Reindeer Use of Alpine Summer Habitats

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Abstract

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Alpine areas in the Scandinavian mountain region are used for grazing by semi-domesticated reindeer (*Rangifer tarandus tarandus*) during the snow-free season. These areas are also used for outdoor recreation and tourism. In summer the reindeer seek nutritive forage and relief from insect harassment during warm weather. Their habitat selection is also expected to be affected by human occurrence in the ranges. Knowledge of reindeer habitat use is needed in management, both within reindeer husbandry and society as a whole.

This thesis presents research on habitat selection by reindeer at the landscape level within three temporal scales (whole summer, four summer periods, and daily cycles). The study was conducted in four study areas (210 to 4000 km^2 each) within three reindeer herding districts in Sweden: *Idre Nya Sameby* (62°00'N)*,* *Handölsdalen* (63°00'N) and *Sirges* (67°00'N). The study areas differed in topography, relative abundance of vegetation types, and occurrence of back-country hikers. The reindeer habitat use was surveyed with pellet-group counts and with 48 adult female reindeer equipped with GPS collars. Reindeer preferences for different habitat attributes and reactions to hiking trails were analysed by fitting resource utilisation functions and by analyses of reindeer movements.

The reindeer showed a general preference for high altitudes at all temporal scales. Selection for high-quality vegetation types was shown, in the reindeer home ranges within the periods, with preference for meadows, grass heath, and heath. The reindeer seemed limited in their forage intake by insect harassment. Effects of hiking trails were small, but the reindeer movement rates increased close to hiking trails in areas with low frequency of hikers. In areas with a higher number of tourist-reindeer encounters the reindeer seemed to have habituated to the hikers. When insect relief areas coincided with high abundance of hikers, the reindeer seemed to accept human disturbance in order to get insect relief. Predictions of habitat selection evaluated by cross-validation of estimated resource utilisation functions showed fairly low predictive capacities with the high resolution of habitat attribute data. For management purposes the results are suggested to be converted to a value point system for range compartments.

Keywords: Rangifer, landscape scale, temporal scale, habitat selection, home ranges, GPS, pellet-group count, resource utilisation functions, human disturbance

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To my father

Contents

Appendix

Papers I–IV

I base my thesis on the following papers, which will be referred to by the corresponding Roman numerals in the text.

I. Skarin, A., Danell, Ö., Bergström, R. & Moen, J. 2004. Insect avoidance may override human disturbances in reindeer habitat selection. *Rangifer 24*, 95–103.

II. Skarin, A., Danell, Ö., Bergström, R. & Moen, J. 2006. Summer habitat preferences of GPS-collared reindeer (*Rangifer tarandus tarandus*). *Wildlife Biology*. In press.

III. Skarin, A. Habitat use of semi-domesticated reindeer estimated with pellet-group counts. Manuscript.

IV. Skarin, A., Danell, Ö., Bergström, R. & Moen, J. Reindeer movements in alpine summer ranges. Manuscript.

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Introduction

There are several grazing systems in the world with large migrating herbivores. Well-known examples are the caribou and reindeer (*Rangifer tarandus*) on the tundra of the northern hemisphere, the Mongolian gazelle (*Procapra gutturosa*) on the steppes of Asia, and the wildebeest (*Connochaetes taurinus*) and other large herbivores of the African savannah. A general characteristic of these animals is their adaptation to seasonally available forage in ranges that are spatially far apart.

Reindeer and caribou are dependent on fresh and nutritive forage, such as herbs and graminoids in summer, while they eat lichens and evergreen plants in winter (Klein, 1990). The summer season is the time when the reindeer and caribou recover from the usually poor winter situation. Besides their dependence on fresh and nutritive forage in summer, the reindeer are also affected by such factors as harassment from insect, human activities and predators in their habitat selection (Mörschel & Klein, 1997; White *et al.*, 1981; Wolfe, Griffith & Wolfe, 2000).

In Sweden, all reindeer are semi-domesticated but live under conditions similar to those of wild reindeer. Most of them move between the nutrient-rich alpine ranges in summer and forests with lichens in winter. There are few studies of summer habitat selection by semi-domesticated reindeer in the Swedish alpine ranges, although they live in a landscape where tourism and infrastructure coincide with their natural environment.

The use of Swedish alpine ranges for reindeer husbandry

The reindeer in Sweden are herded by Sami reindeer herders. The reindeer herding area is divided into 51 reindeer herding districts and range from Idre, in the county of Dalarna in the south, to the Norwegian and Finnish borders in the north. In 33 of these reindeer graze in the alpine ranges during summer. In summer the reindeer graze freely within the borders of reindeer herding districts. One exception is when the herders gather the reindeer for the calf marking in the middle of the summer. The sizes of summer grazing areas of the different districts vary between 300 km^2 and 3200 km^2. Throughout the 20th century the number of reindeer in Sweden has fluctuated between 175,000 and 300,000 animals, and currently there are 266,000 reindeer (Tord Constenius, Board of Agriculture, personal communication, 2006).

Since the reindeer and the landscape mutually affect each other, the question of how and why the reindeer choose a landscape is important. In vegetation types generally considered to be preferred by reindeer, such as meadows and snow-beds or heathland, primary production, species richness, and diversity all increase through grazing by reindeer and other mammals (Olofsson, 2001). However, increased interactions between reindeer and humans may increase the movement of the reindeer (Dyer *et al.*, 2001) and affect their habitat choice. This in turn may lead to a change in distribution of impact and result in wear of the vegetation.

During summer reindeer behaviour is affected by harassing insects. Warble flies and nose botflies (*Hypoderma tarandi* and *Cephenemyia trompe*, respectively, hereafter referred to as oestrids) are common parasites that severely affect reindeer behaviour and may even reduce their grazing time (Colman *et al.*, 2003). Mosquitoes and species of *Simuliidae* also affect their behaviour, especially during the post-calving period, when the reindeer may form large herds at high altitudes to avoid the insects (Downes, Theberge & Smith, 1986; Syroechkovskii, 1995). The insect are active during specified weather conditions, and it is therefore possible to predict the expected insect activity using weather parameters (Hagemoen & Reimers, 2002; Mörschel, 1999).

There are about 8000 km of hiking trails in the Swedish alpine ranges. Apart from the private hostels and resorts, the Swedish Touring Club offers nine mountain stations and 45 lodges to stay at, most of them in remote areas. Since the beginning of the 20th century, hiking tourism in the alpine region has increased (Fredman *et al.*, 2001). Statistics from the Swedish Touring Club report that 4000 people visited Jämtland in 1910, and today the number of tourists in the whole mountain range during summer is about 480,000 each year (Heberlein, Fredman & Vuorio, 2002). Hikers, huts, infrastructure, and human activity have been reported to disturb the reindeer, but there is uncertainty about the magnitude of the disturbance (Colman, Jacobsen & Reimers, 2001; Nellemann *et al.*, 2003; Vistnes & Nellemann, 2001). In a questionnaire to back-country hikers in the northern alpine ranges, 17 percent of the hikers answered that when they encountered reindeer, the reindeer were scared and ran away (Wall-Reinius, 2006). Thirty-five percent of the hikers said that the reindeer noticed them and strolled calmly away. Further, one out of four hikers answered that “the possibility to see reindeer” was an important factor when deciding to visit the area. If they met reindeer a majority of the hikers stopped and watched the reindeer.

Further, the Swedish Government (2000) have pronounced in the environmental objectives that the mountain ecosystems should be managed from a long-term perspective. This includes keeping characteristics such as a grazed landscape, the long-term production capacity, the biological diversity, and the natural, cultural, and recreational assets. To fulfil these goals, and considering the reindeer as a key component in the mountain ecosystem, it is crucial to have knowledge about the ecology and resource selection of the reindeer.

Hierarchical habitat selection in ungulates

Spatial and temporal scales

In studies of resource selection the importance of recognizing scaling has been evident for at least three decades (Johnson, 1980; Peterson & Parker, 1998; Wiens, 1973). In resource selection studies it is common to perform the studies at several spatial scales (e.g. Apps *et al.*, 2004; Johnson *et al.*, 2004). Senft *et al.* (1987) developed the concept of hierarchical foraging in grazing ecology. Their model was based on the way that the herbivore foraging response patterns are displayed at three different levels (regional, landscape, and patch level), where the number of decisions made for one action or the number of actions decides the scale.

At the regional scale, the animal's foraging decisions deal with migration between seasonal areas or home range areas, determined by forage, geomorphology, regional climate, water locations, and physical barriers (Senft *et al.*, 1987). In reindeer husbandry this includes the migration between summer and winter ranges, where the decisions often are made by the reindeer herder. The hierarchical theory also implies that animals should select habitats that permit avoidance of the most limiting factor at large spatial scales, while influence of less important factors should only be evident at fine scales (Dussault *et al.*, 2005; Rettie & Messier, 2000). For example, at the large spatial scale areas with a high density of predators are avoided (Dussault *et al.*, 2005; Rettie & Messier, 2000).

At the landscape level, herbivores select larger patches, plant communities or feeding sites that are attractive. Further, water location, weather, topography, and predators in the plant community may influence selection (Bailey *et al.*, 1996; Senft *et al.*, 1987). Forage depletion in the patch and expectations of intake opportunities in other patches will motivate the animal to move on (Baumont *et al.*, 2000). The distances moved from day to day vary, depending on species and season. Usually stationary caribou and bison do not move more than 2 km a day (Fortin, Fryxell & Pilote, 2002; Johnson *et al.*, 2002b; Rettie & Messier, 2001), while migratory caribou are shown to move an average of 7–8 km a day (Bergman, Schaefer & Luttich, 2000). At the patch level, feeding station, plants, and plant parts are selected. For reindeer during summer there seem to be a weak patch selection, rather a selection for certain plant species (Mårell, Ball & Hofgaard, 2002).

Although spatial and temporal scales are naturally linked, researchers seldom focus on the temporal aspects within one spatial level (Wiens, 1973, 1989). How individuals allocate their time in different habitats is studied at the temporal scale (Mysterud & Ims, 1998). Further, some processes only hold for certain periods of time, after which they attenuate or change (Allen & Hoekstra, 1992).

Survey methods

Several techniques are available for surveys of animal resource selection. Faecal pellet-group counts and counting of animal tracks are examples of indirect observations, while focal sampling, aerial surveys, and equipping animals with radio telemetry or GPS collars are examples of direct observations.

The pellet-group count has the advantage of capturing the total animal abundance over a certain period with a concentrated recording effort (Marques et al., 2001). Faecal standing crop (FSC) and faecal accumulation rate (FAR) are two basic approaches to estimating pellet-group density (Campbell, Swanson & Sales, 2004; Hemami & Dolman, 2005). Another benefit of such techniques is that habitat attributes, such as vegetation type, can be registered at the same time and scale as pellet abundance. However, in pellet-group counts it is not possible to detect when within the investigated period the animals have visited the studied area or to identify animal categories (e.g. age, sex).

Focal sampling is used when the behaviour and activity pattern of an animal is wanted (Altman, 1974). Then the behaviour of a random animal within a group or a herd may be observed at defined intervals during an observation period. Aerial surveys are often used in management to estimate the number of animals within an area (Buckland *et al.*, 2001).

Radio-telemetry has been used in habitat selection studies since 1959 (Millspaugh & Marzluff, 2001). Since then the technique has developed both concerning radio transmitters and statistical modelling. One disadvantage in radio-telemetry is the difficulty of achieving exact positions. However, in the last decade the global positioning system (GPS) has provided an excellent sampling technique. Using GPS one can collect high quality and frequent data on the animals' positions, irrespective of the time of day and weather.

Modelling and evaluation of habitat use models

Predictions of animal distribution and space use are fundamental for conservation and management in ecology (Elith *et al.*, 2006). However, models cannot fully predict the preferences of a species (Levins, 1966). When an appropriate model is found, modelling of animal habitat use can provide valuable information about the ecology of a species and how the animals meet their requirements for survival (Elith *et al.*, 2006; Manly *et al.*, 2002). It is also crucial to correctly evaluate the model in order to make accurate predictions (Alldredge & Griswold, 2006; Guisan & Zimmermann, 2000).

Modelling techniques

There are many analytical techniques available for evaluating resource selection by animals. The most common technique is to compare the used areas with the available areas or with the unused ones (Thomas & Taylor, 2006). A widespread method for estimating habitat use probabilities is to take the actual positions of the animal from telemetry or GPS sampling and apply this to logistic regression with a binary response variable (Apps *et al.*, 2001, 2004; Gibson *et al.*, 2004). However, there can be a sampling problem when using this approach because the whole use of the available landscape is seldom known (Keating & Cherry, 2004). Even if a large proportion of the population is surveyed, the problem remains if it is a gregarious species. Then neighbouring habitats classified as available can be occupied by animals of the same species that are not surveyed. Neither do the logistic procedures account for variability in the intensity of use among the habitat units where locations are recorded (Millspaugh *et al.*, 2006).

Marzluff et al. (2004) developed an approach for resource utilisation functions (RUFs), where the animal's individual utilisation distribution (UD) density within their home range is related to the resource attributes. Using this technique each study animal can also be treated correctly as a sampling unit (Aebischer, Robertson & Kenward, 1993).

Evaluation of models

Evaluation of resource selection models is generally undervalued (Guisan & Zimmermann, 2000). There is a large effort put on the actual model and how well the model fits the data, while the validation of the model is not always done with the same effort. However, one of the most important considerations is whether a model reliably predicts the locations of organisms and can thus be used in management (Boyce *et al.*, 2002). When only small data sets are available, evaluation is often done through cross-validations or resampling techniques such as 'jack-knife' or 'bootstrap'. In these techniques the same data set that was used to parameterise the model is used to evaluate the model (Guisan & Zimmermann, 2000). However, this approach is weak in assessing model credibility and applicability. It is better if two independent data sets are available; then the model can be parameterized with one data set (*training* data set) and evaluated with the other (*evaluation* data set) (Zimmermann & Kienast, 1999).

Aims of the thesis

There are few resource selection studies of semi-domesticated reindeer on a large scale that simultaneously handle habitat quality and how possible human disturbance and insect harassment affect the animal. The reindeer herders' use of their ranges is something that is constantly debated; this may concern the importance of different ranges and how these ranges are used by other interests. In this thesis this issue is brought up from the reindeer and the reindeer herding point of view. The objective of this thesis was to study habitat selection by the semi-domesticated reindeer in alpine regions at the landscape level within three temporal scales (whole summer, four summer periods, and the daily cycles).

Specific questions to investigate were:

1. Which are the important habitat features for the reindeer on the alpine summer ranges?
2. Does reindeer habitat selection at the landscape level differ between temporal scales?
3. How important are weather and expected insect harassment in reindeer habitat selection?
4. To which degree are reindeer displaced from important habitats due to human disturbance?
5. Can reindeer habitat use be predicted in novel areas with the data obtained in this study?

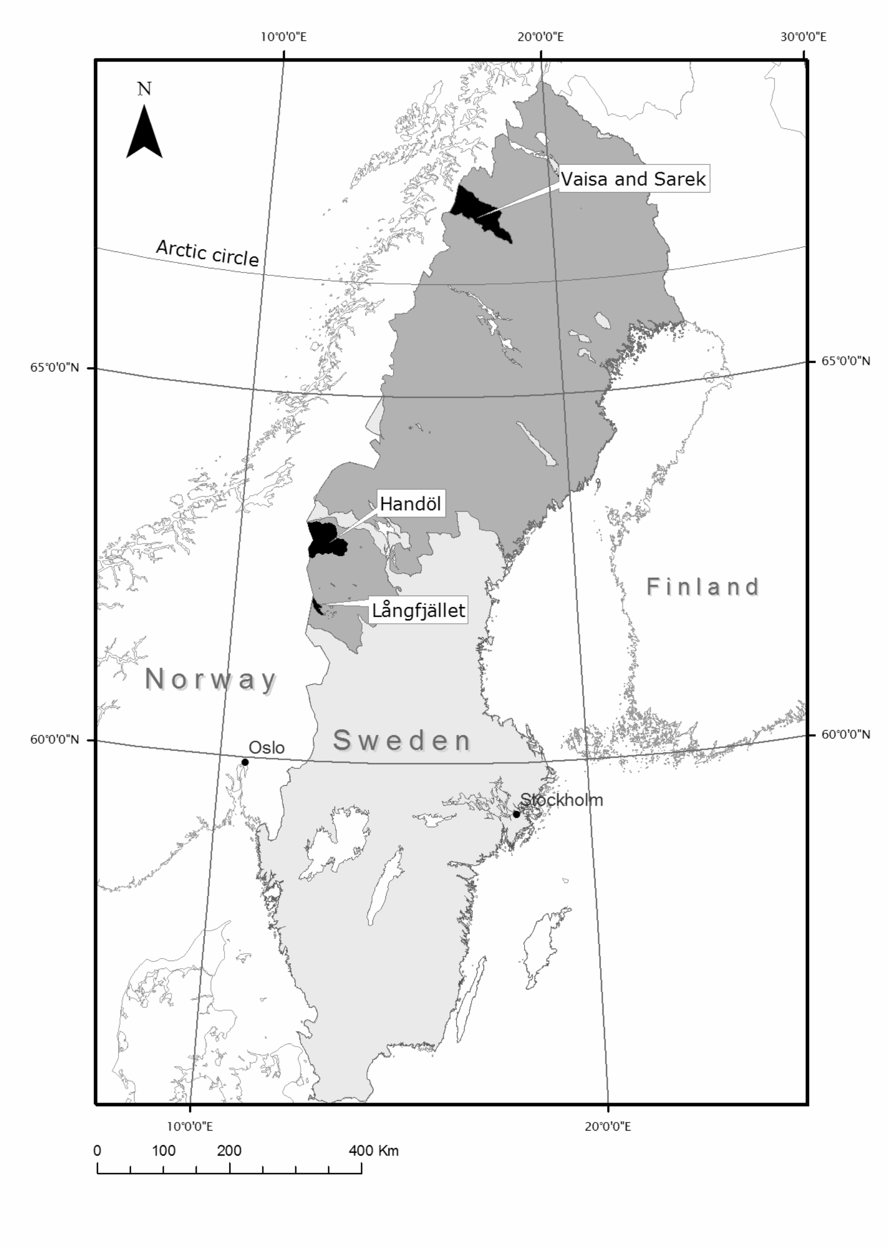

Figure 1. Map of the study areas. The dark grey area show the extension of the reindeer herding districts in Sweden. The study carried out at Långfjället is reported in paper I, and the studies in Handöl, Vaisa, and Sarek resulted in papers II, III, and IV. ©Lantmäteriet Gävle 2006. Permission I 2006/1611.

Study areas

The study was performed in three reindeer herding districts in the Swedish mountain range: *Idre Nya Sameby* at 62°00'N, *Handöldalen* at 63°00'N, and *Sirges* at 67°00'N. Altogether, there were four study areas, *Långfjället* in *Idre Nya Sameby*, *Handöl* situated in *Handölsdalen*, and *Vaisa* and *Sarek* in the *Sirges* reindeer herding district (Fig. 1). The areas were chosen in order to contrast difference in topography, climate, and possible interference from back-country hiking.

Långfjället is the least elevated area, ranging from 800 m to the highest peak at 1204 m, and *Sarek* is the most alpine area, with elevations ranging between 500 and 2015 m. *Handöl* has elevations that range between 600 and nearly 1800 m, and *Vaisa* is slightly lower, ranging between 500 and 1500 m. *Långfjället* has the lowest annual precipitation (800-1000 mm) and the highest mean temperature in July (11°C), followed by *Handöl* (700–1300 mm, 10°C), *Vaisa* (900–1500 mm, 9°C), and *Sarek* (900–1700 mm, 7°C) (during the years 1961–1990; Lantmäteriet, 2002). The vegetation period in *Långfjället* and *Handöl* (temp > 5°C) is 120–130 days, in *Vaisa* and *Sarek* it is somewhat shorter (100–110 days). Since *Långfjället* and *Handöl* is further south than *Vaisa* and *Sarek,* the tree-line reaches higher elevations (900 m compared to 600 m in *Vaisa* and *Sarek*). *Långfjället* is dominated by dry heath, extremely dry heath and extremely dry heath with lichens (Table 1). The vegetation in *Handöl* is also dominated by heaths, ranging from wet to extremely dry. However, there are more grass heaths and meadows than at *Långfjället*. In *Vaisa* common vegetation types are grass heath, meadows, dry heath, bare rock, and sparsely vegetated areas. *Sarek* has approximately the same proportions of vegetation types as *Vaisa* but includes more glaciers and bare rock.

Table 1. Percent of the most common vegetation types in the four study areas.

	Långfjället	*Handöl*	*Vaisa*	*Sarek*
Bare rock and bedrock outcrops	1	8	10	17
Sparsely veg. areas		0	12	9
Dry heath	34	30	17	12
Extremely dry, fresh and wet heath	52	26	17	18
Grass heath	2	6	17	18
Meadow	0	5	9	3
Mires	2	6	2	2
Forests	7	13	1	10
Other	1	5	16	11
Total	100	100	100	100

The hiking season in the Swedish mountain range starts in the beginning of July. Among the study areas, *Långfjället* and *Handöl* are the most popular for back-country hiking. Along the southwest side of *Långfjället* there are two private hotels and areas with cabins and also one large mountain station where the main trails starts. *Handöl* contains three larger mountain stations and four tourist lodges and main trails leading to these (Vuorio, 2003). Along the border between *Vaisa* and *Sarek* there is a hiking trail with lodges. However, this trail is sparsely used compared to the hiking trails in *Långfjället* and *Handöl*. Otherwise, *Vaisa* is sparsely used for human activities besides reindeer husbandry. The central parts of *Sarek* contain no lodges or mountain stations, but there are hiking trails along the major valleys.

Survey of reindeer habitat selection

The survey methods chosen for this study were pellet-group counts and GPS-based technique. The data received were stratified in three temporal scales within the landscape level. The longest scale was the seasonal level, the whole summer season from May to September. The intermediate scale was the periodic level, where the summer was divided into four periods, *Spring*, *Early*, *Mid,* and *Late summer* (the criteria for the division are described in detail in papers II and IV). The circadian cycle within each period was used as the shortest temporal scale. The spatial resolution of collected data about the habitat features in the surveys ranged between 15 m^2 and 2500 m^2. The period for the calf marking was removed from the GPS data sets since the reindeer were handled by the herders at this time.

The faecal standing crop (FSC) technique (see above) was used in *Långfjället* in 2000 (paper I), while the FSC technique was used in *Vaisa* and *Handöl* in 2002 (paper III), and the faecal accumulation rate (FAR) technique in 2003. The pellet groups counted with the FSC technique represented the use of at least three summer seasons (Skarin, 2006, unpublished note on a decay rate experiment), and the pellet groups counted with the FAR technique represented one summer. The surveys were performed using the line transect method (Buckland *et al.*, 2001). The pellet-group counts represented the largest temporal scale; the use over the whole summer season.

The pellet groups were recalculated to numbers of separate pellets and from there to pellets m^{-2}. The pellet densities, separated over years and areas, were then related to topographic characteristics, vegetation type (registered in the field), and distance to hiking trails in multiple linear regressions (papers I and III) and resource selection functions (RSF; Manly et al., 2002; paper I).

The GPS surveys were performed during the two summer seasons of 2002 and 2003. In total 48 adult female reindeer were equipped with GPS collars (GPS Posrec, TVP Positioning AB), which registered the reindeer positions every second hour and every hour, respectively. In 2002 there were 9 reindeer equipped with functioning GPS collars in each of *Vasia* and *Handöl*. In 2003, 10 reindeer in *Handöl*, 7 in *Vaisa*, and 12 in *Sarek* were equipped. In addition, one reindeer moved from *Sarek* to *Vaisa* on the 9 August 2003. Adult female reindeer were chosen as study animals because they represented the majority of the herd. The only additional selection criterion was that the females were judged to be rearing calves (2002) or being pregnant (2003).

The GPS data were stratified and analysed at all three temporal levels (papers II and IV). The GPS survey provided a large number of data sets; one for each individual at each temporal level. At the seasonal level and within the periods, multiple linear regressions of the reindeer movement rates on habitat attributes and temperature and wind speed were fitted. In addition, predicted insect harassment was also used instead of the weather parameters to fit the models for the *Mid summer* periods. In the analyses I grouped this harassment into three groups: warble flies and nose botflies (OES), mosquitoes and species of Simulide (MOS), and no insect harassment (NOI), based on daily weather data from two weather stations (paper IV). The circadian cycle of the movement rates and the reindeer altitudinal positions were tested within each period (paper IV). Within the periods, the utilisation distribution (UD) in the kernel home ranges of individual reindeer was also related to habitat attributes in resource utilisation functions (RUFs) using multiple linear regressions (paper II). The estimated coefficients were averaged across individuals within areas, and over periods or seasons.

Summary of results

General importance of topographic features (I, II, III, and IV)

High altitudes were used by the reindeer at all three temporal scales. At the seasonal level the pellet densities increased with higher altitudes (I and III). Within periods the average altitude of the reindeer home ranges was higher during *Mid summer* and to some degree in *Early summer* (II). In *Mid summer* the daily pattern showed that the reindeer used higher altitudes in daytime when oestrids were expected to be active compared to when they were inactive (IV).

Ruggedness affected the reindeer at both the seasonal and the periodic level. At the seasonal level the reindeer avoided rugged terrain (III) and decreased their movement rates in these terrains (IV). However, at the periodic level in *Handöl* in *Spring* and in *Sarek* in *Late summer* the reindeer avoided the rugged terrain (II) and increased their movement rates (IV). In four other periods they decreased their movement rates in rugged terrain (IV). However, these areas were not avoided (II). Rugged terrain was also correlated with high altitudes. Southwest slopes were found attractive at the seasonal level in *Handöl* and *Långfjället* and at the periodic level in *Handöl* and *Vaisa* (I, II, and III).

Selected vegetation types in alpine areas (I, II, III, and IV)

At the seasonal level, the pellet densities were higher in grass heath, dry heath, extremely dry heath, and fresh heath than in other vegetation types in *Långfjället* and *Vaisa* (I and III). Within the home ranges, the reindeer consistently preferred meadows, grass heath, and other heaths (comprising dry heath, extremely dry heath, fresh heath, and wet heath), within all areas but not in all periods (II). During the expected insect season (*Mid summer*), the only preference for meadows and grass heath was found in *Handöl*, while the reindeer in *Vaisa* and *Sarek* did not show preferences for any specific vegetation type. Bare rocks and bedrock outcrops were generally avoided by the reindeer both at the seasonal and the periodic level.

Within the preferred vegetation types (II), except grass heath, the reindeer had slower movement rates (IV). In avoided vegetation types such as bare rock, they increased their movement rates. In the circadian cycle during *Mid summer* the reindeer used vegetation types with less forage at daytime and vegetation types with high quality forage at night time (IV).

Disturbances from expected insect harassment (IV)

At both the seasonal and the periodic levels, the reindeer increased their movement rates with increasing temperature. In *Mid summer* in all study areas the reindeer increased their movement rates during predicted OES harassment, and decreased their movement rates during predicted MOS harassment (IV). The reindeer also increased their group size with expected insect activity (I).

Influence from human activities (I, II, III, and IV)

At the seasonal level the reindeer in *Långfjället* and *Vaisa* preferred areas close to hiking trails, while in *Handöl* the reindeer were indifferent to hiking trails, but there were indications of the reindeer using areas close to hiking trails (I and III). However, in *Handöl* the reindeer mean distance to highly trafficked hiking trails over the whole summer increased after the tourist season had started (IV). Within their periodic home ranges the reindeer in *Handöl* also avoided areas with houses and camping sites in *Early summer* (II). Otherwise, the reindeer neither preferred nor avoided areas with hiking trails within their home ranges in any of the areas.

In *Spring* the reindeer in *Handöl* increased their movements close to hiking trails. In *Mid summer*, the reindeer in *Vaisa* and *Sarek* also responded with increased movement rates close to hiking trails (IV). Hiking trails were also often situated in preferred vegetation types (II) or at high altitudes (I).

Predictive capacity of the models (II and III)

The adjusted RUF models of reindeer home ranges on habitat attributes had low cross-validation values (ranging between -0.12 and 0.15; paper II). The models of pellet density on the habitat attributes were higher (ranging between 0.29 and 0.51; paper III). However, the reindeer response to vegetation types and altitude was consistent between the years and areas.

General discussion and conclusions

Important habitats for the reindeer

The general habitat preferences of high altitudes and high-quality vegetation types by the reindeer in summer in the alpine ranges were consistent with previous findings. The reindeer also avoided areas scarce in forage. Summer habitat selection studies of reindeer and caribou have shown that high altitudes are important for the reindeer during insect harassment (Anderson & Nilssen, 1998; Downes, Theberge & Smith, 1986; Mörschel & Klein, 1997). Reindeer have also been found to prefer fresh and nutritive forage throughout the summer (Mårell, Ball & Hofgaard, 2002; Skogland, 1980). However, using the three temporal scales also revealed that different parts of the summer range were used during different weather conditions and periods within the summer.

The selection between insect relief and high-quality forage

The consistent preference for high altitudes by the reindeer in the alpine summer ranges across study areas and temporal scales showed that these were important for the reindeer. At the longer temporal scale it also seemed that the altitude had a stronger influence on the reindeer than the vegetation type. At the landscape level abiotic factors are expected to have a strong influence on animal habitat selection (Apps *et al.*, 2001; Johnson, Seip & Boyce, 2004). There may be several reasons for the preferences for high altitudes in my study.

However, although I did not study insect harassment in direct relation to reindeer activity, one of the main reasons for preferences of high altitudes seems to be insect harassment. The daily cycles in *Mid summer* showed that during expected OES and MOS harassment the reindeer increased their movement rate and moved up the hillsides to stay there during harassment. Although this is based on weather parameters, I interpret this movement as a response to insect harassment (Hagemoen & Reimers, 2002; Mörschel, 1999). During insect harassment the reindeer are expected to choose insect relief habitats such as high altitudes and wind-exposed sites (Hagemoen & Reimers, 2002; White *et al.*, 1975).

I also found increased movement rates during expected OES harassment and decreased movement rates during expected MOS harassment. In activity studies of reindeer during insect harassment, the reindeer have particularly been found to increase their insect avoidance behaviour in the presence of oestrids but not in the presence of mosquitoes (Espmark, 1967; Mörschel & Klein, 1997; Downes, Theberge & Smith, 1986). This may also limit the reindeer grazing time (Colman *et al.*, 2003).

The selection for vegetation types was not as strong as the selection for high altitudes. The most important features for the animal should become evident at the larger scale (Rettie & Messier, 2000). At the longer temporal scale, the reindeer only selected for the high-quality vegetation type grass heath and dry heath in two of the areas and fresh heath in one area, while they selected for meadows, grass heath, and heaths (comprising dry heath, extremely dry heath, fresh heath, and wet heath) at the periodic level in all areas investigated. They also had slower movements within all preferred vegetation types except grass heath (IV). This resembles the preferred grazing habitats by reindeer found in other studies (Mårell, Ball & Hofgaard, 2002; Skogland, 1980). The selection for high-quality forage at the landscape level confirms earlier studies (Apps *et al.*, 2001; Johnson, Seip & Boyce, 2004; Mysterud, Lian & Hjermann, 1999). Within a foraging bout the animal may also make frequent short-distance moves (Johnson, Parker & Heard, 2001), which would explain the slower movement rate if the reindeer found forage patches within the vegetation type.

It was not possible to completely separate important grazing habitats and areas that are advantageous during insect harassments. The general preference for southwest slopes may both be explained by high forage abundance and insect relief. These slopes face towards the prevailing wind direction both in winter and summer. Thus, this may result in a shallow snow layer in winter which makes these slopes snow-free early in the season, providing the reindeer with fresh and nutritive forage. During summer the weather is also warmer when the wind comes from the southwest (I). Thus, the insect harassment increases and makes these slopes attractive for the reindeer during insect harassment (cf. Anderson & Nilssen, 1998). Further, the strong preference for meadows and grass heath in *Handöl* in *Mid summer* may also occur since they were situated at higher altitudes and offered insect relief. These vegetation types did not coincide with high altitudes in the other study areas.

However, even if the reindeer preferred high-quality forage when they used high altitudes (II and III), these studies also indicated several ways by which insect harassment may have limited the reindeer in forage intake. The shift of vegetation types in the daily cycles in *Mid summer*, when the reindeer used more sparsely vegetated vegetation types at high altitudes, was quite natural since these vegetation types are more common here (cf. Carlsson, Karlsson & Svensson, 1999). In *Vaisa* and *Sarek,* the lack of selection for meadows and grass heaths during *Mid summer* may be due to preference for high altitudes overriding the selection of vegetation types. The reindeer increased their movement rates in grass heaths. The reindeer also increased their gregarious behaviour during insect harassment, which in turn may limit them to grazing in non-productive habitats (II). Further, if insect harassment limits the reindeer in their forage intake, this would be evident at the large spatial scale (Rettie & Messier, 2000). This is reflected in my studies as a preference for high altitudes as insect relief habitats.

Thus, the selection of insect relief habitats overrides the selection of high-quality forage, which may limit the reindeer in their forage intake.

Disturbance from human activities

The avoidance of huts and camping sites in *Handöl* during the *Early summer* (after the calving; II), and also the increased movements close to hiking trails during the *Spring* period (IV) agree with results in earlier studies of reindeer avoiding human activity during and right after the calving period. In these studies there is an agreement that *Rangifer* are especially sensitive to human disturbance at this time (Aastrup, 2000; Dyer *et al.*, 2001; Nellemann & Cameron, 1998; Vistnes & Nellemann, 2001).

However, outside the calving season the reindeer in *Långfjället*, *Vaisa* and *Handöl* seemed to even prefer areas close to hiking trails, which indicates that the reindeer were not displaced from habitats with human activity during these periods. There are studies which indicate that reindeer may habituate to human disturbance (Colman, Jacobsen & Reimers, 2001), and that animals seem to habituate to the human activity provided that the activity is not too high (Wolfe, Griffith & Wolfe, 2000). This contrasts with other studies which suggest that the reindeer are disturbed and displaced by human activity and infrastructure (Nellemann *et al.*, 2003). The results in this thesis do not generally support this viewpoint.

There seems to be a range with a lower and an upper limit of human disturbance within which the animals can accept the disturbance. In *Vaisa* and also in *Sarek* the reindeer increased their movement rates the closer they were to hiking trails. In a study where a questionnaire was sent to hikers in these areas, the interview answers also indicated that many of the reindeer were scared away by the hikers (Wall-Reinius, 2006). Since the number of hikers was scarce in *Vaisa* and *Sarek* compared to *Långfjället* and *Handöl*, it could mean that the reindeer in *Vaisa* and *Sarek* were not habituated to the hikers, while the reindeer in *Långfjället* and *Handöl* had habituated.

However, for the reindeer in *Handöl* this explanation is not obvious. In paper III there was no significant increase in the number of pellets close to hiking trails in *Handöl*, as was the case in *Långfjället* and *Vaisa*. This might mean that the reindeer in *Handöl* actually avoided hiking trails during the hiking season as indicated by Fig. 5 in paper IV. However, this might be confounded by the fact that the high altitudes used by the reindeer in *Handöl* during insect harassment were located far away from the hiking trails. Nevertheless, the reindeer seemed to go down from the high altitudes during night time. Doing this they may have come closer to the hiking trails when the hikers were more inactive (Wall-Reinius, unpublished results). Thus, they may have allocated their time between high altitudes in daytime and low altitudes at night time to be able to stay in disturbance-free areas throughout the day and still benefit from better grazing at lower altitudes, A trade-off between disturbances was indicated in the study from *Långfjället,* where disturbance from insect harassment seemed to make the reindeer more tolerant of other disturbances. Similarly it has been found that when there is disturbance from other environmental factors such as insect harassment, the reindeer and caribou are least likely to avoid developed areas (Noel *et al.*, 1998; Pollard *et al.*, 1996; Yost & Wright, 2001). *Långfjället* itself was used by the reindeer preferably during insect harassment, since they had few alternatives to find other insect-free habitats.

Management implications

The most important question in this thesis from a management point of view is to which degree these results are useful for predictions of reindeer habitat use in areas not studied. General conclusions from this thesis were that most of the available area above the tree-line containing high-quality vegetation types was used by the reindeer when seen over the whole summer season. The vegetation types avoided by the reindeer above the tree-line were willow thickets, mires, sparsely vegetated areas and places with no vegetation, such as bare rock, bedrock outcrops, and glaciers. The difference in use seems to be a result of interaction between factors such as weather, insect harassment and human disturbance, in addition to vegetation and topography. It may therefore not be possible to do categorical predictions (i.e. important habitats versus unimportant) of reindeer habitat use in novel areas.

A possible approach might be to develop a point system differentiated by periods within the summer season, where value points are given to different habitats. These values should be based on vegetation, topographic features (representing phenology and insect avoidance), degree of human disturbance, and vicinity to other essential habitat types. Calibration of such a system could probably be done with the results in this thesis. Further, validation of these values is also essential and would require empirical habitat selection studies in new areas for which habitat use is predicted.

The higher predictive capacity shown for the models using pellet-group counts (III) indicates that pellet-group counts are better for prediction or validation of habitat use than GPS data is. This may depend on the fact that the two survey methods differed in spatial range and also in the number of animals surveyed. The pellet-group count covered the variation of the whole population and the whole summer range. The GPS data represented less than one percent of the animals which means that the sampling error may be larger because fewer animals were surveyed. Thus, pellet groups may be best suited for the empirical validation of a habitat use prediction system.

In ecological studies it is common for models to be uncertain and have low predictive capacities (Barry & Elith, 2006). This was also the case in our studies; this may have several explanations. For example we did not study insect and hikers abundance in direct relation to the reindeer habitat use and movements. These studies also had a high resolution in the data concerning the study covered a large spatial range. Thus, a lot of statistical noise was registered in the data, which may be reflected in the validations and the R^2-values. Although the predictive capacities were numerically low, the models managed to predict the same patterns in the different areas. Since there was great consistency in the results of the two survey methods and also in relation to earlier studies, this strengthens the models. There was also a larger number of GPS collars in this study compared to earlier studies (Ager *et al.*, 2003; Johnson *et al.*, 2002a), which gives the results further strength.

Future research

An important follow-up to this thesis is to develop a habitat use predictive system, as discussed in the 'Management implications'. Another question that lacks answers is the disturbance from human activities. In this thesis the hikers were only observed indirectly in relation to the reindeer activity. A more detailed study is required, where the frequency of human reindeer encounters are quantified and handled simultaneously with other habitat attributes as done in this thesis.

Something that has not been brought up in this thesis is how the ptarmigan hunt affects reindeer habitat selection. The willow ptarmigan live in the willow thickets and the birch forest vegetation, where the reindeer preferably eat mushrooms during the second half of the summer. The hunt start on 25 August each year and in some reindeer herding districts the hunt is carried out over a large part of the range used during the autumn. However, in most of the reindeer herding districts the hunt is cancelled in sensitive parts of the districts. Nevertheless, the impact of the hunt on the reindeer is unknown.

Another research area that has only been touched on in this thesis is the gregarious behaviour of the reindeer forcing the individual reindeer to forage in non-productive grazing habitats. The results found were only indicatory and it was not possible to analyse them further. However, it would be interesting to investigate if there is any difference in gregariousness during different foraging conditions and disturbances from insect or humans. Thus, the assumption is that the reindeer should spread out more when the nutritive quality of the forage is low, but that this behaviour might be overruled during a disturbance.

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Svensk Sammanfattning

Renen är ett hjortdjur som lever företrädesvis på tundran och i taigan på det norra halvklotet. I Eurasien är de flesta renar tama och hålls av renskötande folkgrupper, medan deras motsvarighet i Nordamerika, caribou, lever i vilt tillstånd. I Sverige finns det för närvarande drygt en kvarts miljon renar som till största delen ägs och sköts av samer. De flesta renarna i Sverige har sina vinterbetesmarker i barrskogen och sommarbetesmarker i fjällen. Under sommaren är renen relativt fri i sitt val av betesområde och därför kan deras beteenden och val jämföras med hur andra vilda hjortdjur använder sina betesområden. Från Sverige finns det få vetenskapliga studier gjorda på hur renarna använder sitt sommarbetesområde, men naturligtvis finns lokal kunskap om detta hos de renskötande samerna. Den kunskapen behöver dock kvantifieras och formaliseras för att ge en mer generell bild av hur renarna använder landskapet; en kunskap som sedan kan användas mer övergripande vid markförvaltning.

Renen är en idisslare som är väl anpassad till stora årstidsvariationer i betestillgång. Under sommaren väljer renen mellan minst ett hundratal olika gröna betesväxter, som gräs, halvgräs och örter. Den betar också blad från buskar och träd. Under vintern är renen i stor utsträckning beroende av lav. Efter en lång och krävande vinter är sommaren en period av återhämtning och uppbyggnad för renen. Hur väl detta sker påverkas av om renen blir störd av myggor och framförallt kormflugor och svalgbroms (som parasiterar på renen). Renen flyr då till svalare och mer vindutsatta områden högre upp i terrängen, vilka samtidigt kan ha sämre bete.

Under sommaren används fjällen också av vandringsturister. I områden som används frekvent av vandrare har renägare märkt att renarna bli störda. Det finns studier gjorda på hur renen påverkas av mänsklig störning men det saknas en samstämmighet om och i vilken grad renar undviker denna typ av områden.

I avhandlingen har jag studerat hur olika faktorer påverkar tamrenen sommartid i dess val av betesområde. För att få en samlad bild, har jag undersökt renens val av område över hela säsongen, inom fyra olika perioder av sommaren (vår, försommar, högsommar, samt sensommar) och under olika delar av dygnet. De fyra tidsperioderna är indelade efter säsongsförändringar i väderleken och händelser i renskötseln.

Studien genomfördes i fyra områden inom tre olika samebyar; *Långfjället* i Idre Nya Sameby i Dalarna, området mellan byn Handöl i Jämtland och byn Ljungdalen i Härjedalen tillhörande Handölsdalens sameby (hädanefter kallat *Handöl*), samt två områden i Sirges sameby, *Vaisa* och *Sarek*, som delvis ligger inom Padjelantas och Sareks nationalparker. För att samla in data om renens användning av områdena gjordes spillningsinventeringar på *Långfjället* år 2000 och i *Handöl* och *Vaisa* år 2002 och 2003. Under somrarna 2002 och 2003 utrustades också sammanlagt 48 renar i *Handöl*, *Vaisa* och *Sarek* med GPS-halsband.

Spillningsinventeringen utfördes genom att renens spillningshögar räknades på provytor (vardera på 15 m^2). Dessa ytor var systematisk utlagda över hela studieområdet för att få en heltäckande bild av hur alla renar under en eller flera somrar använt betesområdet. Inom varje provyta bestämdes också vegetationstyp. Antalet spillingshögar per yta relaterades sedan statistiskt till vegetationstyp, topografi (höjd, brutenhet i terrängen och sluttningens väderstreck), och avstånd till närmaste vandringsled.

I GPS-halsbanden samlades mer detaljerade data om hur renen rörde sig över området, när olika områden var attraktiva under sommaren och vilken tid på dygnet dessa områden nyttjades. GPS-halsbanden registrerade och sparade renens position varannan (2002) respektive varje (2003) timme. Renens positioner analyserades sedan statistiskt, men positionerna räknades först om till individuella hemområden för varje ren. Även den hastighet med vilken renen förflyttade sig räknades ut. Datan relaterades sedan till samma faktorer som spillningsdatat. Renarnas rörelser relaterades också till väderlek i syfte att klarlägga hur möjlig insektsförekomst och avstånd till närmaste vandringsled påverkade deras rörelsemönster.

Oavsett vilken tidsskala jag analyserade var högre terräng viktig för renen. Den föredrog högre områden främst under högsommaren. Genom att undersöka dygnsrytmen hos renarna, under förväntad och icke förväntad insektsstörning, fann jag att renen föredrog högre områden främst under väderförhållanden då insektsstörningar var troliga.

Över hela säsongen var gräshedar, extremt torra rishedar, torra rishedar och friska rishedar attraktiva för renen. Inom sina hemområden föredrog renarna ängsmarker, gräshedar och hedmarker framför områden med fjällbjörkskog, videsnår, myrmarker, blockmark och områden med sparsam vegetation. Detta mönster framträdde oavsett vilken period av sommaren som undersöktes. Under dagtid, på högsommaren använde renarna områden med sparsam vegetation högre upp i terrängen. Nattetid däremot gick de lägre ner för att beta i områden med bättre bete.

Under våren och försommaren, då renarna allmänt anses vara känsliga för störningar på grund av kalvningen, fanns det tydliga tecken på att renarna undvek områden med mänsklig aktivitet. Under högsommaren, i *Vaisa* och *Sarek*, där det är relativt få vandrare jämfört med *Handöl* och *Långfjället*, föredrog renarna områden nära leder. De ökade också sin gånghastighet ju närmare lederna de uppehöll sig. I *Handöl* fanns det inga tydliga tecken på att renen rörde sig snabbare eller föredrog områden nära lederna. I *Handöl* fördelade renarna dygnet mellan högre områden dagtid och lägre områden nattetid för att kunna uppehålla sig i störningsfria områden under hela dygnet och ändå dra nytta av bättre beten på lägre liggande områden. *På Långfjället* verkade renarna acceptera ett visst mått av mänsklig störning för att kunna vistas i insektsfria områden, men här hade renarna få alternativa områden att uppsöka vid insektsstörning. I *Handöl* och *Långfjället* där turister var frekventa kan renarna alltså ha accepterat ett visst mått av mänsklig störning, medan renarna i *Vaisa* och *Sarek* inte gjorde det.

De samlade resultaten visade att det var svårt att få en ”svart-vit” bild av vilka områden som var värdefulla respektive mindre värdefulla för renarna. De olika områdena användes i varierande grad under olika delar av säsongen, vilket alltså berodde på samspel mellan väderlek och insektsaktivitet, beteskvalitet och mänsklig störning. Genom att många faktorer påverkar användningen blir bilden mer komplex. Ett förslag som diskuteras är att översätta de olika faktorernas inverkan i ett poängsystem med vars hjälp ett samlat värde på olika terrängavsnitt beräknas. Därigenom kan olika delområdens betydelse för renskötseln värderas och användas i förvaltningssammanhang.

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