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Reindeer *Rangifer tarandus tarandus* husbandry in Sweden commonly uses the Scandinavian mountain chain as grazing area during the snow-free season and the coniferous forests in the east during winter. Current knowledge of habitat use by reindeer is primarily based on traditional or local knowledge, or on investigations carried out on wild reindeer and caribou in other parts of the world. We identified spatial and temporal habitat use of free-ranging semi-domesticated reindeer by following 48 GPS-equipped reindeer in three summer ranges in the Swedish reindeer herding area. The GPS equipment registered positions every hour or every second hour, during two snow-free seasons. The GPS-collared reindeer were randomly chosen from herds with several thousand animals. Estimated home-range utilisation distributions were used to fit resource utilisation functions (RUFs) including various topographical features, vegetation types, and the vicinity to water and hiking trails. The GPS-equipped reindeer used different parts of the range throughout the snow-free season. Preferred vegetation types were consistently meadows, grass heaths, and other heaths. Avoided vegetation types were all types of forests, sparsely vegetated areas, and bare rocks. The reindeer were seemingly indifferent to hiking trails within their home ranges, which, however, usually coincided with preferred vegetation types, but they avoided areas with houses and holiday huts during early summer. Later in the season, the reindeer preferred higher elevated areas where human constructions were sparse. The home ranges of the GPS-equipped reindeer overlapped considerably during early parts of the season, indicating a dense use of the range by the entire herds. Crowding within the herds appeared to make individual reindeer select non-optimal habitats. However, in our study, we found a non-significant tendency of less predictable individual home ranges when there were large range overlaps. Vegetation types, direction of slopes, time within the season and the possibilities of avoiding insect harassment appear to be key factors for predicting valuable reindeer habitats in novel areas in a land management context.

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During the snow-free season, most of the Swedish mountain chain is used as pastures for semi-domesticated reindeer *Rangifer tarandus tarandus*. Reindeer husbandry uses the landscape in parallel with recreational human activities such as tourism, fishing and hunting. In the environmental goals for the mountain area, the Swedish Government (2000) declared that the mountain landscapes should be managed to preserve long-term productive capacity, characteristics as a grazed landscape, and biological diversity and natural, cultural, and recreational assets. Knowledge about the behaviour and habitat use of the semi-domesticated reindeer is essential for achieving these goals. In a management and land-use perspective, it is important to be able to predict habitat use and locations of animals with established accuracy (Boyce et al. 2002).

In studies of habitat selection by large herbivores, the concept of hierarchical foraging is often used. Herbivore behaviour can be separated into hierarchical levels where the number of decisions made for one action or a number of actions determine the scale (Johnson 1980). Senft et al. (1987) described hierarchical foraging in large herbivores where different foraging response patterns were displayed at three different levels: patch, landscape, and regional level. Studies of reindeer and caribou habitat and resource selection have indicated that selection occurs at all three hierarchical levels (Rettie & Messier 2000, 2001, Johnson et al. 2002, Mårell et al. 2002).

Habitat selection by reindeer and caribou at the landscape level in the snow-free season is believed to be dependent on forage characteristics (Klein 1990, Mårell et al. 2005), insect harassment (Russell et al. 1993, Mörschel & Klein 1997, Mörschel 1999), and also on various human activities and connected infrastructures (Helle & Särkelä 1993, Nellemann & Cameron 1996, Nellemann et al. 2000, Dyer et al. 2001, Vistnes et al. 2001).

Forage for reindeer and caribou in the snow-free season can consist of more than 100 plant species; highly preferred graminoids are wavy hair grass *Dechampsia flexuosa* and sheep's fescue *Festuca ovina* together with dwarf birch *Betula nana*, and several of the Ericaceous dwarf shrub species (Warenberg 1977, Klein 1990). Reindeer are opportunistic feeders, but prefer fresh and nutritive forage, and they often follow the snow-line to explore early stages of plant growth (Mårell et al. 2005). Meadows and grass heaths are vegetation types that are rich in plant species and contain preferred nutritive plants (Skogland 1980). Later in summer, reindeer also have a high preference for mushrooms (Launchbaugh & Urness 1993).

Reindeer and caribou are by nature a highly gregarious species, and domestication has made them even more gregarious (Hemmer 1990). It is also well known that the social acceptance between the animals increase with increased domestication. Spacing and geometry of social animals appear to result from a trade-off between the need to avoid predation and the need to obtain food or other resources (Rayor & Uetz 1990). When reindeer and caribou are within a herd or group, they synchronise their behaviour with the other members of the

group (Maier & White 1998, Colman et al. 2004). Colman et al. (2004) suggested that this is beneficial for all group members and will reduce suboptimal foraging and competition and thereby improve both individual survival and production. However, competition for forage increases with shorter distance between the animals (Romey 1995, Barta et al. 1997).

In studies of the snow-free season, often only parts of the season have been considered (e.g. Downes et al. 1986, Ihl & Klein 2001, Mahoney & Virgl 2003). The effect of season should be taken into account in resource selection studies as the habitat use may shift over time (Aebischer et al. 1993). In our study, we investigated habitat selection at the landscape level continuously throughout the whole snow-free season by following GPS-collared semi-domesticated reindeer. Our aims were to: 1) determine which habitat variables affect the habitat selection within the reindeer home ranges, 2) examine changes in spatial habitat use and herd-behaviour throughout the snow-free season, and finally 3) explore the possibility to predict habitat use with the kind of data obtained here. We used three different areas, and four different periods in order to evaluate the generality of the habitat use in space and time. We also tested the predictive capacity of the habitat model. This has only been considered in few other habitat studies of reindeer and caribou (e.g. Apps et al. 2001, Johnson et al. 2004).

Material and methods

Study areas

Our study was performed in the Scandinavian mountain chain in Vaisa and Sarek situated in Sirges reindeer herding district, at 67°00'N, and in Handöl situated in Handölsdalens reindeer herding district at 63°00'N (Fig. 1). The areas differ in topography and possible interference from back-country hiking.
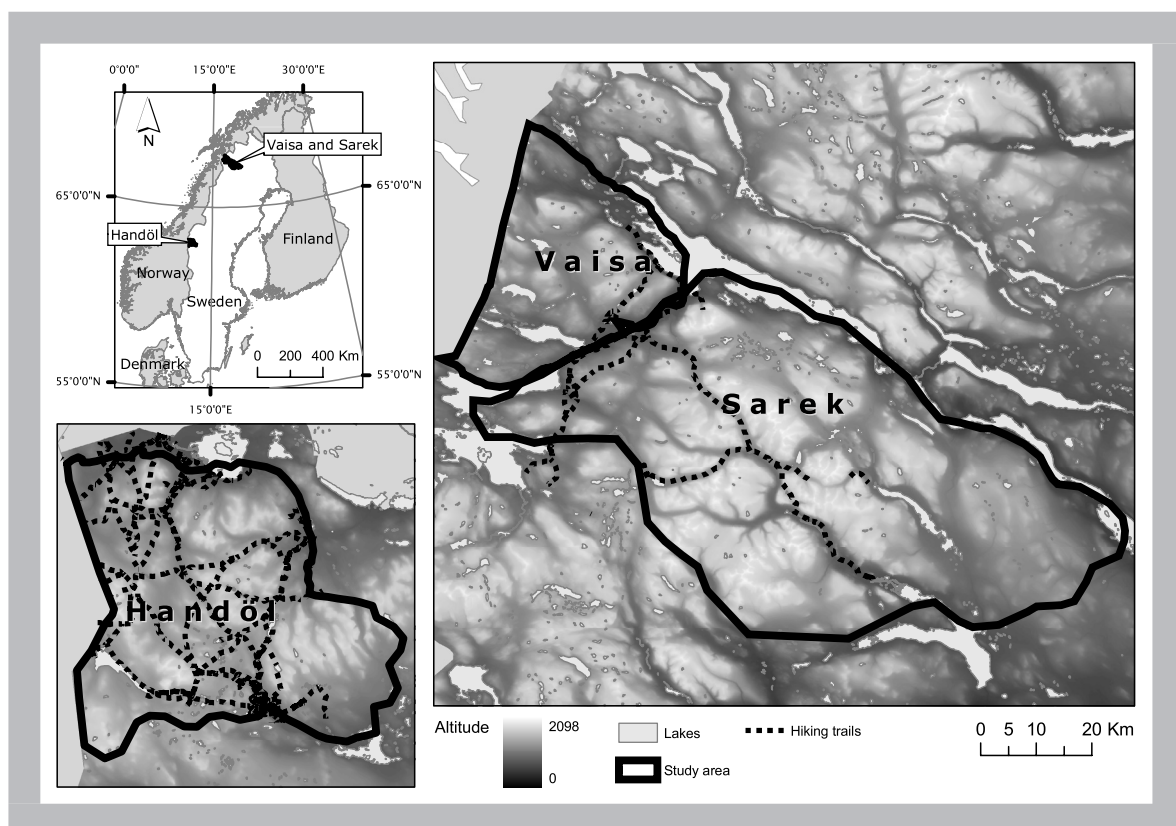

Figure 1. Location of the study areas Handöl, Vaisa and Sarek that were used in our study of the GPS-equipped reindeer, and the surrounding terrain. Vaisa and Sarek are separated by lakes and rivers, hindering extensive migration by the reindeer between the areas. The light colours in the topographic map show higher altitudes. © Lantmäteriverket Gävle 2006. Permission I2006/1119.

Table 1. Distribution and extension of vegetation types in the reindeer study areas Handöl, Vaisa and Sarek. The vegetation classification is from the Swedish CORINE land cover data with a 25 × 25 m resolution.

Vegetation type definition	Handöl (km^2)	(%)	Vaisa (km^2)	(%)	Sarek (km^2)	(%)
Solitary houses with property	0.10	0.00			0.20	0.00
Sand and gravel pits	0.10	0.00			0.07	0.00
Ski slopes	0.19	0.01				
Camping sites and holiday cottage sites	0.88	0.04				
Arable land	0.19	0.01				
Cultivated pastures	0.45	0.02				
Broad-leaved forest not on mires	151.98	6.90	60.72	5.54	303.28	7.49
Broad-leaved forest on mires	0.00	0.00				
Coniferous forest on lichen-dominated areas	25.22	1.14	1.00	0.09	33.15	0.82
Coniferous forest 5-15 m	37.35	1.69	0.55	0.05	41.44	1.02
Coniferous forest >15 m	37.14	1.69	0.01	0.00	7.03	0.17
Coniferous forest on mires	0.54	0.02	0.02	0.00	0.97	0.02
Coniferous forest on open bedrock					0.05	0.00
Coniferous forest not on lichen-dominated areas	3.83	0.17	1.02	0.09	3.39	0.08
Clear-cut areas	2.71	0.12			1.76	0.04
Younger forest	19.50	0.89			2.26	0.06
Mixed forest not on mires	32.86	1.49	0.30	0.03	37.76	0.93
Mixed forest on mires	0.03	0.00			0.04	0.00
Willow thickets	16.27	0.74	11.53	1.05	33.94	0.84
Natural grassland	0.34	0.02			0.01	0.00
Heath including extremely dry heath, dry heath, fresh heath and wet heath	1243.21	56.42	358.21	32.69	1223.39	30.20
Beaches, dunes, and sand plains	0.04	0.00				
Bare rock	168.80	7.66	100.42	9.17	670.15	16.54
Sparsely vegetated areas	5.51	0.25	123.02	11.23	372.15	9.19
Glaciers and perpetual snow	1.18	0.05	1.05	0.10	153.32	3.78
Grass heath	141.46	6.42	173.19	15.81	720.48	17.78
Meadow	115.26	5.23	90.36	8.25	122.47	3.02
Inland marshes	0.28	0.01	0.10	0.01	1.44	0.04
Wet mires	21.80	0.99	3.51	0.32	11.59	0.29
Other mires	115.77	5.25	19.02	1.74	73.62	1.82
Lakes and dams, open surfaces	60.55	2.75	151.57	13.83	237.30	5.86
Total	2203.49	100	1095.60	100	4051.23	100

Within each area, the animals graze freely during May - October under surveillance of outer district borders. Vaisa and Sarek are separated by water bodies which limit but do not completely hinder migration of animals between the areas. During the study periods, there were about 6,000 reindeer altogether in Vaisa and Sarek, and about 8,000 animals in Handöl. The overall densities of adult reindeer were approximately three, two, and five head per km^2, respectively.

Vaisa is situated on a high plateau with elevations mostly ranging within 500 - 1,000 m a.s.l. and with the highest summit (Rautåive) at 1,516 m a.s.l. The annual precipitation in Vaisa is 900-1,500 mm and the mean temperature in July is 9°C (1961-1990). The vegetation period (temperature of >5°C) is 100-110 days (National Land Survey of Sweden

2002). The dominating vegetation types in Vaisa are heaths, meadows, grass heaths, bare rock and sparsely vegetated areas (Table 1). Except for the hunting of willow grouse *Lagopus lagopus* and rock ptarmigan *Lagopus mutus* starting on 25 August and continuing for 2-3 weeks, the area is little used for tourism or other human activities except for reindeer herding.

The elevation in Sarek ranges within 500 - 2,015 m a.s.l., which gives the area an alpine character with deep and long valleys. The annual precipitation is 900-1,700 mm, the mean temperature in July is 7°C, and the vegetation period is 100-110 days (1961-1990). Sarek includes more glaciers and bare rock than Vaisa. Apart from these differences, Sarek and Vaisa have approximately the same proportions of other vegetation types (see Table 1). There

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Table 2. Definitions of periods during the snow-free seasons of 2002 and 2003. N gives the number of GPS-equipped reindeer within each study area and period. The division of the periods is based on seasonal characteristics in weather and interruptions of free grazing due to operations in reindeer herding.

Periods	Handöl		Vaisa		Sarek	
	Date	N	Date	N	Date	N
Spring 2003	11/5-30/5	10	11/5-10/6	7	11/5-10/6	13
Early summer 2003	31/5-3/7	10	11/6-14/7	7	11/6-6/7	13
Mid summer 2002	15/7-31/8	9	19/7-6/9	9		0
Mid summer 2003	15/7-24/8	10	19/7-28/8	7	13/7-28/8	13
Late summer 2002	1/9-15/9	9		0		0
Late summer 2003	25/8-14/9	10	29/8-7/9	7	29/8-13/9	12

are trails along the major valleys in the area used by back-country hikers (see Fig. 1).

The elevation within Handöl ranges from 500 m to the highest peaks Helags at 1,796 m and Sylarna at 1,761 m a.s.l.; these two summits give the area an alpine character. The annual precipitation is 700-1,300 mm, mean temperature in July is 10°C, and the vegetation period is 120-130 days (1961-1990). The vegetation in Handöl varies from wet to extremely dry heaths. The area is popular among back-country hikers, and there are three larger and four smaller public tourist huts and trails leading to the huts within the area (Vuorio 2003). Willow grouse and rock ptarmigan hunting occurs within the area, starting on 25 August.

Data collection and treatment
Position data were collected during two summer seasons in order to capture possible effects of different weather conditions. During 15 July-15 September 2002, 10 randomly sampled adult female reindeer in both the Vaisa and Handöl areas were equipped with GPS collars (Posrec®, 650 gram, manufactured by TVP Positioning AB). This procedure was repeated between 10 May and 15 September 2003, with 10 new reindeer in both areas and 10 additional reindeer in Sarek. The GPS equipment stored the position data (every second hour in 2002 and every hour in 2003, with < 2% of the positions missing), and once the collars were taken off, the data were downloaded. Females were chosen as study animals as they represent the majority of the herds, which in all areas included several thousand animals. The only selection criteria were that they were judged to be rearing calves (2002) or being pregnant (2003). In the summer of 2003, most of the females had a calf (observed at calf marking), but when the collars were taken off in the autumn only 53% of the

reindeer still had a calf. In 2002, two collars (one in each area) failed to collect positions due to technical problems. In 2003, some migration had occurred between Sarek and Vaisa. Instead of 10 reindeer with functioning GPS within each area, there were 12 reindeer in Sarek and seven reindeer in Vaisa, and in addition, one reindeer had moved from Sarek to Vaisa in the middle of the summer (Table 2). One collar in Vaisa stopped working on 18 August.

Data analyses
Based on seasonal characteristics in weather and management activities, the data were divided into two periods in 2002 (mid and late summer) and four periods in 2003 (spring, early, mid, and late summer; see Table 2). The end of the spring was set at the average date of the end of the snow-cover (Pershagen 1969). The end of the early summer period was defined as the time when the reindeer herders started to gather the reindeer for calf marking, and the calf marking period was excluded from the data set. The mid summer period was set to start after the calf marking was over, and to end when the mean daily temperature (during each year) fell below 6°C, corresponding to a temperature at which insect activity is decreasing (Russell et al. 1993, Anderson et al. 1994, Mörschel 1999). The late summer period was defined to end when the herds where gathered for bull slaughter in mid-September before the rut.

To distinguish between foraging movements and movements between foraging patches, we fitted a non-linear curve fitting procedure to the movement rates and identified a breakpoint (r_c) value (Sibly et al. 1990, Johnson et al. 2002). Movement rates smaller than the r_c-value were considered as movements within the forage patches, and movement rates larger than the r_c-value were considered as movements between patches (Johnson et al. 2002).

Only positions considered to represent foraging movements ($<$ r_c-value; on average 98% of the positions) were used in the statistical analyses of habitat use. A downward bias was expected in the r_c-value estimated from the positions registered every second hour in 2002 compared to registrations every hour in 2003. Based on studies of red deer *Cervus elaphus* (Pepin et al. 2004), the magnitude of the bias might be 5-10%. This does, however, not interfere with the identification of breakpoints.

To develop resource utilisation functions (RUFs) for reindeer, we used a multiple linear regression technique to relate reindeer habitat use to habitat attributes (Marzluff et al. 2004). The first step was to estimate the utilisation distributions (UD) from the GPS-positions, using fixed-kernel techniques (Worton 1989, Seaman & Powell 1996). Depending on time periods, between 178 and 900 positions were available for each home-range estimation. For the UD estimation we used ArcView GIS 3.3 software (ESRI Inc © 1992-2002) with the Animal Movement extension (Hooge & Eichenlaub 2001). To decrease computational load, the smoothing parameter was calculated using the *ad hoc* method (Worton 1989). The spatial extent of the UD was defined as the 99% fixed-kernel home range boundary, and was displayed in a 50×50 m raster. The intensity of range use throughout the home range was measured as the height of the kernel density estimate over each grid cell. This could be done by computing the associated probability density function ($\hat{f}_{UD}(x, y)$) throughout the UD using the Focal Patch extension (Hurvitz 2002) as used by Marzluff et al. (2004). However, this appeared to produce exactly the same density values as a reclassification of the cumulative density values for each cell by subtracting it from unity, i.e. 1-0.99, 1-0.98, ... We used the Reclass Function in ArcGIS 9.0™ (ESRI Inc © 1999-2004) to do this. In total, 147 different UD were calculated to be used in the RUF-model. The overlap of home ranges in each area and period was quantified as the intersection of each home range within the 50% boundary with other individual home ranges.

To obtain coefficients of relative use of the habitat, we determined the associated habitat variables to the cells within the UD. The variables were elevation, ruggedness, aspect, vegetation, vegetation diversity, distance to hiking trail, and distance to water obtained from digitised elevation and vegetation data sets. The original raster resolution of the digital elevation map (50×50 m) determined the resolution of the analyses (Marzluff et al. 2004).

From the elevation raster layer slope, aspect, and a topographic ruggedness index developed by Riley et al. (1999), was calculated and modified to a logarithmic scale using ArcGIS 9.0™. The index expresses the amount of elevation difference between adjacent cells of a digital elevation grid. The ruggedness index and the angle of slope were highly correlated ($r = 0.87$, $P < 0.0001$) and slope was therefore omitted from further analyses. The aspect was divided into nine classes: flat areas and eight classes according the slope directions (each class 45° wide). Digitised vegetation data, (Swedish CORINE Land Cover (25×25 m)), were provided from Lantmäteriet, and were processed to fit a raster with 50×50 m cells. The number and areal extents of vegetation types are shown in Table 1. Diversity of vegetation types was defined as the number of different vegetation types found within a radius of three cells (i.e. 150 m) from a centre cell, which the diversity was calculated for. For each 50×50 m cell the Euclidian distance to the nearest hiking trail, and the distance to the nearest lake or stream, were calculated. Slopes steeper than 45°, lakes, and water courses were considered inaccessible for the reindeer and were not included in the analyses.

The multiple regressions were fitted with the SAS 8.2 software (SAS Institute Inc © 1999-2001) using the GLM procedure. The GPS-equipped reindeer were considered a random sample representing the reindeer herd in each study area. The least square solution for each vegetation type effect was solved as the estimated deviation from the mean solution of those vegetation types that were present in all home ranges within each study area and period. The solution of each aspect was obtained as derivates from the mean of all aspect solution since all aspects appeared in all UD. Coefficients for each independent variable in an average RUF were estimated as the arithmetic means ($\bar{\bar{\beta}}$) of coefficients ($\hat{\beta}_i$) obtained in each individual reindeer home range (Marzluff et al. 2004). The variance was estimated by subtracting the inter-animal variation from the total variance, and significances of the average RUF coefficients ($\bar{\bar{\beta}}$) were tested against this variance:

$$\mathrm{Var}(\bar{\bar{\beta}}) = \mathrm{SE}^2_{\bar{\bar{\beta}}} - \frac{\sum \mathrm{SE}^2_{\hat{\beta}_i}}{n^2}.$$

Because adjacent grid cells in the UD are expected to be spatially autocorrelated, we initially explored the possible effect of the autocorrelation

on the outcome of the model fit for 10 reindeer in the mid summer period in Sarek. We randomly assigned every cell in the home ranges a number from one to 10, and sorted the data in 10 separate data sets for each reindeer home range. We fitted 10 separate regression models using the random data sets. The averages of estimated solutions from the 10 separate analyses were compared with the solutions using all data for each reindeer in the analysis. As there were no differences in the coefficients $\bar{\bar{\beta}}$, and the computational burden was considerably smaller when using all data (147 data sets instead of 1,470), the implications of autocorrelation was disregarded. Unexpectedly, standard errors in the analyses using all data were larger than in the subset analyses.

As we did not consider the autocorrelation in the regression analyses, inter-animal variation becomes biased upwards. Therefore, an adjustment value (0.89) was estimated from comparison of the two alternative uses of data and assigned to the SE. We expected fewer $\bar{\bar{\beta}}$s to be significant, but there was no difference in the number of significant coefficients when testing against the two error variances. Therefore, we used the unadjusted standard error for inter-animal variance.

We cross-validated the RUF-model by computing cross-validation correlations (CVC) between observed response values and predicted response values for each animal's home range within each area and time period. The predicted response value was based on average RUF of all home ranges, except the one which was to be predicted. The mean CVC was calculated for each area and period from all the separate CVCs.

Results

Home range characteristics
The general characteristics of the estimated home ranges shifted throughout the snow-free season (Fig. 2). The overlaps for each period and area are shown in Table 3. In spite of being members of large herds, the home ranges of the sampled animals overlapped to some extent. The interpretation of this is that in reality a considerable number of animals used the same home-range areas. As an example the approximate number of reindeer per home range, based on the density of reindeer within an area and the mean size of the home ranges, 50% boundary areas, ranged from eight reindeer in the smallest
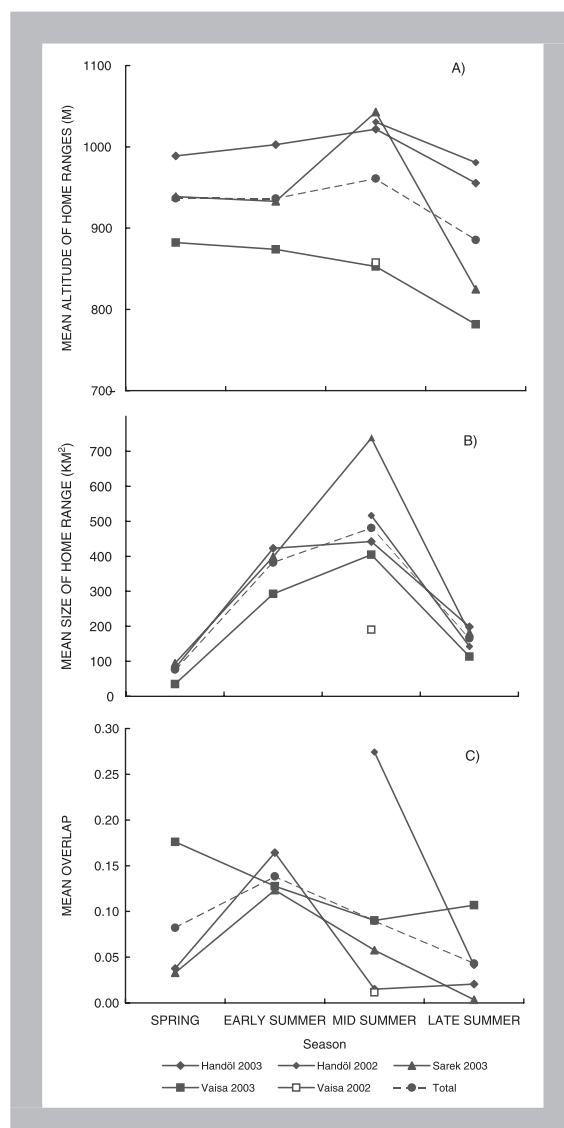

Figure 2. Characteristics of GPS-equipped reindeer's home ranges expressed as the mean altitude of the home ranges (A) in each period and study area, the average home range sizes (in km²; B) within each period and study area, and the mean proportion of overlap between the core areas of the home ranges (50% home range boundary; C) in each period and study area.

mean home range (Vaisa during spring) to 190 reindeer in the largest mean home range (Sarek during mid summer).

The r_c-values for Handöl and Sarek in spring 2003 were 1,748, and 990 m/hour, respectively. In early summer the same year, the breakpoint value in Handöl, Vaisa and Sarek were 2,475, 2,120, and 2,363 m/hour, respectively. No breakpoint values were found for any of the areas in the mid and late

Table 3. Mean regression coefficients of the resource utilisation functions (RUFs) within the home range, on vegetation types for each area and period (only significant values are shown). The first three rows in the overall statistics give the average R^2-values, the mean overlap between the 50 percentile areas of the kernel home ranges, and the cross validation correlation (CVC) for the reindeer within the different periods. See Table 1 for definition of vegetation types. The symbols used in the table express: $*0.01 \leq P < 0.05$, $**0.001 \leq P < 0.01$, $***P < 0.001$, - = not significant, 'empty spaces' = missing values. Note that the vegetation types sand and gravel pit, ski slopes, cultivated pastures, broad-leaved forest (BF) on mires, coniferous forest (CF) on mires, mixed forest (MF) on mires, natural grasslands, clear-cut areas, beaches, dunes, and sand plains were removed from the table since none of these variables had significant coefficients.

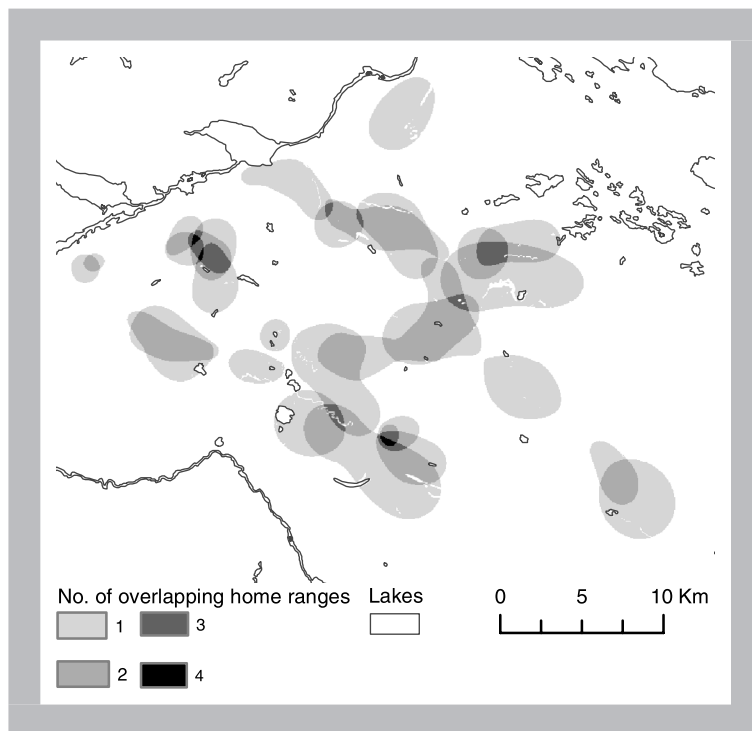| | Spring | | | Early summer | | | Mid summer | | | | | Late summer | | | |
	Handöl 2003	Vaisa 2003	Sarek 2003	Handöl 2003	Vaisa 2003	Sarek 2003	Handöl 2002	Handöl 2003	Vaisa 2002	Vaisa 2003	Sarek 2003	Handöl 2002	Handöl 2003	Vaisa 2003	Sarek 2003
Overall statistics															
R^2-value	0.178	0.261	0.253	0.085	0.152	0.164	0.092	0.156	0.219	0.170	0.122	0.173	0.158	0.259	0.150
Overlap	0.038	0.176	0.033	0.164	0.128	0.123	0.274	0.015	0.012	0.090	0.058	0.041	0.021	0.107	0.003
CVC	0.102	0.093	0.100	0.152	0.088	0.110	0.094	-0.118	0.020	0.118	0.069	0.130	-0.002	-0.001	-0.056
Human intervention															
Houses				-10.749**				-				-	-		
Camping site				-10.140*				-				-	-		
Forested areas															
B F no mire	-		-6.715***	-	-3.418*	-	-1.216*	-	-	-	-	-2.982**	-	-5.659*	-
C F on lichen				-2.678*	-9.858*	-10.889***	-2.672**	-3.827*	-6.201*	-5.335**	-10.506**	-	-	-	-8.050*
C F 5-15 m				-12.702***			-5.833*	-	-	-	-	-	-	-	-
C F > 15 m				-14.446***			-5.244*	-	-	-	-	-	-	-	-
M F no mires	-		-	-6.833**	-	-	-3.214*	-	-	-	-	-5.170*	-	-15.440*	-
Younger forest				-14.348**			-	-6.393*	-	-	-	-	-	-	-
C F no lichen	-		-	-	-	-9.939*	-3.685**	-	-	-	-	-	-	-	-
Open areas															
Willow thickets	-		-6.076***	-	-6.729**	-	-	-	-	-	-	-	-	-	-
Bare rock	-3.020*											-2.208*			
Sparse vegetation	-6.761***														
Glaciers				-8.564**	-	-8.786***						-27.307**			
Heath	-		1.951**	1.671***	2.221*	-	3.462***	2.012*	1.637*	-	-	3.010**	-	4.429*	-
Grass heath	-		2.407**	-	-	-	4.104***	1.871*	-	-	-	-	-	-	-
Meadow	-		2.640*	3.584***	6.118***	3.676***	3.703***	3.087**	-	-	-	5.188***	-	-	-
Inland marshes	-		-	-	-	-	-	-7.852**	-8.055***	-	-	-	-	-	-
Wet mires	-		-9.794***	-	-	-	-	-	-	-6.392**	-	-	-	-	-
Other mires	-		-8.254**	-	-	-	-	-1.739**	-2.655*	-	-	-	-	-	-
Open surfaces	-	-1.701***	-	-	-	-	-	-	-	-	-	-	-	-	-

Figure 3. Overlaps between 50% boundary of the reindeer kernel-home ranges during the early summer period in Sarek in 2003. In this example the average range overlap was 12%. Intersections between home ranges are indicated with shifting grey colour.

from other behaviour. The finding of breakpoint values in only some of the periods gives a clue about the changes in activity over the summer.

During the spring periods, small home ranges were used at lower altitudes in all study areas, and the overlaps between the home ranges were small (mean 8% over all areas; see Fig. 3 for an example of home-range overlap). In the early summer period, the home ranges expanded and the movements were slightly longer. There was no difference in the average altitude of the home ranges compared to the spring period, but the mean range overlap (14%) increased. The breakpoint value (r_c) within the two periods also confirmed that the reindeer made fewer long movements than short movements. In the mid summer period, the home ranges expanded further. The altitude of the positions increased from early summer to mid summer. The largest home ranges and the highest altitudes were found in Sarek. During mid summer, no breakpoint values were found, which indicated that the frequency of longer movements

summer periods. The positions classified to be within a foraging patch could include other behaviour than foraging. However, our collars did not record activity, and thus we cannot separate foraging

Table 4. Mean regression coefficients of the RUFs within the home range on aspect and the continuous range characterising variables (only significant values are shown). The symbols in the table express: *$0.01 \leq P < 0.05$, **$0.001 \leq P < 0.01$, ***$P < 0.001$, - = not significant. Note that the continuous variables altitude and distance to hiking trail were removed because they were non-significant. Handöl 2002 mid and late summer were also removed since none of these had significant coefficients.

	Spring			Early summer			Mid summer				Late summer		
	Handöl 2003	Vaisa 2003	Sarek 2003	Handöl 2003	Vaisa 2003	Sarek 2003	Handöl 2003	Vaisa 2002	Vaisa 2003	Sarek 2003	Handöl 2003	Vaisa 2003	Sarek 2003
Aspect													
Flat	-	-	-4.025**	-	-	-	-	-	-	-	-	-	-4.572*
North	-	-	4.604*	-	-	-	-	-	-	-	-	-	-
Northeast	-	-	-	-	-1.443**	-	-	-3.260**	1.159*	-	-	-	-
East	-	-	-	-2.787**	-1.972**	-	-	-2.087*	-	-	-	-	-2.464*
Southeast	-	-	-	-3.135**	-	-	-	-	-	-	-	-	-
South	-	-	-	-1.727*	-	-	-	-	-	-	-	-	-
Southwest	2.412*	-	-2.780*	1.540*	3.062*	-	-	-	-	-	-	-	-
West	-	-	-	2.893**	-	-	-1.292*	-	-	-	-	-	-
Northwest	-	-	-	2.041**	-	-	-	-	-	-	-	-	-
Continuous variables													
Ruggedness	-0.234*	-	-	-	-	-	-	-	-	-	-	-	-0.273*
Distance to water	-	1.209**	-	-	-	-	-	-	-	-	-	-	-
Vegetation diversity	-1.104*	-	-	-	-	1.450**	-	-	-	0.969*	-	1.252*	-

between forage sites had increased, and compared to early summer the mean range overlap (9%) had decreased. In the late summer period, the home ranges decreased again, the altitude of the positions declined and became lower than during all other periods, and the range overlap also decreased to its lowest value (4%) as a natural consequence of this. Contributing to this was also that low elevation ranges cover larger areas than high elevation ranges.

Home-range use

Multiple regression of UD on range characteristics was fitted with individual R^2-values between 0.04 and 0.44. The mean R^2-values for each period and area are shown in Table 3. The lowest mean degree of explained variation was found in Handöl in the early summer period (0.085) and the highest in Vaisa during the spring period (0.261). Significant average regression coefficients for all the RUFs over all periods and areas are shown in Tables 3 and 4. The RUFs showed that the reindeer only preferred meadows, grass heaths and heaths, whereas most other vegetation types were avoided during some period or in some area. When the coefficients for meadow were significant, it was almost always the highest ranked among the preferred vegetation types. An exception was the mid summer period in Handöl 2002, where grass heath was higher ranked. The avoided vegetation types were all types of forest, bare rock, glaciers, willow thickets, all types of mires, and sparsely vegetated areas. In Handöl during early summer, the reindeer avoided solitary houses, camp sites and holiday cottage sites. In Vaisa and Sarek, these categories were not present.

The effects of aspect shifted between areas and periods. The only cases in which the reindeer responded to ruggedness were in Handöl in spring and in Sarek in late summer, when rugged areas were avoided. Vegetation diversity was a preferred characteristic in Sarek in the early and mid summer periods, and in Vaisa in late summer, whereas it was avoided in Handöl during spring.

Cross validation of the home-range use

The cross validation resulted in a mixture of negative and positive correlations for all periods and areas, except for the early summer period in Handöl where all CVCs were positive. The mean of all CVCs for each period and area are shown in Table 3; the highest mean CVC was found in the early summer period in Handöl 2003 (r = 0.152).
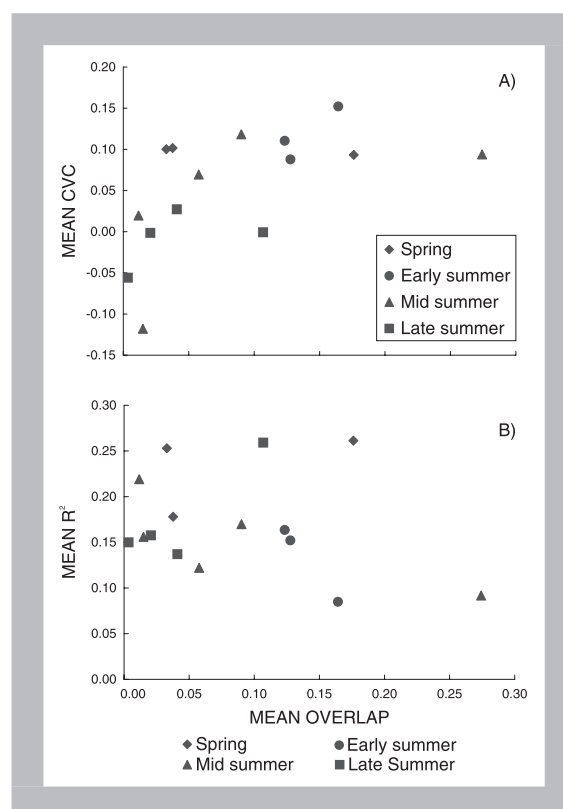

Figure 4. Relationships between home-range overlap and cross validation results. Each point represents the average value of a GPS-equipped reindeer in one period and area. The mean proportions of home-range overlap in relation to the mean cross validation correlation (CVC) for each period are shown in A), and the correlation between mean overlap and the R^2-value for the resource utilisation function (RUF)-model is shown in B).

The relationship between the CVC and the range overlap was positive (r = 0.376, P-value < 0.0001; Fig. 4A). However, the correlation between the range overlaps and the R^2-values for the fitted RUF-models was negative (r = -0.274, P = 0.324; Fig. 4B). We found no relationship between the CVC and the R^2-value. This implies that when reindeer used the same area, the habitat preferences were similar but less distinctive.

Discussion

Expectations from literature on *Rangifer* habitat use are that choices are influenced by forage characteristics (Klein 1990, Mårell et al. 2005), insect harassment (Russell et al. 1993, Mörschel & Klein 1997), various human activities such as tourism (Helle & Särkelä 1993, Nellemann et al. 2000,

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Vistnes & Nellemann 2001), and herd behaviour (Barten et al. 2001).

The observed general pattern in the use of the vegetation types was that the reindeer preferred rich vegetation types above the tree line and avoided sparsely vegetated areas and forests. Meadows, grass heaths and heaths were the only vegetation types that were preferred in all three areas. These vegetation types contained forage species that have been found to be preferred by reindeer in other studies (Klein 1990, Mårell et al. 2002, Mårell et al. 2005). The preferred vegetation types covered 68% of the total area (lakes not included) in Handöl, and 57 and 51% of the total area in Vaisa and Sarek, respectively. Thus, the vegetation types that the reindeer preferably used cover a main part of the total available land. A possible explanation for avoidance of forests in spring is predator vigilance when the calves are small (Barten et al. 2001). In later periods, avoidance of the generally higher insect abundance in forested areas may influence the habitat selection (Skarin et al. 2004). The avoidance of bare rock, glaciers, and sparsely vegetated areas may be a consequence of selection against areas with low forage abundance (Mårell et al. 2002). Avoidance of willow thickets and mires in Sarek and Vaisa in spring and early summer was most likely due to the fact that they were under snow cover. Otherwise these vegetation types usually belong to preferred ones (Warenberg 1977). However, mires are often preferred later in summer (Skogland 1980). In mid summer the mires were probably avoided because of their low altitudinal position, as the reindeer preferred higher altitudes at this time (see Fig. 2A).

There was no difference in the mean altitudinal position of the reindeer from spring to early summer, whereas in mid summer they used higher altitudes. A common observation is that reindeer preferably use higher altitudes during periods when the oestrid flies (warble flies *Hypoderma tarandi* and nose bot flies *Cephenemyia trompe*) are active, i.e. from the end of June (Downes et al. 1986, Anderson & Nilssen 1998, Hagemoen & Reimers 2002). In our study, we did not distinguish between days with predicted low and high insect harassment pressures. Further analyses on reindeer movements during predicted insect harassment days have been performed and presented in another article (Skarin 2006). In Vaisa, however, the altitudinal positions of the reindeer declined consistently throughout the season, probably because attractive vegetation types in lower regions, which were covered with a

thick snow layer early in the season, became available from the mid summer period.

The reindeer preferences for slopes facing southwest in Vaisa in early summer, and southwest to northwest in Handöl during spring and early summer, can be explained by prevailing westerly winds. Such winds make the snow layer shallow and fast-melting at windward slopes, and they provide fresh forage early in the season (Warenberg 1977, Mårell et al. 2005). In Sarek, the preference was reversed; north-facing slopes were favoured and southwest-facing slopes were avoided during spring. One reason for this result might be that the area used by the reindeer during spring was located in the northern part of the study area and on the south side of a larger lake, where, consequently, northern slopes were more abundant. In both Vaisa and Handöl, the landscapes were more open, and the reindeer used the central parts of the areas.

Other studies have shown that reindeer react negatively to human activities (Nellemann et al. 2000, Dyer et al. 2001). In our study areas, the hiking season usually starts at the beginning of July and ends in September. However, we found that the distance to hiking trails did not affect reindeer habitat selection in neither of the periods nor of the areas. On the other hand, if hikers occur frequently, the reindeer may become habituated (Colman et al. 2001), and even though the animals are disturbed by human activities they can increase their tolerance for human activities if insect harassment is severe (Noel et al. 1998, Skarin et al. 2004). Reindeer may run away quite fast if they are disturbed, with little effect on the GPS-registrations. The vegetation types that the reindeer preferred were generally closer to the hiking trails than any other vegetation types, and they remained attractive even though their vicinity to the trails could have disturbed the reindeer.

During early summer, the reindeer in Handöl avoided sites with solitary houses, camping and holiday cottages (the two northern areas had no such sites). This kind of avoidance has also been found among semi-domesticated reindeer in Norway during the calving period (Vistnes & Nellemann 2001). It is likely that human activities are more continuous around residence areas than along hiking trails, and disturbances therefore may become more explicitly recorded in GPS-registrations. Thus there seems to be a trade-off between different types of disturbances and attractions.

Although the preferred vegetation types remained the same, the home-range locations shifted

throughout the snow-free season. Differences in home-range sizes between periods may be a result of the herd structure in relation to growth of the calves, insect harassment, and the phenology of the vegetation. Immediately after birth (beginning of the spring period in our study), the calves lie down at short distances from their mothers and move only when the mothers are too far away (Espmark 1971). The females thus tend to be more stationary, which likely contributes to the smaller home ranges in spring. Range overlap in spring for the individual reindeer was higher in Vaisa than in Handöl and Sarek, which may be ascribed to fewer snow-free foraging patches in Vaisa because of a thicker snow layer (A. Skarin, pers. obs.), and thus fewer choices for the reindeer.

During the early summer period, the home ranges became larger than in spring, and this coincides with the increased calf mobility at about one month of age (Espmark 1971). The overlaps between the GPS-equipped reindeer home ranges were not especially large considering the gregariousness of the species. However, this proves that the GPS-equipped reindeer were widely dispersed in the herds, as we had assumed. Consequently, the range overlap was considered high in all three study areas during this period. The reindeer most likely formed larger herds because of increased harassment from species of mosquitoes and species of Simuliidae (Downes et al. 1986, Mörschel & Klein 1997, Noel et al. 1998, Skarin et al. 2004). This behaviour is also commonly used by reindeer herders to facilitate gathering of the reindeer for calf marking. It has been shown that reindeer and other herd-living ungulates are more influenced by the choices made by the group than by individuals (Colman et al. 2004). Colman et al. (2004) argued that this behaviour improves the animals' possibility to find a good foraging habitat. However, when animals form large herds, density and competition between the animals increase and may force part of the animals to forage in less profitable habitats (Barta et al. 1997, Christman & Lewis 2005). In our study, we found a non-significant tendency of less predictable individual home ranges (low R^2-values; see Fig. 4B) when ranges overlapped much. Thus, our findings do not exclude the point of view that individual reindeer within a herd might have difficulties in occupying optimal home ranges with regard to foraging. As mentioned earlier, each individual home range is occupied by quite many herd members. This in turn suggests that RUF

fitted to individual animal's use of the range likely underestimates the animal's actual preferences. Instead, the RUFs represent the preferences that were possible to achieve for all the herd members under influence from the animal density in the range.

In mid summer, harassment from oestrid flies forces reindeer to run and flee long distances (Mörschel & Klein 1997, Skarin et al. 2004). In our study, this became evident as an increase in the home-range size and a decrease in the overlap between the individual home ranges. The absence of a break-point value (r_c) for the mid summer period also indicates that the reindeer moved longer distances more often during this period. The more equal nutrient value over the different vegetation types later in the snow-free season (Mårell et al. 2005), together with the reindeer's attraction to mushrooms (Launchbaugh & Urness 1993), may also have contributed to the more extensive movements. By this time, the calves are also large enough to follow their mothers for longer distances (Espmark 1971). In addition, the large amount of non-significant coefficients in the RUF-models point towards a more individual behaviour with diverging habitat preferences of the individual reindeer trying to optimise foraging (Rayor & Uetz 1990). This indicates that reindeer make individual choices although the species is a herd-living animal.

In late summer, as the rut approaches and insect harassment decreases, reindeer usually split up in smaller groups (Downes et al. 1986), which may explain the observed lower overlap. When insect harassment decreases, this is likely to result in lower altitudes being used more in the late summer period than in the other periods (Mörschel & Klein 1997). This might, however, also be an effect of cooler weather and emerging wilting of plants at higher altitudes.

The predictive capacity of the estimated reindeer home ranges using the RUF-model differed between periods. The positive correlation between overlap and CVC showed that the predictions of the home ranges became better with increased herd density. This is quite natural as home ranges situated in the same area have a greater chance of being equal, and it gives the opportunity of identifying important habitats during sensitive periods in reindeer herding, in situations of exploitations for other uses of the land. It is likely to be more difficult for reindeer to select a good home range during these periods. As the ranges must be sufficient in all parts of the

season, such areas need to be reserved for reindeer husbandry. Contrary to this, during the mid and late summer periods individual and diverging habitat preferences of reindeer led to a lower predictability of the home ranges using the estimated RUFs.

In conclusion, reindeer habitat selection throughout the snow-free season at the landscape level was mainly dependent on avoidance of insect harassment, the melting snow cover, vegetation types, and plant growth. Thus, when using positioning data in studies of animal habitat selection, a differentiation of the data at the temporal scale is necessary to be able to separate habitat use at different spatial scales. The reindeer habitat use was the same in all areas over the periods with respect to preferred and avoided vegetation types. As our study covered three districts with diverging vegetation types and environmental conditions, our results showed a generality in the reindeer preferences that can also be transferred to other reindeer herding districts in the mountain area not included in our study. However, despite the consistency in the preference of meadows, grass heaths and heaths covering the majority of the range land, there was large individual variation in the habitat selection of reindeer. The reindeer most likely tried to optimise foraging by making individual choices although being influenced by the behaviour of the herd at the same time. Insect harassment apparently had a large impact on the reindeer habitat choice during the mid summer periods. Contrary to extensive reports of avoidance of human activities, hiking trails seemed to have no effect on the habitat selection made by semi-domesticated reindeer. The reindeer even chose vegetation types close to hiking trails, indicating that forage was more important than avoidance of human activities.

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