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Habitat selection of adult moose *Alces alces* at two spatial scales in central Finland

Ari Nikula, Samuli Heikkinen & Eero Helle

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The habitat selection criteria of moose *Alces alces* at several scales are the basic sets of information needed in moose management planning. We studied moose habitat use in central Finland during 1993-1996 using data from radio collared moose, satellite image based forest and land cover data, and applied the principles of compositional analysis. The habitat compositions of 54 home ranges (10 males during summer, six males during winter, 23 females during summer and 15 females during winter) were first compared with the overall landscape. The habitat compositions around moose locations within their home ranges were then compared with the habitat composition of the home range. Seasons and sexes were compared at both scales. In summer, there was only a slight difference between moose home ranges and the overall landscape. Based on tree species composition, home ranges are located in slightly more fertile areas than the overall landscape. Within their home ranges, moose favoured non-pine dominated habitats and mature forests, and avoided human settlements. In winter, the moose home ranges included significantly more pine-dominated plantations and other young successional stages than the overall landscape. The role of pine-dominated peatland forests/ shrub land was especially pronounced in winter. Winter home ranges included less agricultural land and human settlements than the overall landscape, probably due to the more distant location of important winter habitats from man-made landscapes. Within the home ranges, both sexes used non-pine dominated habitats more, and mature forests and human settlements less than expected. At the home range scale, there were no statistical differences between the sexes with respect to habitat use in either season. Within their home ranges, males and females used slightly different habitats during both seasons, suggesting spatially segregated habitat use by the individual sexes. The difference is more clear in winter when males tend to use more pine-dominated, young successional habitats than females. Compared to the situation in the summer, winter ranges are located in slightly more pine-dominated habitats with fewer settlements and agricultural fields. The shift in habitat use between the two seasons is more pronounced with respect to habitat use within the home range. Our results indicate that moose habitat selection criteria vary among different hierarchical levels of selection. We stress the importance of multi-scale assessment of the habitat and other resource selection of animals.

Key words: Alces alces, compositional analysis, GIS, habitat selection, home range, moose, ungulate

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Moose *Alces alces* has been a part of the Fennoscandian fauna since the glaciation period of the last Ice Age which ended about 10,000 years ago (Pulliainen 1987), and today the geographical distribution of the moose covers all the Fennoscandian countries (Cederlund & Markgren 1987, Nygrén 1987, Østgård 1987). In the 1970s and 1980s, the Fennoscandian moose population increased from tens of thousands of animals to several hundred thousand animals and, in some areas, the moose population has probably been the densest in the world (Cederlund & Markgren 1987, Cederlund & Bergström 1996). Because of the high population density, moose has an ambiguous position in Fennoscandian nature: on the one hand it is a valuable game animal (Mattson 1990), and on the other hand it is considered a severe pest in especially forest plantations (Lavsund 1987, Hörnberg 1995).

The rapid increase in population levels has been related to changes in hunting practises and forest management methods after the 1940s-1950s (Ahlén 1975, Lavsund 1987, Østgård 1987) during which period clear-cutting became the established forest regeneration method, and pine became favoured over the other tree species. Furthermore, the economically optimal age class distribution from a forestry point of view includes a high proportion of young forest plantations. It has been hypothesised that large areas of young forest plantation in practise provide an unlimited, continuous supply of food, that allows an effective reproduction of moose (Cederlund & Markgren 1987).

One basic component in moose management is information about moose habitat selection at several scales. The general features of the habitat requirements of Fennoscandian moose have been described by several authors (see e.g. Bergström & Hjeljord (1987) and references therein). In boreal regions, moose is adapted to the mosaic of habitats created by natural disturbances, and moose especially favour young successional stages (Geist 1974, Cederlund & Bergström 1996). Especially in winter and spring, when most of the moose damage in forest plantations occurs, the role of pine in the moose diet is pronounced (Lavsund 1987). Older forests are especially important in winter due to their thinner snow cover, but also during snowfree periods due to the presence of important food plants in the dwarf shrub layer (Hjeljord, Hövik & Pedersen 1990).

An animal's habitat selection can be seen as a hierarchical process in which an individual first selects its home range within the species' distributional range, and then selects between the various habitat types within the home range (Johnson 1980). Recognising this hierarchical nature of selection is essential as it affects our conclusions about the availability and usage of different resource components (Johnson 1980). Studies on the habitat and other resource selections of the moose at different hierarchical levels have indicated that selection occurs at least at the region/landscape level (Forbes & Theberge 1993), at the habitat level (e.g. Cederlund & Okarma 1988, Hjeljord et al. 1990, Bø & Hjeljord 1991, Heikkilä & Härkönen 1993, Ball, Nordengren & Wallin 2001), within habitats in relation to food resource availability (Vivås & Sæther 1987) and composition (Danell, Edenius & Lundberg 1991) and, finally, at the food item level (Niemelä & Danell 1988).

Multi-scale assessments of the habitat selection of moose from the home range to selection within the home range are still rare in the literature. Also, the habitat selection of moose has been studied with radio telemetry on only a few occasions in Fennoscandia (Cederlund & Okarma 1988, Hjeljord et al. 1990, Bø & Hjeljord 1991, Heikkilä, Nygrén, Härkönen & Mykkänen 1996, Ball et al. 2001). Analytically (Aebischer, Robertson & Kenward 1993), most of the telemetry studies have assessed the habitat selection of moose within home ranges or the landscape level in general.

In addition to hierarchical levels of selection, the effect of other factors such as season and sex should also be taken into account in resource selection studies (Aebisher et al. 1993). Seasonal migrations of moose have been studied in several parts of the distributional range of the species, and the distances between summer and winter habitats have been reported to range from a few kilometers to several hundred kilometers (LeResche 1974, Pulliainen 1974, Kuznetsov 1987). The main factors underlying seasonal migrations have been related to seasonal heterogeneity and availability of forage (Bergström & Hjeljord 1987), snow conditions (Sandegren, Bergström & Sweanor 1985) or a combination of these factors (LeResche 1974). However, not all the stud-

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ies have found differences in habitat selection between seasons (Cederlund & Okarma 1988), and in some areas, the moose has been reported to be only partially migratory (Ball et al. 2001). Studies on differences in moose habitat use between sexes in Fennoscandia are lacking, but corresponding studies performed in northern America report differences between males and females in this respect (Leptich & Gilbert 1989, Miller & Litvaitis 1992, Thompson, Gilbert, Matula & Morris 1995).

The aim of our study was to analyse the habitat use of moose at two scales using telemetry data, satellite image based land use and cover data, and applying the principles of compositional analysis (Aebischer et al. 1993). We first analysed whether the habitat composition of home ranges is different from the overall landscape habitat composition. Then, by using individual locations, we analysed whether moose use habitats within their home ranges disproportionally to the habitat composition of their home range. The analyses were made separately for individual seasons, i.e. winter and summer, and males and females were compared within the seasons. The seasons were also compared at both scales.

Material and methods

Study area

The study was carried out in the Province of Oulu in central Finland (65°N, 25°30'E; Fig. 1). This area lies in the middle boreal region of Finland (Ahti, Hämet-Ahti & Jalas 1968), and a high proportion of the area is former sea bottom that has gradually been exposed during the period following the retreat of the glaciers after the last Ice Age, about 10,000 years ago. The topography of the area is rather flat with an average elevation of 90 m a.s.l., and the highest points reaching 190 m a.s.l. The average thickness of the snow cover in the area is 40-70 cm (Climatological statistics of Finland 1971-2000).

The majority of the forests in the area are commercially managed. Of the land area, 65% is forestry land of which most is privately owned. The main tree species are Scots pine *Pinus sylvestris*, Norway spruce *Picea abies* and birch *Betula pubescens* and *B. pendula*. Of the forests, > 70% are dominated (i.e. ≥ 75% of the volume) by Scots pine. Willow species *Salix* spp. comprise most of the shrub layer. The proportion of peatlands is > 50% of the forestry land, and about 56% of the peatlands have been drained (Statistical Yearbook of Forestry 1996).

Locating the radio collared moose

During 1993-1996, 73 moose (37 males and 36 females) were captured and radio collared (Heikkinen 2000). The moose were radio collared in two different areas ca 45 km apart (see Fig. 1). After release, the animals were located by triangulation using a Yagi-type hand held antenna. The location of the radio collared moose was determined once a week all year around, except during periods of intensive movement in spring and autumn when 2-3 locations per week were made. If the moose was not detected from the ground, an aircraft was used to track the animals from the air. In such cases, however, the actual location was always determined on the ground. By the end of 1996, the total number of locations was 4,544. During our study, we adhered to the guidelines for the use of animals in research and the legal requirements of Finland and the Finnish Game and Fisheries Research Institute.

Determination of home ranges

The beginning and the end of the movement periods of moose and their home range periods, respectively, vary between years, and to some degree also among individual moose (Heikkinen 2000). Therefore, instead of using fixed time periods, we distinguished between the home range periods and the intensive movement periods individually for each moose by visually examining the dis-

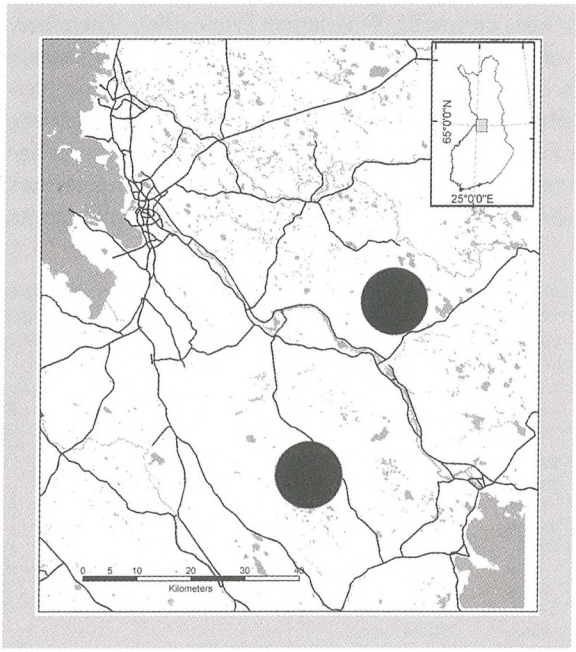


Figure 1. Study area in the province of Oulu, central Finland, showing moose collaring places (●), main roads (–) and water bodies (▒).

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tance, dispersion and timing between locations. When the winter home range period ends and the spring movements start, there is an abrupt increase in the distance of locations to a cluster of locations within the winter home range. When the summer home range period ends and the autumn movements start, the locations start to disperse over a much larger area and at a greater distance from the cluster of locations that constitute the summer home ranges. Similarly, the start of the summer and winter home range periods were determined by examining when the locations started to cluster (Heikkinen 2000).

Home range boundaries were determined using the harmonic mean method (Dixon & Chapman 1980) utilising a grid system with 40 × 40 m squares and Ranges V software (Kenward & Hodder 1996). We used a minimum of 20 locations to determine the home range of each sex as the number of observations per season, especially in winter, was low (for male summer: mean = 30.9, SD = 11.9; for male winter: mean = 28.4, SD = 6.7; for female winter: mean = 24.3; SD = 5.2 and for female summer: mean = 32.5, SD = 11.9). Also, an increase in the total home range size of moose with an increasing number of relocations could be the result of gradual changes in range use over the course of time (Doerr 1983).

Because the 100% isopleths of the home ranges are often influenced by infrequent and outlying locations, especially with a low number of locations per home range, it is preferable to use lower isopleths to obtain a more accurate range representation (Harris, Cresswell, Forde, Trewhella, Woollard & Wray 1990). Therefore, we plotted the utilisation distribution for each moose according to their radio locations, and looked for possible points of inflection in order to determine centres of activity (i.e. core areas). In most cases, the slope discontinuity was found in about 80% of the utilisation area (on average 30.1% (1,200 ha) of the maximum home range area), and therefore it was used to represent the home ranges of the moose (hereon referred to as home range). Coordinates of the home range boundaries were imported to GIS using DXF-interchange files produced with Ranges V (Kenward & Hodder 1996).

Digital maps and landscape variables

Land use and forest data were provided by the Finnish National Forest Inventory (NFI). In Finland, the NFI utilises Landsat TM 5 satellite images concurrently with field plots, as well as digital maps of roads, agricultural land and other non-forest land, to separate non-forest land from forest land. The multi-source method (Tomppo 1991, 1996) uses the k-nn method for producing estimates of e.g. timber volume for each tree species for every pixel corresponding to 25 × 25 m land area. The original satellite image was recorded in 1991.

Digital maps of timber volume estimates for pine, spruce and deciduous trees, as well as digital maps of fields and settlements, roads, waters and peatlands, were imported to GIS as separate layers. For the analysis, we combined timber volume layers and other land use layers to a single land use and cover layer using total timber volume as a proxy of forest age (Tomppo, Katila, Mäkelä & Peräsaari 1998). In the resulting data, each pixel can belong to one of 12 classes (Table 1).

Compositional analysis of home ranges

Aebischer et al. (1993) stated that there are four problems associated with the analysis of many habitat use data sets: 1) Proper determination of sample units, i.e. individual animals should (usually) be used rather than individual radio locations; 2) the proportions of habitats sum up to 1 over all habitat types (unit-sum constraint), which makes the habitat proportions non-independent; 3) analysis should enable testing between-group differences by reference to within-group between

Table 1. Habitat classifications used in the study. The terminology used corresponds approximately to the forestry terminology of the respective successional stages of forests. For instance, the plantations in the classification schedule include both forestry plantations and natural, young successional stages. The source of the age class estimates according to the respective timber volume in the stands is Tomppo et al. (1998).

Class	Class loading	Stand total tree volume criterion	Tree species criterion	Approximate age class	Soil
Openmi	Treeless area on mineral soil	0 m^3/ha	-	-	Mineral
Openpe	Treeless or sparsely stocked peatlands	0 m^3/ha	-	-	Peat
Pinplami	Pine-dominated plantations on mineral soil	1-40 m^3/ha	Pine ≥ 80 % of total volume	1-40 years	Mineral
Pinplape	Pine-dominated plantations/shrub land on peatlands	1-40 m^3/ha	Pine ≥ 80 % of total volume	≥1-40 years	Peat
Planoth	Other plantations/young successional stages	1-40 m^3/ha	Pine < 80 % of total volume	1-40 years	Mineral & peat
Pinthimi	Pine-dominated young thinning forests/pole stage stands	41-95 m^3/ha	Pine ≥ 80 % of total volume	40-80 years	Mineral
Pinthipe	Pine-dominated young thinning forests/pole stage stands	41-95 m^3/ha	Pine ≥ 80 % of total volume	≥40-80 years	Peat
Thinoth	Other young thinning forests/pole stage stands	41-95 m^3/ha	Pine < 80 % of total volume	40-80 years	Mineral & peat
Mature	Mature forests	> 95 m^3/ha	-	>80 years	Mineral & peat
Other	Waters, roads, other non-forested land	-	-	-	-
Settlements	Cities, villages, single buildings	-	-	-	-
Agri	Agricultural fields	-	-	-	-

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animal variation, i.e. comparisons between categories like sex and season; and 4) the definition of available habitats should be based on the consideration of the animals' habitat selection at different levels of hierarchy (Johnson 1980).

To address the above-mentioned problems 1 and 3, we calculated home ranges for each moose separated further by sex (males and females) and season (summer and winter). In the analysis, each home range for each animal and season is thus treated as one sample. Moose tend to show fidelity to their home range areas (Cederlund, Sandegren & Larsson 1987, Cederlund & Okarma 1988) which was a possible source of pseudoreplication (Hurlbert 1984) in our data, as some of the individuals were followed for two or more seasons and the others for only one season. Therefore, although each moose had to make a decision every year concerning its habitat choice, we took the conservative approach and checked whether the home ranges of each moose overlapped in the same season in consecutive years. If this was the case, only one of the overlapping home range boundaries for each moose was randomly selected for the analysis. As a result, our sample size was reduced to 33 summer (10 males and 23 females) and 21 winter home ranges (six males and 15 females) which were used in the analyses.

To address the above-mentioned problem 2, we transformed all habitat proportions to log-ratios using one of the habitat classes as denominator (Aebischer et al. 1993). Thus, given that there are D habitats available and an individual's proportional habitat use is described by $x_1, x_2, \ldots x_D$, where x_i is the proportion of used habitat of type i, the log-ratios are calculated as $y_i = \ln(x_i/x_j)$ where $i = 1,2,\ldots D$, $i \neq j$, and x_j is the proportion of available habitat of type j. In this way, all the log-ratios, y_i, which have the same denominator are rendered linearly independent (Aebischer et al. 1993). We used the class Other (see Table 1) as denominator in the log-ratio transformations.

The logarithmic transformations require that all the habitat types are recorded for all observations, i.e. that there are no zero proportions for any habitat class. In the case of zero proportions, Aebischer et al. (1993) proposed a method in which the zero proportions are substituted by a value of an order of magnitude smaller than the smallest recorded non-zero percentage in the actual data. This method assumes that all the habitats are available and that zero represents use which is so low that it can not be detected (Aebischer et al. 1993). Following this method, we replaced zero proportions with 0.001 which is a value that is an order of magnitude less than the smallest recorded non-zero percentage in our data.

To address the above-mentioned problem 4, we first compared the habitat compositions of home ranges with the overall landscape (Johnson's second-order selection). In order to measure the overall landscape habitat composition in the study area, we used the original home range boundaries (N = 54) and placed them randomly in the area. However, we used two types of criterion based on our telemetry data in the random placing procedure. The home range boundaries were allowed to be located only within the area used by our study animals, i.e. the area was restricted by the outermost boundaries of all the actual home ranges. As our study area extends to the Botnian coast (see Fig. 1) and as there are several large settlements in the area, we also applied some restrictions when randomly placing the home range boundaries within the study area. Moose have been reported to avoid man-made landscapes (Rolley & Keith 1980, Repo & Löyttyniemi 1985), and the randomly placed home range boundaries were therefore restricted to include the class Other (see Table 1) at a maximum of 19.13%, human settlements at 11.75% and agricultural land at 36.32%. These values correspond to the maximum values occurring in the actual home ranges.

When analysing within-home range use (Johnson's third-order selection), we compared habitat compositions around the locations with the habitat compositions of the home ranges. As the accuracy of radio locations varies with, for instance, the distance to the located animal, topography and vegetation cover, we created a 200 m-wide buffer zone around each location and calculated the habitat class proportions from this area. In the analysis, we used only locations that fell within the boundaries of the home ranges (i.e. for male summer home ranges 217 locations, for male winter home ranges 73 locations, for female summer home ranges 628 locations and for female winter home ranges 186 locations).

As we had fewer home ranges than dependent variables for some subgroups, we did not use parametrised multivariate analysis of variance tests (Tabachnick & Fidell 1996), but used randomisation in all the comparisons (see also Pendleton, Titus, Lowell, Degayner & Flatten (1998) about statistical testing of compositional data). Following the presentation of Manly (1997), randomisation is based on the idea that the mean values of observed data for compared groups and the difference D_1 between groups are first calculated. Values from both groups are then randomly allocated to either of the groups, and the difference between the means of groups is recalculated. Repeating the second step numerous times gives an estimate of the distribution D (randomisation distribution) that occurs by randomly allocating

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the values actually observed to either of the groups. Finally, a decision about the significance of the test is made by calculating the proportion of all the observed values in the randomisation distribution D that are greater than or equal to D_1 which corresponds to the P-value.

We used 5,000 randomisations for home range vs overall landscape comparisons, as well as for comparisons between locations, and 10,000 randomisations for home range vs location comparisons. All the comparisons were started by first checking whether moose showed differences in their habitat use among seasons, i.e. summer and winter. We then tested whether males and females showed any differences in their habitat use, and if this was the case for either of the subgroups, further analysis was made separately for each group. Otherwise, the seasons or sexes were grouped. Before deciding whether to use univariate tests of habitats or not, we made a multivariate analysis based on randomisation to check whether the mean differences among groups for a combination of all habitats were likely to have occurred by chance. Depending on the data, different test statistics may yield different results (Manly 1997), and we therefore used Wilk's lambda, sum of log(F) and sum of squares (E-statistics) as parallel measures for multivariate comparisons.

Because of the numerous comparisons between different subgroups (sex and season) within and among scales and the great number of habitat classes, we limited our detailed consideration of the differences mainly to those which were statistically significant ($P < 0.05$) and at the same time showed a reasonable enough difference in absolute proportions for them to be ecologically meaningful. We also calculated a correlation matrix for the original class-proportion values in order to get an impression of which habitat classes were inter-correlated. When combined, this information allows a better focus on the differences in habitat utilisation which are also likely to be a general phenomenon in moose habitat selection.

Results

Characteristics of summer home ranges and habitat use within home ranges

In the multivariate comparison of the summer and winter home range compositions, Wilk's Λ showed a significant difference between groups (0.74% of randomisations < original Wilk's Λ), but the two other statistics did not (86.56% of randomisations < original sum of log(F) and 26.40% for E statistics). Therefore, we analysed the home range level data of habitat compositions separately for summer and winter.

The male and female summer home range multivariate comparison did not show a significant difference between the sexes (45.12% of randomisations < original Wilk's Λ, 71.90% for sum of log(F) and 48.60% for E statistics), and therefore we pooled the data for further analysis. In the multivariate comparison of pooled moose summer home range habitat composition to overall landscape, only Wilk's Λ showed a significant difference between groups (0.02% of randomisations < original Wilk's Λ), but the two other statistics did not (23.56% of randomisations < original sum of log(F) and 24.10% < original E-statistics). Univariate comparisons of habitats between home ranges and the overall landscape show that there was only one statistically significant difference, i.e. non-pine dominated thinning forests were more abundant in the home ranges (Fig. 2A). Based on the tree species composition, and as there was a similar trend for non-pine dominated plantations, the home ranges of moose in summer contain slightly more fertile areas than occur on average in the overall landscape.

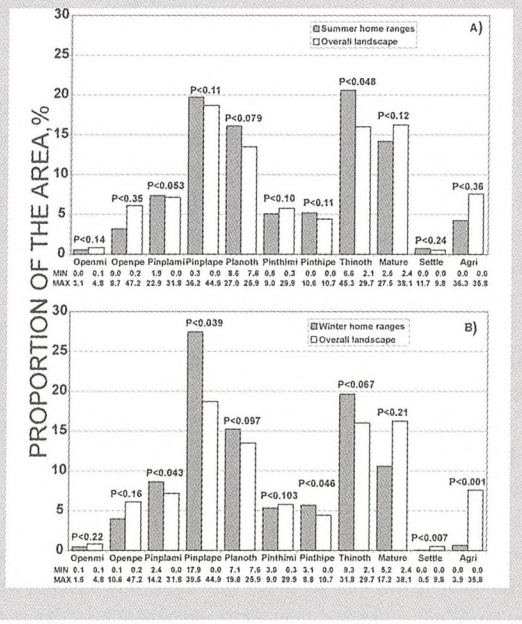


Figure 2. Mean proportions of habitat classes in A) moose summer home ranges (N = 33) and the overall landscape (N = 54), and in B) moose winter home ranges (N = 21) and the overall landscape (N = 54). The significance of group differences (P-values above bars) is based on 5,000 randomisations. Randomisations were made for log-transformed ratios of $Class_i/Class_j$ ($i \neq j$) using the class Other as a denominator. Minimum and maximum values of the original habitat proportions for each class are shown underneath the x-axis and below the bars.

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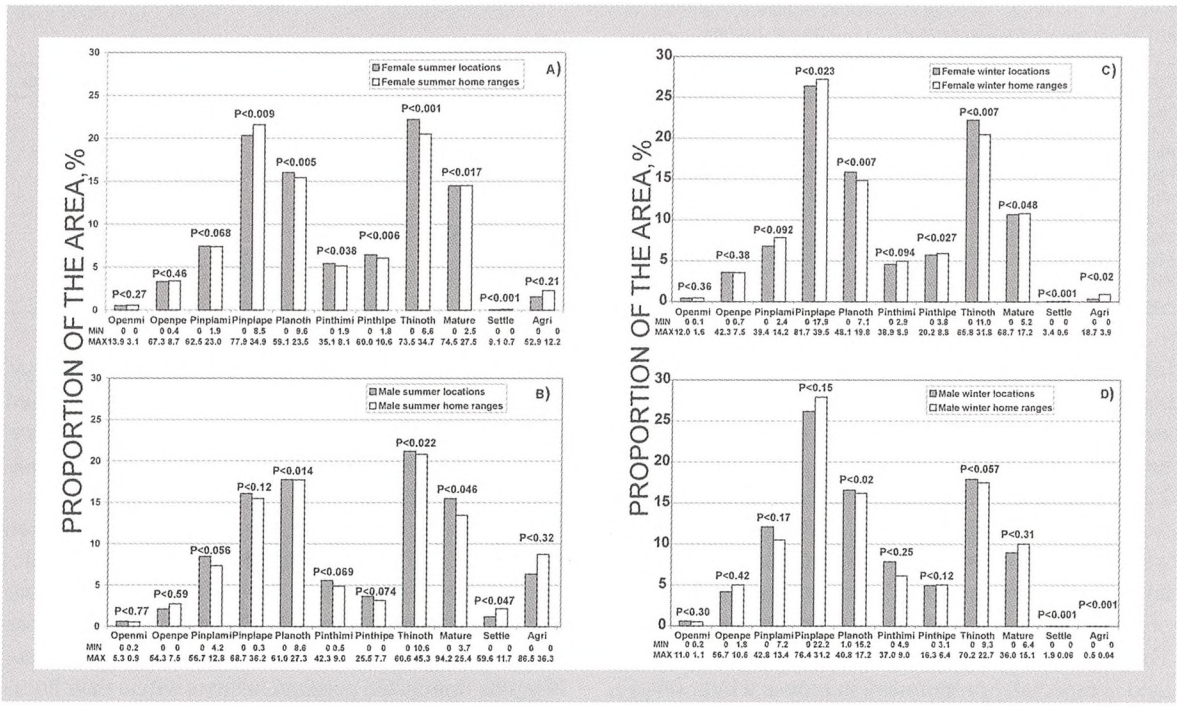


Figure 3. Mean proportions of habitat classes of home ranges and within a distance of 200 m around the moose locations for A) female moose summer locations (■; N = 628) and home ranges (□; N = 23), for B) male moose summer locations (■; N = 217) and summer home ranges (□; N = 10), for C) female winter locations (■; N = 186) and winter home ranges (□; N = 15) and for D) male winter locations (■; N = 73) and winter home ranges (□; N = 6). The significance of group differences (P-values above bars) is based on 10,000 randomisations. Randomisations were made for the log-transformed ratios of $Class_i/Class_j$ ($i \neq j$) using the class Other as a denominator. Minimum and maximum values of the original habitat proportions for each class are shown underneath the x-axis and below the bars.

The multivariate comparison between habitat compositions around the locations of females and males showed a significant difference with all the statistics used (0.01% of randomisations < original Wilk's Λ, 2.38% for sum of log(F) and 0.01% for E statistics), and therefore we made further comparisons separately for each sex. The multivariate comparison of habitat compositions between home ranges and locations showed a significant difference for females (0.01% of randomisations < original Wilk's Λ, 2.17% for sum of log(F) and 0.29% for E statistics), but only a trend for males (9.77% of randomisations < original Wilk's Λ, 5.32% for sum of log(F) and 5.71% for E statistics).

Within home ranges, females used areas with more non-pine dominated plantations and all types of thinning forest (Fig. 3A). Pine-dominated plantations on peatlands/shrub land were significantly less frequent around the female locations than expected on the basis of the home range compositions. Contrary to the results of the home range and overall landscape comparisons, female moose use less pine-dominated plantations on peatlands/shrub land than expected on the basis of the home range compositions.

In summer, males use areas within the home ranges with significantly more mature forests and non-pine dominated young forests (Fig. 3B) than expected on the basis of the home ranges habitat compositions. Males also tend to avoid human settlements and agricultural areas, but the difference is significant only for human settlements. As for females, within home ranges some of the habitat classes were used close to the level or even less than expected, while in the home range vs overall landscape comparisons these habitats were used more than expected. Mature forest dominated areas are found significantly more frequently around male locations, and there are also trends towards pine-dominated thinning forest to be more abundant around male locations than expected on the basis of the home range compositions.

Characteristics of winter home ranges and habitat use within home ranges

The multivariate comparison of male and female winter home ranges did not show a significant difference between the sexes (42.70% of randomisations < original Wilk's Λ, 42.62% for sum of log(F) and 46.80% for E statistics), and the data for both sexes were pooled

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Table 2. Correlations between proportions of habitat classes in moose home ranges (Spearman's rho; N = 54). * indicates a correlation significant at the 0.05 level, ** P < 0.01 and *** P < 0.001.

Class	Openmi	Openpe	Pinplami	Pinplape	Planoth	Pinthimi	Pinthipe	Thinoth	Mature	Settle
Openpe	0.35**									
Pinplami	0.40**	0.49***								
Pinplape	0.16	0.69***	0.50***							
Planoth	0.10	0.28*	0.36**	0.31*						
Pinthimi	0.37**	0.01	0.49***	0.10	-0.15					
Pinthipe	-0.24	-0.18	-0.29*	0.05	-0.62***	-0.04				
Thinoth	-0.42**	-0.64***	-0.52***	-0.51***	-0.18	-0.27*	0.33*			
Mature	-0.38*	-0.47***	-0.54***	-0.68***	-0.54***	-0.06	0.27	0.40**		
Settle	-0.02	-0.08	-0.29*	-0.37**	-0.25	-0.08	-0.14	-0.20	0.36**	
Agri	0.12	-0.17	-0.24	-0.48***	-0.22	0.07	-0.20	-0.16	0.29*	0.74***

for further analysis. Multivariate comparison of the pooled moose winter home ranges and overall landscape showed a significant difference or a trend for such a difference (0.02% of randomisations < original Wilk's Λ, 7.20% for sum of log(F) and 3.22% for E statistics). According to the univariate habitat comparisons, moose winter home ranges included significantly more pine-dominated, young habitats than expected on the basis of the overall landscape habitat composition (Fig. 2B). The role of pine-dominated plantations on peatland/shrub land is especially pronounced in moose winter ranges. Moose winter home ranges are also located in areas with significantly less human settlements and agricultural fields than occurred on average in the overall landscape. The fact that moose winter ranges are characterised by pine-dominated young successional habitats is further supported by the significant negative correlations between these and non-pine dominated habitats, mature forests and settlements (Table 2).

Habitat compositions around the winter locations of females and males were significantly different (3.12% of randomisations < original Wilk's Λ, 5.62% for sum of log(F) and 3.41% for E statistics), and further comparisons were made separately for each sex. Multivariate comparisons of habitat compositions around locations with the home ranges showed a significant difference or a trend for both females (0.01% of randomisations < original Wilk's Λ, 4.03% for sum of log(F) and 1.28% for E statistics) and males (0.01% of randomisations < original Wilk's Λ, 5.72% for sum of log(F) and 3.68% for E statistics).

There were significantly more non-pine dominated plantations and thinning forest and less human settlements and agricultural fields around the female locations than expected on the basis of the habitat distributions of the home ranges (Fig. 3C). Females also tend to use less pine-dominated peatland habitats within their home ranges than expected, but the differences in absolute proportions are small. For males, the only statistically significant difference in forested habitats was found for non-pine dominated plantations which were used slightly more within the home ranges than expected (Fig. 3D).

Comparison of habitat use between females and males

Our data did not show differences in home range level habitat use between the sexes, but several statistically significant differences were found in within home range habitat use both for summer and winter (Table 3). However, taking into account also home range level results and habitat use within home ranges (see Discussion), males and females did not show drastic dif-

Table 3. Differences in within home range habitat use between male and female moose within seasons and between winter and summer for each of the sexes. P-values show the probability of the randomised distribution of group differences being the same as the observed difference between groups (5,000 randomisations). Randomisations were made for the log-transformed ratios of $Class_i/Class_j$ (i≠j) using the class Other as a denominator. See Table 1 for a description of the habitat classes.

Class	Summer ♂♂ (N = 217) vs ♀♀ (N = 628)	Winter ♂♂ (N = 73) vs ♀♀ (N = 186)	♀♀ summer (N = 628) vs winter (N = 186)	♂♂ summer (N = 217) vs winter (N = 73)
Openmi	P < 0.042	P < 0.046	P < 0.005	P < 0.233
Openpe	P < 0.004	P < 0.037	P < 0.457	P < 0.001
Pinplami	P < 0.035	P < 0.001	P < 0.321	P < 0.023
Pinplape	P < 0.001	P < 0.151	P < 0.239	P < 0.001
Planoth	P < 0.321	P < 0.013	P < 0.059	P < 0.049
Pinthimi	P < 0.399	P < 0.009	P < 0.034	P < 0.074
Pinthipe	P < 0.001	P < 0.187	P < 0.176	P < 0.001
Thinoth	P < 0.089	P < 0.201	P < 0.068	P < 0.229
Mature	P < 0.316	P < 0.329	P < 0.007	P < 0.191
Settlements	P < 0.103	P < 0.036	P < 0.054	P < 0.461
Agri	P < 0.001	P < 0.083	P < 0.001	P < 0.001

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ferences in within home range habitat use in neither summer nor winter. In summer, males are located somewhat more in pine-dominated plantations on mineral soils and females more in pine-dominated thinning forests on peatlands. In winter, males are found more in pine-dominated forests on mineral soils than females.

Comparison of moose habitat use in winter and summer

As suggested by the contradictory results obtained in the different measures of significance in the multivariate comparison of the summer and winter home range compositions, there were only a few differences between seasons. In the univariate comparisons, the only significant differences were that there are less human settlements and agricultural fields in the winter home ranges than in summer home ranges ($P < 0.001$ for both sexes). The negative correlations between the proportions of habitat characteristics of winter ranges and settlement areas (see Table 2) further suggest that winter ranges are located further from settlements than summer ranges.

Multivariate comparisons between the habitat distributions around winter and summer locations showed a significant difference for both sexes (for females 0.01% < original Wilk's Λ, 8.59% for sum of log(F) and 2.99% for E statistics; for males 0.01% < original Wilk's Λ, 2.64% for sum of log(F) and 0.03% for E statistics). Compared to winter, in summer, female moose are located more often in areas with more mature forests and pine-dominated thinning forests on mineral soils (see Table 3). There are also less agricultural areas around female winter locations than around female summer locations. For males, there were more significant differences in habitat compositions around summer and winter locations than for females (see Table 3), and the differences are also somewhat larger in absolute proportions. Considering also the home range vs overall landscape comparisons, all types of pine-dominated habitats are found more frequently around male locations in winter than in summer. Non-pine dominated, young forests are important during both seasons for both sexes.

Discussion

Summer home ranges and habitat use within the home range

Relatively few studies in Fennoscandia have addressed the habitat selection of moose in summer (Cederlund & Okarma 1988, Hjeljord et al. 1990, Bø & Hjeljord 1991, Heikkilä et al. 1996). Furthermore, keeping in mind the hierarchical nature of the resource selection of animals (Johnson 1980), most of the moose radio telemetry studies have been based on location vs available habitat comparisons within home ranges or the landscape in general, and the characteristics of entire home ranges have seldomly been assessed (Cederlund & Okarma 1988). As the criteria between habitat selection on a different scale may vary, the direct comparison of different scale studies should be made with caution and, for this reason, the discussion of the home range level results is kept at a rather general level.

According to our results, the habitat compositions of summer home ranges lie relatively close to that of the overall landscape which suggests that moose are able to utilize a variety of habitats in summer instead of being strictly adapted to certain types of habitat (Hjeljord et al. 1990). There were significantly more only non-pine dominated thinning forests in the summer ranges, and a similar trend was also found for non-pine dominated plantations and pine-dominated plantations on mineral soils. The importance of non-pine dominated forests in summer was further supported by the fact that, within the home ranges, moose used areas with significantly more non-pine dominated forests. In our habitat classification, non-pine dominated forests comprise all the combinations from mixed tree species forests to pure deciduous or spruce dominated forests. In the study area, pine is the predominant species in about 75% of the forests, and the remaining forests are either spruce-dominated (~13%) or birch-dominated (~10%) or mixed forests (Statistical Yearbook of Forestry 1996). As a large proportion of deciduous trees or spruce in the forests usually indicates more fertile soils, our data suggest that, at the summer home range level, moose favour areas with more fertile habitats than occur on average in the overall landscape (Bergström & Hjeljord 1987, Hjeljord et al. 1990).

Mature forests have been considered important during snowfree periods due to the presence of food plants in the dwarf shrub layer (Markgren 1974), and especially in late summer due to the delayed phenological changes in food plants (Hjeljord et al. 1990). On the other hand, Cederlund & Okarma (1988) found that, at the home range level, the utilisation of mature forests was close to the expected level. According to our results, the proportion of mature forests in the moose summer home ranges did not differ from that in the overall landscape. Within home ranges, on the other hand, moose are frequently located in areas with significantly more mature forests than expected on the basis of the home range habitat composition. This either implies that mature forests

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do not play an important role in habitat selection at the home range level, or that the proportion of mature forests embedded in forestry-modified landscapes dominated by young successional stages is still above a threshold at which the summer range selection of moose is not affected.

Winter home ranges and habitat use within the home range

The qualitative and quantitative distribution of food in different habitats largely determine the activity patterns and habitat use of large ruminants. In winter, the majority of the browse of moose is nutritionally of low quality, mainly pine (Cederlund, Ljungqvist, Markgren & Stålfelt 1980), and moose spend less time feeding than in summer (Cederlund 1989). Therefore, moose should seek areas with relatively densely distributed feeding habitats in winter (Cederlund 1989). In our study, a large proportion of the habitats in the winter home ranges were pine-dominated young successional stages. The role of pine-dominated plantations in peatlands/shrub land was especially pronounced at the home range level. Within the home ranges, in contrast, moose are more frequently located in non-pine dominated habitats, and pine-dominated habitats are used close to the expected level or even less. As a conclusion, our findings seem to support the idea that moose respond to the food quantity at the home range level (Cederlund 1989, Wallace, Turner, Romme, O'Neill & Wu 1995), but within the ranges they seek habitats with a mixture of tree species in addition to pure pine-dominated habitats also in winter (Hjeljord et al. 1990).

It has been suggested that, due to the increased moose population size, the increasing incidence of young forests and over-browsing, there has been a switch in habitat use, and therefore peatland habitats would not be as important as previously believed (Bergström & Hjeljord 1987). In Finland, however, more peatlands have been found in areas with higher moose densities (Heikkilä & Härkönen 1993), and the evidence from telemetry studies indicates that forested peatland habitats are important for moose all year around (Heikkilä et al. 1996). Our results also indicate that forested peatland habitats are important determinants of moose ranges, especially in winter. It has been hypothesised that drained peatlands would be especially suitable habitats for moose due to the accelerated mobilisation of nutrients affecting the secondary metabolite production and/or increase in the growth of trees and other browse (Heikkilä & Härkönen 1993). The proportion of drained peatlands is high in our study area, and it is likely that drained peatlands comprise a part of the forested peatlands also within the home ranges. However, no geographic information about drained peatlands was available for our analysis, and the role of different types of peatland habitats could not be further assessed.

According to Johnson (1980), the preference in selection can only be reflected if the resource component is relatively scarce. Components that are vital, but also abundant at the same time, might lead to the erroneous conclusion that these habitats are of little value. Also, if some habitat types are important at the home range level, the use of these habitats within the home ranges may appear equal or lower when compared to the availability within home range, which could lead to the erroneous conclusion that these habitats are of little value in within home range habitat selection (Thomas & Taylor 1990). This can partly explain the contradictory results of the importance of pine-dominated peatland forests between home range level and within home range use. According to the statistical tests, within home ranges pine-dominated peatland forests do not seem to be important or are even used less than expected. However, as the amount of forested peatland habitats is high at the home range level, and the differences between home range and within home range use are small, it is more likely that peatland habitats are important at both scales (for a more detailed discussion of the interpretation of results among scales see the section Moose habitat selection at the two levels of scale).

In winter, moose have been reported to select areas with less human settlements and agricultural land (Rolley & Keith 1980). According to moose damage inventories, damaged forest plantations have also been found further from settlements and roads (Repo & Löyttyniemi 1985, Heikkilä 1990, but see also Ball & Dahlgren 2002), and this has been interpreted to mean that moose avoid human disturbance. However, as the summer home ranges did not show a similar pattern, the fact that winter ranges include less settlements and agricultural fields probably reflects the more distant location of important winter habitats from man-made landscapes rather than disturbance. Human settlements and agricultural fields are often located in more productive land originally consisting of other than pine-dominated habitats or peatlands. This is further supported by the significant negative correlations between both settlements and agricultural areas and the proportion of important winter habitats (see Table 2).

Habitat use between seasons

According to our data, the compositions of moose summer and winter home ranges did not show a statistical difference for any type of habitat other than agricultu-

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ral fields and settlements, which were found less frequently in winter ranges than in summer ranges. In this respect, our results are in accordance with those of Cederlund & Okarma (1988) and Ball et al. (2001), who found no drastic differences between summer and winter habitats. According to the overall landscape comparisons, however, there is a slight shift towards pine-dominated habitats in winter (Bergström & Hjeljord 1987). Furthermore, the difference in habitat compositions around summer and winter locations seems to suggest that the change in moose habitat use between seasons is more pronounced in within home range habitat use than at the home range level.

The migration of moose between winter and summer ranges has been related to the snow cover, and several studies have suggested that for winter moose migrate to areas with less snow (Coady 1974, Sandegren et al. 1985). In our study area, the average snow cover is relatively thin (40-70 cm) and perhaps not thick enough to substantially restrict moose movement (Coady 1974). In the autumn, moose mainly migrate from the coast towards the inland, and thus move at least in principle to areas with deeper snow cover than in areas closer to the coast. Also, the relatively flat terrain and the short average migration distances between summer and winter home ranges do not seem to support the idea that migration is related to the snow depth gradient at least in the autumn. On the other hand, the moose winter home ranges were located in areas containing significantly more thinning forests than the overall landscape, and moose also selected areas with more thinning forests within their home ranges. Thus, in addition to the available side-branch forage, at least part of the importance of thinning forests could be related to snow cover depth or snow quality in within home range habitat selection (Ball et al. 2001). However, as there were no data available on the variation in the depth or the quality of snow for the area, the possible mechanisms related to snow and migration from summer ranges to winter ranges can not be further assessed here.

In our study population, the migration distances were generally short, i.e. 15-25 km (Heikkinen 2000), which indicates that migration does not reflect any substantial variation in any habitat characteristic. In spring, moose mainly migrate towards the northwest, i.e. from the inland closer to the coast, although opposite directions have also been reported (Heikkinen 2000). The start of spring migration of northern temperate ungulates has been linked to snow melt and the emergence of fresh green vegetation (LeResche 1974). It is thus possible, although it can not be assessed using our habitat data, that also in our study population the proximate reason for migration from winter to summer ranges is linked to the earlier emergence of vegetation close to the coast. On the other hand, there is evidence that the migratory traditions of the moose can lag far behind environmental changes (Andersen 1991), and considering the relatively short duration of intensive changes in the forest landscapes due e.g. to forestry, it is possible that the migratory behaviour of moose still reflects earlier habitat conditions.

It has been hypothesised that intensive forestry practices increase moose philopatry by creating landscapes in which the different successional stages are evenly distributed over small distances and areas smaller than the home ranges of moose (Cederlund & Sand 1992). Also, Ball et al. (2001) have reported moose populations to be only partially migratory, and they found no drastic differences in habitat compositions between migrants and non-migrants. In our study population, the summer and winter home ranges of the same individuals partially overlapped, especially in the case of females, and the migratory behaviour could thus resemble the behaviour described in Swedish studies. Due to the low number of observations in subsequent years, the effect of different migratory behaviours on habitat use could not be compared in our study. However, as both summer and winter home ranges differed significantly from the overall landscape, our data suggest that, at the scale of the moose home ranges (about 1,200 ha) at least, there is variation in habitat composition that allows a home range level selection. As the intensity and history of forestry and other land use practices varies among countries, and even between regions within countries, the contradicting results of a number of studies might merely reflect differences in the landscape structure and land use history between the areas studied.

Habitat use of male and female moose

Comparison of the habitat use by the sexes (basically, the same applies for comparing seasons or other subgroups) is complicated by the fact that statistical differences between the sexes do not necessary indicate a preference for or an avoidance of habitats by either of the sexes. Statistical differences between the sexes indicate different habitat distributions, but judgements about whether sexes favour or avoid different habitat types require more information about the habitat use of both sexes separately. To be ecologically meaningful, either home range level habitat use (home range vs overall landscape comparisons) or within home range habitat use (home range vs location comparisons) should indicate the same type of pattern for the same habitat types for either of the sexes as found in between

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sex comparisons. This is illustrated by the summer use of pine-dominated peatland plantations/shrub land. Comparisons of the home range to the overall landscape do not show preference or less use of this type of habitat and neither does the within home range use of males. Instead, females tend to use significantly less pine-dominated peatland plantations/shrub land within their home ranges than expected. Still, a between sex comparison shows that pine-dominated young peatland forests/shrub land are significantly more frequent around female locations than around male locations. Keeping in mind the results for the home range level and within home range habitat use, we can conclude that this type of peatland habitat does not seem to be important for either sex in summer.

Female and male moose are spatially segregated during most of the year, and their patterns of habitat use are also likely to be different due to their different nutritional requirements (Cederlund & Sand 1994). According to within home range habitat use, males and females used somewhat different habitat environments which suggest that the sexes are also spatially segregated in our study population. The difference is most clear in winter, when male moose use pine-dominated young forest habitats more than females. Because pine is the main browse species for moose in winter (Cederlund et al. 1980), our result supports the hypothesis that, due to their larger body size, male moose should seek areas with good food availability even at the expense of the food quality (Cederlund & Sand 1994). However, it should be kept in mind that the differences between the sexes found in our study are relatively small, and other possible factors, such as the effect of offspring on habitat selection between the sexes, could not be assessed from our data.

Moose habitat selection at the two levels of scale

In general, our results support the hypothesis that animals select their habitats using different criteria at different hierarchical levels (Johnson 1980, Senft, Coughenor, Bailey, Rittenhouse, Sala & Swift 1987). At the home range level (Johnson's second order selection), in winter especially, moose prefer areas with a high proportion of pine-dominated young successional habitats or thinning forests, but within their home ranges (third order selection), moose select areas with a variety of habitats. This is in agreement with Hjeljord et al. (1990), who concluded that a mosaic of older and younger forests, rather than large areas of young successional stages, is important for moose. However, according to our results, the younger successional stages, especially pine-dominated habitats, seem to direct the habitat selection of moose at the home range level, i.e. the amount of young successional stages has to be high enough to provide a suitable environment for moose. When the proportion of younger successional stages is high enough at the home range level, the mixture of other habitat types becomes important in within home range habitat selection.

According to our results, the actual differences in habitat distributions between home ranges and those around the locations within the home ranges are relatively small in both summer and winter, but the significant differences in univariate comparisons still indicate that moose do select habitats within their home ranges. This is in contrast with Hjeljord et al. (1990), who reported that moose movements and habitat selection within summer home ranges were random in relation to the food resource distribution in the area. Also, Wallace et al. (1995) suggested that ungulates feed randomly within forage patches (at a fine scale), but they respond to forage abundance at a larger landscape scale. There are at least two possible explanations for the discrepancies obtained in the various studies. The first one is related to the definition of available habitat (Johnson 1980, Aebisher et al. 1993). The general method for defining available habitats has been to use more or less arbitrary study area boundaries. If, however, the habitat selection of the animal also happens at the home range level, i.e. the habitat composition is different from the habitat composition of the study area, it can affect the significance of the statistical tests and thus the detection of habitat preferences at different scales.

Second, when interpreting the differences in habitats favoured at the home range scale, which are used equally much or even less within the home ranges than expected by the overall home range habitat distribution, it should be kept in mind that the preference may be conditional on availability (Mysterud & Ims 1998). In such a situation, the use of some habitat is not directly proportional to the availability of that habitat, but changes as the amount of that particular type of habitat increases or decreases. As a consequence, the interpretation of preference for or less use of habitats within home ranges might be obscured if e.g. some threshold value for the amount of favoured habitat is reached or exceeded at the home range level. In our data, this might at least partly explain the differences found between the home range level and the within home range use of habitats that are found in excess at the home range level, such as e.g. pine-dominated peatland habitats. Mysterud & Ims (1998) proposed an approach to test for a change in relative use with changing availability of habitats when two habitat categories are considered. So far, tests for multiple habitat situations, like in our

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data, have not yet been developed (Mysterud & Ims 1998), and the possible effect of changing availability on the change in habitat use of moose remains to be assessed in future studies.

Methodological aspects

Compositional analysis is based merely on the ratios of habitat proportions, and it is the measure of only one landscape structure component, i.e. the composition. As the same amount of a specific habitat can be spatially distributed over the same area in several patterns, measures of the spatial arrangement of different habitat classes, i.e. the landscape configuration, could have potential in explaining the habitat selection of animals (Mysterud & Ims 1998). Although the spatial distribution of moose locations within the home ranges partially addresses the question of the location distribution of different resources within home ranges, it does not answer these questions at the home range level. The location data used in our study were relatively few over time, and the information about the quality of the observation (moose activity) was limited. Constructing the habitat requirements of moose from the landscape level to a single habitat patch requires more intensive (in time) and accurate (location) tracking of moose habitat use. Global positioning system (GPS) equipped radio collars (Lynch & Shumaker 1995), together with automatic data collection of the activity of moose, are potential tools for providing such data. Linking more accurate data about moose movements with landscape structure indices, such as patch density, patch size distribution and interpatch distances, could provide more insight into the processes affecting habitat selection criteria at different scales (Mysterud & Ims 1998). However, studies that utilise spatially and temporally more accurate telemetry data probably also require more accurate data of habitats in addition to data derived from e.g. satellite images (Saveraid, Debinski, Kindscher & Jakubauskas 2001).

Finally, as our sample sizes for seasonal ranges (particularly for males: six winter and 10 summer ranges) were not large, and as selection may only be detectable if important habitat components are not excessively present (Johnson 1980), we recommend and look forward to carrying out further studies using compositional analysis in other geographical areas.

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