ORIGINAL PAPER

Reindeer movement patterns in alpine summer ranges

Anna Skarin · Öje Danell · Roger Bergström · Jon Moen

Abstract To evaluate the movement rates of semi-domesticated reindeer (*Rangifer tarandus tarandus*) during the bare-ground season, we used successive GPS positions from 48 female reindeer. Data were collected during the summers of 2002 and 2003 in two Sámi reindeer herding districts in the Swedish mountains, *Handölsdalen*, and *Sirges*. The movement rates were analysed at five different time periods: over the whole season, and over the sub-seasons *spring*, and *early summer*, *mid summer* and *early autumn*. Variation in movements were analysed in relation to vegetation type, altitude, terrain ruggedness, temperature, wind speed, and proximity to hiking trails. We hypothesised that the foraging quality and different weather conditions is an important factor in determining movement rates. We found that reindeer movement rates were similar between study areas and were dependent on vegetation type and on weather conditions. Studying the circadian movements, in *mid summer* period when daytime oestrid activity are expected to be high, the reindeer stayed at higher altitudes where food quality was low, but moved to low altitudes at night where the food quality was higher. Therefore, we suggest that oestrid activity forces the reindeer to stay in low-quality vegetation types. Reindeer movements were linked to disturbance in areas of intermediate human activity. We found that in *Handölsdalen*, where hikers are abundant, the movement rates of reindeer decreased closer to the trails whereas in *Sirges*, where hikers are less abundant, the movement rates of reindeer increased closer to the trails.

Keywords Movement rates · Temperature · Wind speed · GPS collars · Ungulates · Insect harassment · Human disturbance

Introduction

During the bare-ground season, most of the reindeer in Fennoscandia graze in the mountains. Although the majority of reindeer in Fennoscandia are domesticated and herded, they graze freely during the main part of the summer season, and their behaviour and habitat selection are comparable to wild reindeer. Reindeer play an important ecological and cultural role in Swedish mountain ecosystems (Bråthen et al. 2007; Swedish Government 2000). The Swedish Government has declared that the mountain range should be kept as a grazed landscape with its cultural and recreational assets. In this context, it is important to understand how reindeer use the landscape and how they are affected by different environmental factors.

Animal decision making can be considered a hierarchical process where selection occurs at different scales including: (1) the landscape at the regional level; (2) feeding sites or communities at the landscape level; and (3)

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feeding stations or plants at the patch level (Johnson 1980; Senft et al. 1987). Different factors also affect the animals' decisions or selections at different scales and analyses of animal movements can aid our understanding of animal responses to the environment at these different scales (Ager et al. 2003). Understanding movement patterns is vital in studies of highly mobile species, such as reindeer.

The way in which large herbivores exploit their spatial environment is primarily driven by the distribution of resources (Danell et al. 2006). In summer, reindeer are dependent on fresh and nutritive forage, such as herbs and graminoids (Klein 1990; Skogland 1980). The main preferred vegetation types by reindeer in summer are therefore meadows, snow-beds, and heath lands.

Insect harassment is also a driving force for reindeer behaviour and habitat selection in summer (Espmark and Langvatn 1979; Mörschel and Klein 1997; White et al. 1981). It is well documented that herbivores harassed by insects prefer higher altitudes and wind-exposed sites, which provide relief from the insects (Hagemoen and Reimers 2002; Mooring et al. 2003; Powell et al. 2006; Skarin et al. 2004; White et al. 1975). However, these sites may not necessarily correspond to those preferred for foraging (Mårell et al. 2002; Powell et al. 2006; Skogland 1980). Previous research has also shown that insect activity can be related to weather parameters including temperature and wind speed (e.g. Downes et al. 1986; Gaare et al. 1975; White et al. 1975; Russell et al. 1993; Mörschel and Klein 1997; Hagemoen and Reimers 2002).

With the expansion of urban areas and increased levels of hunting and ecotourism, human–reindeer interactions have also increased. In the Swedish mountain chain, there are 8000 km of hiking trails, and these are unevenly distributed across the region. Hikers are abundant along the trails during certain time periods and they are more abundant in certain areas (Vuorio 2003). Many hikers expect to see reindeer during their treks, especially hikers from other countries (Wall-Reinius 2009). The eagerness to spot or interact with reindeer can create a potential conflict if the reindeer flee as hikers approach. This extra activity causes the reindeer to use energy, loose grazing time and potentially takes them from better habitats and pastures to poorer locations.

Previous studies of reindeer during the bare-ground season have considered their reactions and responses to harassment by oestrids (*Hypoderma tarandi* and *Cephenemyia trompe*), mosquitoes and species of *Simuliidae* (Colman et al. 2003; Mörschel and Klein 1997), and to disturbance from human activities (Colman et al. 2001; Dyer et al. 2001; Vistnes 2008). Although previous studies have focused on reindeer responses to insect harassment and human activities during the summer season, these two factors have rarely been considered together. However, there is some evidence to suggest that reindeer movement occurs in order to avoid insect harassment more than to avoid human activity (Noel et al. 1998; Skarin et al. 2004). Studying reindeer movement rates simultaneously with other environmental factors in areas with different hiking pressures may enable reindeer responses to hiking pressure to be distinguished.

In a previous study, Skarin et al. (2008) described resource utilisation function models (RUF; Marzluff et al. 2004), in which reindeer home range use was correlated to vegetation type, topography, distance to hiking trails and other human interactions. These models showed that the reindeer home range use was dependent on vegetation type, aspect, and landscape ruggedness. However, an analysis of reindeer behaviour and movement rate within the boundaries of the home range is necessary to fully understand habitat selection and the extent of home ranges in relation to different environmental factors.

The aim of this study was to evaluate reindeer movement rates at two different temporal extents (whole season and sub-seasons) using GPS-location fixes with 1-hour time intervals. We assessed the reindeer movement rates over the whole summer season as well as over different sub-seasons in relation to different environmental factors to identify general patterns of reindeer movement. The factors assessed were vegetation type, altitude, terrain ruggedness, temperature, wind speed, and disturbance from human activities (measured as the distance to the nearest hiking trail). We further describe the reindeer circadian movements within the sub-seasons, and we investigate the correlations between reindeer movement rate and their home range size in an effort to explain some of the results found.

Materials and methods

Study areas

The study was conducted in the summer ranges of *Handölsdalen* (63°00′N, 12°30′E) and *Sirges* (67°00′, 17°10′E), which are both reindeer herding districts in the Scandinavian mountain range. This included three study areas, *Handöl* situated in *Handölsdalen*, and *Vaisa* and *Sarek* located in *Sirges* (Fig. 1). *Vaisa* and *Sarek* are separated by lakes and rivers, which limit but do not completely prevent migration of reindeer between the areas. The reindeer graze freely from May to October within the study areas, but are gathered for calf marking in July and bull slaughter in September. There were approximately 8,000 reindeer in *Handöl*, and 6,000 reindeer between *Vaisa* and *Sarek*.

The hiking season in the Swedish mountain range starts in July and ends in mid September (Vuorio 2003). The study areas were chosen dependent on the number of
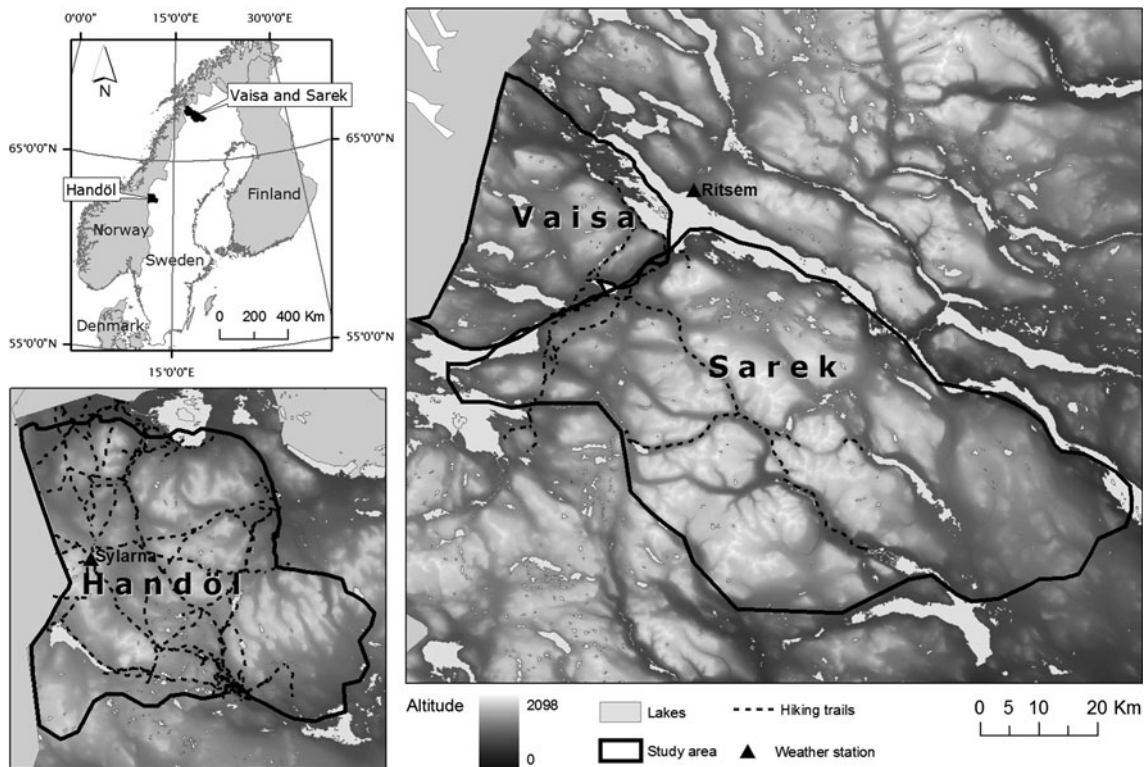
Fig. 1 Location of the three study areas: *Handöl*, *Vaisa,* and *Sarek*. Lakes and rivers separate *Vaisa* and *Sarek*, making extensive migration between these areas difficult for reindeer. *Light colours* in the topographic maps are higher altitudes. The weather stations Ritsem and Sylarna are also marked on the maps ©Lantmäteriet Gävle 2010. Permission I 2010/0055

visitors. *Handöl* is the most popular of the three areas for backcountry hiking, and has a number of main trails connecting three mountain stations and four lodges. Generally, the highest frequency of visitors to the area occurs during the last week of July and first week of August (Mats Almlöf, Swedish Touring Club, Sylarna, personal communication, July 2006). Fewer tourists visit *Vaisa* and the area is mainly used for reindeer husbandry. In *Sarek*, the hiking trails follow the major valleys and are frequently used by backcountry hikers.

The area of the *Handöl* study site is 2,000 km², *Vaisa* 1,000 km², and *Sarek* 4,000 km². The elevation in *Handöl* ranges from 600 m to the highest peaks at 1,796 and 1,761 m at *Helags* and *Sylarna*, respectively. In *Vaisa*, the elevations mostly range between 500 and 1,000 m, with the highest summit (*Rautåive*) at 1,516 m. *Sarek* has the broadest elevation range of the three sites from 500 to 2,015 m; this site also has long deep valleys and a more alpine character than the other two sites. All three areas have an alpine climate. The annual precipitation in *Handöl* is 700–1,300 mm, the mean daytime temperature in July is 10°C and the vegetation period (mean daytime temp >5°C) is 120–130 days (data averages for 1961–1990; Lantmäteriet 2002). In *Vaisa*, the annual precipitation is 900–1,500 mm and the mean temperature in July is 9°C. *Sarek* has an annual precipitation of 900–1,700 mm and the lowest mean temperature (7°C in July) of the three areas.

The vegetation period in both *Vaisa* and *Sarek* is 100–110 days. Since *Handöl* is further south than *Vaisa* and *Sarek*, the tree line occurs at higher elevations (900 m compared to 600 m in *Vaisa* and *Sarek*). The vegetation in *Handöl* is dominated by heaths, ranging from wet to extremely dry (Table 1). In *Vaisa*, the common vegetation types are dry heaths, meadows, grass heaths, bare rock, and sparsely vegetated areas. *Sarek* has approximately the same distribution of vegetation types as *Vaisa,* but with more glaciers and bare rock. In *Handöl*, 85% of the area consisted of high-quality vegetation, and in *Vaisa* and *Sarek* it covered approximately 60% of the area.

GPS data collection

The data was collected in two phases. From July 15th to September 15th 2002, 10 randomly sampled adult female reindeer at both *Vaisa* and *Handöl* were fitted with GPS collars (Posrec®, 650 g, manufactured by TVP Positioning AB). From May 10th to September 15th 2003, 10 new adult female reindeer in both areas and 10 additional reindeer in *Sarek* were fitted with GPS collars. Adult females were chosen as study animals since they represent the majority of

Table 1 Percentage of the total area of each vegetation type in the three study areas

	Handöl %	Vaisa %	Sarek %
High-quality vegetation type			
Grass heath	6.4	16.6	17.7
Dry heath	30.0	16.6	11.8
Fresh heath	19.2	9.3	6.3
Wet heath	2.7	2.2	3.0
Heaths[a]	2.9	4.2	7.2
Meadow	5.2	8.6	3.0
Mires	6.1	2.1	2.1
Thickets and willows	0.7	1.1	0.8
Birch forest	6.9	1.1	7.5
Coniferous forest	4.6	0.2	2.1
Mixed forest	1.4	0.0	0.9
Young forest	1.0		0.1
Sum of high quality	87.1	62.1	62.6
Low-quality vegetation types			
Infrastructure[b]	0.1		0.0
Lakes, shores	3.4	14.4	6.3
Blocky areas	7.7	9.8	16.6
Sparsely vegetated areas	0.3	11.9	9.2
Glaciers and snowfields	0.0	0.1	3.6
Extremely dry heath	1.4	1.7	1.8
Sum of low quality	12.8	37.9	37.4
Total area size (km^2)	2210	1050	4070

The vegetation classification is from the Swedish CORINE land cover data, with 25 × 25 m resolution. The vegetation types are also divided into two groups whether they contain high- or low-quality forage according to Klein (1990) and Skogland (1980)

[a] According to the coarser classification of Swedish CORINE Land cover map—includes dry, extremely dry, fresh, and wet heath

[b] 'Infrastructure' represents camping sites, ski slopes, and private property

the herds and they also tend to remain with the herd (Thomson 1972), and thus are likely to provide the most representative picture of how the reindeer herds use their ranges. The females were randomly sampled among those which were either rearing calves (2002) or pregnant (2003). In 2002 all reindeer had a calf, both at the calf marking stage and when the collars were removed in September. In 2003, most of the marked females had a calf (visually confirmed at calf marking), but when the collars were taken off in autumn 2003 only 60% of the reindeer still had a calf following them. The GPS equipment recorded and stored positions, and the data were downloaded after the collars were removed. In 2002, positions were collected every 2 h to increase battery life for the following year and in 2003 data were collected every hour. Less than 2% of the positions were missing due to malfunctioning equipment. In 2002, two collars (one in each area) failed to collect positions due

to technical problems. In 2003, some migration occurred between *Sarek* and *Vaisa*: 12 reindeer spent most of their time in *Sarek* and 7 in *Vaisa*. In addition, one reindeer moved from *Sarek* to *Vaisa* on the 9th of August. One collar in *Vaisa* stopped working on the 18th of August 2003.

Data analyses

Linear mixed models of movement rates and associated habitat data were fitted for each area and period with individual reindeer as random effect using the Mixed Model procedure in the SAS 9.2 software (SAS Institute Inc© 2002–2008).

In the statistical analyses, the data from 2003 were sorted into five different time periods: the whole study season and four sub-seasons: *spring*, *early summer*, *mid summer* and *early autumn*. The sub-seasons were the same as those used by Skarin et al. (2008) for home range calculations; however, for this paper we changed the name *late summer* to *early autumn* since this is more appropriate. In 2002, we only collected data during half the season and every second hour. Therefore, this data set was only used to verify the analyses of the 2003 data set within the sub-seasons, *mid summer* and *early autumn*. The movement rates determined from the two-hourly dataset are expected to underestimate movement rate by 40% compared to 30% for the hourly data (Pepin et al. 2004). The time periods for the sub-seasons were set according to seasonal weather characteristics and with respect to handling events in reindeer husbandry (Table 2). The last day of the *spring* was defined as the average date when snow cover ended (Pershagen 1969); this sub-season has scarce forage due to snow cover. The last day of *early summer* was defined as the day before the reindeer herders started to gather the reindeer for calf marking. The *early summer* is the sub-season where vegetation growth begins, providing relatively good forage availability (Mårell and Edenius 2006). *Mid summer* started after the calf marking had finished and ended when the mean daily temperature during each study year fell below 6°C. This is the temperature at which insect activity is shown to decrease (Anderson et al. 1994; Mörschel and Klein 1997; Russell et al. 1993). The *mid summer* is the main growth season when the reindeer had good access to forage (Mårell and Edenius 2006). The end of the *early autumn* corresponded to the day before the reindeer were gathered for the bull slaughter in mid-September. *Early autumn* is a sub-season with good grazing conditions but with reduced insect harassment compared to *mid summer*.

The movement rates were calculated as the distance moved between every successive GPS location recorded divided by the time elapsed (Table 2 show the mean numbers of positions used). Movement rates were not calculated if there were one or more positions missing between the

Table 2 The sub-seasons in 2003 used in the analyses distinguished according to seasonal weather characteristics and handling events in reindeer herding, and the number of reindeers with collars and mean number of successive positions per reindeer (±SD) within each sub-season and area

	Area	Date	Days	Reindeers	Mean no. of positions ± SD	Mean MR (m/h) SD	Mean HR size (km²) SE	$r_{MR, HR}$
Spring	*Handöl*	11/5–30/5	19	10	477 ± 6	216 ± 330	80 ± 13	0.739*
	Vaisa	11/5–10/6	29	7	736 ± 17	174 ± 251	35 ± 9	0.066
	Sarek	11/5–10/6	29	13	721 ± 50	188 ± 292	94 ± 13	0.724**
Early summer	*Handöl*	31/5–3/7	33	10	812 ± 5	352 ± 509	423 ± 39	0.688*
	Vaisa	11/6–14/7	33	7	611 ± 27	419 ± 567	293 ± 21	−0.12
	Sarek	11/6–6/7	25	13	798 ± 39	381 ± 510	398 ± 38	0.648*
Mid summer	*Handöl*	15/7–24/8	40	10	955 ± 41	321 ± 459	442 ± 78	0.760*
	Vaisa	19/7–28/8	40	7	1,075 ± 86	439 ± 507	404 ± 91	0.637
	Sarek	13/7–28/8	46	13	889 ± 221	445 ± 535	737 ± 66	0.404
Early autumn	*Handöl*	25/8–14/9	20	10	468 ± 79	341 ± 361	198 ± 43	0.258
	Vaisa	29/8–7/9	9	7	355 ± 45	342 ± 342	113 ± 45	0.535
	Sarek	29/8–13/9	15	12	236 ± 4	337 ± 374	181 ± 61	0.511

Mean movement rate (MR) per hour ± SD, mean kernel home range (HR) size (Skarin et al. 2008), Pearson's correlation coefficients ($r_{MR, HR}$) between movement rate and home range size

successive locations. The reindeer were actively herded during the calf marking periods, and therefore the positions from these periods were removed from the datasets before analyses.

Variables used to explain the movement rates were vegetation type; the altitudinal position of the reindeer; a terrain ruggedness index (a scale from 1 to 59, representing the difference in elevation between adjacent grid cells of a digital elevation grid as described by Riley et al. 1999, but transformed to a logarithmic scale); the slope of the movement (the altitudinal change between two positions divided by the distance moved); temperature; wind speed; and distance to the nearest hiking trail transformed to a logarithmic scale (since a trail far away most likely do not affect the reindeer). The digitised geographical data for vegetation type (Swedish CORINE Land Cover, 25 m raster resolution) and altitude (digital elevation model, 50 m raster resolution) were provided by The National Land Survey (http://www.lantmateriet.se). For the 'heaths' vegetation types, two different classification resolutions were available. We used the finer classification where available; otherwise the coarser classification was used. For the coarser resolution, all heath vegetation types (except grass heath) were combined into one category called 'heaths'. This represented less than seven per cent of all the vegetation types available within each area (Table 1). The areas with the coarser classification are also in the outskirts of the study areas where the reindeer spent less time. Rare or similar vegetation types were further combined in all analyses to reduce the number of vegetation classes. For interpretation of our results, we also classified vegetation types into high- or low-quality vegetation type according to Klein (1990) and

Skogland (1980), as shown in Table 1. Temperature (°C) and wind speed (m s⁻¹) records from the weather stations at *Sylarna* and *Ritsem* (Fig. 1) for the *Handölsdalen* and *Sirges* study areas, respectively, were obtained at three-hourly intervals from the Swedish Meteorological and Hydrological Institute (http://www.smhi.se). Temperatures and wind speeds for every hour were calculated by linear interpolations. Possible correlations between the continuous variables were checked and significant correlations were found only between wind speed and temperature at Sylarna weather station ($r = -0.135$, $P < 0.001$). Therefore, a combination of temperature and wind speed was derived [temperature × (wind speed + 1)⁻¹], but this variable had no significant effects in the analyses. In the mixed model analyses, the mean values of the continuous habitat attributes at the two successive GPS locations were used for each rate observation. The dominating vegetation type at each position was given the value 1 and other the value 0. For each rate observation, the mean values of the vegetation types were used as vegetation variable to which the models were fitted.

In addition, during the *mid summer* sub-season, temperature and wind speed were used to derive two variables reflecting oestrid, and mosquito and *Simuliidae* activities. Although, there are several studies that have investigated insect activity with respect to weather conditions, it is not possible to find sharp temperature thresholds or exact wind speed intervals that determine insect activity. For this reason, these variables were only used to discuss the possible correlations between reindeer movement rate and insect harassment. Temperature thresholds reported for oestrid (OES) fly activity are 7°C (Downes et al. 1986), 10°C

(Mörschel [1999]; Anderson et al. [1994]), and 13°C (Colman [2000]; White et al. [1975]). The upper wind speed limit for OES activity has been reported as 8–9 m/s (Anderson et al. [1994]), and 4 m/s as the average wind speed (Mörschel [1999]). Mosquitoes and species of *Simuliidae* (MOS) have been reported to be active at temperatures between 6 and 18°C and wind speeds below 6 m/s (Russell et al. [1993]), to decline in activity above 16°C and 7.5 m/s (Hagemoen and Reimers [2002]), or to have the highest activity at 10.3°C and 3.8 m/s (Downes et al. [1986]). Based on these studies, we assumed that OES activity occurred when wind speed was below 9 m/s and the temperature was above 11°C, and that MOS were mainly active at temperatures between 7 and 17°C and at wind speeds below 7 m/s, with discrepancy for *Siimulidae* that probably also is active above 17°C. Temperatures and wind speeds outside these ranges were assumed to have no insect activity (NOI). The OES and MOS variables are confounded to some extent.

To estimate the reindeer utilisation distributions (UD) or home ranges within each sub-season from the GPS-positions, we used fixed-kernel techniques (Worton [1989]; Seaman and Powell [1996]). Depending on time periods, between 236 and 1075 positions were available in the home-range estimations (Table 2). For the UD estimation, we used ArcView GIS 3.3 software (ESRI©1992–2002) with the Animal Movement extension (Hooge and 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.

Using the whole dataset, we initially tried to fit a single mixed model, with areas and sub-season as fixed effects and reindeer as random with first order interactions between fixed effects and continuous variables. However, in an effort to find a parsimonious model using Akakie information criterion (AIC), we found that removing non-significant interactions terms increased the AIC-value. Thus, the full model was probably the most appropriate among models with first-order interactions, but this model left us with interaction terms difficult to explain. We therefore divided the data by each sub-season, and fitted separate linear mixed models of the movement rates for the different habitat variables for each area and period with reindeer as random effect. We also fitted separate mixed models at the whole season scale within each area with reindeer as random effect. A least squares estimate for each vegetation type was obtained and expressed as deviation from the mean of estimates of those vegetation types that all the reindeer had visited in each study area. We used AIC to select the most parsimonious model. We compared AIC-values for the full model in each subset with models where continues variables with the highest *P*-value >0.20 were removed; if this model had a

lower AIC-value we continued and excluded next variable until we found the most parsimonious model. The individual average movement rates within each sub-season were also correlated with the individual home range size using Pearson's correlation. Further, we plotted circadian movement rate and mean altitude change within the three different weather categories of expected insect activity within the *mid summer* period. We also plotted the per cent of positions by the hour within high- and low-quality vegetation type during each sub-season.

Results

Movement rates over the whole summer

The mean movement rate for all animals was 344 ± 460 m/h, and there was no difference in the movement rate between the three areas (ANOVA, $P = 0.711$). The model selection ended up with using the full model for each area at this temporal interval. Furthermore, the reindeer in *Handöl* moved faster within five out of seven of the significant high-quality vegetation types (fresh heaths, grass heaths, meadow, birch forest and lakes (which included open surfaces and shores)), while they moved slower in the lower-quality vegetation types bare rock and sparsely vegetated areas (Table 3). In *Vaisa*, the reindeer moved slower within four out of six high-quality vegetation types (dry heath, fresh heaths, meadow, and mires), and in *Sarek* the reindeer moved slower through fresh heaths and willow thickets. In grass heaths though, the reindeer always moved faster. The reindeer also increased their movement rates with increasing temperature in all study areas. In *Handöl* and *Sarek*, the movement rates decreased with wind speed. The reindeer movement rates decreased with increasing altitude and in rugged terrain (*Handöl* and *Sarek*). In *Sarek*, the reindeer also increased their movement rate with increased distance to the hiking trails.

Movement rates within sub-seasons

Movement rates varied between the sub-seasons, with an increase from *spring* to *mid summer* and then a decrease in *early autumn* (Table 2). The model selection for the sub-season interval models resulted in excluding altitude in the model for *Handöl* in *early summer* and *mid summer*, and for *Vaisa* in *spring* and *early autumn*, otherwise the full model was used. There was a divergent pattern of movement rate within the different vegetation types (Tables 4, 5). Within *spring* the reindeer moved slower in the open high-quality vegetation types, while they moved faster in the forested high-quality vegetation types. In *early summer*, the reindeer moved slower within the majority of the

Table 3 Mixed model coefficients of reindeer movement rates (m/h) and habitat types over the whole season (May–September 2003)

	Handöl		Vaisa		Sarek	
	β	SE	β	SE	β	SE
Intercept	282.2	81.1**	560.2	250.8	180.0	67.3*
High-quality vegetation types						
Dry heath	−7.5	10.6	−56.0	15.7***	−6.7	7.5
Fresh heath	28.4	11.4*	−98.5	17.4***	−29.5	9.3**
Wet heaths	20.7	24.4	141.5	60.6*	6.9	17.5
Heaths	25.1	28.5	2.1	33.2	−20.4	13.5
Grass heath	55.1	19.1**	33.6	16.6*	18.0	6.7**
Meadow	48.9	15.7**	−58.0	14.9***	−2.8	10.2
Mires	16.7	22.9	−111.3	50.7*	−34.2	37.0
Willow thickets	−21.7	48.0	91.5	92.7	−98.0	41.2*
Birch forest	62.0	19.3**	−86.0	65.1	−24.8	28.7
Mixed forest	−116.8	70.6	–	–	–	–
Coniferous forest	−167.0	36.5***	446.4	292.7	–	–
Young forest	−235.0	46.6***	–	–	–	–
Lakes	232.9	65.0***	43.0	44.5	5.2	43.3
Other	−82.2	68.9	63.2	98.5	96.5	67.3
Low-quality vegetation types						
Bare rock	−109.1	18.4***	36.3	22.6	9.5	11.5
Glacier	–	–	–	–	208.9	79.2**
Extremely dry heaths	−21.6	27.2	30.7	30.9	18.0	13.8
Sparsely vegetated areas	−247.9	36.9***	3.6	19.5	−13.4	11.3
Abiotic factors						
Temperature	15.8	0.6***	26.1	0.9***	22.9	0.6***
Wind speed	−2.8	1.0**	−2.0	2.4	−4.9	1.7**
Slope of movement	−0.3	0.2	−0.1	0.2	−0.1	0.1
Altitude	−0.1	0.0*	−0.3	0.0***	−0.3	0.0***
Terrain ruggedness	−3.3	0.5***	−1.2	0.7	−3.5	0.5***
Hiking trail	9.1	6.3	11.6	8.6	22.2	4.8***

For full names of the vegetation types see Table 1, high- and low-quality vegetation types are according to Klein (1990) and Skogland (1980)

* $0.01 \leq P < 0.05$, **$0.001 \leq P < 0.01$, *** $P < 0.001$, '–' missing values

high-quality vegetation types and faster within the low-quality vegetation, and in *mid summer* the pattern was reversed. Further, we found increased movement rates within grass heath in all areas in *early summer* and in *Sarek* in *mid summer*. In the *early autumn*, there was no obvious response in the movement rates within the different vegetation types. For further details about the movement rates within the vegetation type in each area and sub-season see Tables 4 and 5.

The reindeer response to the weather parameters was quite consistent. Movement rates increased with temperature in all sub-seasons. In all areas, the reindeer movement rates decreased with wind speed during *mid summer*, while an increase in reindeer movement rate with wind speed occurred in *spring* in *Handöl*, in *Vaisa* in *early summer*, and in all areas in *early autumn*. The reindeer movement

rates were generally lower in rugged terrain and with increasing altitude. However, in *Handöl* in *spring* and in *Sarek* in *early autumn*, movement rates were higher when the reindeer moved over rugged terrain. Furthermore, the reindeer showed increased movement rates with increasing distance to hiking trails in most areas and sub-seasons; however, in *Handöl* during *spring* and in *Vaisa* and *Sarek* during *mid summer*, the reindeer increased their movement rate with decreasing distance to the hiking trails.

A strong positive correlation was found between the reindeer average home range sizes and average movement rate over the sub-seasons ($r_{MR,HR} = 0.722$, $P = 0.0001$, $N = 117$). However, splitting the data into a single sub-season and one area, only a few correlations were found between home range size and movement rates (Table 2). In *mid summer*, the reindeer home ranges in *Sarek* were almost twice as

Table 4 Mixed model coefficients of reindeer movement rates (m/h) and habitat types and within *spring* and *early summer* and each area

| | Spring | | | | | | Early summer | | | | | |
| | Handöl | | Vaisa | | Sarek | | Handöl | | Vaisa | | Sarek | |
	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE
Intercept	99.7	242.0	460.1	169.9*	351.1	89.7**	406.3	178.1*	776.6	780.0	306.5	712.6
High-quality vegetation types												
Dry heath	−122.4	17.8***	−7.8	7.9	9.7	9.1	−54.7	17.6**	−99.9	27.5***	−70.5	17.4***
Fresh heath	−114.8	18.8***	−24.6	8.6**	−7.0	12.0	−14.8	18.7	−64.6	35.3	−27.9	21.7
Wet heaths	−125.1	63.5*	−64.4	71.6	60.6	23.3**	−85.1	42.9*	526.2	304.6	−49.8	40.6
Heaths	104.3	104.3	127.3	69.4	113.1	92.4	1.2	31.7	52.2	214.4	−468.9	168.4**
Grass heath	−14.2	50.1	18.8	10.0	−11.4	7.7	148.2	44.6***	100.4	28.9***	44.4	16.3**
Meadow	−37.6	27.4	13.7	7.5	−23.6	14.5	−5.1	25.8	−148.5	22.1***	−19.1	18.8
Mires	−70.6	48.5	−49.2	45.0	38.8	65.1	−9.0	73.8	−295.5	110.2**	−171.0	411.4
Willow thickets	−87.7	129.9	129.7	80.3	212.0	72.9**	−113.7	77.2	−16.2	246.0	−343.8	113.5**
Birch forest	274.8	45.2***	29.1	45.4	373.6	169.1*	42.0	44.6	−454.6	236.6	−266.8	63.4***
Mixed forest	–	–	–	–	–	–	−191.2	280.9	–	–	–	–
Coniferous forest	655.9	208.5**	235.8	248.8	–	–	375.1	356.9	–	–	–	–
Young forest	–	–	–	–	–	–	–	–	–	–	–	–
Lakes	136.0	115.3	−2.2	44.4	291.2	56.0***	280.0	165.4	−23.5	102.7	−18.4	162.3
Other	−508.1	232.9*	369.4	248.6	38.5	81.4	188.4	174.2	48.3	291.3	159.6	133.8
Low-quality vegetation types												
Bare rock	0.7	113.8	−57.4	25.8*	−12.1	13.0	−0.3	52.6	261.3	48.2***	66.9	35.0
Glacier	–	–	–	–	–	–	–	–	–	–	–	–
Extremely dry heaths	−241.0	54.2***	95.9	82.4	14.0	24.5	−22.5	57.8	−70.6	50.1	−39.2	24.2
Sparsely vegetated areas	–	–	40.3	31.6	−16.3	18.1	–	–	45.4	34.0	95.1	29.7**
Abiotic factors												
Temperature	5.1	1.8**	0.4	1.3	−2.7	1.1*	20.0	1.5***	22.8	1.6***	16.4	1.3***
Wind speed	5.4	1.7**	2.5	2.1	−2.2	1.8	0.4	2.6	13.6	5.2**	−3.3	4.1
Altitude	−0.4	0.1***	–[a]	–[a]	−0.2	0.0***	–[a]	–[a]	−0.5	0.1***	−0.3	0.1***
Slope of movement	−0.1	0.4	0.1	0.2	−0.1	0.2	−0.5	0.4	−0.6	0.5	−0.6	0.3
Terrain ruggedness	6.3	1.1***	2.5	0.6***	−1.8	0.6**	−3.7	1.1**	−0.8	1.6	−5.9	1.2***
Hiking trail	−33.0	11.8**	74.8	16.9***	34.6	7.4***	37.2	12.8**	87.0	19.0***	19.5	12.3

For full names of the vegetation types see Table 1, high- and low-quality vegetation types are according to Klein (1990) and Skogland (1980)

* $0.01 \leq P < 0.05$, ** $0.001 \leq P < 0.01$, *** $P < 0.001$, '–' missing values ([a]variable excluded due to the model selection)

large as those in the other areas, while their movement rates were similar at all sites. In *Vaisa* in all sub-seasons, but especially in *spring* and *early summer,* the reindeer had smaller home ranges compared to the other areas.

Circadian movements

During the days of expected insect harassment in *mid summer,* the movement rates had pronounced peaks at the beginning (around 0500 h) and at the end of the day (around 1900 h) as shown in Fig. 2a. These movements appeared to be associated with cyclical altitude positioning, i.e., the reindeer increased their movement rates as they moved up the hillsides in the mornings and down in the evenings (Fig. 2b).

The number of positions registered in vegetation types with high or low forage quality (Klein 1990; Skogland 1980; Table 1) differed over a 24-h cycle within the different sub-seasons (Fig. 3). Within the *mid summer* period, in all three areas, there was an increase in the number of positions registered in low-quality vegetation types in the day, while there were more positions found in vegetation types with high-quality forage at night. In *spring* and *early summer* and *early autumn*, there were no major differences in the use of different vegetation types during the circadian cycle.

Table 5 Mixed model coefficients of reindeer movement rates (m/h) and habitat types and within *mid summer* and *autumn* and each area

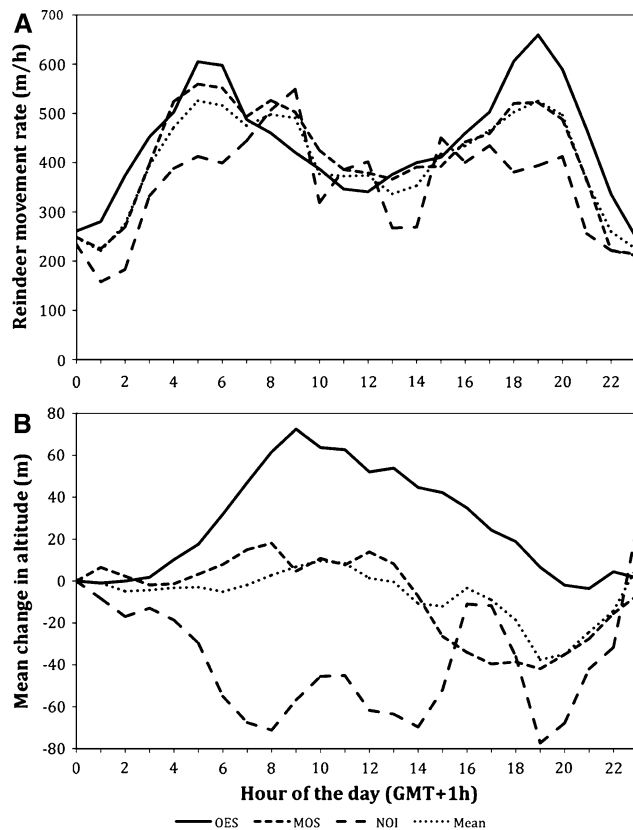|	Mid summer						Autumn					
	Handöl		Vaisa		Sarek		Handöl		Vaisa		Sarek	
	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE
Intercept	252.7	112.2	8.0	729.0	550.6	527.1	365.2	171.3	45.3	279.9	522.3	202.1*
High-quality vegetation types												
Dry heath	5.6	13.6	−34.3	23.5	10.5	15.4	4.0	15.6	42.5	26.7	15.1	12.3
Fresh heath	53.0	16.2**	−39.5	29.6	−75.7	17.2	−18.5	15.1	26.9	32.5	41.9	28.2
Wet heaths	84.9	45.4	256.4	106.6*	−44.0	30.7	53.0	31.4	50.2	81.5	43.0	51.3
Heaths	−39.9	39.4	−1.6	68.4	66.8	28.8*	247.8	75.8**	33.2	53.4	−37.0	20.3
Grass heath	14.4	21.7	−14.1	22.1	86.4	13.1	10.0	46.5	−46.6	31.5	−15.1	12.3
Meadow	71.7	24.5**	−41.0	25.5	1.2	20.0	−43.4	29.5	−22.8	29.1	45.0	39.0
Mires	17.0	41.1	165.2	104.6	−107.4	77.4	−47.5	29.2	−2.7	130.0	20.1	43.5
Mixed forest	−141.9	90.0	–	–	–	–	70.7	112.1	–	–	–	–
Birch forest	58.5	31.2	344.7	161.1*	144.4	73.5*	52.3	26.0*	−3.9	140.8	18.1	38.3
Willow thickets	203.8	140.5	140.2	256.1	−123.2	63.6	−82.3	112.5	368.6	142.5**	12.7	89.4
Coniferous forest	−176.3	42.2***	−683.9	720.2	–	–	−211.4	88.9*	1608.8	356.3***	–	–
Young forest	227.2	51.0***	–	–	–	–	−56.6	195.2	–	–	–	–
Lakes	223.2	131.6	139.0	80.8	−245.6	75.5**	238.1	131.2	222.0	113.3	197.0	75.9**
Other	−156.9	104.6	53.6	151.7	146.6	126.2	−106.4	153.0	−192.3	251.8	–	–
Low-quality vegetation types												
Bare rock	−111.4	18.8***	−5.6	30.9	3.5	19.5	75.8	89.8	37.4	83.3	−15.7	67.4
Glacier	–	–	–	–	205.3	92.7*	–	–	–	–	–	–
Extremely dry heaths	−4.8	43.3	26.5	47.9	55.9	26.2*	−39.1	50.8	87.3	123.4	70.5	67.8
Sparsely vegetated areas	−188.9	37.8***	−31.2	25.8	−37.7	17.7*	–	–	0.9	107.4	70.8	66.8
Abiotic factors												
Temperature	11.5	1.2***	33.4	2.5	22.1	1.5***	1.6	1.6	12.1	4.5**	9.0	1.7***
Wind speed	−6.5	1.8***	−27.9	5.2	−14.3	3.6***	4.8	2.0*	35.8	11.3**	36.8	5.8***
Altitude	–[a]	–[a]	−0.5	0.1	−0.3	0.0***	−0.1	0.1	–[a]	–[a]	−0.3	0.1***
Slope of movement	−0.3	0.2	0.0	0.4	0.0	0.2	−0.1	0.3	0.1	0.8	−0.1	0.5
Terrain ruggedness	−7.8	0.9***	−5.9	1.3	−7.8	0.8***	−2.6	1.1*	1.1	2.2	2.3	1.1*
Hiking trail	31.3	11.6**	−47.6	16.4**	−28.3	10.0**	−8.0	13.3	−22.7	29.4	39.8	19.7*

For full names of the vegetation types see Table 1, high- and low-quality vegetation types are according to Klein (1990) and Skogland (1980)

* $0.01 \leq P < 0.05$, ** $0.001 \leq P < 0.01$, *** $P < 0.001$, '–' missing values ([a]variable excluded due to the model selection)

Discussion

We found evidence for association of forage quality and movement rate in the response of movement rate on the different vegetation types. Within *early summer*, the reindeer had slower movement rates within the high-quality vegetation types (Klein 1990; Skogland 1980), dry heaths, wet heaths, heaths, meadows, willow thickets and birch forest and higher movement rates through low-quality vegetation types, such as bare rock and bedrock outcrops and sparsely vegetated areas. This implies that the reindeer stopped for foraging at the high-quality sites and passed over the lower-quality sites. Mårell et al. (2002) also found that reindeer preferentially browsed within heath and willow vegetation types especially at the beginning of the
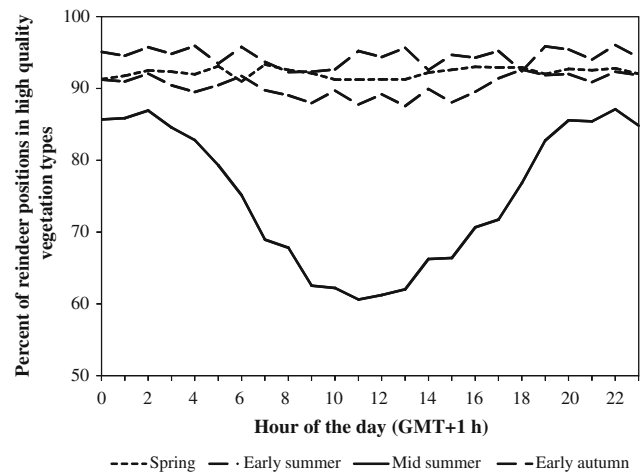
summer season. The unexpected high movement rates in grass heath; although this is normally a preferred vegetation type (Skarin 2007), may be the result of reindeer moving across them quickly to seek insect relief. According to the reindeer herders in *Vaisa*, the reindeer in this area preferentially graze on grass heath close to snow patches, where they are close to insect relief habitats (Nils-Johan Utsi, reindeer herder in *Vaisa*, personal communication February 2003). The faster movements over high-quality vegetation types in *mid summer* may also be explained by the reindeer seeking insect relief and will be discussed later. In rugged terrain, slower movement may depend on higher forage quality (Mårell and Edenius 2006) or it could simply be due to the ruggedness of the terrain making it difficult to move across the area. The slower movements in the high and

Fig. 3 The percentage of reindeer positions (by the hour of the day) on the high-quality vegetation types (meadows, grass heath, dry heath, fresh heath, wet heath, thickets and birch, and coniferous forests) in 2003, (according to Klein 1990). (Bare rock, glaciers and permanent snowfields, extremely dry heath, and sparsely vegetated areas were classified as sparsely vegetated habitat types)

Fig. 2 **a** Patterns of average reindeer movement rates (m/h) in all three study areas in *mid summer* 2003, within the different weather categories, when the insects were predicted to be active. The assumed active insects were oestrid flies (OES) when temperature was ≥11°C and wind speed was ≤9 m/s, and mosquitoes and *Simuliidae* (MOS) when temperatures were ≥7°C and <17°C and wind speed was ≤7 m/s. The weather categories outside these thresholds were assumed to result in no insect harassment (NOI). Between 1400 and 1900 h, there were no NOI observations from *Vaisa* and *Sarek*. **b** The average altitude change (m) in the position of reindeer in all three study areas during *mid summer* 2003

dense vegetation types such as, willow thickets, fresh heath and wet heath may also be caused by the vegetation restricting the reindeer movements.

The distribution of the reindeer within each study area also seemed to be a reflection of forage availability. Interestingly, we found that the reindeer movement rate was the same irrespective of the size of the study area and the size of the home range, but differed between sub-seasons. This indicates that the movement are mostly associated with the forage quality and the characteristics of the different areas. The large home ranges in *Sarek* in *mid summer* was probably caused by the more alpine character of the area, with long deep valleys; which forced reindeer to walk along the valleys to reach new grazing areas, thus enlarging their home ranges. The smaller home ranges in *Vaisa* might be a reflection of its flat landscape compared to the other areas. Thus, the reindeer did not need to expand their home ranges

to the same extent as at other sites to reach new areas. According to the herders in the *Sirges* reindeer-herding district, the reindeer from *Vaisa* always weigh more and are in good physical shape, while the reindeer in *Sarek* have lower slaughter weights and are not as healthy. Our results suggest that the forage quality at *Vaisa* is exceptionally good, since the reindeer have such small home ranges. The reindeer manage to gain more weight even though they forage over a smaller area than the reindeer in the other areas.

The gradual increase in movement rate and home range size throughout the bare ground season may have several explanations. One possible explanation for the continuous change is the increase in body size and moving capacity of the calves. The mothers stay in close contact with the calves during the first month, when the calves only move short distances. At one-month old, the calves become gradually more independent, after which their positions within the grazing herd are as random as that of any other individual (Espmark 1971). However, our results show that the behaviour is due to a combination of factors.

Irrespective of the temporal period investigated, weather conditions were important in determining reindeer movement rates. Insect avoidance at higher altitudes and at wind-exposed sites might be an explanation for the pattern we report (Downes et al. 1986; Gaare et al. 1975; Mooring et al. 2003; Powell et al. 2006). Insect harassment, especially from oestrids, has been found to be most severe in the middle of the summer (Anderson et al. 1994; Hagemoen and Reimers 2002). Therefore, the reindeer response to changes in weather conditions and correlated changes in insect activity probably interact, especially during the *mid summer*

sub-season. As there was a strong response to the weather parameters during this sub-season, we tried to relate the variables derived from temperature and wind speed, aiming to reflect insect activity, with reindeer movement rates. However, as we did not have direct observations of insect activity these results are not shown. Nevertheless, the models showed that the reindeer had higher movement rates during periods of expected OES activity and lower movement rates during periods of expected MOS activity, as seen in Fig. 2a. This supports the view that insect activity causes the movement patterns found. The increased movement during the assumed OES activity periods appears to be specific to *Rangifer*, since other ungulates are known to decrease their activity during parasite attack (Espmark and Langvatn 1979; Mooring and Hart 1992; Mörschel and Klein 1997). The decrease of movement rate in the *mid summer* sub-season with increasing altitude and within the low-quality vegetation types, bare rock and sparsely vegetated area was probably also a response to finding insect relief at higher altitudes. Decreased movement rates during expected mosquito harassment have been reported previously (Downes et al. 1986; Mörschel and Klein 1997) and this is common herder knowledge that is used to facilitate herding since the reindeer form large herds at this time. It has also been suggested that an individual is less likely to be harassed by insects if it stands still in a larger herd, because of the increased probability of neighbours being harassed instead (Helle and Aspi 1983; Mooring and Hart 1992).

In *mid summer*, reindeer appeared to use sparsely vegetated habitat types in the day and vegetation of high quality at night (Fig. 3), which may be linked to the assumed insect activity. The high movement rates in the high-quality vegetation types during this sub-season may also be linked to the insect harassment. This implies, that not only does the reindeer lose grazing time due to insect harassment (Colman et al. 2003), they are also forced into areas with lower grazing quality. When forage quality decreases, the search time for forage also increases, making feeding more difficult (Illius 2006). The reindeer's own impact on the vegetation by trampling may also increase, which in turn might lead to increased wear of the vegetation, especially in vegetation types that are sensitive to trampling (Moen and Lagerström 2008; Bråthen et al. 2007). Outside the insect season, the reindeer habitat selection within the home range seemed to be more dependent on forage quality, since they stayed in high-quality vegetation types during both day and night.

We expected a response to human disturbance along the hiking trails, especially in *mid summer*, which coincides with the hiking season. The response to expected human activity differed among the areas, however. In *Handöl* during *mid summer*, where hikers are frequent, the reindeer appeared to have habituated to human activity; it seemed more important to avoid insect harassment and to reach high-quality grazing grounds than to totally avoid hiking trails. This contradicts with our findings in *Sarek*, where the reindeer showed increased movement rates with decreased distance to the hiking trails. In *Sarek* there are few hikers (Wall-Reinius 2009) compared to *Handöl* (Vuorio 2003). As a result, the reindeer in *Sarek* may not have become habituated to hikers, to the same degree as in *Handöl*. On the other hand, the reindeer in *Handöl* had less opportunities to avoid the hiking trails; the mean distance (for each day and reindeer) to hiking trails in *Handöl* never exceeded 4.2 km while in *Sarek* the reindeer mean distance to hiking trails was up to 18 km. Vistnes (2008) suggests that reindeer is affected by human activities within a zone of 4 km from the activity, but in *Handöl* this was hardly possible. Even though, our result supports the view that if animals perceive an activity as spatially predictable and non-threatening, they may habituate to that activity (Colman et al. 2001; Whittaker and Knight 1998), and the question remains if reindeer may perceive human activities as predictable. The reindeer response to hiking trails in *Handöl* in *spring* was not expected, since human activity would have been low in the area but still they avoided hiking trails. However, one explanation may be the presence of snowmobiles and skiers in the early *spring* sub-season. Further, the reindeer use of areas close to hiking trails probably coincided with the fact that these often contain preferred vegetation types that are snow-free early (Skarin 2007). The slower movement rates of reindeer closer to the hiking trails in *spring* and *early summer* probably coincided with proximity to attractive vegetation types.

In conclusion, reindeer movement rates were dependent on forage quality, topography and weather parameters. During periods of expected insect harassment, the reindeer seemed more occupied by finding insect relief than finding good forage. In areas with low hiking activity, the reindeer reacted on both expected insect harassment and human activity. Thus, in management and planning of new hiking areas or hiking trails it is important to take in consideration reindeer and reindeer husbandry, especially during the high season of insect harassment. However, this might be difficult since this often is the high season for hiking and trails often are located in productive parts of the landscape. Therefore, we suggest a careful spatial planning of mountain areas, where vegetation types or areas with high-quality forage attractive to reindeer need to be prioritised.

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