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Habitat use by semi-domesticated reindeer, estimated with pellet-group counts

Anna Skarin

Swedish University of Agricultural Sciences, Reindeer Husbandry Unit, P.O. Box 7023, S-750 07 Uppsala, Sweden (anna.skarin@rene.slu.se).

Abstract: Habitat selection theory predicts that herbivores should select for or against different factors at different spatial scales. For instance, quantity of forage is expected to be a strong factor influencing habitat choice at large scales, while forage quality may be important at finer scales. However, during summer, herbivores such as reindeer (*Rangifer tarandus tarandus*) can be limited in their grazing time by insect harassment, and do not always have the possibility to select for high quality forage. Human disturbances from hikers, etc., can also have a limiting effect on the possibility for reindeer to graze in high quality foraging habitats. Reindeer habitat selection at the landscape level was investigated through faecal pellet-group counts during the summers of 2002 and 2003 in two reindeer herding districts in Sweden. Resource utilization functions (RUFs) were developed using multiple linear regressions, where the pellet densities were related to vegetation types, topographic features, distances to tourist resorts, and distances to hiking trails. Validations of the models were performed through cross-validation correlations. Results show that high altitudes with high quality forage were important habitats. Areas that offer both snow patches and fresh forage plants for the reindeer were used in relation to their availability. The reindeer also seemed able to habituate to human intervention to a certain extent. The predictive capabilities of the RUF models were high and pellet-group counts seemed well suited to study how abiotic factors affect the habitat use at large temporal and spatial scales.

Key words: disturbance, insect harassment, multiple linear regression, landscape level, ungulates.

Rangifer, 27 (2): 121-132

Introduction

The Fennoscandian mountain range is the predominant grazing area for semi-domesticated reindeer (*Rangifer tarandus tarandus*) during the snow-free season. There are few large-scale habitat studies performed earlier on reindeer in these areas (e.g. Skogland, 1984). The Swedish Government has declared that the Swedish mountain ecosystem should be managed with a sustainable perspective, which includes preserving the characteristics of a grazed landscape, the long-term productive capacity, biological diversity and natural, cultural and recreational assets (Prop. 2000/01:130). In these contexts, it is important to gain knowledge about the landscape use by reindeer and identify the general habitat use at the large spatial scale.

Based on hierarchical foraging theory (Johnson, 1980; Senft *et al.,* 1987), animals are predicted to select habitats that permit avoidance of the most limiting factor at large spatial scales, while influences of less important factors should only be evident at finer scales (Rettie & Messier, 2000; Dussault *et al.,* 2004). It is known that *Rangifer* avoid predators (Rettie & Messier, 2000) and select forage quantity (Mårell *et al.,* 2002) at large spatial scales, and select patches with forage of high nutritive quality at finer scales (Johnson *et al.,* 2001; Mårell *et al.,* 2002). Other known limiting factors for reindeer and caribou in the snow-free season are harassment from insects such as oestrid flies and mosquitoes (Downes *et al.,* 1986; Hagemoen & Reimers, 2002; Colman *et* *al.,* 2003). Thus, at the larger spatial scales there should be a selection against areas with high levels of insect harassment. *Rangifer* can also respond negatively to human activities, especially during the calving season (Nellemann & Cameron, 1996; Vistnes & Nellemann, 2001; Frid & Dill, 2002). However, it is uncertain how important human activities are and at which scale they interact with reindeer habitat selection. It has been suggested that insect harassment may override human disturbances at the landscape level (Pollard *et al.,* 1996; Skarin *et al.,* 2004).

In summer, the reindeer prefer rich and nutritive forage and follow the receding snowline to explore the early stages of plant-growth (Skogland, 1984). In June and July they prefer new-growth forage such as leaves and floral parts of shrubs, forbs and grasses in heaths, meadows and grass heaths (Skogland, 1984; Klein, 1990). In August they shift to forage more grasses and sedges in mires. According to Skogland (1984) the meadows in the low-middle alpine region seem to be the most preferred vegetation type throughout the summer.

Several techniques are available for surveys of animal habitat selection, e.g. using GPS collars for registration of positions of individual animals, flight observations, and faecal pellet-group counts. Pellet-group surveys have the advantage that the overall animal abundance over several months is captured at a large spatial scale, with a concentrated recording effort (Marques *et al.,* 2001). Another benefit is that habitat attributes, such as vegetation type, can be registered simultaneously at the same spatial scale as pellet abundance. A large number of habitat selection studies on large herbivores have used faecal pellet-group counts to collect data on habitat use (e.g. Neff, 1968; Guillet *et al.,* 1995; Härkönen & Heikkilä, 1999), compared with only a few investigations performed on *Rangifer* (Helle & Särkelä, 1993; Quayle & Kershaw, 1996; Teterukovskiy & Edenius, 2003; Skarin *et al.,* 2004).

Faecal standing crop (FSC) and faecal accumulation rate (FAR) are two basic approaches to estimating pellet-group density (Campbell *et al.,* 2004; Hemami & Dolman, 2005). In the FSC method, the pellet group density is measured on a first visit to a plot and related to a known pellet-group decay rate. In the FAR method, the pellet-group accumulation over a fixed time period is measured in previously cleared plots, and therefore there is no need to estimate the decay rate of the pellet groups. With both techniques, defecation rate is needed for calculation of the absolute animal abundances in the area. If defecation rate is not available, the relative abundance in the different habitats can be used (Neff, 1968; Van der Wal *et al.,* 2001). Campbell *et al.* (2004) found that the FSC method is generally less precise and cost effective than the FAR technique.

The aim of this paper was to investigate how vegetation type, altitude, direction of slope, ruggedness, hiking trails, tourist resorts and huts affect habitat selection by reindeer at the landscape scale within two different summer ranges. The predictive capacity of a habitat model based on a faecal pellet-group count was also evaluated. The faecal pellet-group count was performed using both the FSC and the FAR techniques.

Materials and methods

Study area

The study was performed in the summer ranges of two reindeer herding districts in the Scandinavian mountain range: *Handöl* (63°00'N; 12°30'E), situated in the *Handölsdalen* reindeer herding district, and *Vaisa* (67°40'N; 17°00'E), located in the *Sirges* reindeer herding district (Fig. 1). Within these areas the reindeer graze freely from May to October, with exception for the calf marking period, when the reindeer are gathered by the reindeer herders.

The size of *Handöl* is about 1700 km^2. The elevation ranges from 500 m to the highest peaks, *Helags* at 1796 m and *Sylarna* at 1761 m. The annual precipitation is 700–1300 mm, mean temperature in July is 10 °C, and the vegetation period (temp > 5 °C) was 120–130 days during the years 1961–1990 (National Land Survey of Sweden, 2002). The vegetation is dominated by heaths, ranging from wet to extremely dry (Table 1). The area is popular for back-country hiking, and within the area there are three mountain stations and four tourist huts, with main trails leading to them (Vuorio, 2003).

Vaisa has a size of 900 km^2 and is situated on a high plateau, with elevations mostly ranging between 500 m and 1000 m and with the highest summit (*Rautåive*) at 1516 m. The annual precipitation is 900–1500 mm and the mean temperature in July is 9 °C (1961–1990). The vegetation period (temp > 5 °C) is 100–110 days (1961–1990). The dominating vegetation types are heaths, meadows, grass heaths, bare rock and sparsely vegetated areas (Table 1). There are three tourist lodges in the southeast part of the area. Besides that, the area is sparsely used for back-country hiking or human activities other than reindeer husbandry.

Pellet-group counts

The pellet-group counts were performed during two summer seasons. The FSC was inventoried between 18 June and 3 July 2002 at 305 points in *Handöl*, and from 17 to 30 August at 218 points in *Vaisa*.

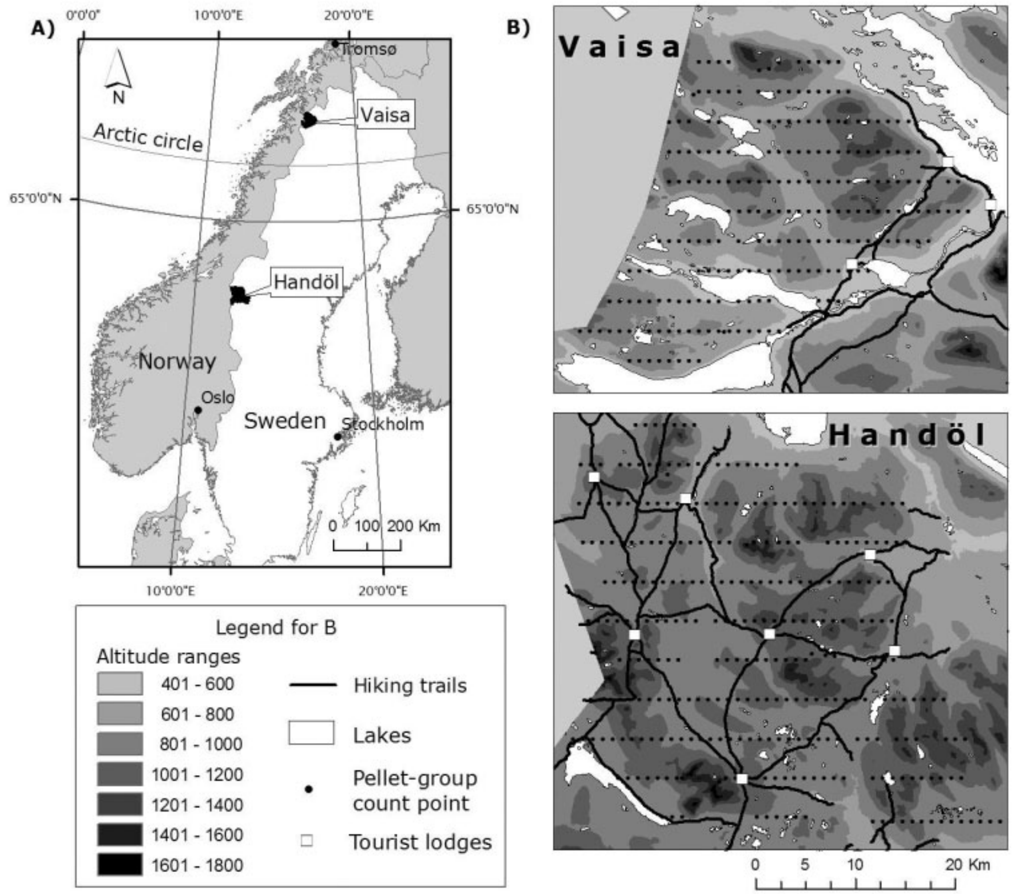

Fig. 1A-B. A. The two study areas *Handöl* and *Vaisa* localized in Sweden, near to the Norwegian-Swedish national border. B. The two study areas shown with altitude ranges, hiking trails and tourist lodges (key to symbols at bottom left). The inventory points for the pellet-group counts are marked with dots in the transect lines. ©Lantmäteriet Gävle, 2006. Permission I 2006/1611.

The FAR was conducted in 2003 in *Handöl* between 23 June and 8 July, and in *Vaisa* between 11 and 21 August. Thus, in *Handöl* the FSC from 2002 represents the habitat use in the summer of 2001 and previous summers, and the FAR counts from 2003 represent the habitat use after counting in 2002 and the early parts of the snow-free season in 2003. In *Vaisa*, the FSC counts from 2002 include most of the habitat use in the summer of 2002 and previous summers, and the FAR counts in 2003 represent the use during 2003.

In the pellet-group counts, a point transect survey design was used (Buckland *et al.,* 2001). The distance between each transect was 4 km in *Handöl*, and 3 km in *Vaisa* (Fig. 1). The distance between the points on each transect was 1 km. At each point, 75 m^2 was inventoried in five circular plots of 15 m^2 (radius = 2.18 m): one in the centre, and one in each cardinal point of the compass, 20 m from the centre plot. The coordinates of the centre plots were registered, and the centre of each plot was marked with a small orange wooden stick. The pellet groups were counted and removed from the plots the first year. To be counted, the centre of the pellet group had to be inside the plot. As the animals often move when they defecate, pellets could be spread over a large area or separated in smaller groups. If there were less than 20 pellets in a group, the separate pellets were counted instead.

Prior to the statistical analyses, the sum of the pellet groups at each point was converted into separate pellets, using an estimated mean number of pellets per pellet group (127 ±7, estimated by counting pellets in 34 pellet groups sampled in the field). The distribution of the pellets m^{-2} was assumed to be negative binomial. A square root transformation of the pellet data was therefore done after adding 1 to the observations, in order to approach a normal distribution.

Habitat variables

All spatial data were handled with Arc GIS 9.0™ software (ESRI Inc., © 1999–2004). The digitized geographical data were provided from Lantmäteriet (http://www.lantmateriet.se), which distributes national geographic and land information data. Habitat variables initially derived for each pellet-group point were vegetation types (defined for each plot), vegetation diversity, topographic features (altitude, slope, direction of slope, and ruggedness), and the shortest distance to a tourist resort or hut and to a hiking trail. The vegetation at each plot (Table 1) was classified in the field according to the categories used in the Swedish vegetation map (von Sydow 1983). When a plot contained a mixture of vegetation types, the dominant type was noted. To make the results in *Handöl* and *Vaisa* comparable, vegetation types that only were represented in one study area were, if possible, merged with a similar vegetation type represented in both areas. To test if the number of different vegeta-

Table 1. Distributions of vegetation types at the inventory plots, observed percentages of pellets within each vegetation type and mean altitudes, with standard deviations (SD) for each vegetation type.

		Handöl					*Vaisa*				
		Veg. type	Pellets (%)		Altitude (m)		Veg. type	Pellets (%)		Altitude (m)	
Vegetation zones[a]	*Vegetation type*[a]	(%)	FSC	FAR	mean	±SD	(%)	FSC	FAR	mean	±SD
High alpine region (starts above 1200–1600 m)[b]	Bare rock and bed-rock outcrops	6.1	3.05	2.44	1260	(142)	15.13	8.85	6.00	1003	(142)
Middle alpine region (starts above 1100–1300 m)[b]	Extreme snow bed	-	-	-	-	-	2.03	2.17	0.31	1042	(157)
	Moderate snow bed	7.0	8.01	6.89	1114	(108)	28.51	28.33	27.85	898	(130)
	Extremely dry heath	15.1	16.88	16.46	1077	(121)	10.24	17.64	18.05	888	(143)
	Grass heath	5.8	8.39	6.36	1044	(109)	5.35	6.84	7.31	839	(122)
Low alpine region (starts above 600–950 m)[b]	Meadow with low herbs	5.0	6.68	5.67	993	(97)	4.52	4.13	4.55	790	(67)
	Meadow with tall herbs	0.3	0.29	0.44	867	(68)	-	-	-	-	-
	Dry heath	28.8	35.73	38.09	980	(88)	16.88	26.16	24.65	752	(113)
	Fresh heath	9.6	8.27	8.23	910	(60)	6.00	1.44	5.54	628	(84)
	Wet heath	3.6	1.60	2.66	911	(76)	0.37	0.00	0.00	695	(130)
	Willow thickets	0.6	0.47	0.42	932	(62)	2.40	0.51	1.55	674	(129)
	Dry fen	5.1	2.97	3.99	921	(86)	4.80	3.03	3.47	719	(115)
	Wet fen	0.8	0.42	0.65	891	(71)	-	-	-	-	-
	Sloping fen	0.6	0.39	0.34	880	(109)	-	-	-	-	-
	Bog and fen hum-mock vegetation	2.5	1.48	0.90	865	(79)	0.65	0.14	0.22	634	(103)
	Mosaic mire	1.7	0.16	0.28	888	(72)	0.28	0.02	0.00	546	(9)
Birch forest region (starts above 400–800 m)[b]	Birch forest – heath type w/ lichens	0.1	0.02	0.04	955		0.18	0.07	0.00	-	-
	Birch forest – heath type w/ mosses	2.0	0.71	1.15	778	(38)	-	-	-	580	(99)
	Birch forest – meadow type w/ tall herbs	0.5	0.00	0.40	778	(41)	1.29	0.66	0.50	569	(55)
	Other	4.8	4.48	4.55	-	-	1.38	0.00	0.00	-	-

Note: The faecal standing crop (FSC) counts were conducted in 2002, and the faecal accumulation rate (FAR) counts in 2003.
[a] Classification according to the Swedish vegetation map (von Sydow, 1983).
[b] Range for zone borders in northern and southern mountain regions, respectively.

tion types found at each plot within an inventory point had any effect on the pellet-group density, a vegetation diversity index was defined as the number of different vegetation types found at each inventory point. Thus, there could not be more than five classes (one for each plot) at one point; therefore the index was maximised to 5. The topographic measures of ruggedness, degree of slope, direction of slopes, and altitude were generated from a digital elevation model with a resolution of 50 m. The ruggedness was quantified with an index (1–59) that expresses the elevation differences between adjacent cells of a digital elevation grid (Riley *et al.,* 1999). The direction of slope was divided into four classes northwest, northeast, southwest and southeast, (each class was 90° wide). The distances to the nearest hiking trail and to the nearest tourist resort or hut from each inventory point were used to quantify disturbances from human activities on reindeer habitat selection.

Habitat selection models

Resource utilization functions (RUFs) were developed using multiple linear regressions of the number of pellets m^{-2} at each inventory point on the habitat attributes (Marzluff *et al.,* 2004). The regression analyses were performed with SAS 8.2 software (SAS Institute Inc., © 1999–2001). Separate regression models were fitted, one for each year and area. To avoid co-linearity and to obtain the most parsimonious models (Burnham and Anderson 2002), the set of habitat variables was reduced according to five different criteria. Continuous independent variables were first evaluated for independence using Pearson correlations. When two variables were highly correlated ($r > 0.5$), one of them was deleted. The appropriateness of the included remaining variables in the models was evaluated based on significance of regression coefficients, Akaike's information criterion (Akaike, 1973) with difference for small samples ($AIC_C\ \Delta$), AIC_C weights (w), and the determination coefficient of the models (R^2). The models with the highest R^2 values included the following independent variables: vegetation type, vegetation diversity, altitude, altitude squared, ruggedness index, direction of slope, distance to tourist resort or hut, and distance to hiking trail (only the RUF-models based on the *Handöl* survey). The altitude and the class variables vegetation type and direction of slope were always included in the models. This gave 32 models remained to be evaluated on $AIC_C\ \Delta$ -values in each of the two model sets of *Handöl* and the 16 models in sets of *Vaisa*. The models were evaluated based on AIC_C weights, which were calculated in relation to all models in each set (Burnham & Anderson, 2002). The models for each year and area with the highest AIC_C weights were chosen as the final RUF models.

Model validation

The selected RUF models were validated with Spearman rank correlations computed between the observed and the predicted pellet density. Predictions of pellet density were calculated with the fitted RUF from one area and the habitat data from the other area. This resulted in four correlations to evaluate, one for each RUF-model.

Results

Comparison between years

The percentage of pellet groups in the vegetation types did not differ between the years (Table 1 and Fig. 2). A chi-square test indicated that the percentages of pellets in each vegetation type were randomly distributed (χ^2 (20) < 0.97 for both years and areas). The mean number of pellets in *Handöl* was 5.67 pellets m^{-2} and 3.74 pellets m^{-2} in the FSC and the FAR count, respectively. In *Vaisa*, it was 6.02 pellets m^{-2} in the FSC count and 5.72 pellets m^{-2} in the FAR count. The number of pellets m^{-2} in the FAR count was naturally lower. However, in *Vaisa* there was a smaller difference between the years.

Habitat selection

Independent variables in the final RUF model based on FSC counts in *Handöl* were vegetation type, direction of slope, altitude, altitude squared, distance to tourist resort or hut, distance to hiking trail, and ruggedness. In *Vaisa* the same model included these variables except distance to hiking trail (Table 2). In the RUF-model based on FAR counts done in *Handöl* vegetation type, direction of slope and altitude was included, and in the RUF for Vaisa these variables together with altitude squared and distance to tourist resorts or huts were included.

The estimated RUF coefficients (Table 3) showed that the use by reindeer increased with altitude. However, in the models including altitude squared the reindeer utilisation abundances increased asymptotically towards a certain altitude. Using the FSC counts, the use declined above 1250 m in *Handöl* and above 950 m in *Vaisa*. Using the FAR counts in *Vaisa*, it declined above 800 m. Thus, the low-middle alpine zones were preferred while the highest altitudes in the high alpine zones were not preferred. Further, the pellet densities in the FSC counts in *Handöl* were lower in rugged terrain. The FSC counts in *Handöl* showed that the reindeer preferred areas closer to hiking trails, but also that the reindeer avoided areas near tourist resorts or huts. In *Vaisa* the reindeer had a preference for areas closer to tourist resorts and huts. The only significant response to vegetation types in the FSC counts was the preference for *grass*

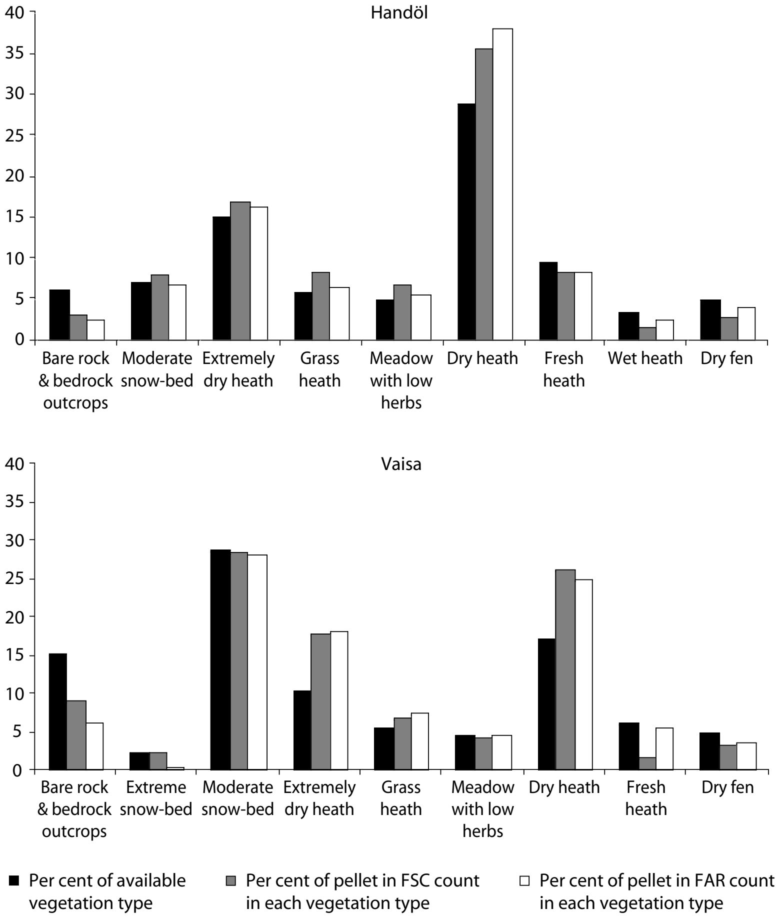

Fig. 2. Per cent available vegetation type and per cent pellets from the FSC count and FAR count in *Handöl* and *Vaisa* respectively. The histograms only show the vegetation types were the availability exceeded two per cent.

heaths and *meadows* and the avoidance of *dry heaths* and *mosaic mires* in *Handöl*. However, the RUF based on the FAR counts showed that the reindeer in *Handöl* avoided *bare rock and bedrock outcrops* which occur mainly within the high alpine zone. In *Vaisa* the reindeer preferred *grass heaths*, *dry heaths* and *extremely dry heaths*. All the preferred vegetation types were within the low to middle alpine zones, thus corresponding to the preferred altitudes.

Model Validation

When predicting the pellet distribution in Handöl with the Vaisa RUF based on FSC counts, the Spearman rank correlation was $r = 0.36$ ($P < 0.0001$), while it was $r = 0.42$ ($P < 0.0001$) when using the *Handöl* RUF for prediction of *Vaisa* pellet distribution. When predicting the FAR distributions with the RUF models, the correlations were $r = 0.39$ ($P < 0.0001$) for the *Handöl* RUF, and $r = 0.27$ ($P < 0.0001$) for the *Vaisa* RUF.

Discussion

The fitted RUFs clearly confirmed that the reindeer have a strong preference for rather high altitudes in the low-middle alpine region throughout the snow-free season. Explanations for this may be insect harassment, predator vigilance, higher forage quantity and quality at higher altitudes, and possibly strengthen by a bias caused by irregular defecation rates and differences in pellet-group decay rate. Reindeer, being *Cervids* and ruminants, tend to follow regular cycles of consumption, rumination, and defecation (Russell *et al.,* 1993; Skogland, 1984). However, for some deer species (e.g., mule deer, *Odocoileus hemionus*), it has been questioned whether the defecation rate is constant over time and whether pellet groups represent how much time the animals actually spend in different habitats (Collins & Urness, 1981; Neff, 1968). Quayle and Kershaw (1996) suggested that the high densities of caribou pellet groups at high altitudes depended on the caribou resting and ruminating at the sum-

Table 2. Included independent variables in the candidate RUF regressions models for each survey method (faecal standing crop (FSC) and faecal accumulation rate (FAR)) and area, number of parameters (*k*), the coefficient of determination (R^2), difference among AIC_C scores (AIC_C Δ), and AIC_C weights (*w*), only the models with AIC_C Δ < 2 are shown (Burnham & Anderson, 2002).

	Veg [a]	Asp [b]	Alt [c]	Alt^2 [d]	TRI [e]	Resort [f]	Trail [g]	Div [h]	*k*	R^2	AIC_C Δ	w
FSC												
Handöl	×	×	×	×	×	×	×		21	0.342	0	0.354
	×	×	×		×	×	×		20	0.335	1.222	0.192
	×	×	×	×	×	×	×	×	22	0.342	1.948	0.134
Vaisa	×	×	×	×	×	×	-		20	0.464	0	0.388
	×	×	×	×		×	-		19	0.457	0.757	0.266
	×	×	×	×	×	×	-	×	21	0.466	1.272	0.206
FAR												
Handöl	×	×	×						17	0.207	0	0.081
	×	×	×		×				18	0.212	0.223	0.073
	×	×	×					×	18	0.212	0.305	0.070
	×	×	×		×			×	19	0.217	0.349	0.068
	×	×	×	×					18	0.211	0.557	0.061
	×	×	×	×	×				19	0.216	0.824	0.054
	×	×	×	×				×	19	0.214	1.260	0.043
	×	×	×				×		18	0.209	1.322	0.042
	×	×	×	×	×			×	20	0.219	1.364	0.041
	×	×	×				×	×	19	0.213	1.664	0.035
	×	×	×		×		×		19	0.213	1.767	0.034
	×	×	×		×		×	×	20	0.218	1.934	0.031
	×	×	×	×			×		19	0.213	1.974	0.030
	×	×	×			×			18	0.207	1.989	0.030
Vaisa	×	×	×	×		×	-		19	0.363	0	0.271
	×	×	×	×	×	×	-		20	0.368	0.318	0.231
	×	×	×	×		×	-	×	20	0.364	1.692	0.116
	×	×	×	×	×	×	-	×	21	0.369	1.993	0.100

[a] Veg = vegetation type; [b] Asp = direction of slope (aspect); [c] Alt = altitude; [d] Alt^2 = altitude squared; [e] TRI = terrain ruggedness index; [f] Resort = distance to tourist resort or hut; [g] Trail = distance to hiking trail; [h] Div = diversity index.

mits, and that they then defecated as they rose and walked away from the resting site. However, in a study of 48 GPS-collared reindeer partly in the same areas as in this study, the reindeer had high movement rates both at high altitudes and at low altitudes, and seemed not to use high altitudes for rest more exclusively than low altitudes (Skarin, 2006). Differences in pellet-group decay rates between different types of substrates might also have biased the results. However, the majority of the study areas (>75 %) consisted of vegetation types, where no or very small difference in decay rate between vegetation types can be assumed (Skarin, submitted).

Other studies have shown that reindeer as well as other ungulates seek insect avoidance at high altitudes and at wind-exposed sites (Downes *et al.,* 1986;

Hagemoen & Reimers, 2002; Skarin *et al.,* 2004; Syroechkovskii, 1995). The summers of 2002 and 2003 were very warm, especially in *Vaisa* (the mean temperature in July was 3 °C and 6 °C above normal in *Vaisa* 2002 and 2003 respectively). This could have made the high altitudes even more important due to increased insect harassment compared to a normal summer. However, the insect activity usually starts at the end of June and has a peak in the beginning of July (Nilssen, 1997), and can therefore not solely explain the preferences for high altitudes throughout the summer season in this study. Predator vigilance may also force the female reindeer to higher altitudes, especially early in the season, when the calves are small and not capable of moving longer distances to escape possible predators (Barten *et al.,* 2001).

The reindeer seemed to primarily occupy vegetation types with high nutritive quality when they used high altitudes. Although rugged terrain and bare rock are positively correlated with altitude, these areas were avoided by the reindeer (however, this might also be confounded with the avoidance of the highest altitudes). More generally, plants growing at higher altitudes can have high nutritious quality during a longer time period since the growth period can be prolonged at higher altitudes. The vegetation types *grass heaths* preferred in *Handöl* and *Vaisa*, *extremely dry heath* preferred in *Vaisa*, and *moderate*

Table 3. Regression coefficients for the RUF based on faecal standing crop (FSC) and faecal accumulation rate (FAR) counts.

	Handöl FSC		*Vaisa* FSC		*Handöl* FAR		*Vaisa* FAR	
Abiotic factors								
Altitude (km)	11.33	*	17.70	***	2.31	***	6.71	(*)
Altitude² (km²)	-4.41	(*)	-9.16	***	×		-4.13	(*)
Ruggedness	-0.02	*	-0.02		×		×	
Northwest slope	-0.12		-0.01		0.01		-0.06	
Southwest slope	0.24		0.21		0.02		0.19	
Southeast slope	0.20		0.27		-0.05		0.11	
Resort	0.05	**	-0.06	***	×		-0.03	**
Hiking trail	-0.08	*	×		×		×	
Vegetation types								
Bare rock	-0.96		-1.21		-1.94	***	1.02	
Grass heaths	0.96	(*)	0.17		-0.44		2.51	*
E dry heaths	-0.06		0.63		-0.41		3.10	**
Dry heaths	0.45		0.71		0.32		2.46	*
Fresh heaths	-0.23		-0.83		-0.33		1.89	
Wet heaths	-0.83		-2.70		-0.36		-2.17	
Meadows	1.01	(*)	-0.85		-0.03		1.57	
Moderate snow bed	-0.08		-0.67		-0.77		1.61	
Fen	-0.65		-0.53		-0.94		0.94	
Dry fen	-0.94	(*)	-1.49		-0.28		0.34	
Mosaic mire	-1.59	*	-0.50		-0.92		-0.93	
Willow thickets	-1.19		-1.50		-0.85		0.98	
Birch forest	-0.13		-1.02		-0.08		0.26	

(*)$0.05 \leq P < 0.1$. *$0.01 \leq P < 0.05$. **$0.001 \leq P < 0.01$. ***$P < 0.001$.
The variables not used in the model are marked with ×.

snow beds used in relation to its availability in both years and areas (Fig. 2), were all within the middle alpine zone which is situated at rather high altitudes. *Grass heaths* and *moderate snow beds* contain high quality plant species which are easily digested and preferred by the reindeer during the early and mid parts of the summer (Klein, 1990; Skogland, 1980). In addition, *moderate snow beds* often occur in proximity to *grass heaths* and *meadows* (von Sydow, 1983), and usually have a thick snow cover that gradually melts throughout the season and provides new ground with fresh forage for the reindeer and snow-fields for relief during insect harassment and warm weather (Skogland, 1980). Further, during these warm summers a prolonged growth period at higher altitudes could have been even more important for the availability of high quality forage at the large spatial scale. This might be reflected in the vegetation type preferences in especially *Vaisa* in 2003 when the temp was 6 °C above normal in July.

In *Vaisa*, the reindeer seemed to have greater opportunity to forage when they selected for higher altitudes. Almost one-third of the inventoried area in *Vaisa* consisted of the vegetation type *moderate snow beds* compared to 7 percent in *Handöl*. In addition, the RUF based on the FAR counts in *Handöl* showed that the reindeer did not prefer any particular vegetation type, except that they avoided bare rock and bedrock outcrops.

The reindeer in this study appeared to have accepted a certain degree of human disturbance in order to use preferred vegetation types. Reindeer are considered to avoid areas with human activities (Vistnes & Nellemann, 2001; Vistnes *et al.,* 2001); therefore, the preference for areas near hiking trails in *Handöl*, where there are many hikers (Vuorio, 2003), was unexpected. However, the pellet density decreased closer to tourist resorts and huts in *Handöl*. This may be explained by the continuous activity around the huts in *Handöl* compared to the more shifting activity at the hiking trails. In *Vaisa*, there are only three smaller huts used by a low number of hikers (Wall-Reinius, 2006), which might explain the preference for areas in proximity to the huts. Further, the reindeer herders in *Handöl* claim that the reindeer avoid otherwise preferred grazing grounds when there are too many hikers in the area (Lennart Blind, reindeer herder in *Handöl*, pers. comm.. May 2002). The mean distance from hiking trails to preferred vegetation types, such as *meadows* and *dry heaths* was 1500 m, and 2100 m to *grass heaths*, while it was 2700 m to *bare rock and bedrock outcrops*. Thus, the reindeer may be attracted to the area around the hiking trails in *Handöl*, but they may use it at times when the number of hikers is low. In areas with many hikers the reindeer also seem to habituate to human activity in order to reach insect free areas and good grazing ground (Pollard *et al.,* 1996; Skarin, 2006).

The reindeer avoided mosaic mires and dry fen in *Handöl* although these vegetation types are normally preferred late in summer (Skogland, 1980). Another explanation may be the reindeer preference for high altitudes, since these vegetation types are more common at lower altitudes. However, this may also be explained by the pellet groups being less visible and disappearing faster in such moist vegetation types (Hemami & Dolman, 2005; Skarin, submitted). In *Vaisa*, the occurrence of pellet groups in the birch forest might likewise have been underestimated, since the counting was performed at the end of the growing season when the vegetation was taller. However, there were only a few observations in total in these vegetation types, and it is unlikely that they have affected the main result of the RUF models. A limiting factor for the interpretation of the results is also the large temporal scale at which this survey was performed which does not reveal a detailed use of vegetation types during separate periods within the summer season (Schooley 1994; Skarin *et al.*, in press).

In *Vaisa*, movements of reindeer to and from the study area could have caused the higher density of pellets the second year. In *Vaisa*, the number of animals during the calf-marking period was about the same both years, but it is likely that a number of reindeer from the eastern part (not inventoried in this study) in the herding district moved to the western part of the district after the calf-marking period according to herder observations (Nils-Johan Utsi, reindeer herder in *Vaisa*, pers. comm., March 2006).

The predictive capacity of the estimated RUFs was considered high. In the cross-validation correlations based on the counts done in *Handöl*, the RUFs explained about 50 per cent of R^2 when fitting the RUF models. This indicates a high accuracy when using the RUFs to predict reindeer habitat use in a new area. In the cross-validation correlations of the *Vaisa* RUFs predictive capacity was lower (about 25 per cent of R^2). One explanation for this, and especially for the FAR counts, could be that the pellet-group counts in the two areas were done during different periods of the summer: in *Handöl* at the beginning of the snow-free season, representing the summer of 2002, and those in *Vaisa* at the end of the season, representing the summer of 2003. Further, the R^2-values when fitting the *Vaisa* RUFs were higher than for the *Handöl* RUFs, which might compensate for the lower explanation of variation in predicting habitat use in *Handöl* with *Vaisa* RUFs.

The cross-validation correlations were also higher than that of the RUFs based on reindeer home range use estimated from GPS-collared reindeer in the same areas (Skarin *et al.,* in press). In GPS- or VHF-collar surveys, often only a small part of the herbivore population can be surveyed. A pellet-group count measures how the whole population uses a landscape over a longer time period. Counting pellet groups and assigning them to different vegetation types also obviates the problem of misclassifications of vegetation type (Guillet *et al.,* 1995). Here the cross-validation of the models was also done with RUFs based on datasets from another area (*Vaisa* versus *Handöl* and vice versa), and not by splitting up the same dataset, as in k-fold cross-validation (Boyce *et al.,* 2002). K-fold cross-validation naturally gives a higher predictive capacity, since datasets from the same area likely are more consistent.

A higher degree of significance for the RUF- coefficients were found with the FSC surveys compared to the FAR surveys. This may depend on the resolution of the independent factors not being appropriate for the time scale that the FAR count represents. However, for this study these factors were convenient and cost effective to use. On the other hand, it might also depend on the different study periods that the two different survey methods represent (c.f. Schooley, 1994). In the FSC count the habitat use over several years (at least four years: Skarin, submitted) are registered, and pellets are accumulated at preferred sites, while the FAR count only represent one summer of use (in this case). However, the summers of 2002 and 2003 were comparable in that they both were very warm summers. Therefore, for the purpose of this study the FSC counts seemed to be more efficient than FAR counts, contradicting previously mentioned suggestions in the literature.

Conclusion

The pellet-group surveys showed that reindeer preferred higher altitudes, although they seemed to avoid extreme summits. Moreover, strong selection for individual vegetation types could not be detected on a seasonal scale. This indicates that, at the landscape scale and at this long time interval abiotic factors had a larger impact on the reindeer habitat selection than the forage. There was a difference between the two areas in the choice of vegetation types, which may correspond to differences in the structure of the areas. The results indicated that the reindeer used areas close to hiking trails in both areas, although there was a difference in intensity of disturbance from hikers. The areas around the hiking trails offered more often high quality grazing grounds. The reindeer habituated to the human activity at the hiking trails in order to reach these grazing grounds. However, when the intensity of human activity increased significantly, as around the tourist resorts and huts visited throughout the summer, the reindeer avoided the area.

Acknowledgements

This work was financed by the Foundation for Strategic Environmental Research (MISTRA), through the Swedish Mountain Mistra Programme. The study was made possible thanks to the loyal cooperation of the reindeer herders in *Handölsdalen* and *Sirges* reindeer herding districts. The field co-workers are acknowledged. Sincere thanks also to Öje Danell, Roger Bergström and Jon Moen for valuable contributions and discussions throughout the study, and to Erik Frykman for his linguistic comments on the manuscript.

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Manuscript received 24 January, 2007
revision accepted 17 October, 2007

Renens användning av sommarbetesområdet, uppskattat med spillningsinventeringar

Abstract in Swedish / Sammanfattning: Hierarkiskt habitatval innebär att djur väljer för och emot olika faktorer beroende på den rumsliga skalan. Mängden bete kan t ex spela stor roll för en växtätares habitatval på en stor skala medan kvalitén på betet kan ha större betydelse på en mindre skala. För renar (*Rangifer tarandus tarandus*), kan betestiden och möjligheten att hitta bra bete sommartid begränsas både på stor och liten skala pga. störningar från insekter och mänsklig aktivitet. Här studerades renarnas val av betesområde på landskapsnivå med hjälp av spillningsinventering under somrarna 2002 och 2003 i två samebyar i Sverige. Spillningstätheten för respektive område och år undersöktes statistiskt med hjälp av multipel linjär regression eller sk "resource utilisation functions" (RUF). Där relaterades spillningstätheten till vegetationstyp, olika topografiska faktorer, avstånd till vandringsleder, stugplatser och fjällstationer. Resultaten visade att områden högt upp i terrängen med hög beteskvalitet var attraktiva. Vegetationstypen moderat snölega som anses ha hög beteskvalitet användes av renarna i relation till dess förekomst. Däremot verkade renarna undvika områden kring välbesökta fjällstugor och fjällstationer medan de däremot t o m föredrog områden nära vandringsleder. Det kan bero på att vandringslederna går genom attraktiva vegetationstyper. RUF-modellerna hade en hög prediktiv förmåga vilket visar att spillningsinventeringar är användbara när man önskar studera hur djuren använder ett betesområde i relation till olika faktorer på en relativt stor rumslig och temporal skala.