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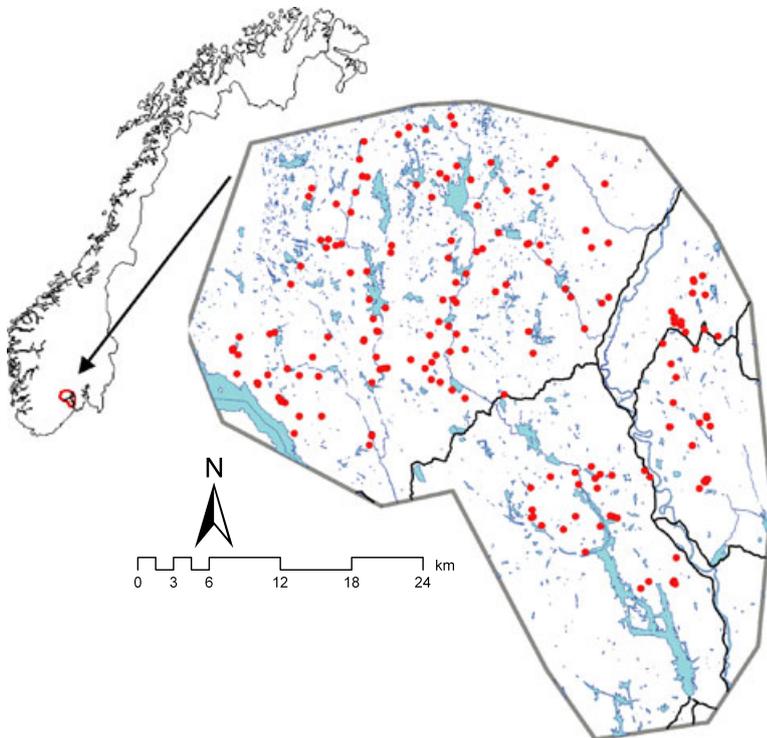
Fig. 1. Map of the study area in southern Norway (part of Telemark, Buskerud and Vestfold counties). The map shows the spatial distribution of forest stands sampled for browse biomass availability ($n = 189$), lakes, rivers, major roads and boundary of the study area.

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 ($\pm$ SE) snow-depths in the centre of the study area (430 m a.s.l) during January–April 2007 and 2008 were 49 $\pm$ 2·4 cm and 72 $\pm$ 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

(m³: 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 m² 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/50m²) 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 m³	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 $P_{2.1}$). 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 ($P_{2.1}$) 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 $P_{2.2}$ and $P_{3.1}$) but also with biomass of the lower
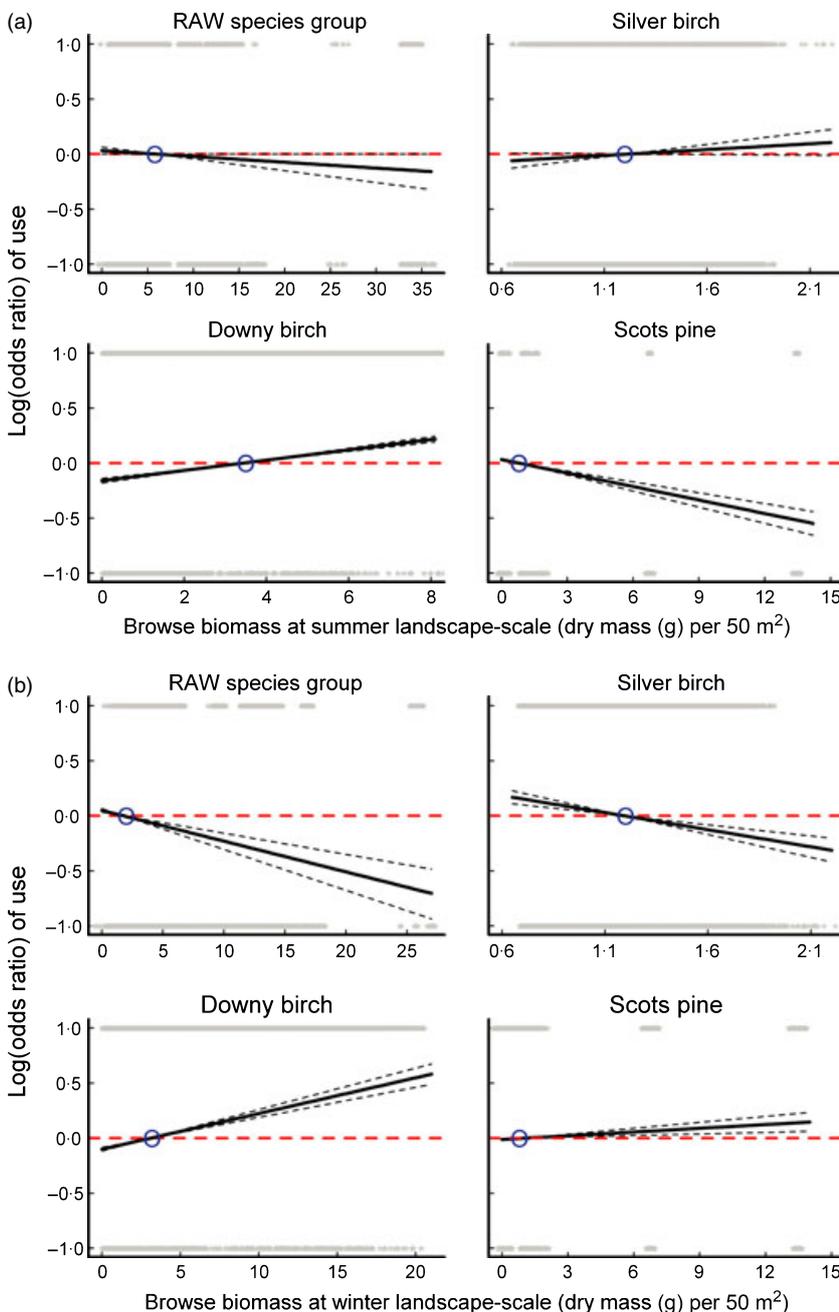

Fig. 2. Selection estimates (log odds ratio of use ± 95% highest posterior density intervals) for available browse biomass for each target species at the (a) summer and (b) winter landscape-scale, where the log odds ratios are calculated relative to the average available browse biomass for that target 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.
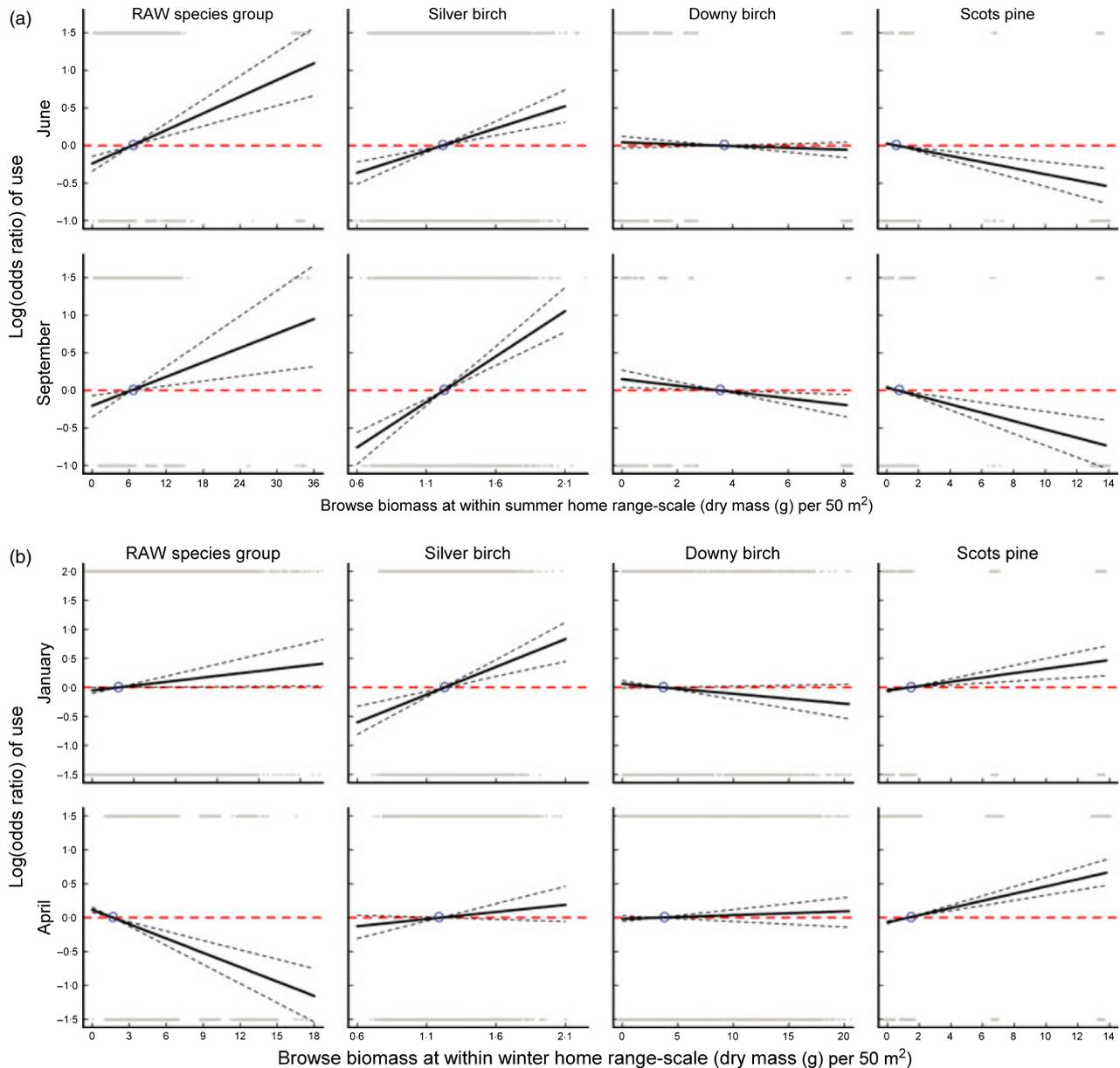
Fig. 3. Selection estimates (log odds ratio of use ± 95% highest posterior density intervals) for available browse biomass for each target species at the (a) within-summer, and (b) within-winter home range-scale, where the log odds ratios are calculated relative to the average available browse biomass 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
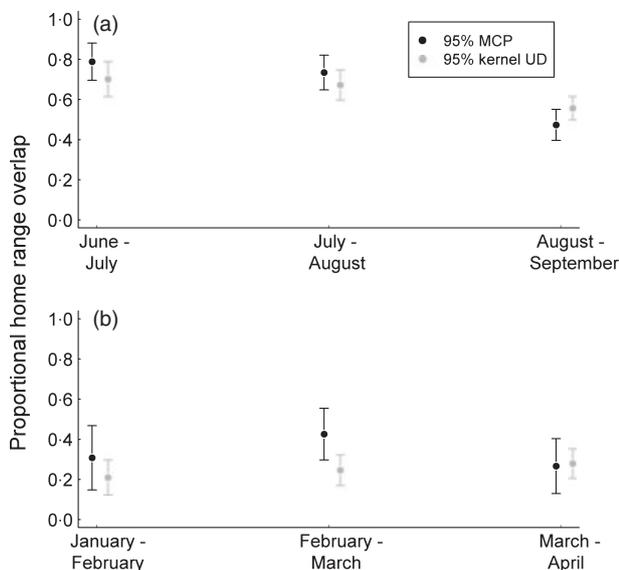
Fig. 4. Mean (and 95% confidence intervals) proportion of bimonthly home range overlap within-summer (a) and winter (b) using 95% MCP and 95% kernel UD. Sample size (*n* = total number of monthly home ranges for all moose) = 66 and 92 for summer and winter, respectively.

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 $P_{4.1}$ and $P_{4.2}$) 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 ($P_{4.3}$; 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 $P_{2.1}$ and $P_{2.2}$). We found that the pattern of habitat selection within-home ranges changed during winter but remained stable during summer (supporting $P_{3.1}$ and $P_{4.1}$). Furthermore, bimonthly home range overlap within seasons (an index for site fidelity) was high in summer and low in winter (support-

ing $P_{3.2}$ and $P_{4.2}$). 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 $P_{4.3}$). 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.

Acknowledgements

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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).

Table S3. Mean (SD) strip length (cm) and bite diameter (mm) by moose for six target species as observed in the study area.

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.

Table S5. Results of model selection for summer and winter RSF models for moose at the home range-scale and landscape-scale.

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.

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.

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).

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