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

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

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

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

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

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

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

Material and methods

Study area

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

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

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

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

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

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

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

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

Habitat types

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

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

Moose data

We used data from 64 GPS-collared moose for which the GPS attempted to acquire one position (or fix) at two hour intervals. For each hour of the day we recorded between 38,151 and 38,413 fixes during the study period, 2006-2009. The analysis

was divided in two parts: analysis of land cover utilisation and analysis of forest type and forest stage utilisation. In the analysis of land cover utilisation, we included 11 males and 53 females for which >10 GPS-fixes were available every second hour of the day per month during one or several years (May-April). We tracked 10 males and 27 females for more than one year. We knew the reproductive status (calf/calves: N = 81, or no calf: N = 12) for all females each year.

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

Statistical analyses

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

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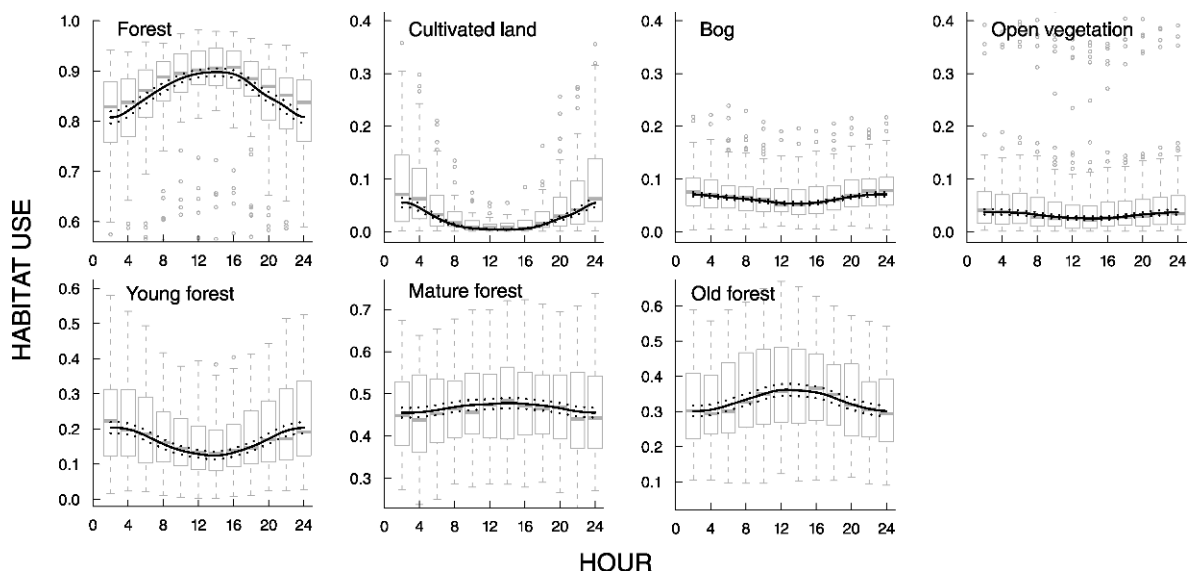
Figure 1. Circadian variation in moose habitat use for different land cover types (upper four panels) and forest stages (lower three panels). The curves were estimated by GAMMs and dashed lines indicate ± 1 SE. The box plots show the distribution of the GPS-observations.

and distance within two km (the 99% quantile of the observed step lengths) from the GPS-location. The GPS-locations represent areas used by moose, whereas the random locations represent the available areas. Given the high total number of locations (1,590,799 for the land cover analysis and 634,668 for the forest analysis), the random and the animal locations should provide a representative measure of used and available habitat types within the study area.
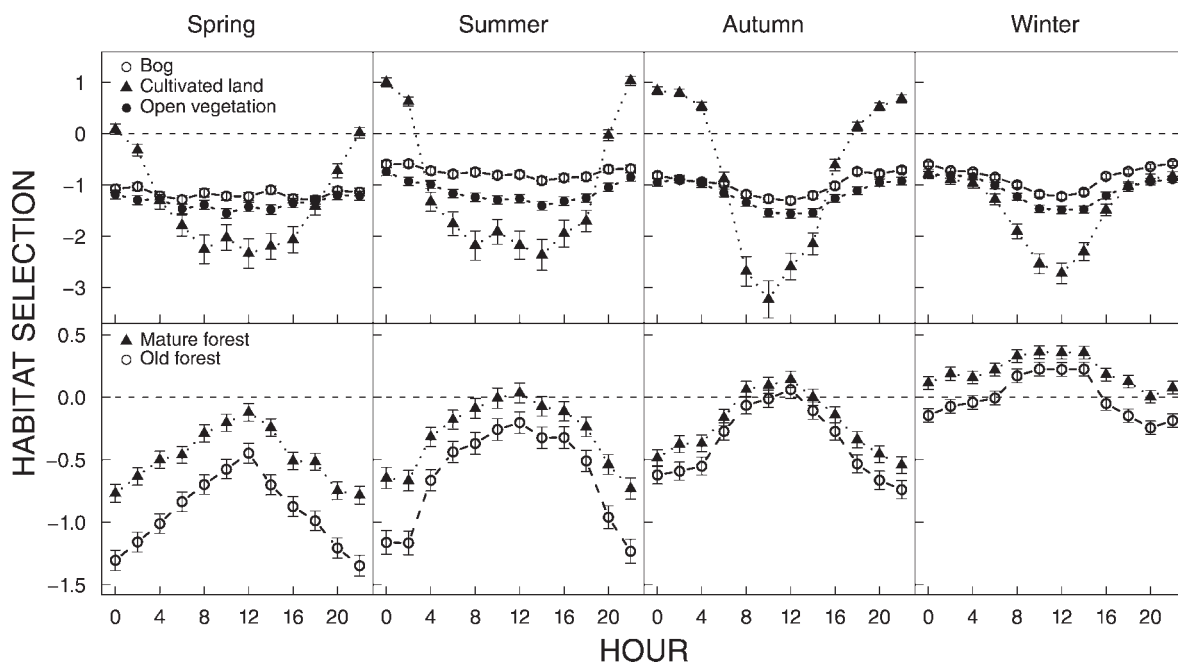

Figure 2. Step Selection Function-scores showing circadian habitat selection in four seasons by moose in central Norway. The upper panels show land cover selection with forest as reference land cover whereas the lower panels show selection of different forest stages with young forest (< 40 years old) as reference stage. The highest values indicate the selected habitat type at a given hour. The reference habitat type is selected when other habitat types have values below zero. Bars show robust standard errors.

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

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

Results

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

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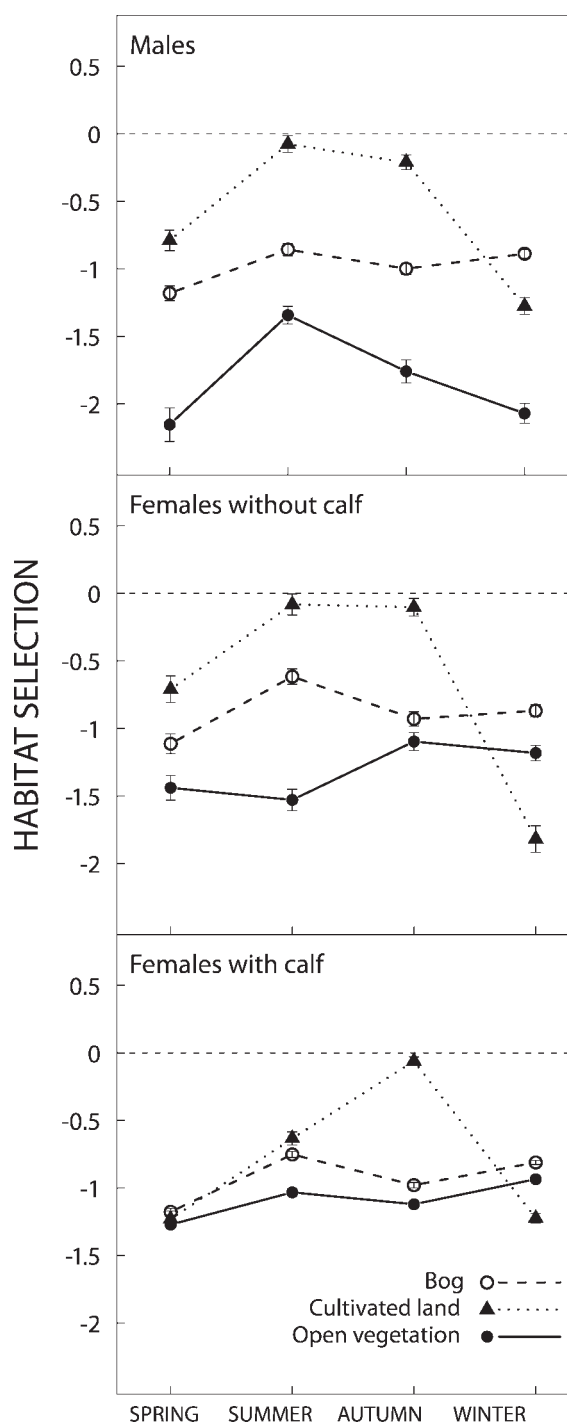

Figure 3. Step Selection Function-scores showing seasonal land cover selection by moose in central Norway, forest being the reference land cover. The land cover with the highest values is the selected land cover at a given season. The reference land cover is selected when other land cover types have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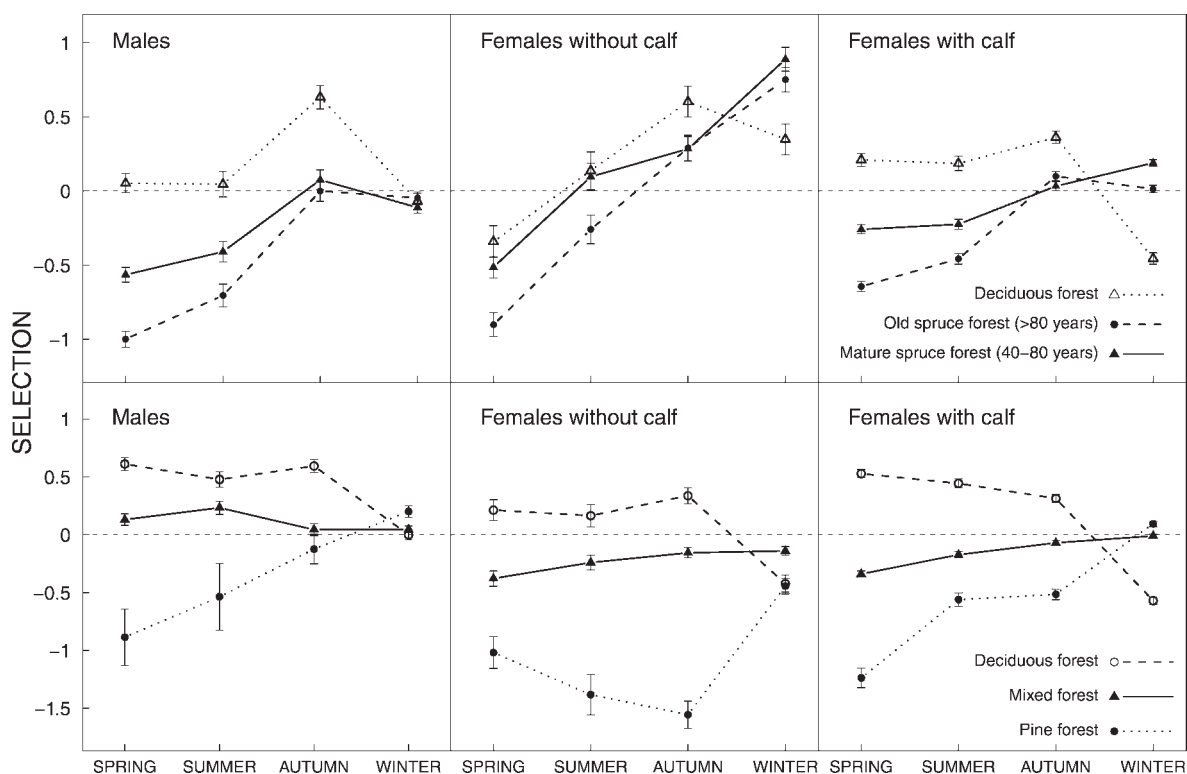
Figure 4. Step Selection Function-scores showing seasonal selection of forest type and forest stage by moose in central Norway. The forests with the highest values are the selected forest type or stage at a given season. Values below zero indicate that this forest type or stage is less selected than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

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

Conclusion

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

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