet. The temporal increase in Norway spruce browsing in the vicinity of feeding stations might also be attributed to a high demand for natural browse or roughage to balance the intake of the artificially supplied forage (Doenier et al., 1997).

Browsing pressure on lateral twigs decreased rather than increased close to the feeding stations, particularly on Scots pine, in contrast to P_1. Browsing pressure was defined and calculated as the proportion of the available twigs bitten during the last winter, but we did not record the size of the available twigs. We suggest that intense browsing over a long time period (15–20 years) has caused a decrease in size and/or nutritious quality of shoots, leading to a reduced acceptability to moose (Price, 1991). Repeated browsing is known to negatively affect tree productivity

Table 4

Parameter estimates of species-specific GAMM models predicting leader stem browsing by moose up to 1000 m from feeding stations in 2008 in Stor-Elvdal, Norway. The models include a random intercept for transect ID within feeding station ID. The models form the analytical basis for Fig. 5. Sample size (no. of trees) for Scots pine = 86, Norway spruce = 136; RAW species group = 62; and Birch species = 192.

Model species	Parametric coefficients	Estimate	S.E.	*t*-Value	*p*-Value
Scots pine	Intercept	−0.293	0.543	−0.54	0.590
	Active (yes)	1.005	0.737	1.364	0.176
	Smooth terms	edf	Est. rank	*F*-value	*p*-Value
	s(Distance = 2008)	1	1	0.323	0.571
		N	Std. dev.	Residual	
	Random intercept	43	1.485	0.793	
Norway spruce	Intercept	−2.546	0.602	−4.227	<0.001
	Active (yes)	1.417	0.616	2.300	0.023
	Smooth terms	edf	Est. rank	*F*-value	*p*-Value
	s(Distance = 2008)	1	1	10.65	0.001
		N	Std. dev.	Residual	
	Random intercept	78	0.922	0.847	
RAW species	Intercept	1.836	0.647	2.84	0.006
	Active (yes)	0.228	0.803	0.28	0.778
	Smooth terms	edf	Est. rank	*F*-value	*p*-Value
	s(Distance = 2008)	1	1	0.65	0.422
		N	Std. dev.	Residual	
	Random intercept	31	<0.001	0.980	
Birch species	Intercept	0.422	0.365	1.158	0.248
	Active (yes)	0.666	0.449	1.483	0.139
	Smooth terms	edf	Est. rank	*F*-value	*p*-Value
	s(Distance = 2008)	1	1	1.48	0.225
		N	Std. dev.	Residual	
	Random intercept	81	0.139	0.945	

(Stroh et al., 2008) and browse availability for herbivores (Edenius, 1993) which can, eventually, lead to forage depletion (Andrew, 1988; Edenius, 1991; Persson et al., 2005; Cooper et al., 2006). In a long-term moose browsing simulation experiment in Sweden, Persson et al. (2005, 2007) showed that production of browse biomass in birch species often increased with moderate to heavy moose browsing, particularly in highly productive habitats, but decreased with the heaviest browsing intensity (5 moose per km^2). Such decrease in browse production due to excessive browsing on birch is associated with reduced size and nutritive quality of shoots (Danell et al., 1985). This finding may correspond with the pattern found for birch around the feeding stations, with decreased browsing pressure over time closest to the stations, due to reduced forage acceptability, and little change further away. Scots pine showed the strongest decrease in browsing pressure in our study. Similarly, Persson et al. (2005, 2007) showed that simulated moose browsing had a consistent negative effect on Scots pine browse production independent of habitat productivity. Scots pine has a fixed growth pattern with little flexibility in shoot production for compensatory growth. Moreover, as an evergreen, Scots pine does not store nutrients in roots or stems as most deciduous species do, but nutrients remain in the needles where they are vulnerable to browsing (Millard et al., 2001). Although, we did not quantify compensatory tree growth in response to moose browsing in our study, it seems probable that the decrease in lateral twig browsing over time observed at distances $\leq$200 m from feeding stations is associated with an overall decrease in shoot size and available twig biomass (i.e. resource depletion) due to intensive browsing over an extended time period (15–20 years). Evidence of induced chemical defense in Scots pine twigs by moose browsing is scarce but the initial differences in acid concentrations between trees may explain why some trees are browsed more than others (Danell et al., 1990).

4.2. Spatial development of browsing pressure

As expected (P_2), browsing pressure on leader stems was high even at 1000 m from feeding station for all species except Norway spruce, suggesting that increasing numbers of moose at the feeding stations leads to an increased radius of the zone with heavy browsing. Furthermore, we found no differences in leader stem browsing between active and inactive feeding stations, except for Norway spruce, which might indicate the occurrence of rebrowsing (Bergqvist et al., 2003; Danell et al., 2003). Correspondingly, we observed high browsing pressure on lateral twigs of the preferred RAW species group at inactive feeding stations, although browsing pressure on birch species and Norway spruce was considerably lower on inactive compared to active feeding stations. Scots pine lateral twig browsing peaked at ca. 600 m from feeding stations, suggesting that this distance provided the closest available Scots pine forage. That lateral twig browsing of Scots pine peaked at the same distance at inactive feeding stations also suggests rebrowsing.

Assessments of spatial changes in browsing impact around animal attractants such as diversionary feeding stations or near physical barriers such as fences may, from a forest-management standpoint, be important for predicting which forest stands are at risk of being severely browsed in the future. Conifer leader stem browsing by deer is considered an important problem to commercial forest management (Bergquist et al., 2009) as it may lead to loss in revenue and profitability due to lower yield, and lower timber quality (Welch et al., 1992). Timber production has long been the main source of revenue from Norwegian forest and remains so even when browsing damage by moose is taken into consideration (Wam et al., 2005; Wam and Hofstad, 2007). Ward et al. (2004) showed that economic losses become evident at leader stem browsing levels of $\geq$55%. In our study, browsing levels on leader stems around active feeding stations were above this

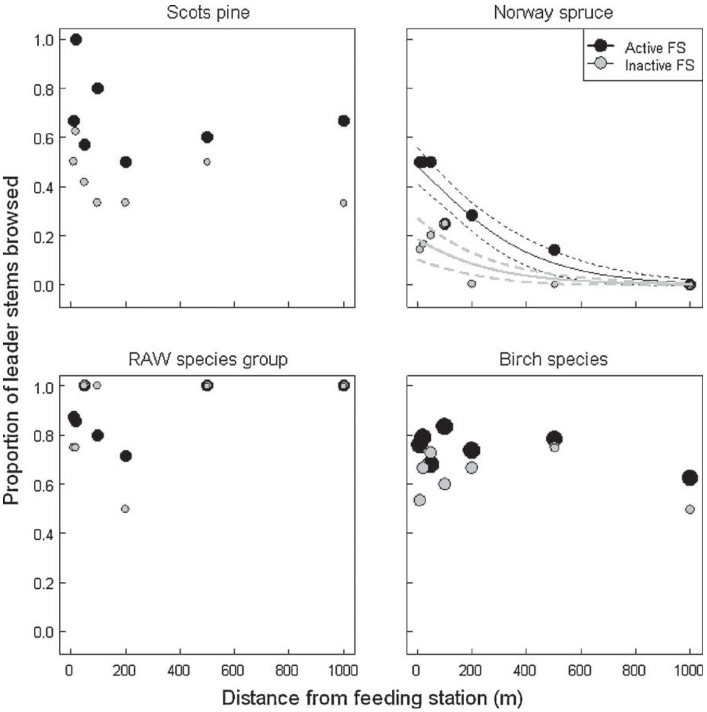

Fig. 5. Proportion of leader stems browsed for each target species up to 1000 m from feeding stations after winter 2008 (black lines and circles = active feeding stations, grey lines and circles = inactive feeding stations). The plotted raw data points are the mean proportion of leader stems browsed in seven distance classes (12.5, 25, 50, 100, 200, 500, and 1000 m). The area of the circles is proportional to the amount of data in each category. Solid lines represent the mean predicted values and dashed lines the 95% confidence limits (see model estimates in Table 4).

proposed threshold even at 1000 m from feeding stations except for Norway spruce. This implies that in forested areas where diversionary feeding of browsing herbivores is practiced for extended periods (i.e. decades), leader stem browsing will increase spatially and may, eventually, impact the profitability of timber in forest stands far from feeding stations.

4.3. Implications of long-term diversionary feeding

The presence of permanent feeding stations is known to restrict seasonal space use patterns of herbivores to the vicinity of feeding stations and may even change the foraging behavior of moose to that of central-place foragers in less than 10 years of diversionary feeding (van Beest et al., 2010). In agreement and as expected by P_3, we observed a negative relationship between browsing pressure and distance from feeding station in 1998 (after 5–10 years of feeding) for all species and for both leader stem and lateral twig browsing (Figs. 3 and 4). However, after 10 years of additional winter feeding (in 2008), browsing pressure at the same spatial scale ($\leq$200 m from feeding stations) was no longer negatively correlated with distance from feeding station for most target species in contrast to expectations from central-place foraging theory. Moreover, when assessing browsing pressure at a slightly larger scale ($\leq$1 km from feeding stations in 2008), browsing pressure decreased only on Norway spruce leader stems (Fig. 5) and on the lateral twigs of deciduous species (Fig. 6). This apparent inconsistency between leader stem browsing patterns in 2008 and our expectation based on central-place foraging theory (P_3) could be an artifact of our sampling design (i.e. the absence of sampling plots at distances >1 km from feeding stations) or a general increase in landscape-level browsing pressure. There is some evidence, from a different area in southern Norway, that browsing pressure on Scots pine leader stems can remain constant up to 4 km from feeding stations (80% of available leader stem browsed) before decreasing to 20% at 6 km from feeding stations (Tange, 2007). More evidence is needed to evaluate the effect of long-term diversionary feeding on changes in browsing pressure at the landscape-scale. Furthermore, the discrepancy between central-place foraging theory and lateral twig browsing might be confounded by the depletion of lateral twig biomass following long-term browsing pressure as discussed above. This suggests that the potential of central-place foraging theory to successfully predict foraging behavior of browsing herbivores and concomitant forest damage around feeding stations declines as winter feeding continuous over time. Nevertheless, the observed browsing patterns in 2008 do, to some extent, support central-place foraging theory in terms of variation in species-specific browsing pressure as a function of distance from feeding stations. For example, central-place foragers are expected to increase selection of preferred forage resources at greater distances from the focal point compared to lower ranked species (Schoener, 1979; Rosenberg and McKelvey, 1999). Indeed, browsing pressure on leader stems of the preferred RAW species was high at 1 km from feeding stations (100% of available stems browsed), lower for medium preference species (60% of Scots pine and birch species) and completely absent for the least preferred Norway spruce (Fig. 5).

During this study we had no control over the spatial positioning of the feeding stations which makes it difficult to assess potential

Table 5
Parameter estimates of species-specific GAMM models predicting lateral twig browsing by moose up to 1000 m from feeding stations in 2008 in Stor-Elvdal, Norway. The models include a random intercept for plot ID within transect ID within feeding station ID. The models form the analytical basis for Fig. 6. Sample size (no. of twigs) for Scots pine = 1391, Norway spruce = 88867; RAW species group = 845; and Birch species = 9319.

Model species	Parametric coefficients	Estimate	S.E.	*t*-Value	*p*-Value
Scots pine	Intercept	−3.814	0.673	−5.669	<0.001
	Active (yes)	0.459	0.826	0.556	0.578
	Smooth terms	edf	Est. rank	*F*-value	*p*-Value
	s(Distance = 2008)	2.802	3	9.55	<0.001
		N	Std. dev.	Residual	
	Random intercept	80	2.569	0.496	
Norway spruce	Intercept	−14.207	0.584	−24.32	<0.001
	Active (yes)	3.127	0.152	20.61	<0.001
	Smooth terms	edf	Est. rank	χ^2	*p*-Value
	s(Distance = 2008)	2.995	3	431.5	<0.001
RAW species	Intercept	−1.577	0.521	−3.030	0.002
	Active (yes)	−1.042	0.737	−1.414	0.158
	Smooth terms	edf	Est. rank	*F*-value	*p*-Value
	s(Distance = 2008)	1	1	2.399	0.122
		N	Std. dev.	Residual	
	Random intercept	54	1.258	0.633	
Birch species	Intercept	−3.244	0.357	−7.865	<0.001
	Active (yes)	1.253	0.409	3.063	0.002
	Smooth terms	edf	Est. rank	*F*-value	*p*-Value
	s(Distance = 2008)	2.947	3	23.91	<0.001
		N	Std. dev.	Residual	
	Random intercept	162	1.279	0.906	

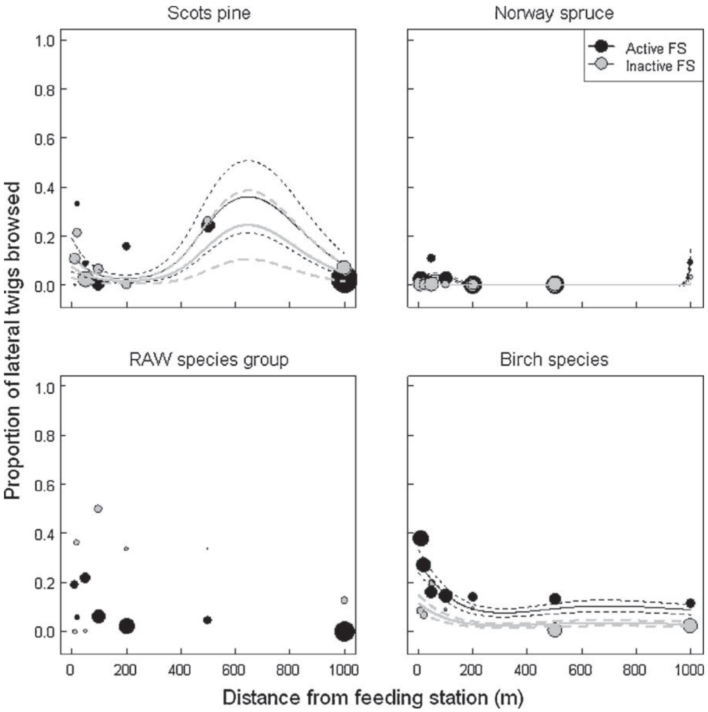

Fig. 6. Proportion of lateral twigs browsed for each target species up to 1000 m from feeding stations after winter 2008 (black lines and circles = active feeding stations, grey lines and circles = inactive feeding stations). The plotted raw data points are the mean proportion of lateral twigs browsed in seven distance classes (12.5, 25, 50, 100, 200, 500, and 1000 m). The area of the circles is proportional to the amount of data in each distance class. Solid lines represent the mean predicted values and dashed lines the 95% confidence limits (see model estimates in Table 5).

confounding effects. For example, site properties are known to affect foraging decisions of moose (Danell et al., 1991a) and browsing pressure on food items may differ between sites within the same region (Suominen et al., 2008). Indeed, the slight misfit between real data points and model predictions for some target species could be due to small scale differences in site properties among feeding stations. Nevertheless, because feeding stations are typically placed in areas where animals are likely to occur (Putman and Staines, 2004), and not at random, our results are useful for applied forest and wildlife management.

5. Conclusion

Browsing ungulates provided with supplemental feed continue to forage on the natural vegetation, creating a gradient in browsing pressure which is typically greatest near the feeding station and decreases as a function of distance from it (Schmitz, 1990; Doenier et al., 1997; Gundersen et al., 2004). Here we have presented clear evidence that as winter feeding continues over time, there is an increased risk of excessive browsing close to feeding stations. Leader stem browsing in particular remained high up to 1 km from feeding stations which can have important economic implications (Ward et al., 2004). Browsing on commercially valuable Norway spruce (a species normally avoided by moose) increased after 15–20 years of diversionary feeding. Central-place foraging theory successfully predicted browsing patterns around feeding stations after 5–10 years of feeding. Long-term winter feeding shifted peak browsing pressure on important winter forage further away from feeding stations due to fine-scale resource limitation, which caused browsing patterns to deviate from central-place foraging theory after 15–20 years of feeding. As such, sacrifice areas around feeding stations will continue to expand over time, which warrants caution against long-term diversionary feeding in fixed locations. Our study emphasizes the importance of considering the appropriate time frame when deciding to initiate winter feeding and can assist in developing more effective feeding programs in areas where both wildlife management and commercial timber production need to produce benefits at the same spatial scale (Wam et al., 2005; Wam and Hofstad, 2007; Visscher and Merrill, 2009).

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