

Does forest harvesting and linear infrastructure change the usability value of pastureland for semi-domesticated reindeer (*Rangifer tarandus tarandus*)?

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During the harshest winter, preference of forest habitat by reindeer should be dependent on the availability of energy-rich lichens, while in summer and easy snow conditions on the availability of protein-richer food. Reindeer should also avoid linear infrastructure (roads, power lines) if it causes disturbance and energy loss. We tested seasonal home range and habitat selection by semi-domesticated reindeer (*Rangifer tarandus tarandus*) in a sub-arctic pine forest area, northern Finland by tracking 29 female reindeer with GPS collars from 1999–2002. As expected, reindeer preferred old-growth forest and avoided felled areas and linear infrastructure in the selection and use of their wintering areas. Old-growth forest had high preference especially in late winter. During summer and early winter, reindeer also used sapling stand areas, young cultivated forests, mires and high-elevation open land. The net energy balance hypothesis including the total energy profits and expenditures could primarily explain habitat selection by reindeer during winter in intensively grazed and logged forest areas. Maintaining a certain amount of old-growth forest and minimizing linear infrastructure in wintering areas considerably improves the suitability of these ranges for reindeer herding.

Introduction

Reindeer and caribou (*Rangifer tarandus*) are physiologically well adapted to utilise lichens, which are rich in digestible carbohydrates but low in protein and minerals (Nieminen & Heiskari 1989). In particular, certain common terrestrial lichens (mostly *Cladina* sp.) are highly consumed winter feeds, although other terrestrial

plants with higher protein content, like dwarf shrubs, grasses and sedges supplement or compensate the lichen diet (Bergerud 1974, Kojola *et al.* 1995). When there is a lack of terrestrial lichens in wintering areas or snow conditions considerably hamper digging of these lichens, reindeer and caribou living in woodland areas shift to use arboreal lichens (*Bryoria*, *Alectoria* sp.), especially in late winter (Helle 1984,

Rominger & Oldemeyer 1990, Rominger *et al.* 1996, Poole *et al.* 2000, Terry *et al.* 2000, Johnson *et al.* 2001). The consumption rate of arboreal lichens is, however, greatly dependent upon the amount of available old-growth forest with an abundance of these lichens (Rominger & Oldemeyer 1990, Rominger *et al.* 1996, Kumpula *et al.* 2003, Johnson *et al.* 2004).

The value of lichen resources to the successful wintering of reindeer and caribou is evident since, in particular, the availability of terrestrial lichens within closed predator-free or nearly predator-free, intensively grazed areas have been observed to correlate positively with calf production and body weight, and negatively with mortality rate in these populations (Klein 1968, Skogland 1983, 1985, Kojola *et al.* 1993, 1995, 1998, Ouellet *et al.* 1996, Kumpula *et al.* 1998, Kumpula 2001a). Furthermore, the proportion of terrestrial lichen ranges of the total land area may partly affect the average long-term reindeer densities (Kumpula *et al.* 2000). The effects of arboreal lichen resources on the demography of reindeer and caribou populations have not been studied comprehensively, but there are some suggestions that calf production and mortality rates are balanced, and body mass of calves in the following autumn increased if there was an adequate amount of old-growth forest with plenty of arboreal lichens available for reindeer over winter (Kumpula & Nieminen 1992, Helle & Kojola 1993, Kumpula *et al.* 1998).

There are only few studies, where the impacts of forest harvesting on habitat selection, pasture quality or demography of reindeer and caribou populations have been documented. In winter, woodland caribou have been observed to select old spruce–fir forests with abundant reserves of arboreal lichens (Rominger & Oldemeyer 1990, Poole *et al.* 2000, Johnson *et al.* 2001, 2004, Mosnier *et al.* 2003) and they avoid areas where forest felling has been intensive (Smith *et al.* 2000). In a similar way, semi-domesticated reindeer living in the coniferous forest area and grazing freely are known to prefer old-growth forests when digging for terrestrial lichens or searching for arboreal lichens during winter (Helle & Saastamoinen 1979, Helle & Tarvainen 1984, Helle *et al.* 1990).

Coniferous forests cover over two thirds of the reindeer herding area in Finland, and most of these are designated as commercial forests. Forest harvesting has gradually changed the composition and age structure of commercial forests completely, especially during the past 50 years (Mattila 1996, Tomppo & Henttonen 1996). At the same time, the reindeer herding system in Finland was intensifying utilization of the pastureland. Calf slaughtering, supplementary winter-feeding and antiparasitic treatment of reindeer have made reindeer herds increasingly less vulnerable to natural population regulation mechanisms and enabled herders to maintain average reindeer densities at a level at which winter pastures have gradually become overgrazed in many areas (Kojola & Helle 1993, Kojola *et al.* 1993, 1995, Väre *et al.* 1996, Kumpula *et al.* 2000, Kumpula 2001b). The complicated process of deterioration and reduction of winter ranges made reindeer herding more dependent on supplementary winter-feeding, creating extra costs for the herders and reducing profit margins (Kumpula 2001b).

For a long time, there has been a heated debate between the stakeholders in reindeer herding and forest industry in Finland on how forest harvesting affects reindeer pastures and reindeer herding (Kyllönen & Raitio 2004, Raitio & Rytteri 2005). Forest harvesting practices clearly reduce the area of old-growth forest and the amount of arboreal lichen resources (Armleder & Stevenson 1996, Proceviat *et al.* 2003, Stevenson & Coxson 2003). Forest harvesting, felling residue, wood transportation, cultivation of soil and road networks also reduce the amount of terrestrial lichens and disturb or prevent the utilisation of these lichens (Kumpula 2003). Removal of forest cover may also affect snow conditions in large felled areas (Kirchoff & Schoen 1987). All these changes can drive reindeer away from new logging areas as has been observed with caribou (*see* Smith *et al.* 2000, Terry *et al.* 2000). On the other hand, the growth of ground lichens, grasses and herbs gradually increase in felled areas, sapling stands and thinned forests as the amount of light at the forest floor increases (Kumpula 2003). This may cause an increase in use of felled areas, sapling stands and young for-

ests, especially in summer and autumn. Reindeer adapt to changes in a forest landscape if they are able to obtain sufficient winter feed from different aged forests, and herders can also improve the nutritional condition of reindeer by introducing supplementary winter feed to the animals.

In the debate between the forest industry and reindeer herders the following issues have repeatedly been brought up: How do reindeer prefer or avoid different kinds of forest habitats during different seasons? Are old-growth forests still as important for reindeer and reindeer herding during winter as many herders emphasise? Do human perturbations such the constructions of roads and power lines on pastureland cause disturbance for reindeer? We searched answers for these questions by analysing home range and habitat selection of semi-domesticated reindeer (*Rangifer tarandus tarandus*) in the Ivalo Reindeer Herding District, northern Finland. For this work we used the GPS tracking data of 29 female reindeer from 1999–2002. The main focus of the work was to compare the usability value of different forest age classes in different seasons. We also studied the avoidance of linear infrastructure (roads and power lines) by reindeer.

Material and methods

Study area

The Ivalo Reindeer Herding District (Fig. 1) belongs to the Specific area where reindeer herding has a special status with respect to other land use (Finnish Reindeer Herding Act 1990: chapter 1, section 2). The total area of the Ivalo district is 2861 km², of which 8% is covered by lakes and rivers and 9% by mires (Kumpula *et al.* 2004). The area is characterised by dry nutrient poor lichen (*Cladina* and *Cladonia* sp.) dominated Scots pine (*Pinus sylvestris*) forest, where certain dwarf shrubs (mainly, *Empetrum nigrum*, *Calluna vulgaris*, *Vaccinium vitis-idaea*, *V. myrtillus*) and mosses (*Dicranum* sp., *Pleurozium schreberi*) are grown. There are also submesic pine or pine–birch (*Betula pubescens*) forests and small occurrences of Norwegian spruce (*Picea abies*) forests in the area. In all these



Fig. 1. Location of the Ivalo Reindeer Herding District in the reindeer management area of Finland.

submesic types, dwarf shrubs (*Vaccinium vitis-idaea*, *V. myrtillus*, *V. uliginosum*, *Empetrum nigrum*), grasses (*Deschampsia flexuosa*, *Festuca ovina*) and mosses (*Pleurozium schreberi*, *Dicranum* sp.) are the most common terrestrial plants with some amount of terrestrial lichens (*Cladina* sp.).

Forest harvesting has been practised intensively in the study area for over 80 years, creating a mosaic of forest stands of various ages. During the study, 31% of the total area was still covered by mature and old-growth coniferous

forests. *Bryoria* sp. is the most common epiphytic lichen in these predominantly pine forests. In the scarce old-spruce forest areas *Alectoria* sp. in contrast, is common. The remaining forestland areas are covered with cultivated forests of varying age, sapling stands and felled areas (data: digital forest map by Metsähallitus). The relief of the area is rugged with several treeless tops of low and smooth fell mountains. According to the Digital Elevation Model (DEM) obtained from the National Land Survey of Finland, the highest mountaintops in the Ivalo district reach just over 500 metres above sea level. The lowest areas are found along Lake Inari, at 120 metres above sea level and altogether 50% of the area is below 210 metres. The tree line is approximately 350 metres above sea level.

The lichen-dominated ranges in the Ivalo district are heavily worn-out since the average amount of reindeer lichens (*Cladina* spp.) in these pastures was only 240 kg DM (dry mass) lichen ha⁻¹ in the year 2000 (Kumpula *et al.* 2004). This is only 9% of lichens in the maximum productive stage and 3% in the climax stage (Kumpula *et al.* 2000). However, the abundance of lichens varied to some extent between different aged forests in the actual lichen ranges, being 220 kg DM ha⁻¹ on average in felled areas and sapling stands, and 260 kg DM ha⁻¹ in young and mature cultivated forests and old-growth forests. Terrestrial lichens in submesic pine forests were less abundant with only 20 kg DM ha⁻¹ in felled areas and 150 kg DM ha⁻¹ in old-growth forests. In submesic felled areas grasses occurred in excess of 40 kg DM ha⁻¹ while in all other submesic pine forest types it was less than 5 kg DM ha⁻¹. Both dry (nutrient poor) and submesic old-growth forests also had clearly more arboreal lichens (mainly *Bryoria* sp.) than mature and young cultivated forests, although the index of arboreal lichen abundance varied from low to moderate in these forests. For obvious reasons, there were no or very little arboreal lichens in felled areas (Kumpula *et al.* 2003).

The climate of the study area is sub-arctic, characterised by a long and cold winter, and a short, relatively warm summer. Continuous snow cover occurs over a seven-month period, from October to May. Meteorological data obtained from the Ivalo Airport Station during 1971–2000

represents the average situation of the area relatively well (Drebs *et al.* 2002). During this period, the mean temperature of the coldest month, January, was –13.6 °C and the warmest month, July, +13.9 °C. The annual mean temperature was –0.8 °C. Annual precipitation was 435 mm and monthly values varied from 23 mm (January) to 66 mm (August). The maximum average snow depth, 67 centimetres, occurred in March.

The mean number of reindeer in winter, following the autumn slaughtering season in the Ivalo district during the last ten years has been 5500 animals (maximum number permitted is 6000 reindeer). The density of reindeer during winter was therefore 2.1 animals per km². During the study period, reindeer were herded in winter in two main herds with some differences in management system. In the southern and central areas, approximately 4000 reindeer were provided with supplementary feed (mainly pre-dried hay silage) from January to April. Feeding sites were always situated near cratering areas and reallocated in accordance with reindeer movements. In spite of systematic supplementary feeding, reindeer still acquired 2/3 of their nutrition from natural pastures (calculated from the daily amount of given feed). In the northern part of the district, supplementary winter feeding was used less frequently in a herd of 1500 reindeer.

GPS tracking of reindeer

From December 1999 to November 2002, we tracked 29 female reindeer in the Ivalo herding district using GPS collars produced by VECTORNIC Aerospace GmbH in Germany (model types GPS 2000 and GPS PLUS). Collar weights varied between 550 and 700 g depending on the model. In the autumn and winter round-ups, we installed the GPS collars on adult females whose calves were previously slaughtered. Collars were divided among the northern and central-southern herds in the same proportion as the relative size of the herds (7 collars *versus* 22 collars). The collars were programmed to measure the location of a reindeer with an interval of eight hours. We assumed that this interval was suitable for data collection on the basis of mobility of

reindeer as well as the battery capacity of GPS collars. The data was stored in the GPS memory and downloaded after retrieval of the collars. Due to problems in GPS engineering, primarily reduced battery life, the total amount of locations obtained with a GPS collar varied from 32 to 1075 locations. The oldest types of our collars were programmed to indicate accuracy of each location only as validated or invalidated, meaning that at least five satellites were available and the DOP value was below ten. For the study, we used only observations with a validated status. During the entire study period we received a total of 10 977 valid locations, 9229 of which were located on state land (Table 1).

Habitat types and habitat selection analyses

State land covers 85% of the total area in the Ivalo district. For the habitat selection analyses, we acquired digital forest stand and habitat-type maps from Metsähallitus (Finnish Forest and Park Service), which is responsible for the management of state land in Finland. These maps were originally created by delineating forest patches from aerial photographs and verified by field checking. The maps are updated annually by digitising all treated forest stands. The accuracy of these maps is not given, but it can be estimated that for forest age classes it is at least

Table 1. GPS locations of the study reindeer from December 1999 to November 2002. Number (*n*) and proportion (%) of locations in the state land per reindeer and seasonal period is reported.

Reindeer ID	November–January			February–April			May–October			Grand total
	Total	In state land	% in state land	Total	In state land	% in state land	Total	In state land	% in state land	
101	169	166	98.2	120	116	96.7	290	290	100.0	579
102	29	29	100.0	56	56	100.0				85
103A	25	25	100.0	152	142	93.4				177
103B	188	188	100.0	29	29	100.0	257	255	99.2	474
104A	30	30	100.0	178	170	95.5	4	4	100.0	212
104B				178	178	100.0	134	104	77.6	312
105A	31	31	100.0	192	156	81.2	195	175	89.7	418
105B				56	56	100.0	2	2	100.0	58
106A	29	29	100.0	242	241	99.6	247	205	83.0	518
106B	69	67	97.1				10	10	100.0	79
107A	26	26	100.0	167	62	37.1				193
107B	12	5	41.7	10	10	100.0	10	8	80.0	32
108A	167	154	92.2	196	178	90.8				363
108B	273	271	99.3	180	180	100.0	15	15	100.0	468
109A	153	2	1.3	144	2	1.4				297
109B				37	25	67.6	227	146	64.3	264
109C	243	239	98.4	176	176	100.0	461	436	94.6	880
110A	147	4	2.6	30		0				177
110B	275	266	96.7	86	86	100.0	367	318	86.6	728
203	284	255	89.8	261	232	88.9	530	432	81.5	1075
204	276	255	92.4	268	268	100.0	106	106	100.0	650
205	279	279	100.0	270	145	53.7	136	77	56.6	685
209	58	40	69.0							58
210	192	168	87.5	196	168	85.7	331	266	80.4	719
212	183	56	30.6	186	79	42.5	64	58	90.6	433
214	209	152	72.7	56	56	100.0				265
216	76	74	97.4	41	41	100.0	8	7	87.5	125
217	79	79	100.0	104	104	100.0	144	143	99.3	327
218	80	80	100.0	88	88	100.0	158	158	100.0	326
All	3582	2970	82.9	3699	3044	82.3	3696	3215	87.0	10977

90%, and the quality of the spatial content is estimated to be better than ten meters.

In the forest-type maps, the defined age classes for true forest types were: Felled area (approx. 0–10 yrs.), Sapling stand area (11–35 yrs.), Young cultivated forest (36–80 yrs.), Mature cultivated forest (81–140 yrs.), Forest stand with diverse age structure (in addition to the dominant old-growth tree layer, this forest type comprises a sub-layer of young trees) and Old-growth forest (at least 140 yrs., and often greater than 200 yrs.). Other defined habitat types were: Open forestland with low productivity (scrubby forestland where the annual growth rate of trees is $< 1 \text{ m}^3$ wood per year and which is mainly located at high elevation), Open land (land above the tree line), Mires, Gravel pits/forest roads/power lines and Water. The group, Gravel pits/forest roads/power lines, was primarily formed by forest roads. The original digital map was reclassified into 14 separate habitat classes (Table 2). The class, Forest stand with a diverse age structure, was combined with the Old-growth forest class. Also the classes, Open forestland and Open land, were combined into one habitat class (High-elevation open land/open forestland). All true forest classes were divided into two main categories according to the composition of the forest floor: either lichen domi-

nated or dwarf shrubs/grass dominated types.

On the basis of the constructed map, we calculated the area (ha) and the proportion (%) of different habitat classes on state land in the entire movement area for all study reindeer tracked (Table 2). We divided the GPS location data into three seasonal periods (November–January, February–April and May–October) (Fig. 2). It was not possible to make a more detailed seasonal division in our data due to restrictions of the statistical analysis techniques. We created Minimum Convex Polygon (MCP) home-range areas (Mohr 1947) for the entire roaming area of the study reindeer and separately for each reindeer in each seasonal period by employing the Animal Movement extension in ArcView 3.2 (Hooge & Eichenlaub 1997). To improve the accuracy of the analyses, we excluded all the reindeer home-range areas containing less than 50% of the total locations on state land or having fewer than 30 locations per seasonal period on state land. We then calculated the area and the proportion of different habitat classes in each accepted seasonal MCP. The distribution of GPS locations in different habitat classes in each seasonal MCP home-range area was calculated as a percentage.

In this work, preference/avoidance estimations of different habitat classes were based on

Table 2. Habitat classes with ID abbreviations obtained from the digital maps of Metsähallitus. Area (ha) and proportion (%) of classes in the entire roaming area for all reindeer studied on state land in the Ivalo district reported.

ID	Class type	Area	
		ha	%
FeLi	Felled area, lichen	4031	1.92
FeSG	Felled area, dwarf shrub/grass	8722	4.16
SaLi	Sapling stand area, lichen	21115	10.08
SaSG	Sapling stand area, dwarf shrub/grass	19924	9.51
YoLi	Young cultivated forest, lichen	5417	2.59
YoSG	Young cultivated forest, dwarf shrub/grass	12419	5.93
MaLi	Mature cultivated forest, lichen	1071	0.51
MaSG	Mature cultivated forest, dwarf shrub/grass	7585	3.62
OiLi	Old-growth forest, lichen	9469	4.52
OiSG	Old-growth forest, dwarf shrub/grass	55407	26.44
HiLa	High-elevation open land/open forestland	25781	12.30
Mire	Mires	24351	11.62
GRL	Gravel pits/forest roads/power lines	1624	0.78
Wate	Water	12611	6.02
	Total	209527	100.00

the log-ratio analysis method (Aitchison 1986) of statistical analysis of compositional data also referred to as Compositional Analysis. We applied Compositional Analysis with two-stage comparisons described by Aebischer *et al.* 1993 using the Compositional Analysis Excel tool ver. 4.1 (Smith 2003). Compositional Analysis is a technique that uses MANOVA to analyse two sets of data in which variables are represented as proportions. It is used to determine the statistical significance of differences and the rank order of differences between variables. The significance of Λ and t values were first determined by randomisation tests as recommended by Aebischer *et al.* (1993) to overcome problems arising when the distribution of log-ratio differences is not multivariate normal. If the random P value for Λ was smaller than 0.05, the habitat selection of reindeer was directly considered non-random, implying that reindeer either prefer or avoid certain habitat classes when selecting home-range area or when using habitats within the home range. In cases where the significance of randomisation test for Λ was $P > 0.05$, but the results from a less conservative Chi-square test seemed to be significant ($P < 0.05$), we briefly present results from the Chi-square test (*see also* Smith 2003).

To avoid the need to drop variables (e.g. habitat types) or cases (e.g. animals) when habitat availability for some of the cases is zero, the method recommended by Aebischer *et al.* (1993) was implemented, i.e. replacement of missing values in particular residual log-ratios by the mean of all non-missing values for that log-ratio and then computation of the mean Λ by weighting each denominator-dependent value of Λ by the number of non-missing values involved in its calculation, and determination of the level of significance by randomisation (Smith 2003). Correspondingly, in cases where the habitat was available but not utilised (or use of the habitat was so low that it could not be detected) meaning that ‘used’ data equalled zero, this zero value was substituted as recommend by Aebischer *et al.* (1993) by using a value of an order of magnitude smaller than the smallest recorded non-zero proportion in the data.

In the first stage of the analysis, the proportion of habitat classes in the entire roaming area

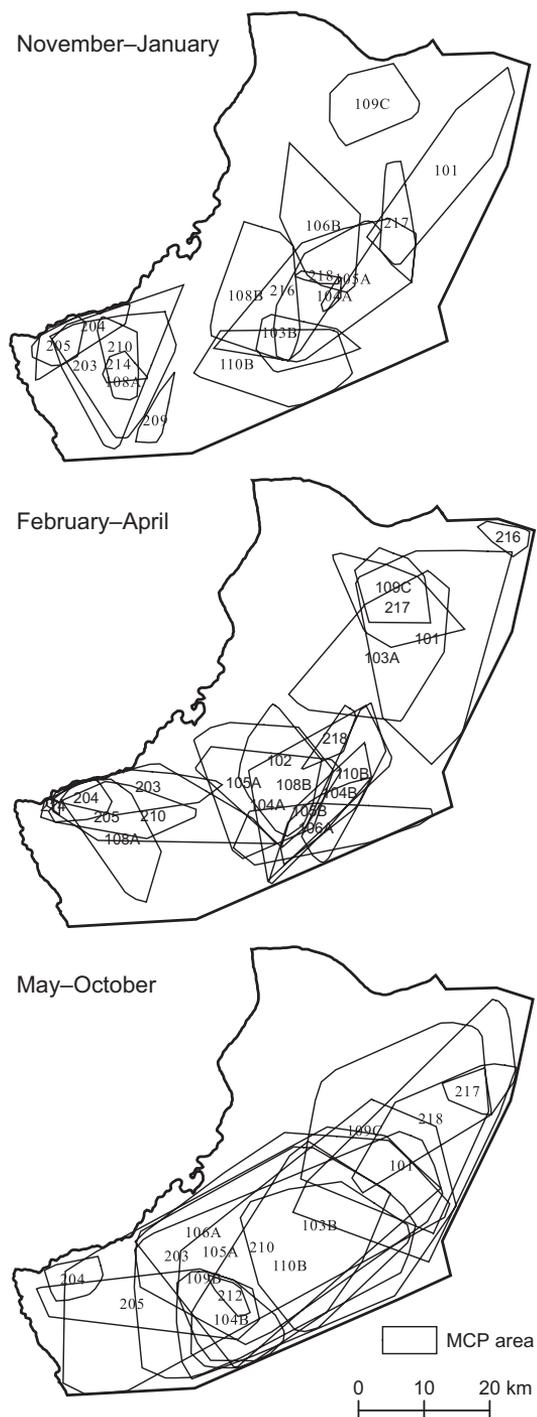


Fig. 2. Seasonal MCP areas of the study reindeer used in the compositional analysis.

for all reindeer (available) is compared with the proportions of these habitat classes within the

individual MCP areas (used) in each season. The first stage of analysis shows if reindeer favour or avoid some habitat or landscape classes when they select seasonal home-range areas. In the second stage of the analysis, the proportion of habitat classes inside the individual MCP areas (available) was compared with the distribution of GPS locations in habitat classes within the individual MCP areas (used) in each season. Thus, the second stage of analysis shows if reindeer still favour or avoid some habitat or landscape classes when they roam inside their seasonal home ranges.

Note that although the preference/avoidance of certain habitat or landscape classes could be very clear in the first stage of the analysis, it may not appear as strong in the second stage of the analysis. This is the result of the fact that reindeer have already been able to make such a clear choice in the composition of seasonal home-range area that the preference/avoidance is hidden in the second stage of analysis. In both stages of analysis the preference/avoidance was first analysed by using all 14 habitat classes (Table 2) and after that by combining all forestland classes according to the same development stage (age), resulting in nine habitat classes for the analysis. However, in the second stage of the analysis for the period May–October we excluded the class Water. After conducting all composition analyses, we calculated the mean proportion of different habitat classes in seasonal MCP areas and GPS locations in each seasonal period.

Effect of snow conditions on habitat selection

Snow conditions in various habitat types and in different areas were monitored at regular intervals during three consecutive winters (1999–2002) (Kumpula & Colpaert 2007). On the basis of these snow measurements and long-term snow data (see Kumpula & Colpaert 2003) we know that our GPS tracking period consisted of three winter seasons with different snow and digging conditions (difficult: 1999–2000; easy: 2000–2001 and normal: 2001–2002). Thus, our GPS tracking period covers all possible snow conditions and represents average snow condi-

tions in the study area. The number of locations per winter is limited and we were not able to analyse possible changes in habitat selection between winters. However, we could still detect the effect of snow conditions on habitat selection by comparing early-mid- and late-winter periods. Results from the analysis of the early-mid-winter period represent habitat selection in easy/moderate snow conditions while results from the late-winter period correspond to difficult snow conditions. On the basis of the analyses of our snow measurement data (Kumpula & Colpaert 2007), there were no essential differences in snow conditions between forest habitat classes during the winters 1999–2002. Noticeable differences in snow cover characteristics would probably affect the preference of forest habitat classes.

Results

Home range composition in three seasons

During the study period, the GPS tracked reindeer used 93.6% of the total land area in the Ivalo Reindeer Herding District. Of all locations, 84.1% were located on state land (Table 1). On the basis of size of seasonal MCP areas and the dispersions of GPS locations the reindeer were much more sedentary during the winter periods (November–April) than during the period from May to October (Figs. 2 and 3).

When all 14 habitat classes were used in the randomisation test for Λ , the preference of habitat classes in the selection of home-range area during November–January by the studied reindeer was random ($\Lambda = 0.143$, $df = 13$, $n = 18$, $P = 0.168$). However, the results from the less conservative Chi-square test, indicated differences in the preference of habitat classes when reindeer selected home-range area during November–January ($\chi^2 = 35.05$, $df = 13$, $P < 0.001$). The classes: Old-growth forest–lichen, Old-growth forest–dwarf shrubs/grass, and Mire obtained the highest three ranks; and the classes: Felled area–dwarf shrubs/grass, Sapling stand area–dwarf shrubs/grass, and Felled area–lichen the lowest three ranks (rank order: OILi > OISG > Mire > HiLa > YoLi > Water > MaSG > SaLi > MaLi > YoSG > GRL > FeLi >

SaSG > FeSG). Also, when using the randomisation test for Λ and combining forest classes with the same age in this period, the preference of habitat classes in the selection of home-range area was non-random ($\Lambda = 0.184$, $df = 8$, $n = 18$, $P = 0.004$). According to the pair-wise comparisons Old-growth forest obtained the highest rank, and Felled area and Gravel pits/forest roads/power lines the lowest ranks (Table 3).

During February–April the preference of habitat in the selection of home-range area by the study reindeer was non-random for all 14 habitat classes ($\Lambda = 0.059$, $df = 13$, $n = 20$, $P = 0.008$). The classes: Old-growth forest–lichen, Mire, and Old-growth forest–dwarf shrubs/grass obtained the highest three ranks; and the classes: Felled area–dwarf shrubs/grass, Felled area–lichen, and Sapling stand–dwarf shrubs/grass the lowest three ranks (rank order: OILi > Mire > OISG > MaLi > HiLa > MaSG > Wate > SaLi > GRL > YoLi > YoSG > SaSG > FeLi > FeSG). When forest classes of the same age were combined, the preference of habitat in the selection of home-range area during February–April was still non-random ($\Lambda = 0.184$, $df = 8$, $n = 20$, $P = 0.003$). In this test, the class Old-growth forest obtained the highest rank, and Felled area and Gravel pits/forest roads/power lines the lowest ranks (Table 4).

During May–October, the preference of habitat in the selection of home-range area was again non-random for all 14 habitat classes ($\Lambda = 0.004$, $df = 13$, $n = 15$, $P = 0.013$). The classes: Sapling stand area–lichen, Old-growth forest–lichen, and High-elevation land had the highest three ranks; and the classes: Mature forest–lichen, Felled area–dwarf shrubs/grass, and Felled area–lichen the lowest three ranks (rank order: SaLi > OILi > HiLa > Mire > OISG > Wate > SaSG > GRL > YoSG > YoLi > MaSG > FeLi > FeSG > MaLi). However, when forest classes of the same age were combined, the habitat preference in the selection of home-range area during May–October was random ($\Lambda = 0.283$, $df = 8$, $n = 15$, $P = 0.116$). In contrast, the Chi-square test indicated that the preference of habitat in the selection of home-range area during May–October could be non-random ($\chi^2 = 18.94$, $df = 8$, $P = 0.015$). Sapling stand areas obtained the highest rank value and Mature cultivated forest the lowest

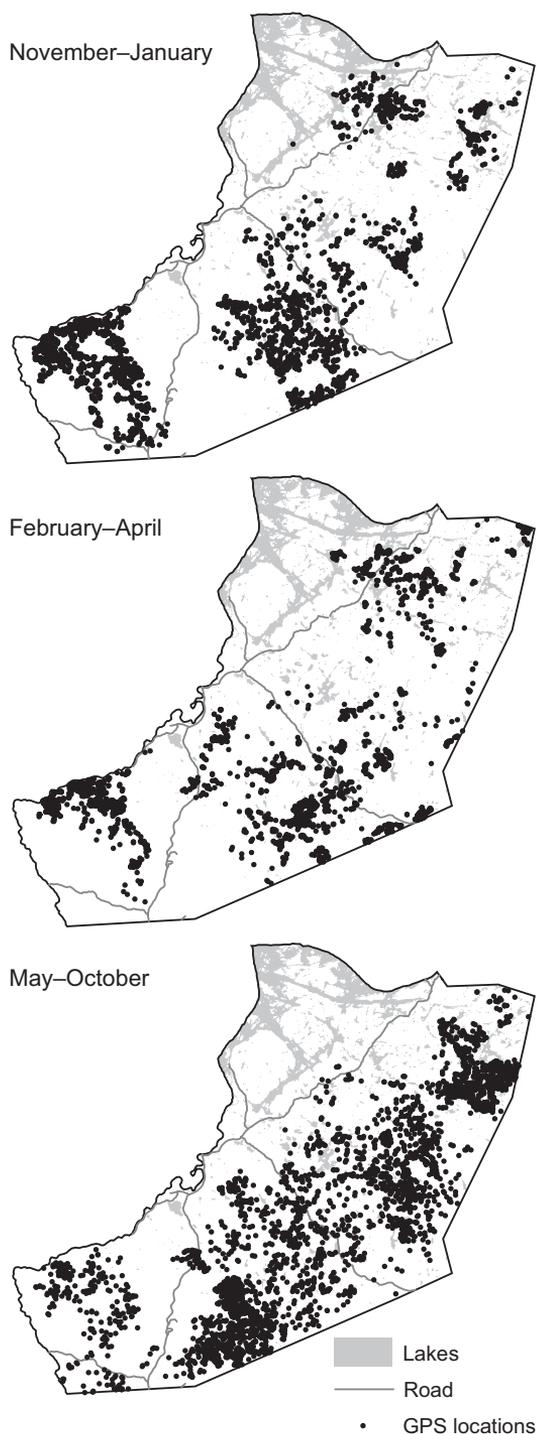


Fig. 3. GPS locations of the study reindeer in each seasonal period in the Ivalo Reindeer Herding District.

(rank order: Sa > HiLa > Mire > Ol > Yo > GRL > Wate > Fe > Ma).

Habitat selection within the home range

When moving inside home-range areas during November–January, the selection of habitat by

the study reindeer was random for all 14 habitat classes ($\Lambda = 0.097$, $df = 13$, $n = 18$, $P = 0.194$) and also for the combined nine classes ($\Lambda = 0.319$, $df = 8$, $n = 18$, $P = 0.097$). However, the Chi-square test again indicated that there could be some differences between habitat classes in the latter analysis ($\chi^2 = 20.55$, $df = 8$, $P = 0.008$), indicating the highest rank for Old-growth forest

Table 3. Preference and ranking matrices of combined habitat classes for reindeer in November–January in the first stage of compositional analysis where preference of habitat classes in the selection of home-range area was analysed (the entire roaming area for all reindeer versus individual MCP areas).

Numerator	Denominator									
	Fe	Sa	Yo	Ma	Ol	HiLa	Mire	GRL	Wate	Rank
Fe		-	—	—	—	-	—	-	-	0
Sa	+		-	-	-	-	-	+	-	2
Yo	+++	+		+	-	+	+	+++	+	7
Ma	+++	+	-		-	+	-	+	+	5
Ol	+++	+	+	+		+	+	+++	+++	8
HiLa	+	+	-	-	-		-	+	+	4
Mire	+++	+	-	+	-	+		+++	+++	6
GRL	+	-	—	-	—	-	—		-	1
Wate	+	+	-	-	—	-	—	+		3

$\Lambda = 0.184$, $df = 8$, $n = 18$, $P = 0.004$.

Rank order: Ol > Yo > Mire > Ma > HiLa > Wate > Sa > GRL > Fe.

+ represents higher preference by numerator, +++ represents significant deviation from random at $P \leq 0.05$; - and — have a reverse meaning.

> reports preference direction, >>> means significant difference between adjacent classes.

Fe = Felled area; Sa = Sapling stand area; Yo = Young cultivated forest; Ma = Mature cultivated forest; Ol = Old-growth forest; HiLa = High-elevation land; Mire = Mire; GRL = Gravel pits/forest roads/power lines, and Wate = Water.

Table 4. Preference and ranking matrices of combined habitat classes for reindeer in February–April in the first stage of compositional analysis where preference of habitat classes in the selection of home-range area was analysed (the entire roaming area for all reindeer versus individual MCP areas).

Numerator	Denominator									
	Fe	Sa	Yo	Ma	Ol	HiLa	Mire	GRL	Wate	Rank
Fe		-	-	-	—	-	—	—	-	0
Sa	+		+	-	-	-	-	+	-	3
Yo	+	-		-	-	-	—	+	-	2
Ma	+	+	+		-	+	-	+	+	6
Ol	+++	+	+	+		+++	+	+	+++	8
HiLa	+	+	+	-	—		-	+	+	5
Mire	+++	+	+++	+	-	+		+	+++	7
GRL	+++	-	-	-	-	-	-		-	1
Wate	+	+	+	-	—	-	—	+		4

$\Lambda = 0.184$, $df = 8$, $n = 20$, $P = 0.003$.

Rank order: Ol > Mire > Ma > HiLa > Wate > Sa > Yo > GRL >>> Fe.

For symbol explanations see Table 3.

and the lowest for Gravel pits/forest roads/power lines (rank order: Ol > Sa > Yo > Mire > Fe > Ma > HiLa > Wate > GRL).

During February–April the selection of habitat inside the MCP areas by the study reindeer was non-random for all 14 habitat classes ($\Lambda = 0.083$, $df = 13$, $n = 20$, $P = 0.024$). The classes: Old-growth forest–lichen, Old-growth forest–dwarf shrubs/grass, and equally Sapling stand area–dwarf shrubs/grass and Water obtained the highest three ranks; and the classes: Young cultivated forest–lichen, Felled area–dwarf shrubs/grass, and Felled area–lichen the lowest three ranks (rank order: OLi >>> OISG > SaSG = Wate >>> SaLi > GRL = MaSG > Mire > YoSG > HiLa > MaLi > FeLi > FeSG > YoLi). When forest classes of the same age were combined, the selection of habitat inside the MCP areas during February–April was still non-random ($\Lambda = 0.300$, $df = 8$, $n = 20$, $P = 0.015$). Old-growth forest clearly obtained the highest rank and Felled area the lowest rank (Table 5).

During May–October the selection of habitat inside the MCP areas by the study reindeer was random for all 13 habitat classes (class Water excluded) ($\Lambda = 0.062$, $df = 12$, $n = 15$, $P = 0.215$) and also for the eight combined habitat classes ($\Lambda = 0.312$, $df = 7$, $n = 15$, $P = 0.109$). However, the Chi-square test indicated that there could be some differences in the utilisation between habitat groups in the latter analysis ($\chi^2 = 17.46$, df

$= 7$, $P = 0.015$), giving the Mire class the highest rank value and the Gravel pits/forest roads/power lines the lowest (rank order: Mire > Sa > Ol > HiLa > Yo > Fe > Ma > GRL).

Utilisation of habitat classes

Two classes, Old-growth forest and Sapling stand area, were used most frequently during the winter months (November–April), although Old-growth forest clearly had a higher preference than Sapling stand areas (Figs. 4–5). Old-growth forest covered 31.0% of the total area in the entire roaming area for all reindeer. During the early-mid-winter, Old-growth forest consisted 31.6% of the individual MCP areas and during late winter 32.7%. The proportions of GPS locations in Old-growth forest during these two periods were 37.5% and 37.2%, respectively. Correspondingly, Sapling stand areas covered 19.6% of the combined roaming area for all reindeer and 19.9% and 23.2% of the individual MCP areas in the two winter periods, respectively. The proportions of GPS locations in Sapling stand areas during these two winter periods were 22.0% and 27.1%, respectively.

During May–October the proportions of Old-growth forest in the MCP areas and GPS locations decreased, while the proportion of Sapling stand areas clearly increased (Fig. 6).

Table 5. Preference and ranking matrices of combined habitat classes for reindeer in February–April in the second stage of compositional analysis where preference of habitat classes within home-range area was analysed (proportion of habitat classes within individual MCP areas versus GPS locations).

Numerator	Denominator									
	Fe	Sa	Yo	Ma	Ol	HiLa	Mire	GRL	Wate	Rank
Fe		—	-	-	—	-	—	—	—	0
Sa	+++		+	-	-	+	+	+	-	5
Yo	+	-		-	—	+	-	-	-	2
Ma	+	+	+		-	+	+	-	+	6
Ol	+++	+	+++	+		+++	+++	+	+++	8
HiLa	+	-	-	-	—		-	-	-	1
Mire	+++	-	+	-	—	+		-	-	3
GRL	+++	-	+	+	-	+	+		-	5
Wate	+++	+	+	-	—	+	+	+		6

$\Lambda = 0.300$, $df = 8$, $n = 20$, $P = 0.015$.

Rank order: Ol >>> Ma = Wate > GRL > Sa > Mire > Yo > HiLa > Fe.

For symbol explanations see Table 3.

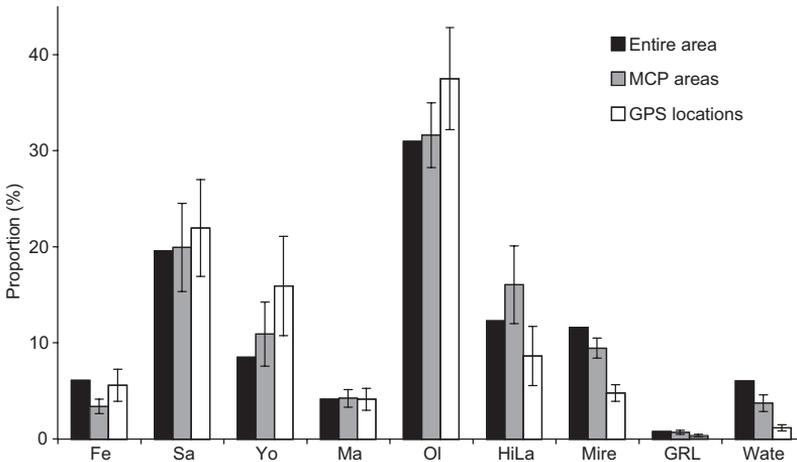


Fig. 4. Average proportions (%) \pm SE of different habitat classes during November–January in the entire roaming area for all reindeer, in seasonal home-range (MCP) areas, and in GPS locations within MCP areas.

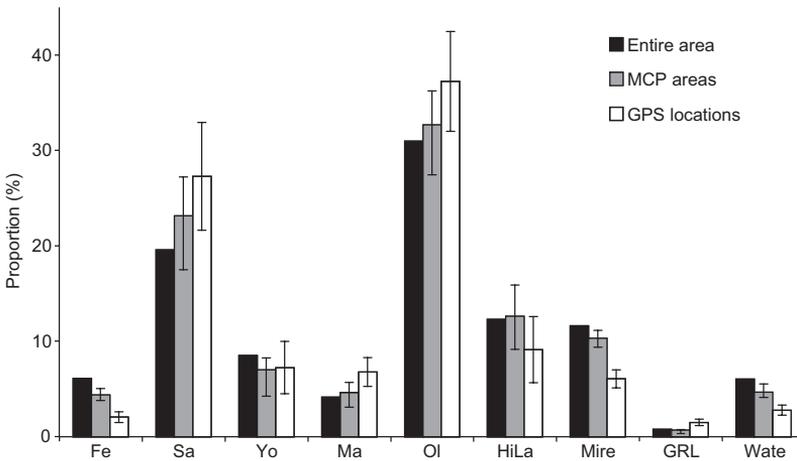


Fig. 5. Average proportions (%) \pm SE of different habitat classes during February–April in the entire roaming area for all reindeer, in seasonal home-range (MCP) areas, and in GPS locations within MCP areas.

Also, the proportions of High-elevation land and Mire both in the MCP areas and GPS locations increased markedly during May–October.

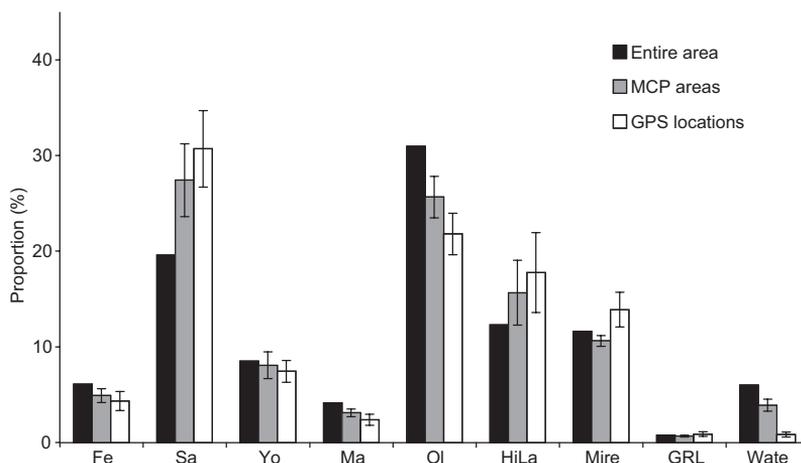
Discussion

This study shows that when reindeer selected a composition of home-range area in winter, the class Old-growth forest acquired the highest rank values while the classes Felled area and Gravel pits/forest roads/power lines the lowest. Furthermore, when reindeer used the late-winter home-range areas, Old-growth forest still gained highest rank value and Felled area lowest. Preference for old-growth forests and avoidance of felled areas were evidently caused by the availability of lichens, since according to a previous study made in the Ivalo district, both terrestrial

and arboreal lichens were most abundant in old-growth forests and scarce in felled areas (Kumpula *et al.* 2003). Besides lichen availability, reindeer probably also have difficulties digging in felled areas during winter since felled residue has been measured to cover 16%–39% of the total area after logging (Kumpula 2003). Also, the ground layer may suffer from mechanical harvesting and the soil is often treated for cultivation. It seems indisputable that old-growth forests have a special value for reindeer especially as late-winter habitat when snow conditions are usually harshest and reindeer have difficulties satisfying their energy expenditures.

In good pasture and grazing conditions, terrestrial lichens comprise 50%–80% of the reindeer and caribou winter diet, but if lichen pastures are scanty or heavily grazed, as in our study area, they possibly constitute only 30%

Fig. 6. Average proportions (%) \pm SE of different habitat classes during May–October in the entire roaming area for all reindeer, in seasonal home-range (MCP) areas, and in GPS locations within MCP areas.



of all winter food (Scotter 1967, Miller 1978, Russell & Martell 1984, Kojola *et al.* 1995). It is therefore evident in our study area that reindeer had to search for other food components (dwarf shrubs, grass and sedges as well as arboreal lichens) in order to satisfy their nutritional needs during winter. Traditionally, the winter nutrition of reindeer in this area has been based on terrestrial lichens (Helle & Tarvainen 1984), and the preference for terrestrial lichens still appeared in our data since terrestrial lichen-dominated old-growth forest acquired higher rank values than submesic old-growth forest at both stages of the compositional analysis. On the other hand, high rank value of submesic old-growth forest clearly indicated that reindeer also rely on arboreal lichens. The amount of arboreal lichens in the diet cannot be continuously high since there was only a limited amount of these lichens available to reindeer ($2\text{--}5 \text{ kg DM ha}^{-1} < 2 \text{ meter level}$) in old-growth submesic forests (Kumpula *et al.* 1997). However, this amount is frequently exceeded when winter storms sweep through the forest and arboreal lichens drop on the surface of the snow (Rominger & Oldemeyer 1991, Terry *et al.* 2000, Stevenson & Coxson 2003). Therefore the importance of arboreal lichens for reindeer's well-being is evident. Energy expenditures for browsing arboreal lichens are lower than energy expenditures for digging terrestrial lichens (*see* Boertje 1985). They also most likely facilitate the digging of other food plants, like dwarf shrubs and grasses, by providing extra energy and promoting the rumen fermentation

in reindeer, as terrestrial lichens do (Russell & Martell 1984, Aagnes *et al.* 1995).

The relatively high incidence and rank values of Sapling stand area and Young cultivated forest in the early winter home-range areas were probably related to easy snow conditions which allowed reindeer to dig food components richer in protein (*see* Adamczewski *et al.* 1988). In fact, dwarf shrubs and grasses/sedges may comprise nearly half of the winter diet of reindeer in our study area (Kojola *et al.* 1995) and there are plenty of sapling stand areas and young forests available to reindeer. Especially sapling stand areas where felling residue has already decomposed and where the growth of either lichens or grasses has already increased (*see* Colpaert *et al.* 1995, 2003, Kumpula 2003), have a relatively good usability value for reindeer, especially in early and mid winter. Sapling stand areas are even more important from spring to autumn when reindeer need a lot of protein and mineral rich green plants (Nieminen & Heiskari 1989). For the same reason, reindeer also used mires and high-elevation land. On the basis of the nutrition physiology and energy expenditures of reindeer (McEwan & Whitehead 1970, Soppela *et al.* 1992, Cuyler & Øritsland 1993, Aagnes *et al.* 1995), we suppose that especially in late winter reindeer that are able to obtain terrestrial or arboreal lichens at least to a certain degree, are also more capable of digging up other food components richer in proteins, like dwarf shrubs, grasses and sedges. On the other hand, supplementary winter feed offered by reindeer herders

may also provide extra energy enabling reindeer to dig and gain access to other terrestrial vegetation.

Helle (1981) observed that wild forest reindeer (*Rangifer tarandus fennicus*) in Finland frequented ice-covered lakes. The reindeer in this study also spent a relatively large amount of time on ice-covered lakes in late winter since the class Water received an intermediate rank value during that season. This behaviour can partly be related to the hereditary adaptation of reindeer to observe and avoid predators, but it is more likely that reindeer only rested on lake ice in the mild late-winter weather and in this way reduced their energy expenditures (*see* Cuyler & Øritsland 1993). On the contrary, during May–October, reindeer preferred high-elevation open (and windy) land which was probably partly caused by the avoidance of insect harassment. Especially during the warmest summer season, insect harassment may cause considerable stress and energy loss for reindeer (Mörschel & Klein 1997, Skarin *et al.* 2004).

A distinct avoidance of infrastructure (e.g., roads, settlements, mineral exploration, power and pipe lines) has been documented for caribou (Bradshaw *et al.* 1998, Dryer *et al.* 2001, 2002, Johnson *et al.* 2005) and for both wild and semi-domesticated reindeer (Vistnes & Nellemann 2001, Vistnes *et al.* 2001, 2004, Nellemann *et al.* 2003). Nevertheless, it has also been observed that caribou and reindeer may somehow adapt to infrastructure and human disturbance (Noel *et al.* 2004, Skarin *et al.* 2004). We observed that the class Gravel pits/forest roads/power lines received very low rank values when reindeer selected home-range areas during the winter periods, but not during the period from spring to autumn. From the seasonal home ranges it appears that this class was lowly ranked especially in early winter. It is likely that reindeer prefer winter habitat with little linear infrastructure and perturbations such as forest roads or power lines. Besides the fact that these landscape classes are of limited nutritional value, the reason of avoidance is likely human disturbance. Forest roads in the Ivalo district are open for all traffic in early winter and there is also snowmobile and dog sledge traffic on these roads and along power lines, which may

cause considerable disturbance for reindeer and reindeer herding. This disturbance probably also increases the energy expenditure of reindeer. In late winter, disturbance is decreasing when snow accumulation closes many roads. Additionally, reindeer herders commence supplementary feeding along forest roads. In deep snow, reindeer can also use snowmobile tracks along roads and power lines as these form a suitable track for their movement. Similarly, during the summer season, when reindeer continuously migrate over large areas, human disturbance is probably not as important as during winter (Skarin *et al.* 2004) and forest roads may even offer some relief from insect harassment.

The ability to balance the energy budget by fulfilling minimum energy expenditures and saving energy is very important for the successful wintering of reindeer (McEwan & Whitehead 1970, Soppela *et al.* 1992, Cuyler & Øritsland 1993). Lichens contain a lot of easily digestible carbohydrates (Russell & Martell 1984, Nieminen & Heiskari 1989) and a diet containing lichens is effectively fermented by reindeer and it also promotes the digestion of other plant fibre in the rumen (Aagnes *et al.* 1995). Reindeer utilising a lichen-rich diet have a lower thermal energy cost of daily water intake than reindeer utilising a protein rich diet (Soppela *et al.* 1992). On the basis of the Optimal Foraging theory (MacArthur & Pianka 1966, Pyke *et al.* 1977), we can therefore assume that reindeer living in lichen woodland areas should prefer habitat abundant in lichens and avoid lichen-poor habitat. The foraging process of ungulates with various energetic benefits and expenditures (searching, obtaining, handling and fermentation of food) has been modelled e.g. by Fryxell (1991), Murray (1991) and Bergman *et al.* (2001). However, there are also other energetic costs like weather, biting insects and disturbance, than those caused by the foraging process itself. Therefore a model of net energy balance for explaining foraging behaviour and population dynamics of large herbivores has been proposed (Armstrong & Robertson 2000). On the basis of this model, we can present a more focused hypothesis for habitat selection by reindeer. In a sedentary grazing system (like our study area) with few predators and intensive grazing and logging, small energetic benefits and

expenditures caused by winter range quality and human disturbance primarily control home range and habitat selection by reindeer.

We conclude that old-growth forest is a very important habitat for reindeer in lichen woodland, especially in late winter. Various kinds of human perturbations and activities may also cause substantial disturbance to reindeer and reindeer herding during winter. Therefore, maintaining a certain amount of old-growth forest and, at the same time, minimising infrastructure construction and disturbance in winter ranges, considerably improves the suitability of these ranges. However, besides old-growth forest, reindeer utilise and require various other habitat types, each of which may offer a certain food, shelter or relief during a specific seasonal period. In managed forests, sapling stand areas especially provide a significant part of the seasonal nutritional requirements for reindeer. Still, the main concern in terms of reindeer herding comes from the fact that it is very difficult to maintain a satisfactory amount of old-growth conifer forest within important winter ranges in intensively harvested forest areas (*see e.g. Kyllönen & Raitio 2004, Kyllönen et al. 2006*). It is essential to realize that the increasing multidimensional targets in land use practices do not necessarily mean the reduction of combined benefits, not even when measured purely as an economic value (Bosted *et al.* 2003, Zhou & Gong 2004, Kyllönen *et al.* 2006).

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