

Effects of a holiday resort on the distribution of semi-domesticated reindeer

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We studied the impacts of a large skiing and hiking resort on the distribution of semi-domesticated reindeer in Saariselkä, eastern Finnish Lapland, in 1986 and 2000. The effect of intensity of outdoor activities on reindeer density in terms of pellet-group density was dependent variably on habitat, the year of inventory and season. Despite the overall doubling of visitor numbers between the inventory years, pellet-group density in winter increased in the study area by 20%. The sex ratio of reindeer in summer 1986 was male-biased up to a distance of 8–12 km, indicating that females with calves avoided the vicinity of the resort, but in 2000 the bias existed only at a distance of 0–4 km. However, pellet-group density in summer at the distance of 0–4 km was 53% and 28% lower than that at 4–8 km and 8–12 km, respectively. In winter, a similar pattern was observed in lichen-rich coniferous habitats. *Cladonia stellaris*, which has low tolerance to heavy grazing, reached its maximum abundance at the distance of 0–4 km. Observations on the increased tolerance of reindeer were very probably associated with improved channeling of tourists into fewer and better marked hiking and skiing routes, changes in the reindeer herd-management and frequent contacts with humans, but the adverse effects of outdoor activities could not be avoided.

Introduction

Northern wildlife species, including reindeer and North-American caribou (*Rangifer tarandus*), face increasing anthropogenic impacts associated with intensified use of natural resources. Such uses include forest cuttings, water reservoirs, oil drilling, mining, population settlement and infrastructure (e.g. Klein 1971, Nellemann & Cameron 1998, Mahoney & Schaefer 2002,

Kumpula *et al.* 2007, Weir *et al.* 2007, Dahle *et al.* 2008) as well as tourism with associated outdoor recreation recently reviewed by Wolfe *et al.* (2000), Weladji and Forbes (2002) and Vistnes and Nellemann (2008).

Up until the mid-1980s, the focus of impact assessment research on reindeer was on short-term responses (escape distance, length of flight, etc.) at a local level; the impacts, both on direct habitat loss and disturbance effects, were com-

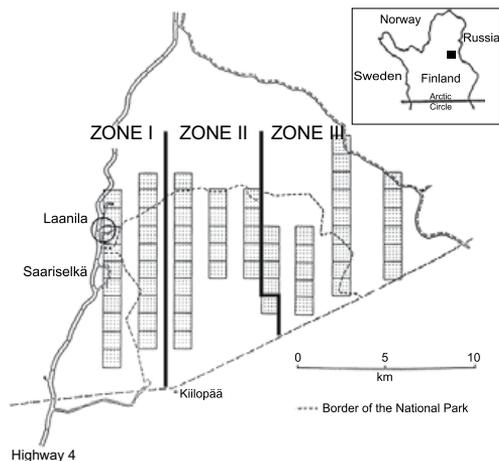


Fig. 1. The study area in the vicinity of the Saariselkä resort in Finnish Lapland and the sampling design used in 1986. The design was the same in 2000 with the exception that the number of the sample plots was about 50% smaller.

monly assessed to be negligible. The more recent approach, considering the long-term impacts at the regional level, commonly suggests stronger negative impacts (Vistnes & Nellemann 2008). Although disturbance stimuli associated with outdoor recreation (excluding hunting) are non-lethal, the reindeer behave, according to the risk-disturbance hypothesis (Berger *et al.* 1983, Frid & Dill 2002), in a similar manner to when they encounter great predators, resulting in an increase in energy costs (Tyler 1991, Bradshaw *et al.* 1998).

Avoidance of disturbance might result in increased use of the remaining habitats (Nellemann *et al.* 2000, Vistnes & Nellemann 2001, Dahle *et al.* 2008), and at worst the disturbance-mediated overexploitation of the pastures reduces reproductive success (Nellemann *et al.* 2003, Cameron *et al.* 2005), which corresponds to the strictest definition of disturbance as a process reducing the population size (Petraitis *et al.* 1989). Another commonly used definition refers to disturbance as a deviation of the animals' behaviour without any human influences (Frid & Dill 2002).

From the viewpoint of the management of semi-domesticated reindeer, the attribute "peaceful" is an important determinant of pasture quality (Kitti *et al.* 2006). Therefore, as tourism and

recreational use continue to expand in the north, it is increasingly important to know to what extent the reindeer adapt to disturbance and how the possible negative effects could be mitigated. In this study we compared the distribution of semi-domesticated reindeer in the vicinity of a large holiday resort in Finnish Lapland in 1986 and 2000. During that period, the number of reindeer in the local Ivalo herding association slightly decreased, meanwhile the number of overnight visits almost doubled (Niva 2002).

We report how the increase in outdoor activities influenced the relative reindeer densities and how estimated disturbance levels, habitat and season influenced the distribution of reindeer. Because the male reindeer tolerate disturbances better than females with calves (Smith & Cameron 1983, Helle & Särkelä 1993, Nellemann *et al.* 2000), we used the sex ratio as an indication of avoidance responses in summer. Furthermore, we studied the main characteristics of lichen vegetation in order to discover the possible indications of uneven distribution of grazing. The coverage and height of lichens are generally inversely related to grazing intensity (Kumpula *et al.* 2000, Nellemann & Vistnes 2001, Dahle *et al.* 2008), and *Cladonia stellaris* in particular resists heavy grazing poorly (Ahti 1961, Helle & Aspi 1983). Thus we hypothesised that if the reindeer avoid the resort, the coverage and height of the lichens would be at their maxima in the vicinity of the resort (Nellemann *et al.* 2000, 2001, Dahle *et al.* 2008).

Material and methods

Study area

The study was carried out in Finnish Lapland in the north-western edge of Saariselkä, in an area consisting of approximately 180 km² of forest and fells; about 50% of the area belongs to the Urho Kekkonen National Park, established in 1983 (Fig. 1). A more comprehensive description of the nature in the Saariselkä area is given by Saastamoinen (1982) and the Finnish Forest and Park Service (Metsähallitus 2001). The study area covers 7% of the land area of the herding association of Ivalo, where the impacts of other

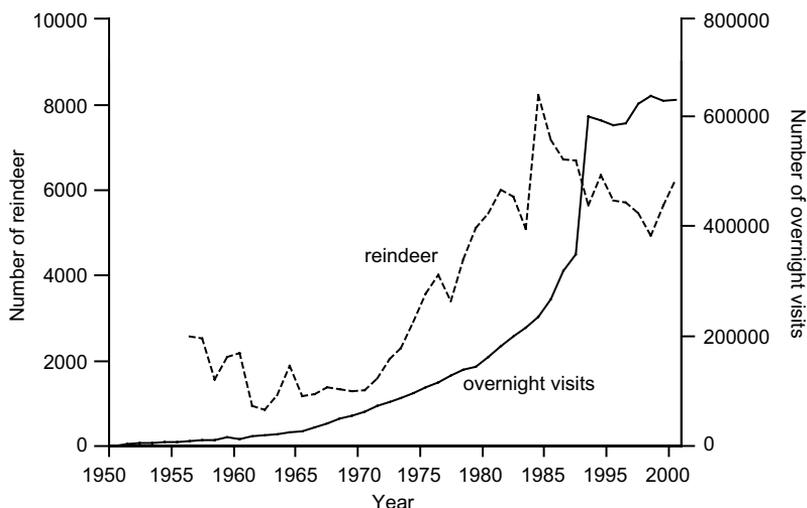


Fig. 2. The number of semi-domesticated reindeer in the herding association of Ivalo during 1956–2000, and overnight visits to the Saariselkä area, Finnish Lapland, during 1950–2000.

land uses, such as settlement and infrastructure, roads and forest cuttings, have recently been discussed by Kumpula *et al.* (2007) and Anttonen *et al.* (2011).

The number of reindeer started to increase in the Ivalo herding association in the middle of the 1970s, peaked in 1984 (density of winter herd 3.1 indiv. km⁻²), and declined by 2000 by 23% (Fig. 2). The basic pattern was similar, apart from the exceptionally low numbers during the 1960s, to that reported for semi-domesticated reindeer populations elsewhere in northern Finland, Sweden and Norway (Helle & Kojola 2006), and reflected the variation in winter weather that affected the reproduction and mortality of the reindeer (Helle & Kojola 2008). The herding association of Ivalo was the first in Upper Lapland to adopt regular supplementary feeding in winter in the mid-1970s, either in yard corrals or on natural pastures (Helle & Saastamoinen 1979, Nieminen & Autto 1989), but there are reindeer still relying on natural pastures only.

Until the early 1960s, Saariselkä had been visited primarily by wilderness-orientated recreational users, and the subsequent development of the Saariselkä holiday resort concentrated on downhill and cross-country skiing, hiking, and other kinds of outdoor recreation. The number of overnight visits in 1986 amounted to 300 000 and had doubled by 1993 (Fig. 2). From the viewpoint of tourism, the year is divided into several seasons. The most popular is the skiing

season in March–April, and the second is the hiking season in September (Haapalehto 2001).

Field sampling

Based on the estimated intensity of recreational use, the study area was divided into three zones, each 4–7 km wide.

Zone I. This includes the town-like resort and its surroundings with slalom slopes, lit skiing network, hiking and jogging routes, and so on. In 2000, the built-up area (including buildings, roads, parking places, and downhill skiing slopes) covered about 4 km², and accounted for around 5% of the total area of Zone I. In 1986, overnight visits had amounted to 300 000 (Helle & Särkelä 1993), and in 1993 reached ca. 600 000, the level at which they remained until 2000 (Saarinen 2001). The total number of tourists, including short-stay visitors, in 1988 was estimated to be 1 000 000 (Helle & Särkelä 1993), and in 2000 about twice that number. The eastern half of the area is located in the Urho Kekkonen National Park.

Zone II. The day-use area visited by people skiing or hiking from the resort. Most of the zone is located within the national park. The annual number of visitors in 1986 and 2000 was estimated to be 46 000–80 000 and

about 150 000, respectively (Helle & Särkelä 1993, Haapalehto 2001).

Zone III. Defined as a wilderness area, with only one small hut for skiers and hikers. In 1986 and 2000, the visitor's book in the hut had 500 and 300 names, respectively. The actual number of skiers and hikers, especially in 2000, might have been somewhat greater, since all of them did not enter the hut or sign the visitor's book (Haapalehto 2001). The southern and western parts of the study area are located within the national park, and the other parts in the protected forest zone or within normal commercial forests.

The sampling design for the inventories carried out in summer 1986 and 2000 is presented in Fig. 1. One-km-wide strips were delineated in each zone according to the approximate distribution of the habitat types occurring in the respective zones. Inside the strips, the sample plots were located systematically at a distance of 200 m from each other; 1557 and 771 sample plots were investigated in 1986 and 2000 respectively. The plots were located outside the area where reindeer received dry hay as a feeding supplement in winter.

The following variables were measured in each sample plot:

- Habitat type (alpine fell, sub-alpine birch forest, Scots pine forest).
- Number of winter and summer reindeer pellet-groups within a radius of 3.99 m (50 m²) around the centre of the sample plot.
- The *Cladonia stellaris* and other lichens, mainly *Cladonia* (*C. rangiferina*, *C. mitis*, including *Cetraria nivalis* and *Stereocaulon paschale*) height (living part), and their coverage within a square of 0.25 m².

The pellet-group density in terms of the faecal standing crop is a widely used method in studying population trends and habitat use of ungulates (Campbell *et al.* 2004), and it has also been applied to reindeer (Helle *et al.* 1990, Helle & Särkelä 1993, Skarin *et al.* 2004, Skarin 2007). The pellet-groups from winter remain visible in Scots pine forest for about five years (Helle *et al.* 1990), and the pellet-groups from

summer persist in dry habitats for four years, at least (Skarin 2008).

In the area of the herding association of Ivalo, ground lichens are the most preferred winter food of reindeer (Kojola *et al.* 1995), and measurements of lichen height and coverage have been used to determine the distribution of reindeer in winter (Vistnes *et al.* 2001, Dahle *et al.* 2008). In summer, reindeer lichens are highly sensitive to trampling by reindeer and humans (Pegau 1970, Törn *et al.* 2006). In order to assess the principal reason for the short and trimmed lichen vegetation in the area, in autumn 2002 we examined how the distance from main hiking trails influenced height and coverage of lichens in Zone I, most prone to human trampling. We assumed that human trampling occurred most pronouncedly in the nearest vicinity of the trails and decreased with the increasing distance. Sixty 100-m-long strips were placed 100 m apart across the eight main trails leaving 50 meters of the strip on each side of a trail. Habitat types around the strips were recorded. The coverage and height of lichens were measured in three sample plots (0.25 m²) at 5, 10, 20, 30 and 50-m distance from a trail. The means of these three plots were used in the analysis.

Data on the sex ratio of the reindeer in the study area were collected and mapped in the field during the period from 2 June to 15 September 1986 and from 19 June to 23 August 2000. In 1986 and 2000, 603 and 595 adult reindeer were sexed, respectively.

Statistical analyses

The two inventories could not be treated as repeated measurements, because the locations of the sample plots were not exactly the same. The distribution of the plots inside a block also differed in the two inventories. Thus, although the study area and zoning corresponded to each other in the two inventories, they can be considered two different samples, or cross-sectional studies. Therefore, the field data from 1986 and 2000 were re-organised for the statistical analysis. The inventories were carried out using the same block pattern in summer 1986 and 2000, but there were different numbers of sample plots

inside the 65 blocks in the two inventories. The blocks, 1 km² in size, were organised systematically along the strips from south to north. In the first inventory, a network of 25 plots was located systematically in each block, the total number being about one half of the number in the second inventory. The difference in the number of sample plots in the two inventories was balanced by randomly selecting 12 plots from each block in the first inventory. The final 1986 and 2000 data sets consisted of 109 and 114 sample plots, respectively, distributed among zones and habitats (Table 1). Topographically, the zones were rather similar; the highest fells being in Zone I, Zone II and Zone III; 454 m, 440 m and 469 m a.s.l., respectively.

Spatial correlation (Koenig 1999, Fortin *et al.* 2002) between the adjacent blocks was investigated using autocorrelation-function (ACF) plots to study the interdependence of the blocks. In general, the autocorrelations for the number of summer and winter pellet-groups between the adjacent blocks were not significant in the inventories or in the zones. In the first inventory in Zone II, the ACF plots for the winter pellet-groups suggested that adjacent blocks might correlate slightly stronger than those located further away. However, this was not considered to be a serious problem affecting the GLM analysis.

Five general linear models were constructed to test the effects of inventory, habitat, zone and their interactions (cross effects) on the number of summer and winter pellet-groups and the height of lichens, the coverage of *C. stellaris* and other lichens as well.

Both the ACF plots and GLM analysis were carried out using the SYSTAT statistical software (www.systat.com).

The differences between the groups (e.g. alpine habitat *versus* coniferous) were tested depending on the significance of the terms, main effects or interactions. The main focus in the pair-wise comparisons was to test the differences between the inventories and between the zones. If the three-way interaction of Inventory, Habitat and Zone was significant, then 27 pair-wise comparisons were required. On the other hand, if only the main effect of the zones was significant, then only three comparisons were required. Taking Bonferroni's inequality (Chiang 2003)

into account, the significance level of a comparison was corrected by multiplying the *p* value by the number of pair-wise comparisons. If the *p* value of a comparison was after the correction equal to or greater than 0.05, then the difference could not strictly be considered statistically significant. Uncorrected significant *p*-values for the pair-wise comparisons were presented but with cautions if the Bonferroni-corrected *p*-value was not significant at *p* < 0.05. Although the transformations homogenised the variances in the groups of cases rather well, separate variance estimates for the error term were used in the *F*-test of pair-wise comparisons in order to ensure corrected significances if the variances of contrasted groups differed from each other (Milliken & Johnson 1984, Wilkinson & Coward 2004).

In order to study lichen characteristics in relation to the distance to the trail, linear mixed models (the models with a random factor) were constructed for lichen height and lichen coverage using the MIXED procedure of the SAS statistical software (SAS Institute Inc. 2002–2005). A random factor was included because the sample plots inside the strips were not assumed to be independent observations (e.g. Hox 2002).

The differences in the sex ratios of the reindeer between the study area and the Ivalo herding association in 1986 and 2000 were tested using the Fischer exact test for 2 × 2 tables. The tests were calculated for the zones with the habitats pooled together. The expected values for the sex ratio were calculated from the official reindeer statistics, presenting the total number of males and females in each year. The correlations were computed using the SAS statistical

Table 1. The sample size by zones and habitats in 1986 and 2000 in the vicinity of the Saariselkä resort, Finnish Lapland.

Year	Zone	Habitat			Total
		Alpine	Subalpine	Coniferous	
1986	I	8	17	13	38
	II	8	17	10	35
	III	3	11	22	36
2000	I	8	16	14	38
	II	11	16	15	42
	III	4	9	21	34

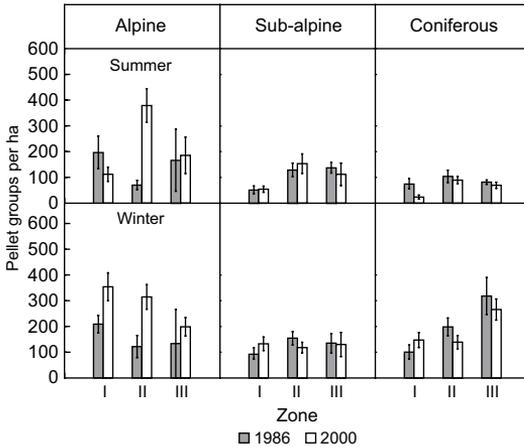


Fig. 3. Pellet-group densities (mean \pm SE) of semi-domesticated reindeer by season (summer/winter), habitats and zones in the vicinity of the Saariselkä resort, Finnish Lapland, in 1986 and 2000.

software and its CORR procedure (SAS Institute Inc. 2002–2005).

Results

Pellet-group densities

The GLM model explained 11.8% and 33.1%

of the variation in pellet-group density in winter and summer, respectively (Table 2 and Fig. 3). Among the main effects (Habitat, Inventory, Zone), Habitat described the relative preference of the habitats and influenced the pellet-group densities in summer and winter. In summer, the pellet-group density in alpine habitats (204 ha^{-1}) was almost three-fold that found in the coniferous habitats (73 ha^{-1}) ($F_{1,47.85} = 12.81$, Bonferroni-corrected $p = 0.003$), which could be expected since alpine habitats offer better relief from insect harassment (Helle & Särkelä 1993) and better availability of grasses and other summer food of reindeer (Nieminen & Heiskari 1988, Kumpula *et al.* 1999). In winter, the pellet-group densities in alpine (241 ha^{-1}) and in coniferous habitats (197 ha^{-1}) did not differ from each other, but the pellet-group densities in these habitats were significantly higher than the in sub-alpine habitats (127 ha^{-1}) (alpine *vs.* sub-alpine: $F_{1,68.68} = 10.03$, Bonferroni-corrected $p = 0.006$; coniferous *vs.* sub-alpine: $p = 0.018$, $F_{1,175.69} = 7.79$, Bonferroni-corrected). The low pellet-group density in sub-alpine habitats in winter was probably associated with the deep snow cover characteristic of sub-alpine birch forests at the timber line (Kumpula & Colpaert 2007, Helle *et al.* 2008).

Table 2. GLM models for pellet-group densities and lichen characteristics in the vicinity of the Saariselkä resort, Finnish Lapland. Values of the response variable in models 1 and 2 were log-transformed and values in models 4 and 5 were subject to arc-sin of the square-root transformation. p values at which models are considered significant are set in boldface.

Variable/term in the model	Model 1: number of summer pellet-groups per ha		Model 2: number of winter pellet-groups per ha		Model 3: height of <i>Cladonia</i> sp.		Model 4: coverage of <i>Cladonia</i> <i>stellaris</i>		Model 5: coverage of other <i>Cladonia</i> sp.	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Inventory	0.45	0.504	5.40	0.021	6.86	0.010	55.37	< 0.001	20.71	0.000
Zone	7.86	0.001	0.03	0.971	3.09	0.048	4.63	0.011	2.09	0.127
Habitat	12.35	< 0.001	7.17	0.001	4.46	0.013	23.50	< 0.001	5.50	0.005
Zone \times Habitat	0.65	0.631	4.36	0.002	4.17	0.003	2.47	0.046	0.72	0.579
Inventory \times Habitat	3.57	0.030	4.19	0.017	1.56	0.213	7.09	0.001	1.70	0.185
Inventory \times Zone	7.61	0.001	0.61	0.544	8.75	< 0.001	0	0.313	0.99	0.373
Inventory \times Habitat \times Zone	4.10	0.003	0.80	0.524	0.64	0.638	1.46	0.214	1.26	0.286
Error										
Sum of squares (SS)	15.2		22.1		10358.2		1.74		2.84	
Degrees of freedom (df)	204		203		197		205		205	
Mean square (MS)	0.08		0.11		52.58		0.01		0.01	

In testing the avoidance hypothesis, the central variables were the year of Inventory and Zone. Inventory revealed the possible differences in pellet-group densities between 1986 and 2000 and the comparisons between the Zones tested the differences in pellet-group densities in relation to the estimated intensity of outdoor recreation.

The impact of Inventory was not significant in summer, whilst in winter 2000 the pellet-group density was 20% higher than that in winter 1986 ($F_{1,21,91} = 4.487, p = 0.035$) despite a doubling of the visitor numbers in Zones I and II and a slight decline in the number of reindeer in the Ivalo herding association since the mid-1980s (Fig. 2).

The Zone influenced pellet-group density only in summer. In Zone I, it was 53% lower than that in Zone II ($F_{1,136,44} = 10.761$, Bonferroni-corrected $p = 0.003$) and 28% lower than in Zone III ($F_{1,142,6} = 5.371, p = 0.022$), respectively, thus supporting the avoidance hypothesis.

The interaction of Zone \times Habitat occurred repeatedly in winter in the coniferous habitats (Table 2). The pellet-group density in Zone I was 52% lower than that in Zone III ($F_{1,63,5} = 14.63$, Bonferroni-corrected $p = 0.001$) and in Zone II 55% lower than that in Zone III ($F_{1,61,7} = 4.98, p = 0.029$). The support to the avoidance hypothesis was of particular importance, since 47% of pellet-groups were located in coniferous habitats, the corresponding figure being 26% and 27% for alpine and sub-alpine habitats, respectively. The calculation was based on the zone-specific means for pellet-group density (Zone I 125 ha⁻¹; Zone II 119 ha⁻¹; Zone III 262 ha⁻¹) and frequency of various habitat types (Table 1, average frequencies were used).

The Inventory \times Zone interaction was significant in summer. In 2000, the pellet-group density in Zone I was 52% lower than in Zone II ($F_{1,59,9} = 21.01$, Bonferroni-corrected $p = 0.005$) and 43% lower than in Zone III ($F_{1,72,13} = 3.99, p = 0.050$), in accordance with the avoidance hypothesis.

The pellet-group densities by Inventory \times Habitat \times Zone was significant only in summer (Table 2). In summer 1986, the pellet-group density in sub-alpine habitats in Zone I was lower than that in Zone II ($F_{1,28,6} = 6.80, p = 0.014$) and in Zone III ($F_{1,20,9} = 11.37, p = 0.003$). In summer 2000, the pellet-group density in Zone I was lower than that in Zone II in all habitats (alpine: $F_{1,15,6} = 12.16, p = 0.003$; sub-alpine: $F_{1,21,1} = 5.93, p = 0.024$; coniferous: $F_{1,22,9} = 14.69$, Bonferroni-corrected $p < 0.001$). Furthermore, in coniferous habitats it was lower in Zone II than in Zone III ($F_{1,33,0} = 10.75, p = 0.002$). In alpine habitats, the pellet-group density in Zone II in 2000 was much higher than in 1986 ($F_{1,14,6} = 21.04$, Bonferroni-corrected $p < 0.001$), although visitor numbers had doubled.

Sex ratio of the reindeer

The sex ratio of the reindeer were compared in the study area by Zones with that reported for the whole area of the Ivalo herding association in the respective years (Table 3). In 1986, the sex ratio of reindeer was significantly male-biased in all three Zones. In 2000, the proportion of males in Zone I was still of almost the same magnitude as 14 years earlier, but in Zones II and III the difference in the sex ratio was no longer significant.

Table 3. Sex ratio of the reindeer in the Ivalo herding association and in the study area by zones in 1986 and 2000 in the Finnish Lapland.

Year	Area	Zone	Male (%)	Female (%)	<i>n</i>	Fisher's exact test <i>p</i>
1986	Ivalo Study area		19.6	80.4	5944	
		I	69.3	30.7	332	< 0.001
		II	11.0	89.0	173	0.003
		III	10.0	90.0	90	0.022
2000	Ivalo Study area		21.1	78.9	6409	
		I	67.3	32.7	217	< 0.001
		II	18.9	81.1	106	0.632
		III	22.4	77.6	58	0.749

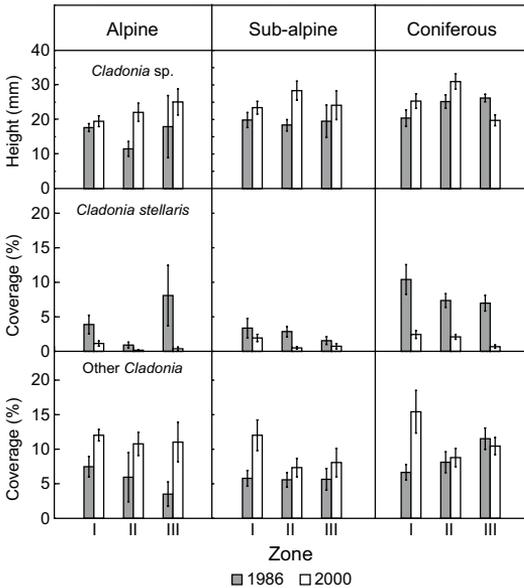


Fig. 4. Lichen characteristics (mean \pm SE) by the habitats and zones in the vicinity of the Saariselkä resort, Finnish Lapland, in 1986 and 2000.

However, females still tended to avoid Zone I in 2000.

Lichen characteristics

In 2002, the lichen coverage in the vicinity of the trails showed that only habitats (alpine, sub-alpine, coniferous) differed significantly from each other ($F_{2,585} = 38.79$, Bonferroni-corrected $p < 0.001$). Similarly, significant differences in lichen height existed only between the habitats ($F_{2,520.96} = 2.574$, Bonferroni-corrected $p < 0.001$). The results suggested that reindeer grazing and trampling were the main factor affecting the lichen vegetation. Comparable data from 1986 were lacking, but because the impacts of human trampling ten years earlier was concentrated only in the closest vicinity of the wilderness cabins (Hoogesteger 1976) we assumed that trampling and grazing by the reindeer were the main determinants of the lichen vegetation in 1986 as well.

In the study area, the overall mean for lichen coverage (including *C. stellaris* and other lichens) amounted to 12% and lichen height to 22 mm. The GLM models explained 30.0%, 44.3% and 18.4% of the variation in lichen height, cover-

age of *C. stellaris*, and coverage of other lichens, respectively (Table 2). Of the main effects, both Habitat and Inventory had a significant effect on all the lichen characteristics (Table 2 and Fig. 4).

The coverage of *C. stellaris* was higher in coniferous habitats than in alpine ($F_{1,173.72} = 27.40$, Bonferroni-corrected $p = 0.018$) and sub-alpine habitats ($F_{1,94.66} = 14.85$, Bonferroni-corrected $p < 0.001$). Similarly, the coverage of other lichen species was higher in coniferous habitats than in alpine habitats ($F_{1,172.88} = 9.88$, Bonferroni-corrected $p = 0.006$), and lichen height was higher in coniferous and sub-alpine habitats than in alpine habitats (coniferous vs. alpine: $F_{1,77.46} = 7.86$, Bonferroni-corrected $p = 0.018$; alpine vs. sub-alpine: $F_{1,93.70} = 5.44$, $p = 0.022$). One should note, however, that the reason for the relative deficiency of lichens in alpine habitats was not only heavy grazing and trampling by the reindeer, but also in open habitat the growth rate of lichens is lower (Helle et al. 1983, Dahle et al. 2008).

Between 1986 and 2000, the coverage of *C. stellaris* decreased by 74% ($F_{1,167.70} = 40.23$, Bonferroni-corrected $p < 0.001$), whilst the lichen height and coverage of other lichen species increased by 22% and 45%, respectively (height: $F_{1,21.29} = 5.42$, Bonferroni-corrected $p = 0.042$; coverage: $F_{1,21.99} = 19.28$, Bonferroni-corrected $p < 0.001$). The result was ambiguous in two ways. First, it contradicted the finding that pellet-group density in winter was higher in 2000 than in 1986, suggesting increased grazing intensity and resultant lower lichen height; second, the changes in lichen height and coverage of *C. stellaris* were opposite. However, these same features also appeared in an extensive pasture inventory data set in northernmost Lapland from 1976–1978 and 2004 (Mattila 2006). The reasons remain unclear, but it seems to be obvious that despite the increase in lichen height, the intensity of grazing was still too heavy for *C. stellaris*, which suffered in particular from reindeer grazing and responded slowly the decrease in grazing intensity (Ahti 1961, Helle & Aspi 1983).

The impacts of Zone were variable. The coverage of *C. stellaris* in Zone I was higher than that in Zone II ($F_{1,144.33} = 5.64$, $p = 0.019$), which suggests avoidance of the area most heavily used for recreation. Instead, lichen height in Zone III

was greater than that in Zone I ($F_{1,130,06} = 5.92$, Bonferroni-corrected $p = 0.048$), which contradicted the earlier observation that in winter, when lichens are mainly used by reindeer, pellet-group density in Zone III was higher than that in Zones I and II.

The interaction of Zone \times Habitat revealed that the coverage of *C. stellaris* in alpine habitats in Zone I was higher than in Zone II ($F_{1,23,0} = 8.58$, $p = 0.008$), and in sub-alpine habitats it was higher in Zone I than in Zone III ($F_{1,48,6} = 4.50$, $p = 0.039$). This supported the avoidance hypothesis, but lichen height varied unpredictably. It was greater in alpine habitats in Zone III than in Zone I ($F_{1,6,6} = 7.26$, $p = 0.033$) and Zone II ($F_{1,13,2} = 7.31$, $p = 0.018$), whilst in coniferous habitats lichen height in Zone III was smaller than in Zone II ($F_{1,44,0} = 6.80$, $p = 0.012$).

The interaction of Inventory \times Habitat \times Zone for lichen characteristics was not significant (Table 2).

Discussion

The terminology describing changes in the animals' behaviour in relation to anthropogenic disturbance is variable and the same words are commonly used with different meanings (Bejder *et al.* 2009). The history of reindeer management in the study area suggested an even distribution of reindeer (Anon. 1973, Helle & Särkelä 1993), therefore we use disturbance to refer to a deviation from that pattern (Frid & Dill 2002). In interpreting trends in the avoidance responses of reindeer between 1986 and 2000, we follow the definitions introduced by Bejder *et al.* (2009). The term habituation for individuals was justified, as they learned, with repeated exposure, not to respond to a given disturbance stimulus; otherwise the animals exhibited varying degrees of tolerance, i.e. tolerance could increase, decrease or remain unchanged. However, increased tolerance is difficult to distinguish from the positive impacts of habitat restoration (Nellemann *et al.* 2010), which must be taken into account in interpreting the results.

The overall pellet-group density in winter was higher in 2000 than in 1986, despite the doubling of visitor numbers at the distances of

0–4 km and 4–8 km from the resort and a slight decrease in the number of reindeer in the Ivalo herding association. We suggested that there was no difference between the study years in the reindeer's capability to migrate from the area. In summer, field observations on sex ratio indicated lesser avoidance in 2000 than in 1986 by the females, tolerating various kinds of disturbance less than the male reindeer (Smith & Cameron 1983, Vistnes & Nellemann 2008). In 2000, the herd structure was male-biased only at 0–4 km from the resort, meanwhile in 1986 the bias was visible at a range of 8–12 km.

As pointed out by Frid and Dill (2002) and Bejder *et al.* (2009), increased tolerance does not mean that disturbance would be insignificant to the animals, as evidenced in this study by the uneven distribution of the reindeer. In summer the pellet-group density at 0–4 km from the resort was lower than that at 4–8 and 8–12 km, and basically a similar pattern was found in winter for coniferous habitats, the most important winter pasture. In summer, reindeer prefer open fell-tops, probably because of the windiness and resultant low insect harassment (Helle & Särkelä 1993), but they were not forced to live in the vicinity of the holiday resort, because good insect refuges, i.e. open fells, windy open areas, sandy forest roads with sand pits (Helle & Aspi 1984), as well as good pastures were also to be found outside the study area (Kumpula *et al.* 1999). Instead, in winter tolerance of the local reindeer to human activities is variable; the avoidance responses are lowest in early and strongest in late winter (Anttonen *et al.* 2011), which difference could not be taken into account in this study.

Cladonia stellaris reached the maximum abundance levels close to the resort with the lowest grazing pressure in terms of pellet-group density. Otherwise the expected uneven pasture use only poorly reflected lichen characteristics, which might be associated with very small amounts of lichens as a result of long-term heavy grazing (Kojola *et al.* 1995, Kumpula *et al.* 2000). In our study area, lichen coverage was on average 12%, while in a Norwegian impact-assessment study, under the heaviest grazing pressure it was 17% and was more than 80% in areas avoided by wild reindeer (Nellemann *et al.* 2001). In terms of the lichen biomass,

the difference in lichen vegetation was even more pronounced. Using the conversion function of Kumpula *et al.* (2000), the lichen biomass (dry matter) in our study area averaged at 19 g m² as compared with the Norwegian figures of 50–1100 g m² (Nellemann *et al.* 2001) and 250–1200 g m² (Nellemann *et al.* 2000).

The weak association between pellet-group density and lichen characteristics of reindeer was reported also in Swedish mountains, mainly due to trampling by reindeer during the snow-free season (Skarin 2001). In our study area, several other reasons were obvious. The results from 1986 suggested that in winter the significant positive correlations between pellet-group density and lichen abundance occurred mainly in areas, where reindeer could select the feeding site without human disturbance (Helle & Särkelä 1993). In addition, as the snow depth increased, the reindeer chose sites with the shallowest snow coverage (Kumpula & Colpaert 2007, Helle *et al.* 2008), which commonly takes place at the micro-site level at the cost of lichen biomass (Helle & Aspi 1983). Similarly, this had an impact on the composition of diet, which comprised considerable amounts of dwarf shrubs in relation to increasing snow depth (Kojola *et al.* 1995). Furthermore, a lowered grazing intensity due to disturbance is reflected only slowly in lichens, because the recovery of heavily grazed lichen vegetation, even without grazing, might take about 30 years (Kärenlampi 1973).

The results of our analyses on pellet-group density and abundance of *C. stellaris* were fairly consistent with earlier observations (Vistnes & Nellemann 2008). Wild reindeer in Norway almost totally avoided in winter areas closer than 5–10 km to a relatively small holiday resort (Nellemann *et al.* 2000), and in another study, lichen height decreased 35% over an 8-km distance from a highway/tourist cabins (impacts were not separated) as a result of anthropogenic disturbance (Dahle *et al.* 2008). In summer, wild reindeer selected insect refuges several kilometres from human-activity areas (Vistnes *et al.* 2008). In northern Norway during calving, the density of semi-domesticated reindeer closer than 4 km to cabins was about one fifth as compared with that in the area 4 km away (Vistnes & Nellemann 2001).

A great variation in tolerance to anthropogenic disturbance exists between *Rangifer* populations (Reimers & Colman 2006, Vistnes & Nellemann 2008), but this study, as compared with earlier observations of the local reindeer population, indicated that tolerance can be highly variable even within the same population. The most drastic change took place between the 1970s and 1986, the first study year. Until the late 1960s, the western edge of the Saariselkä fell area was known as an important calving area, but later the reindeer moved away due the disturbance associated with outdoor recreation and they reacted vigorously to any kind of human contact (Anon. 1973, Helle & Särkelä 1993). Because frequent and regular human activity increase the tolerance of reindeer (Colman *et al.* 2001, Skarin *et al.* 2004, Reimers & Colman 2006), the shock impact of outdoor recreation in our study area in the late 1960s was obviously related to an emergency of the wholly new phenomenon of skiers and hikers, despite very low visitor numbers (Fig. 2).

In addition, that happened at the same time as the snowmobile revolution triggered the transition from intensive herding to extensive herding or to a free-range management system (Pelto *et al.* 1968, Ingold 1980). The earlier close relationship between the reindeer and herders was broken. Reindeer feared the new vehicle with which the herders could compel the reindeer to move as they required, causing them to become more alert and timid (Ingold 1980). In ungulates, this behaviour is the sum of the effects of all human activity (Jeppesen 1987, Stankowich 2008), thus decreased tolerance of the reindeer is reflected in the strong avoidance responses to hikers and skiers (Helle & Särkelä 1993).

However, herders quickly learned to use the vehicle properly (Helle & Särkelä 1993), and the population decline around 1970 led to intensification of management practices, including the artificial or supplementary feeding of the reindeer in winter in yard corrals or on natural pastures (Helle & Saastamoinen 1979). Feeding developed into a normal routine and increased the levels of tameness of the reindeer in every kind of human encounter, as often reflected anecdotally. For instance, individual reindeer could follow wholly unknown people picking cloud-

berries in summer months, because these people carried similar buckets to those that the reindeer herder used to deliver feed to the animals in a yard corral during winter.

We did not monitor in detail the changes in the infrastructure of the resort and its surroundings, but some of these very probably mitigated the disturbance effect of the resort. The new lodges, hotels, roads, etc., were built largely within the same town-plan area that existed in the 1980s by condensing the urban structure. Several studies showed that the continued development in an already developed area has smaller impacts than extensive development over a larger area (Vistnes *et al.* 2001, Cameron *et al.* 2005, Joly *et al.* 2006). By 2000 the numerous “unofficial” trails that were still in use in the 1980s (Helle & Särkelä 1993) were replaced by fewer, more clearly marked trails equipped with duckboards over the wetlands and steps on the slopes. They channel the recreational use effectively (S. Kankaanpää, the head of Urho Kekkonen National Park, pers. comm.). Nellemann *et al.* (2010) showed that wild reindeer responded rapidly to closing of a trail and were capable to occupy a lost pasture again. Thus our findings that pellet-group density increased in the study area despite the overall doubling of visitor numbers could be mainly a result of improved channelling of tourists into fewer trails, and that applied also to reduced avoidance responses by female reindeer in summer. In the Swedish mountains, permanent hiking trails had little or no impact on the disturbance behaviour of semi-domesticated reindeer especially during severe insect harassment (Skarin *et al.* 2004, 2008).

Rather few papers have dealt with disturbance behaviour of semi-domesticated reindeer as compared with the wild *Rangifer* (Vistnes & Nellemann 2008). Semi-domesticated reindeer are subject to artificial and natural selection, promoting, for instance, white coloration at the cost of an increased parasite intensity (Rodven *et al.* 2009). In behavioural traits, tameness and herd fidelity are highly preferred (Kitti *et al.* 2006). Wild reindeer, originating from bewildered semi-domesticated animals in the 1950s, have still a shorter flying distance than the original wild reindeer (Reimers & Colman 2006), suggesting that tolerance to humans owes a genetic component.

In northern Finland, shooting of alert and shy reindeer has been a normal practice already in the 18th century, i.e. tameness of each individual has been tested annually, because shy animals could not be managed in a normal manner (Helle 1982). Despite such artificial selection semi-domesticated reindeer seem to have an upper limit for disturbance, as suggested by Wolfe *et al.* (2000) and Skarin *et al.* (2004), and evidenced in this study by avoidance of areas in the vicinity of a great holiday resort. Furthermore, one should note that tourism and outdoor recreation are not the only land use forms affecting reindeer. In the herding association of Ivalo, where our study area was located, Anttonen *et al.* (2011) found that the impacts of settlement, buildings, main roads, official snow mobile tracks and gold digging areas, covered with varying intensity 28%–39% of the entire area.

References

- Ahti, T. 1961: Taxonomic studies on reindeer lichens (*Cladonia*, subgenus *Cladina*). — *Annales Botanici Societatis 'Vanamo'* 32: 1–160.
- Anonymous 1973: *Matkailu/porotaloustoimikunnan mietintö. Komiteanmietintö 123*. — Maa- ja metsätalousministeriö, Helsinki.
- Anttonen, M., Kumpula, J. & Colpaert, A. 2011: Range selection by semi-domesticated reindeer (*Rangifer tarandus tarandus*) in relation to infrastructure and human activity in boreal environment, northern Finland. — *Arctic* 64: 1–14.
- Bejder, L., Samuels, A., Whitehead, H., Finn, H. & Allen, S. 2009: Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. — *Marine Ecology Progress Series* 395: 177–185.
- Berger, J., Daneke, D., Johnson, J. & Berwick, S. 1983: Pronghorn foraging economy and predator avoidance in a desert ecosystem: implications for the conservation of large mammalian herbivores. — *Biological Conservation* 25: 193–208.
- Bradshaw, C., Boutin, S. & Hebert, D. 1998: Energetic implications of disturbance caused by petroleum exploration to woodland caribou. — *Canadian Journal of Zoology* 76: 1319–1324.
- Cameron, R., Smith, W., White, R. & Griffith, B. 2005: Central Arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. — *Arctic* 58: 1–9.
- Campbell, D., Swanson, G. & Sales, J. 2004: Comparing the precision and cost-effectiveness of faecal pellet group count methods. — *Journal of Applied Ecology* 41:

- 1185–1196.
- Chiang, L. 2003: *Statistical methods of analysis*. — World Scientific Publishing Co. Pte. Ltd., New Jersey.
- Colman, J., Jacobsen, B. & Reimers, E. 2001: Summer response distances of Svalbard reindeer *Rangifer tarandus platyrhynchus* to provocation by humans on foot. — *Wildlife Biology* 7: 275–283.
- Dahle, B., Reimers, E. & Colman, J. 2008: Reindeer (*Rangifer tarandus*) avoidance of a highway as revealed by lichen measurements. — *European Journal of Wildlife Research* 54: 27–35.
- Fortin, M.-J., Dale, M. R. T. & ver Hoef, J. 2002: Spatial analysis in ecology, vol. 4. — In: El-Shaarawi, A. H. & Piegorisch, W. W. (eds.), *Encyclopedia of environmental metrics*: 2051–2058. John Wiley & Sons Ltd., Chichester.
- Frid, A. & Dill, L. 2002: Human-caused disturbance stimuli as a form of predation risk. — *Conservation Ecology* 6(1): 11. [online] URL: <http://www.consecol.org/vol6/iss1/art11/>.
- Haapalehto, M. 2001: *Virkistyskäytön vaikutus porojen laidunmenon käyttöön Saariselällä*. — Lopputyö, Rovaniemen ammattikorkeakoulu.
- Helle, T. 1982: *Poron ja peuran jäljillä*. — Kirjayhtymä, Vaasa.
- Helle, T. & Aspi, J. 1983: Effects of winter grazing by reindeer on vegetation. — *Oikos* 40: 337–343.
- Helle, T. & Aspi, J. 1984: Do sandy patches help reindeer against insects? — *Reports from Kevo Subarctic Research Station* 19: 57–62.
- Helle, T. & Kojola, I. 2006: Population trends of semi-domesticated reindeer in Fennoscandia — evaluation of explanations. — In: Forbes, B., Bölder, M., Müller-Wille, L., Hukkinen, J., Müller, F., Gunsley, N. & Konstantinov, Y. (eds.), *Reindeer management in northernmost Europe*: 319–339. Ecological Studies 184, Part II, Springer-Verlag Berlin Heidelberg.
- Helle, T. & Kojola, I. 2008: Demographics in an alpine reindeer herd: effects of density and winter weather. — *Ecography* 31: 221–230.
- Helle, T. & Särkelä, M. 1993: The effects of outdoor recreation on range use by semi-domesticated reindeer. — *Scandinavian Journal of Forest Research* 8: 123–133.
- Helle, T. & Saastamoinen, O. 1979: The winter use of food resources of semi-domestic reindeer in northern Finland. — *Communicationes Instituti Forestaliae Fenniae* 95: 1–26.
- Helle, T., Aspi, J. & Kilpelä, S.-S. 1990: The effects of stand characteristics on reindeer lichens and range used by semi-domesticated reindeer. — *Rangifer, Special Issue* 3: 107–114.
- Helle, T., Aspi, J. & Tarvainen, L. 1983: The growth rate of *Cladonia rangiferina* and *C. mitis* in relation to forest characteristics. — *Rangifer* 3: 2–5.
- Helle, T., Horstkotte, T., Mikkola, K., Niva, A. & Posio, H. 2008: Lumipeitteen ominaisuudet ja suurilmaston vaihtelu vaikuttavat poroelon menestymiseen. — *Luonnon Tutkija* 112: 58–60.
- Hoogesteger, M. 1976: Changes in vegetation around the refuge huts in Koilliskaira forest area. — *Silva Fennica* 10: 40–53.
- Hox, J. 2002: *Multilevel analysis. Techniques and applications*. — Lawrence Erlbaum Associates, Publishers, Mahwah, London.
- Ingold, T. 1980: *Hunters, pastoralists and ranchers*. — Cambridge University Press, Cambridge.
- Jeppesen, J. 1987: Impact of human disturbance in home range movement and activity of red deer (*Cervus elaphus*) in a Danish environment. — *Danish Review of Game Biology* 13: 1–38.
- Kitti, H., Gunsley, N. & Forbes, B. 2006: Defining the quality of reindeer pasture. — In: Forbes, B., Bölder, M., Müller-Wille, L., Hukkinen, J., Müller, F., Gunsley, N. & Konstantinov, Y. (eds.), *Reindeer management in northernmost Europe*: 141–165. Ecological Studies 184, Part II, Springer-Verlag Berlin Heidelberg.
- Klein, D. 1971: Reactions of reindeer to obstructions and disturbances. — *Science* 173: 393–398.
- Koenig, W. D. 1999: Spatial autocorrelation of ecological phenomena. — *Trends Evol. Ecol.* 14: 22–26.
- Kojola, I., Helle, T., Niskanen, M. & Aikio, P. 1995: Effects of lichen biomass on winter diet, body mass and reproduction of semi-domesticated reindeer *Rangifer t. tarandus* in Finland. — *Wildlife Biology* 1: 33–38.
- Kumpula, J. & Colpaert, A. 2007: Snow conditions and usability value of pastureland for semi-domesticated reindeer (*Rangifer tarandus tarandus*) in northern boreal forest area. — *Rangifer* 27: 25–39.
- Kumpula, J., Colpaert, A. & Anttonen, M. 2007: Does forest harvesting and linear infrastructure change the usability value of pastureland for semi-domesticated reindeer (*Rangifer tarandus tarandus*)? — *Annales Zoologici Fennici* 44: 161–178.
- Kumpula, J., Colpaert, A. & Nieminen, M. 1999: Suomen poronhoitoalueen kesälaidunvarat. — *Kala- ja riistatiedotteita* 152: 1–54.
- Kumpula, J., Colpaert, A. & Nieminen, M. 2000: Condition, potential recovery, and productivity of lichen (*Cladonia* spp.) ranges in the Finnish reindeer management area. — *Arctic* 53: 152–160.
- Kärenlampi, L. 1973: Suomen poronhoitoalueen jäkälämäiden kunto, jäkälämäärät ja tuottoarvot vuonna 1972. — *Poromies* 40: 15–19.
- Mahoney, S. & Schaefer, J. 2002: Hydroelectric development and the disruption of migration in caribou. — *Biological Conservation* 107: 147–153.
- Mattila, E. 2006: Porojen talvilaitumien kunto Ylä-Lapin paliskunnissa vuonna 2004. — *Metlan työraportteja* 28: 1–54.
- Metsähallitus 2001: Urho Kekkonen kansallispuiston hoito- ja käyttösuunnitelma. — *Metsähallituksen luonnonsuojelujulkaisuja B* 60: 1–64.
- Milliken, G. & Johnson, D. 1984: *Analysis of messy data*. — Van Nostrand Reinhold, New York.
- Nellemann, C. & Cameron, R. 1998: Cumulative impacts of an evolving oilfield complex on the distribution on calving caribou. — *Canadian Journal of Zoology* 76: 425–430.
- Nellemann, C., Jordhøy, P., Stöen, O.-G. & Strand, O. 2000: Cumulative impacts of tourist resorts on wild reindeer (*Rangifer tarandus tarandus*) during winter. — *Arctic*

- 53: 9–17.
- Nellemann, C., Vistnes, I., Jordhoy, P. & Strand, O. 2001: Winter distribution of wild reindeer in relation to power lines, roads and resorts. — *Biological Conservation* 101: 351–360.
- Nellemann, C., Jordhoy, P., Vistnes, I., Strand, O. & Newton, A. 2003: Progressive impacts of piecemeal development on wild reindeer. — *Biological Conservation* 113: 307–317.
- Nellemann, C., Vistnes, I., Jordhoy, P., Stoen, O.-G., Kaltenborn, B., Hanssen, F. & Helgesen, R. 2010. Effects of recreational cabins, trails and their removal for restoration of reindeer winter ranges. — *Restoration Ecology* 18: 873–881.
- Nieminen, M. & Heiskari, U. 1988: Diets of freely grazing and captive reindeer during summer and winter. — *Rangifer* 9: 17–34.
- Nieminen, M. & Autto, P. 1989: Porojen laitumet ja ruokinta talvella 1986–87. — *Poromies* 56: 38–43.
- Niva, A. 2002: *Matkailu, porojen laidunnus ja laidunten kuluminen Saariselällä; vuosien 1986 ja 2000 vertailu*. — Päättyöyö, Hämeen amk, metsätalous, Evo.
- Pegau, R. 1970: Effects of reindeer trampling and grazing on lichen. — *Journal of Wildlife Management* 23: 95–97.
- Pelto, P., Linkola, M. & Sammallahti, P. 1968: The snowmobile revolution in Lapland. — *Suomalais-Ugrilaisen Seuran aikakauskirja* 69: 1–42.
- Petraitis, P., Latham, R. & Niesenbaum, R. 1989: The maintenance of species-diversity by disturbance. — *Quarterly Review of Biology* 64: 393–418.
- Reimers, E. & Colman, J. 2006: Reindeer and caribou (*Rangifer tarandus*) response towards human activities. — *Rangifer* 26: 55–71.
- Rodven, R., Männikkö, I., Ims, R., Yoccoz, G. & Folstad, I. 2009: Parasite intensity and coloration in reindeer calves — contrasting artificial and natural selection. — *Journal of Animal Ecology* 78: 600–607.
- Saastamoinen, O. 1982: Economics of multiple-use forestry in the Saariselkä forest and fell area. — *Communicationes Instituti Forestalis Fenniae* 104: 1–102.
- Skarin, A. 2001: *Interactions between reindeer, humans, topography and weather — spatial patterns in reindeer pellet groups and lichen characteristics*. — Examensarbete 221, Sveriges Lantbruksuniversitet, Institutionen för husdjursgenetik, Uppsala.
- Skarin, A. 2007: Habitat use by semi-domesticated reindeer, estimated with pellet-group counts. — *Rangifer* 27: 121–132.
- Skarin, A. 2008: Decay rate of reindeer pellet-groups. — *Rangifer* 28: 47–52.
- Skarin, A., Danell, Ö., Bergström, R. & Moen, J. 2004: Insect avoidance may override human disturbances in reindeer habitat selection. — *Rangifer* 24: 95–103.
- Skarin, A., Danell, Ö., Bergström, R. & Moen, J. 2008: Summer habitat preferences of GPS-collared reindeer *Rangifer tarandus tarandus*. — *Wildlife Biology* 14: 1–15.
- Smith, W. & Cameron, R. 1983: Responses of caribou to industrial development on Alaska's Arctic Slope. — *Acta Zoologica Fennica* 175: 43–45.
- Stankowich, T. 2008: Ungulate flight responses to human disturbance: a review and meta-analysis. — *Biological Conservation* 141: 2159–2173.
- Tyler, N. 1991: Short-term behavioural responses of Svalbard reindeer *Rangifer tarandus platyrhynchus* to direct provocation by a snowmobile. — *Biological Conservation* 56: 179–194.
- Törn, A., Rautio, J., Norokorpi, Y. & Tolvanen, A. 2006: Revegetation after short-term trampling at subalpine heath vegetation. — *Annales Botanici Fennici* 43: 129–138.
- Vistnes, I. & Nellemann, C. 2001: Avoidance of cabins, roads, and power lines by semi-domesticated reindeer during winter. — *Journal of Wildlife Management* 65: 915–925.
- Vistnes, I. & Nellemann, C. 2008: The matter of spatial and temporal scales: a review of reindeer and caribou response to human activity. — *Polar Biology* 31: 399–407.
- Vistnes, I., Nellemann, C., Jordhoy, P. & Strand, O. 2001: Wild reindeer: impacts of progressive infrastructure development on distribution and range use. — *Polar Biology* 24: 531–537.
- Vistnes, I., Nellemann, C., Jordhoy, P. & Stoen, O. 2008: Summer distribution of wild reindeer in relation to human activity and insect stress. — *Polar Biology* 31: 1307–1317.
- Weir, J., Mahoney, S., McLaren, B. & Ferguson, S. 2007: Effects of mine development on woodland caribou *Rangifer tarandus* distribution. — *Wildlife Biology* 13: 66–74.
- Weladji, R. & Forbes, B. 2002: Disturbance effects of human activities on *Rangifer tarandus* habitat — implications to life-history and population dynamics. — *Polar Geography* 26: 171–186.
- Wilkinson, L. & Coward, M. 2004: Linear models II: analysis of variance. — In: *SYSTAT II. Statistics II*: 81–138. SYSTAT Software Inc., Richmond.
- Wolfe, S., Griffith, B. & Wolfe, C. 2000: Response of reindeer and caribou to human activities. — *Polar Research* 19: 63–73.