ARCTIC
VOL. 64, NO. 1 (MARCH 2011) P. 1–14

# Range Selection by Semi-Domesticated Reindeer (*Rangifer tarandus tarandus*) in Relation to Infrastructure and Human Activity in the Boreal Forest Environment, Northern Finland

MARJA ANTTONEN,[1,2] JOUKO KUMPULA[3] and ALFRED COLPAERT[4]

(*Received 3 June 2008; accepted in revised form 9 June 2010*)

ABSTRACT. During past decades, the amounts of infrastructure and human activity have increased in northern latitudes. Although the effects of human development on wild reindeer and caribou have been widely examined, its effects on semi-domesticated reindeer and the reindeer herding environment are still poorly understood. We studied how seven different human activities (population centres, buildings, main roads, forest roads, snowmobile tracks, skiing trails, and gold digging areas) affect the range selection by semi-domesticated reindeer in northern Finnish Lapland using GPS tracking data on 29 female reindeer. Data were analyzed using compositional analysis on two spatial scales (home range selection and within-home-range selection) and in three seasonal periods (early winter, late winter, and summer-autumn). Results showed that during winter, reindeer strongly avoided almost all studied human activities when selecting home range areas (for forest roads, the direction of the effect was unclear), but in summer and autumn, only some of those activities were important. Within the selected home range areas, pasture use by reindeer appears to be less sensitive to infrastructure and human activity, probably because reindeer were able to avoid these anthropogenic disturbances at the upper level of habitat selection. The size of the potential cumulative area affected by infrastructure varied seasonally between 27.5% and 39.0% of the study area when calculated on the basis of home range selection, and between 7.2% and 20.3% when calculated from within-home-range selection. The strongest avoidance of infrastructure was found in late winter on both scales of range selection, but weakest avoidance was in early winter for home range selection and in summer for within-home-range selection. Cumulative impacts of different human activities on the usability value of reindeer ranges should be taken into account when planning new land-use operations in the areas important for the reindeer herding.

Key words: *Rangifer tarandus tarandus*, semi-domesticated reindeer, reindeer herding, infrastructure, human activity, human disturbance, avoidance, compositional analysis, GPS tracking

RÉSUMÉ. Au cours des dernières décennies, la quantité d'infrastructures et d'activités humaines s'est accrue dans les latitudes nordiques. Bien que les incidences du développement humain sur le renne sauvage et le caribou aient été examinées à grande échelle, ses incidences sur le renne semi-domestiqué et sur le domaine vital du renne sont toujours mal comprises. Nous avons étudié la manière dont sept activités humaines différentes (centres de population, bâtiments, routes principales, routes forestières, pistes de motoneige, pistes de ski et zones d'exploitation aurifère) exercent une influence sur la sélection du domaine du renne semi-domestiqué dans la partie finlandaise de la Laponie du nord à l'aide de données de poursuite obtenues au moyen d'un GPS apposé à 29 rennes femelles. Les données ont été analysées au moyen d'une analyse compositionnelle fondée sur deux échelles spatiales (la sélection du domaine vital et la sélection à l'intérieur du domaine vital) et sur trois périodes saisonnières (début de l'hiver, fin de l'hiver et été-automne). Les résultats ont indiqué que pendant l'hiver, le renne évitait dans la plus grande mesure du possible presque toutes les activités humaines étudiées quand il choisissait son domaine vital (dans le cas des routes forestières, le sens de l'effet n'était pas clair), mais à l'été et à l'automne, seulement certaines de ces activités revêtaient de l'importance. À l'intérieur des domaines vitaux sélectionnés, le pâturage utilisé par le renne semble moins sensible à l'infrastructure et à l'activité humaine, probablement parce que le renne était capable d'éviter ces perturbations anthropogéniques au niveau supérieur de la sélection de l'habitat. La grandeur de la zone cumulative potentielle touchée par l'infrastructure variait s'une saison à l'autre entre 27,5 % et 39,0 % de l'aire étudiée lorsque calculée en fonction de la sélection du domaine vital, et entre 7,2 % et 20,3 % lorsque calculée en fonction de la sélection de l'intérieur du domaine vital. C'est à la fin de l'hiver que le renne évitait le plus possible l'infrastructure pour ce qui est des deux échelles de sélection du domaine vital, tandis que c'est au début de l'hiver que le renne faisait le moins d'évitement dans le cas de la sélection du domaine vital, et à l'été dans le cas de la sélection de l'intérieur du domaine vital. Les incidences cumulatives de diverses activités humaines

[1] University of Oulu, Department of Geography, PO Box 3000, FI-90014 University of Oulu, Finland
[2] Corresponding author: marja.anttonen@oulu.fi
[3] Finnish Game and Fisheries Research Institute, Reindeer Research Station, FI-99910 Kaamanen, Finland
[4] University of Eastern Finland, Department of Geographical and Historical Studies, Geography, FI-80101 Joensuu, Finland

sur la valeur d'utilisation des domaines vitaux du renne devraient être prises en considération dans le cadre de la planification de nouvelles exploitations d'utilisation des terres dans les zones où les formations de troupeaux de rennes sont importantes.

Mots clés : *Rangifer tarandus tarandus*, renne semi-domestiqué, troupeau de rennes, infrastructure, activité humaine, perturbation humaine, évitement, analyse compositionnelle, poursuite GPS

Traduit pour la revue *Arctic* par Nicole Giguère.

## INTRODUCTION

Arctic and subarctic areas have gone through rapid growth in human activity during the late 20th century as the industrialized world has expanded its search for and exploitation of natural resources like energy, minerals, and timber into the high latitudes. Other kinds of land use, like tourism and recreational activities, have also become more important. This increased human presence has many effects on the environmental, cultural, social, and economic conditions of these northern areas (Klein, 2000). It has been estimated that today 15–20% of the Arctic land areas are subjected to anthropogenic impacts and disturbance. High levels of disturbance are likely to occur in 50–80% of the area by 2050, and in northern Fennoscandia even sooner, within 20–30 years (UNEP, 2001). Reindeer and caribou (*Rangifer tarandus* subspecies) are considered to be among the species most sensitive to the impact of human disturbance in Arctic regions (UNEP, 2001). Therefore, the loss of pastures is one of the main challenges for semi-domesticated reindeer husbandry today (Jernsletten and Klokov, 2002).

Within the last decades, several studies relating to responses of *Rangifer* to human activities have been conducted (e.g., reviews by Wolfe et al., 2000; UNEP, 2001; Weladji and Forbes, 2002; Reimers and Colman, 2006; Vistnes and Nellemann, 2008). Most studies concern wild reindeer and caribou, and only a few have addressed the responses of semi-domesticated reindeer (see Helle and Särkelä, 1993; Vistnes and Nellemann, 2001; Skarin et al., 2004; Skarin, 2006). Infrastructure (e.g., roads, trails, pipelines, oil wells, mines, and settlements) and human activity (e.g., forestry, tourism, recreation) have been shown to cause disturbance and avoidance behaviour, act as a barrier to migration routes, and lead to fragmentation and degradation of rangelands occupied by reindeer and caribou populations (Cameron et al., 1992; Nellemann and Cameron, 1998; Nellemann et al., 2000, 2001, 2003; Smith et al., 2000; Dyer et al., 2001, 2002; Vistnes and Nellemann, 2001; Vistnes et al., 2001, 2004; Johnson et al., 2005; Kumpula et al., 2007; Weir et al., 2007). However, some opposite results have also been reported. For example, Reimers et al. (2007) observed that wild reindeer migration and grazing in North Ottadalen, Norway, were not disturbed by power lines transecting their rangelands.

Avoidance can be defined as a lower-than-expected animal density in areas near the source of anthropogenic disturbance (Vistnes and Nellemann, 2001). Vistnes (2008:8) suggested that avoidance occurs because reindeer and man have a long evolutionary history together: "It seems that it is beneficial for *Rangifer* to reduce the risk of encountering human hunters by avoiding the signs of human presence." The reindeer avoidance of human disturbance extends beyond the actual construction area (Nellemann and Cameron, 1998). The first constructions built in an area may have the greatest impact on the distribution of the animals (Haskell et al., 2006), but subsequent development may strengthen the avoidance behaviour, producing a cumulative impact (Nellemann and Cameron, 1996, 1998; Vistnes and Nellemann, 2001; Vistnes et al., 2001). It has been shown that heavily fragmented and developed areas have greater effect than less-developed areas on the avoidance behaviour of reindeer, and that wild reindeer may even abandon areas where infrastructure densities reach a certain level (Vistnes et al., 2001). In the long term, avoidance can lead to lower productivity of reindeer or caribou herds because heavier use of areas with less or low-quality forage may result in poorer body condition or decreased calf production (Cameron et al., 1992; Nellemann et al., 2000, 2003; Vistnes and Nellemann, 2001). Also, fragmented pasture areas, increased human activities, and lower quality and quantity of pasture due to higher reindeer densities can affect the profitability of reindeer herding because supplementary feeding may be needed in winter. In addition to adding expense, supplementary feeding allows herders to maintain the reindeer in the reduced wintering areas at densities so high that the pastures cannot recover. Over time, therefore, reindeer husbandry may become even more dependent on supplementary feeding (Kumpula, 2001).

The avoidance behaviour of reindeer varies seasonally and by gender (Vistnes, 2008). Late winter and calving are the most sensitive periods for disturbance (e.g., Dyer et al., 2001; Vistnes and Nellemann, 2001), but avoidance has been observed throughout the year (e.g., Dyer et al., 2001; Weir et al., 2007). Females, and especially females with calves, are more sensitive to disturbance than males (Cameron et al., 1992; Helle and Särkelä, 1993; Nellemann and Cameron, 1998; Nellemann et al., 2000; Vistnes and Nellemann, 2001; Schaefer and Mahoney, 2007). On the other hand, reindeer can also habituate to human activities (Colman et al., 2001; Haskell et al., 2006; Reimers and Colman, 2006; Skarin, 2006, 2007), and in some situations, other, apparently stronger limiting factors may make the reindeer more tolerant of disturbance (Pollard et al., 1996; Skarin et al., 2004; Skarin, 2006). For example, it has been observed that during insect harassment or warm weather in mid-summer, reindeer use high-altitude areas despite the presence of hikers, which might normally cause reindeer avoidance (Skarin et al., 2004; Skarin, 2006).

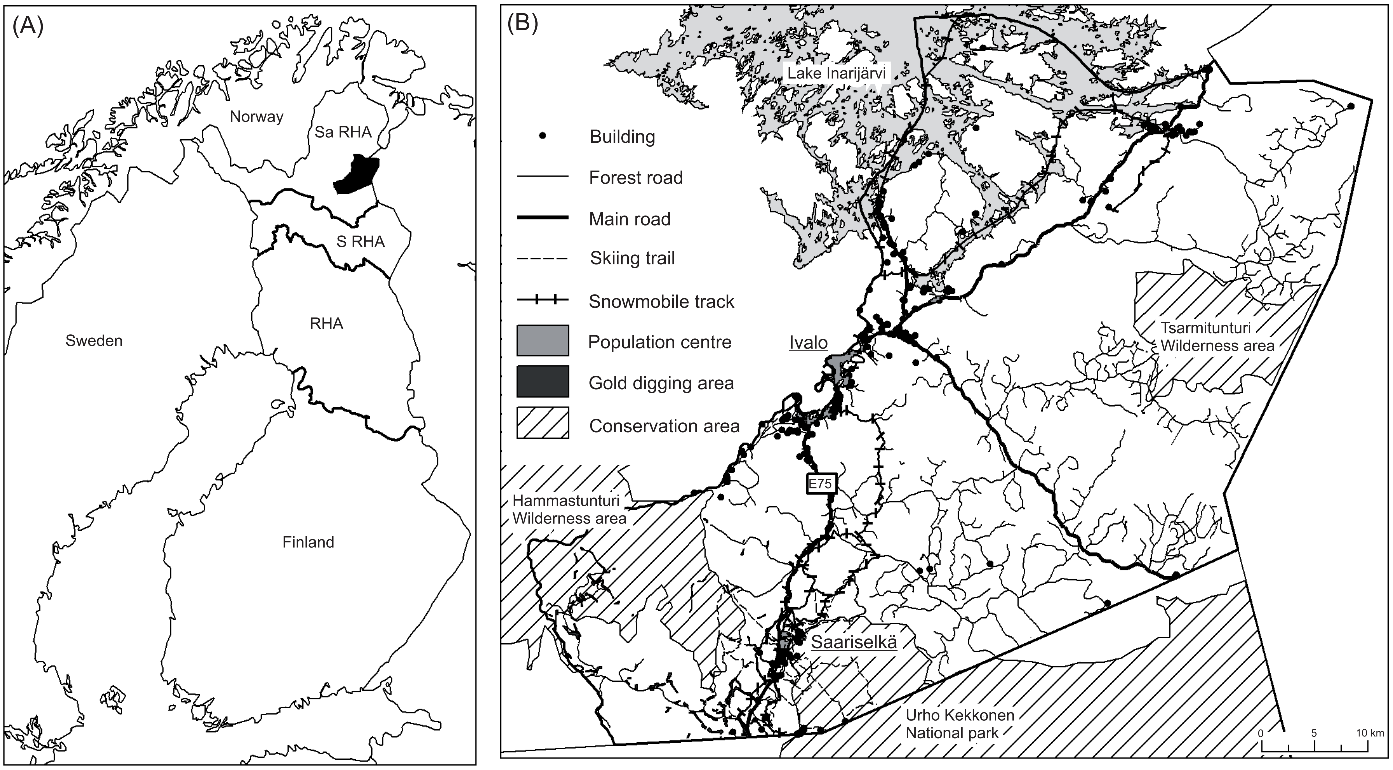


FIG. 1. Map of northern Scandinavia. (A) shows the Ivalo reindeer-herding district (black area) and the location and borders of the three Finnish reindeer-herding areas: RHA = Reindeer husbandry area (56 districts), S RHA = Special reindeer husbandry area (20 northernmost districts of the RHA), Sa RHA = Sami reindeer husbandry area (13 northernmost districts of the S RHA). Map of the study area (B) shows places mentioned in the text and the main types of land use and infrastructure in the Ivalo reindeer-herding district. The forest industry operates mainly outside the conservation areas.

In this study, we examined how semi-domesticated reindeer inhabiting boreal forest areas responded to infrastructure and human activity in three different seasons and on two spatial scales. Our hypothesis was that semi-domesticated reindeer avoid infrastructure and human activity when selecting both their seasonal home range and the pasture areas inside that home range. We tested the hypothesis separately with seven different forms of infrastructure, using empirical data on reindeer movements. We wanted to determine whether the reindeer response to human activity differs between the two spatial scales of habitat selection and to increase our knowledge of the cumulative impacts of different land-use activities on reindeer herding in this boreal forest environment.

## STUDY AREA

The study area, the Ivalo reindeer-herding district (black area in Fig. 1A), is situated in northern Finland. It is located within the municipality of Inari (boundaries not shown), which includes eight reindeer-herding districts. The total area of the Ivalo district is 2861 km$^2$ (Fig. 1B). About 8% (235 km$^2$) of the area is covered by water, and another 8% (226 km$^2$) by mire (Kumpula et al., 2004). The area belongs to the northern boreal forest zone, and the landscape is characterized by dry pine (*Pinus sylvestris*) forests of different ages, where the ground layer is dominated by lichens (*Cladina* and *Cladonia* sp.). The relief of the area is rugged, with several treeless tops of relatively low, smooth fells. The snowy-forest climate is characterized by long, cold winters and short, relatively warm summers.

This area is intensively exploited for different kinds of land-use activities. Intensive forestry has been practiced in the area over the past 80 years (Luhta, 1999). Saariselkä, one of Lapland's largest winter tourism centres, and Ivalo, the administrative centre of the municipality, are within the area. One of the major north-south roads through Finnish Lapland (No. E 75) runs throughout the southern part of the district. On the other hand, there are also three conservation areas—the Hammastunturi and Tsarmitunturi wilderness areas and a small part of the Urho Kekkonen National Park—where reindeer herding is allowed.

During the past 10 years, the average reindeer winter stock of the Ivalo district after the slaughter season has been about 5500 reindeer; the maximum number permitted is 6000 animals. Over the study period, reindeer were herded during wintertime in two main herds, using somewhat different management systems. The herd of about 4000 reindeer populating the southern and central parts of the district was offered supplementary forage, mainly pre-dried hay silage, from January to April. Our calculations indicate that supplementary feeding supplied one-third of total nutrition for this herd, and natural pastures provided the remainder. Herders fed the animals in the areas near their cratering (winter feeding) sites, and when reindeer moved, feeding places were shifted accordingly. In the northern part of the district, where about 1500 reindeer were herded, supplementary winter feeding was not used as systematically.

## MATERIAL AND METHODS

### *GPS Tracking*

We tracked 29 female reindeer equipped with GPS collars in the Ivalo herding district from December 1999 to November 2002. We used female reindeer because they form the largest proportion (70% to 80%) of the reindeer herd. Before fitting the collars, we tested the functioning of the GPS devices in different types of terrain and did not observe any differences in GPS accuracy or observation rate between open land and closed forest. We placed the collars on adult females whose calves were slaughtered during the autumn and winter round-ups. We deployed the collars on reindeer in the northern and central/southern herds in proportion to the relative size of the herds: seven collars for the northern herd and 22 collars for the central/southern herd. Each reindeer was tracked for about one year. The devices were programmed to measure the location of a reindeer at eight-hour intervals. This location interval was selected on the basis of the animal's mobility and to optimize battery life during the long surveillance period. The data were stored in the GPS memory and downloaded after the retrieval of the collar. Each GPS position accepted for the study had to fulfill two criteria: at least five satellites were available at the time of the measurement, and the DOP-value was below 10. Thus, the true spatial accuracy of the reindeer GPS positions was about 15 m or better.

For the entire tracking period, we collected a total of 10 977 valid locations, and the total number of locations per reindeer varied from 32 to 1075. Before further analysis, we removed the GPS positions that were located inside round-up corrals and therefore may not have represented free-ranging animals. In order to study the differences in the reindeer response to infrastructure and human activity in different seasons, we divided the GPS location data for each individual into three seasonal periods: 1) early winter: November–January, 2) late winter: February–April, and 3) summer-autumn: May–October. Restrictions in statistical analysis precluded a more detailed seasonal division of the data. In the three seasons, we eventually had observation data for 20, 25, and 15 reindeer, respectively. The mean number of GPS locations per reindeer varied from 170.8 (SD = 84.1) in early winter, to 146.3 (SD = 75.3) in late winter and 243.1 (SD = 133.4) in summer-autumn. Two types of infrastructure, gold digging areas and skiing trails, occur only in the southern and southwestern parts of the herding district (Fig. 1). Therefore, in analyses of these forms of infrastructure, we used only the reindeer of the central/southern herd, and we left out seven reindeer inhabiting the northern parts of the district whose home ranges never reached the southern area. In these analyses, the data were

TABLE 1. Distance in metres of buffers created around different types of infrastructure.

| Infrastructure | Buffer 1 | Buffer 2 | Buffer 3 | External area |
|---|---|---|---|---|
| Population centres | 0–200 m | 200–1000 m | 1000–2500 m | > 2500 m |
| Buildings | 0–100 m | 100–400 m | 400–1500 m | > 1500 m |
| Main roads | 0–100 m | 100–400 m | 400–1500 m | > 1500 m |
| Forest roads | 0–100 m | 100–400 m | 400–1500 m | > 1500 m |
| Snowmobile tracks | 0–100 m | 100–400 m | 400–1500 m | > 1500 m |
| Skiing trails | 0–100 m | 100–400 m | 400–1500 m | > 1500 m |
| Gold digging areas | 0–100 m | 100–400 m | 400–1500 m | > 1500 m |

from 14 reindeer in early winter, 19 reindeer in late winter, and 11 reindeer in summer-autumn. We formed Minimum Convex Polygon (MCP) home range areas (Mohr, 1947) for the population range of all reindeer in the study and separately for each reindeer in every seasonal period by employing the Animal Movement application in Arc View 3.2 software (Hooge and Eichenlaub, 1997).

### *Infrastructure Data*

Digital infrastructure data (1:250 000) on roads, population centres, and buildings were obtained from the National Land Survey of Finland. In addition, the Finnish State Forest Enterprise (Metsähallitus) provided the spatial data on skiing trails and snowmobile tracks in the area. The spatial data on gold mining reservations, mining claims, and mining concessions were downloaded from the Mining Register of the Ministry of Trade and Industry. When processing the infrastructure data, we classified the administrative centre of the municipality, Ivalo, and two smaller settlements (Siskeli and Nellim), as well as the tourist resort of Saariselkä, as "population centres" (see Fig. 1). "Buildings" data represent the most important buildings or groups of buildings located in the area. Roads were divided into two categories: "main roads" (covered with asphalt and in heavy or intermediate use all year round) and "forest roads" (minor gravel roads, partly closed in wintertime, and used mainly for forestry and outdoor recreation purposes). We combined the data on gold mining reservations, mining claims, and mining concessions of the area and called this infrastructure layer "gold digging areas."

We created multiple buffers based on three distances for each infrastructure type (Table 1). Areas inside the reindeers' home range but beyond the buffers were named "external areas." We used greater distances for population centres than for other infrastructure studied because major developments have a higher level of human activity than small developments and therefore may produce greater avoidance effects. We calculated the proportions of infrastructure buffer areas, first within the entire roaming area (MCP) of all reindeer, and then within each seasonal home range area of each reindeer. We also calculated the percentage of GPS locations found in each infrastructure buffer within each of these individual seasonal home ranges. From all infrastructure buffers and GPS locations, we then subtracted the overlapping buffer areas and the GPS locations of the first buffers of all other infrastructure types in order to remove the possible immediate effect of other land use in the area. For example, if a population centre and a road overlapped, and no reindeer were located in the area of a population centre, then including buffer 1 of the population centre could have confused the results of the road analysis. However, this approach may introduce some bias if there are more complicated interactions between disturbance types, for example, if reindeer avoid roads, but not roads near population centres. It is not possible, however, to eliminate all potential interactions between all infrastructure types since it would make the analyses prohibitively complex.

*Analysis of Reindeers' Responses to Infrastructure*

To analyze the reindeers' use (preference or avoidance) of different buffers around the infrastructure, we used a log-ratio analysis of compositions (Aitchison, 1986), also referred to as compositional analysis (Aebischer et al., 1993), using specialized software, Compositional Analysis Excel tool, version 4.1 (Smith, 2003). Compositional analysis is a method that uses two sets of proportional data, in this case, the proportions of available habitat and used habitat to total area. In compositional analysis, the experimental unit is one animal instead of one individual observation point. Compositional analysis uses multivariate analysis of variance (MANOVA; statistic Wilks' lambda) to determine the significance and the rank order of differences between variables in two datasets (available and used proportions).

We first tested whether the use of habitats (different buffers of infrastructure) was random with respect to the composition of habitats within a certain area by comparing the observations of available and used habitat ($H_0$: habitat use does not differ from random). When habitat use differed from random, i.e., when the animal preferred or avoided certain habitats, the habitat types were compared pairwise (using a t-test) and ranked in the order of use, from preferred to least preferred or avoided habitats. To overcome the problems arising when the distribution of log-ratio differences is not multivariate normal (Smith, 2003), we used a Monte Carlo randomization test to determine the significance of the Wilks' lambda and t-values. If the random $p$ for Wilks' lambda or the t-value was smaller than 0.05, then the habitat selection was considered as non-random (or the difference of use between habitat types was considered significant). The analysis requires that all habitat types be recorded, so in cases (animals) for which the proportion of "used habitat" was zero—i.e., their use of the infrastructure buffer was so small that it could not be observed—a value of an order of magnitude smaller than the smallest recorded non-zero proportion in the data was substituted, as recommended by Aebischer et al. (1993). This value varied from 0.01 to 0.0001 in our analyses.

Following Aebischer et al. (1993), we tested reindeer responses to infrastructure in two stages, on two different spatial scales: the first (home range selection) describes how reindeer select their seasonal home ranges, and the second (within-home-range selection), how reindeer use the areas within their seasonal home ranges in relation to infrastructure. These two stages of compositional analysis correspond to the second and third orders in Johnson's (1980) habitat selection hierarchy, in which the first order was the selection of the physical or geographical range of a species.

In the home range selection analysis, we studied the preference for or avoidance of infrastructure buffers by comparing the proportion of buffers within the entire roaming area of all reindeer with the proportion of these buffers within the seasonal home ranges. In the cases of skiing trails and gold digging areas, we made the comparisons only in the roaming area of the southern/central reindeer herd. In the within-home-range selection analysis, we compared the proportion of infrastructure buffers within seasonal home ranges with the distribution of GPS locations inside infrastructure buffers within the home ranges. If the analysis shows that an animal avoided or preferred certain habitat or landscape in selecting the home range area, but similar avoidance or preference is not visible in within-home-range selection, this may mean that the home range choice eliminated the habitat not avoided or selected, precluding a similar choice within the home range (Kumpula et al., 2007).

*Pasture Composition Inside the Infrastructure Buffers*

To ensure that reindeer use of infrastructure buffers was not confounded by differences in habitat composition, we analyzed the habitat composition inside the infrastructure buffers in cases where reindeer avoidance at the within-home-range selection was indicated. For this we used the reindeer pasture classification data derived from a Landsat ETM+ satellite image from the year 2001. First, we classified the image into 20 habitat classes with a supervised classification method (maximum likelihood). These 20 classes were then combined into eight reindeer pasture classes: 1) lichen pasture – all nutrient-poor and dry pine and birch forests and dry open highland habitat types; 2) grass pasture – grass, herb, and deciduous tree pastures, including all mesic and submesic forest types and similar open highland habitats; 3) arboreal lichen pasture – old growth and mature pine and spruce forests; 4) mires and fens; 5) sand, rock, and gravel, including fell tops with no vegetation; 6) fields; 7) water; and 8) cloud (Kumpula et al., 2004). Then we tested whether in winter the infrastructure buffers differed from each other in the proportions of lichen, grass, and arboreal lichen pasture. For the summer-autumn season, we analyzed the potential differences between the buffers in the proportions of grass pastures and mires using one-way analysis of variance (ANOVA), followed by Tukey's post hoc test in cases where we observed significant differences between buffer areas in the proportions of pasture types. Similarly, when the assumptions of the parametric tests were not satisfied, we used non-parametric tests: the Kruskal-Wallis one-way analysis of variance on ranks, followed by Dunn's post hoc test. The analyses were carried out using SigmaStat software version 3.5.

*Estimation of the Cumulative Areas Covered and Affected by Infrastructure*

To analyze the total effect of infrastructure on reindeer herding over the study area, we calculated the cumulative area covered and potentially affected by infrastructure and human activity (i.e., subject to functional habitat loss as a result of avoidance or reduced use by reindeer). First we calculated the area covered by infrastructure by estimating the width of the roads and recreational routes and the average size of the buildings and creating coverage buffers for each infrastructure type. Then we defined the areas potentially affected by infrastructure at both studied spatial scales of reindeer habitat selection. If the compositional analysis showed that infrastructure affected reindeer home range selection, we defined the avoidance area around this infrastructure by comparing the use of buffers 1 to 3 with the use of the "external area" (i.e., the t-test results from compositional analysis). A significant difference between buffers 1 to 3 and the external area, with respect to either the reindeers' selection of seasonal home ranges or their use of land within those ranges, was interpreted as avoidance of infrastructure and was taken as the distance by which the area affected was calculated. Finally, we created coverage buffers for all infrastructure types and extrapolated the cumulative area affected by infrastructure and human activity for the entire reindeer herding district in all studied seasons. However, since this study used buffers rather than measuring exact avoidance distances from infrastructure, these cumulative areas affected are only estimates.

## RESULTS

*Responses of Reindeer to the Infrastructure in Seasonal Home Range Selection*

When reindeer chose their home range within the entire roaming area in early winter season, the selection was affected by the population centres ($\Lambda = 0.1346$, random $p = 0.0010$), buildings ($\Lambda = 0.3463$, random $p = 0.0010$), main roads ($\Lambda = 0.4622$, random $p = 0.0030$), snowmobile tracks ($\Lambda = 0.5019$, random $p = 0.0050$) and forest roads ($\Lambda = 0.6847$, random $p = 0.0440$); that is, the selection was non-random in respect to these infrastructure types. The pairwise comparisons for population centres, buildings, main roads, and snowmobile tracks showed that reindeer used buffers 1, 2, and 3 significantly less than they used the external area (Table 2). However, for forest roads the pairwise comparisons did not show significant differences in use between any buffers (random $p > 0.162$). In the early winter season, the reindeers' home range selection was random in relation to the skiing trails ($\Lambda = 0.7744$, random $p = 0.4240$) and gold digging areas ($\Lambda = 0.6804$, random $p = 0.1950$), indicating that these developments did not affect the reindeer home range selection.

During late winter, the home range selection by reindeer was non-random with respect to the population centres ($\Lambda = 0.0000$, random $p = 0.0010$), buildings ($\Lambda = 0.3160$, random $p = 0.0010$), main roads ($\Lambda = 0.6788$, random $p = 0.0170$), snowmobile tracks ($\Lambda = 0.3263$, random $p = 0.0010$), skiing trails ($\Lambda = 0.1005$, random $p = 0.0010$), and gold digging areas ($\Lambda = 0.6293$, random $p = 0.0340$). In all of these cases except the gold digging areas, the pairwise comparisons showed that the reindeer used buffers 1, 2, and 3 significantly less than they used the external area (Table 2). In gold digging areas, only buffer number 3 was significantly less used than the external area (at significance level $p < 0.05$). However, results between external area and buffers 1 and 2 were also close to 0.05 level (random $p = 0.065$ and 0.056, respectively) (Table 2). Reindeer home range selection was not affected by the forest roads during late winter ($\Lambda = 0.7935$, random $p = 0.1260$).

In the summer-autumn season, the selection of home range area by reindeer was affected by the population centres ($\Lambda = 0.2079$, random $p = 0.0020$), buildings ($\Lambda = 0.1623$, random $p = 0.0010$) main roads ($\Lambda = 0.5277$, random $p = 0.0310$), and gold digging areas ($\Lambda = 0.3051$, random $p = 0.0140$). Pairwise comparisons showed that in all of these infrastructure types, the external area was significantly more used than buffers 1, 2, and 3 (Table 2). Results did not indicate effects on reindeer home range selection in respect to forest roads ($\Lambda = 0.8190$, random $p = 0.5110$), snowmobile tracks ($\Lambda = 0.6497$, random $p = 0.1480$), or skiing trails ($\Lambda = 0.8507$, random $p = 0.7370$) in this season.

*Responses of Reindeer to the Infrastructure within the Seasonal Home Ranges*

In early winter, only four of the reindeer had small parts of the population centre buffers inside their home range, and only two of the reindeer used these buffers. Thus, the population centres had to be omitted from this stage of the analysis. During early winter, reindeer within-home-range selection was affected by buildings ($\Lambda = 0.0699$, random $p = 0.0020$). According to the pairwise comparisons, reindeer used the external area of building buffers significantly more than they used buffers 1 and 2 (Table 3). Within-home-range selection was also affected by main roads ($\Lambda = 0.2738$, random $p = 0.0410$), so that reindeer used buffers 1, 2, and 3 significantly less than the external area (Table 3). In contrast, the use of home ranges during the early winter season was not affected by forest roads ($\Lambda = 0.7951$, random $p = 0.2250$), snowmobile tracks ($\Lambda = 0.4769$, random $p = 0.4770$), skiing trails ($\Lambda = 0.8002$, random $p = 0.8750$), or gold digging areas ($\Lambda = 0.5893$, random $p = 0.3650$).

In the late winter season, reindeer within-home-range selection was affected by the main roads ($\Lambda = 0.3898$, random $p = 0.0090$). The pairwise comparisons showed that only buffer 1 was significantly less used than the external area (Table 3). During this season, the use of home range was also affected by the snowmobile tracks ($\Lambda = 0.1857$,

TABLE 2. Mean pairwise log-ratio differences in home range selection for cases in which significant avoidance effects were detected. The selection of buffers 1, 2, and 3 is compared with the selection of external area. Both observed and random *p*-values are given, but only the random *p* values (determined with Monte Carlo randomization tests and considered to have stronger significance) are used in the text.

| Infrastructure | External area, m (denominator) | Buffer, m (numerator) | Mean log-ratio (SE) | t | df | *p* | Random *p* |
|---|---|---|---|---|---|---|---|
| **Early winter**: | | | | | | | |
| Population centres | > 2500 | 0–200 | -3.94 (0.43) | -9.1498 | 19 | 0.0000 | 0.0010 |
| | > 2500 | 200–1000 | -3.91 (0.50) | -7.8685 | 19 | 0.0000 | 0.0010 |
| | > 2500 | 1000–2500 | -5.36 (0.64) | -8.4128 | 19 | 0.0000 | 0.0010 |
| Buildings | > 1500 | 0–100 | -3.62 (0.71) | -5.1272 | 19 | 0.0001 | 0.0010 |
| | > 1500 | 100–400 | -4.03 (0.99) | -4.0521 | 19 | 0.0007 | 0.0010 |
| | > 1500 | 400–1500 | -3.44 (1.13) | -3.0545 | 19 | 0.0065 | 0.0020 |
| Main roads | > 1500 | 0–100 | -5.25 (1.12) | -4.7000 | 19 | 0.0002 | 0.0010 |
| | > 1500 | 100–400 | -4.93 (1.19) | -4.1410 | 19 | 0.0006 | 0.0010 |
| | > 1500 | 400–1500 | -4.33 (1.28) | -3.3950 | 19 | 0.0030 | 0.0040 |
| Snowmobile tracks | > 1500 | 0–100 | -3.69 (1.04) | -3.5314 | 19 | 0.0022 | 0.0030 |
| | > 1500 | 100–400 | -4.21 (1.16) | -3.6332 | 19 | 0.0018 | 0.0030 |
| | > 1500 | 400–1500 | -4.78 (1.26) | -3.8052 | 19 | 0.0012 | 0.0020 |
| **Late winter**: | | | | | | | |
| Population centres | > 2500 | 0–200 | -4.55 (0.00) | -1318.72 | 24 | 0.0000 | 0.0010 |
| | > 2500 | 200–1000 | -4.39 (0.22) | -19.6891 | 24 | 0.0000 | 0.0010 |
| | > 2500 | 1000–2500 | -5.44 (0.47) | -11.5109 | 24 | 0.0000 | 0.0010 |
| Buildings | > 1500 | 0–100 | -4.22 (0.61) | -6.9495 | 24 | 0.0000 | 0.0010 |
| | > 1500 | 100–400 | -4.29 (0.85) | -5.0678 | 24 | 0.0000 | 0.0010 |
| | > 1500 | 400–1500 | -3.03 (1.00) | -3.0300 | 24 | 0.0058 | 0.0020 |
| Main roads | > 1500 | 0–100 | -1.50 (0.44) | -3.3630 | 24 | 0.0026 | 0.0030 |
| | > 1500 | 100–400 | -1.75 (0.53) | -3.2949 | 24 | 0.0030 | 0.0030 |
| | > 1500 | 400–1500 | -1.57 (0.55) | -2.8442 | 24 | 0.0090 | 0.0080 |
| Snowmobile tracks | > 1500 | 0–100 | -3.73 (0.65) | -5.6965 | 24 | 0.0000 | 0.0010 |
| | > 1500 | 100–400 | -3.99 (0.82) | -4.8414 | 24 | 0.0001 | 0.0010 |
| | > 1500 | 400–1500 | -4.14 (0.94) | -4.4241 | 24 | 0.0002 | 0.0010 |
| Skiing trails | > 1500 | 0–100 | -4.10 (0.42) | -9.6929 | 18 | 0.0000 | 0.0010 |
| | > 1500 | 100–400 | -4.91 (0.52) | -9.4214 | 18 | 0.0000 | 0.0010 |
| | > 1500 | 400–1500 | -5.32 (0.63) | -8.4020 | 18 | 0.0000 | 0.0010 |
| Gold digging areas | > 1500 | 0–100 | -1.91 (0.98) | -1.9562 | 18 | 0.0661 | 0.0650 |
| | > 1500 | 100–400 | -2.31 (1.07) | -2.1620 | 18 | 0.0443 | 0.0560 |
| | > 1500 | 400–1500 | -2.82 (1.20) | -2.3528 | 18 | 0.0302 | 0.0370 |
| **Summer-autumn**: | | | | | | | |
| Population centres | > 2500 | 0–200 | -4.89 (0.75) | -6.5026 | 14 | 0.0000 | 0.0010 |
| | > 2500 | 200–1000 | -4.38 (0.81) | -5.3850 | 14 | 0.0001 | 0.0010 |
| | > 2500 | 1000–2500 | -5.05 (1.02) | -4.9583 | 14 | 0.0002 | 0.0010 |
| Buildings | > 1500 | 0–100 | -3.69 (0.71) | -5.2104 | 14 | 0.0001 | 0.0010 |
| | > 1500 | 100–400 | -4.39 (1.03) | -4.2861 | 14 | 0.0008 | 0.0010 |
| | > 1500 | 400–1500 | -4.06 (1.24) | -3.2842 | 14 | 0.0054 | 0.0010 |
| Main roads | > 1500 | 0–100 | -1.56 (0.51) | -3.0653 | 14 | 0.0084 | 0.0040 |
| | > 1500 | 100–400 | -1.88 (0.64) | -2.9315 | 14 | 0.0109 | 0.0040 |
| | > 1500 | 400–1500 | -2.21 (0.80) | -2.7696 | 14 | 0.0151 | 0.0030 |
| Gold digging areas | > 1500 | 0–100 | -5.51 (1.74) | -3.1608 | 10 | 0.0101 | 0.0200 |
| | > 1500 | 100–400 | -5.51 (1.86) | -2.9670 | 10 | 0.0141 | 0.0200 |
| | > 1500 | 400–1500 | -5.51 (2.09) | -2.6331 | 10 | 0.0250 | 0.0290 |

random $p = 0.0030$), so that all three buffers were significantly less used than the external area (Table 3). During late winter the within-home-range selection of reindeer was not affected by buildings ($\Lambda = 0.4625$, random $p = 0.0870$), forest roads ($\Lambda = 0.7825$, random $p = 0.1650$), or gold digging areas ($\Lambda = 0.6193$, random $p = 0.8194$). Furthermore, in late winter as in early winter, it was not possible to test the within-home-range selection near the population centres because there were so few reindeer whose home ranges or GPS-observations contained population centre buffers. This was also the case with skiing trails: only four of the 19 reindeer had the skiing trail buffers inside their late winter home range area (available proportions).

During the summer-autumn season, the within-home-range selection was affected by the population centres ($\Lambda = 0.0067$, random $p = 0.0110$). Only buffer 2 differed significantly from the external area on the significance level of $p < 0.05$. However, use of buffers 1 and 3 was also smaller compared to use of the external area (Table 3). Reindeer also showed selection in respect to buildings when they used their home range areas ($\Lambda = 0.0171$, random $p = 0.0040$). The use of buffers 1 and 2 was significantly smaller than use of the external area (Table 3). The main roads also affected the use of home range areas during this season ($\Lambda = 0.2965$, random $p = 0.0210$). Reindeer used the external areas significantly more than the main road buffers 1 and 3 (Table 3). During the summer-autumn season, within-home-range selection was random with respect to forest roads ($\Lambda = 0.6100$, random $p = 0.0910$), snowmobile tracks ($\Lambda = 0.6858$, random $p = 0.5990$), skiing trails ($\Lambda = 0.3275$,

TABLE 3. Mean pairwise log-ratio differences in within-home-range selection for cases in which significant avoidance effects were detected. The selection of buffers 1, 2, and 3 is compared with the selection of external area. Random *p*-values were determined with Monte Carlo randomization tests.

| Infrastructure | External area, m (denominator) | Buffer, m (numerator) | Mean log-ratio (SE) | t | df | *p* | Random *p* |
|---|---|---|---|---|---|---|---|
| **Early winter**: | | | | | | | |
| Buildings | > 1500 | 0–100 | -5.57 (0.50) | -11.1516 | 12 | 0.0000 | 0.0020 |
| | > 1500 | 100–400 | -4.48 (1.34) | -3.3537 | 12 | 0.0057 | 0.0170 |
| Main roads | > 1500 | 0–100 | -4.41 (1.64) | -2.6918 | 7 | 0.0310 | 0.0450 |
| | > 1500 | 100–400 | -4.79 (1.49) | -3.2232 | 10 | 0.0091 | 0.0220 |
| | > 1500 | 400–1500 | -2.09 (0.99) | -2.1120 | 12 | 0.0563 | 0.0010 |
| **Late winter**: | | | | | | | |
| Main roads | > 1500 | 0–100 | -2.70 (0.58) | -4.6461 | 16 | 0.0003 | 0.0020 |
| Snowmobile tracks | > 1500 | 0–100 | -4.27 (0.82) | -5.1999 | 12 | 0.0002 | 0.0020 |
| | > 1500 | 100–400 | -2.86 (1.05) | -2.7116 | 12 | 0.0189 | 0.0190 |
| | > 1500 | 400–1500 | -2.19 (0.98) | -2.2369 | 13 | 0.0434 | 0.0200 |
| **Summer-autumn**: | | | | | | | |
| Population centres | > 2500 | 0–200 | -5.86 (0.45) | -13.1496 | 4 | 0.0002 | 0.0710 |
| | > 2500 | 200–1000 | -5.79 (0.56) | -10.4002 | 6 | 0.0000 | 0.0150 |
| | > 2500 | 1000–2500 | -2.28 (1.08) | -2.1113 | 7 | 0.0727 | 0.0570 |
| Buildings | > 1500 | 0–100 | -5.38 (0.28) | -19.0817 | 9 | 0.0000 | 0.0010 |
| | > 1500 | 100–400 | -6.27 (1.13) | -5.5505 | 9 | 0.0004 | 0.0080 |
| Main roads | > 1500 | 0–100 | -2.50 (0.64) | -3.8745 | 10 | 0.0031 | 0.0080 |
| | > 1500 | 400–1500 | -0.87 (0.47) | -1.8530 | 10 | 0.0936 | 0.0310 |

random $p = 0.1690$), and gold digging areas ($\Lambda = 0.2954$, random $p = 0.1214$).

*Pasture Composition inside the Infrastructure Buffers*

Differences of pasture composition between infrastructure buffers were examined if there were indications of avoidance of buffer areas in within-home-range selection. In the early winter season, no differences between buffers were found when testing proportions of lichen pastures ($F = 1.234$, $p = 0.307$) and grass pastures ($H = 0.497$, $p = 0.919$) in buffers around buildings. However, there was significantly less arboreal lichen pasture in buffer 1 than in the external area ($H = 13.232$, $p = 0.004$, post hoc $p < 0.05$). Buffers around the main roads did not differ from each other in proportions of the three tested pasture classes (Table 4).

During late winter, when testing the proportions of arboreal lichen pastures in buffers around the main roads, no differences were found (Table 4). However, there were differences in proportions of the two other pasture types tested. There was significantly less lichen pasture in buffers 1 and 2 than in the external area ($H = 19.734$, $p < 0.001$, post hoc $p < 0.05$, and $< 0.05$) and significantly less grass pasture in buffer 2 than in the external area ($H = 11.374$, $p = 0.01$, post hoc $p < 0.05$). Buffers around the snowmobile tracks did not differ from each other in their proportions of the three tested habitat classes (Table 4).

In the summer-autumn season, there was significantly less grass pasture in buffer 1 than in the external area around population centres ($H = 9.494$, $p = 0.023$, post hoc $p < 0.05$). Furthermore, buffers 1, 2, and 3 also contained less mire and fen habitat than the external area ($F = 10.067$, $p < 0.001$, post hoc $p < 0.001$, 0.001, and 0.002, respectively). No differences in the proportions of grass pastures were found in buffers around buildings (Table 4). However, in buffer 1 there was significantly less mire and fen than in buffer 3 ($F = 3.653$, $p = 0.022$, post hoc $p = 0.028$). No differences in proportions of grass pasture were found between buffers around the main roads (Table 4). Again, there was significantly less mire and fen in buffer 1 than in buffer 2 ($H = 8.903$, $p = 0.031$, post hoc $p < 0.05$) (Table 4).

*Cumulative Areas Covered and Affected by Infrastructure*

The total area covered by infrastructure within the Ivalo reindeer-herding district was 29.9 $km^2$, which is 1.2% of the total district area (Table 5). The infrastructure types that cover the most area inside the herding district are population centres (9.9 $km^2$), gold digging areas (9.0 $km^2$), and forest roads (8.5 $km^2$). The cumulative areas affected in different seasons, and therefore potentially used less than expected by reindeer, were calculated by combining the spatial data of the infrastructure layers where evidence of reindeer avoidance was detected in both home-range and within-home-range selection. According to the distances determined, the potential area affected for home range selection varied from 39% in late winter to 27.5% in early winter season (Table 6). For within-home-range selection, the cumulative areas affected were smaller, varying from 20.3% in late winter to 7.2% in summer-autumn.

## DISCUSSION

The results clearly showed that infrastructure and human activity affect range selection by reindeer at two spatial scales: the selection of home range areas and pasture use within the seasonal home range areas selected. In general, it seems that all the infrastructure types studied affect reindeer range selection in some seasonal period or at some spatial scale. Avoidance was most evident when reindeer selected their seasonal home ranges. The main

TABLE 4. Differences in pasture composition between the infrastructure buffers in cases with indications that reindeer avoided buffers in within-home-range selection. F is the statistic of the ANOVA test, and H is the statistic of the Kruskal-Wallis test. In post hoc results, Tukey's or Dunn's test is reported when it was performed. The numbers after the post hoc test indicate which buffers differ significantly: e.g., in early winter there is significantly less arboreal lichen pasture in buffer 1 than in the external area ("buffer 4" in this table).

| Infrastructure | Pasture type | Df | F/H | *p* | Post hoc | Post hoc *p* |
|---|---|---|---|---|---|---|
| **Early winter**: | | | | | | |
| Buildings | Lichen | 3 | F = 1.234 | 0.307 | - | |
| | Grass | 3 | H = 0.497 | 0.919 | - | |
| | Arboreal | 3 | H = 13.232 | 0.004 | Dunn:1 vs 4 | < 0.05 |
| Main roads | Lichen | 3 | F = 2.342 | 0.087 | - | |
| | Grass | 3 | F = 1.123 | 0.351 | - | |
| | Arboreal | 3 | F = 0.567 | 0.64 | - | |
| **Late winter**: | | | | | | |
| Main roads | Lichen | 3 | H = 19.734 | < 0.001 | Dunn:1 vs 4;<br>2 vs 4 | < 0.05<br>< 0.05; |
| | Grass | 3 | H = 11.374 | 0.01 | Dunn: 2 vs 4 | < 0.05 |
| | Arboreal | 3 | F = 0.92 | 0.436 | - | |
| Snowmobile tracks | Lichen | 3 | H = 3.085 | 0.379 | - | |
| | Grass | 3 | F = 2.13 | 0.108 | - | |
| | Arboreal | 3 | H = 8.304 | 0.04 | Dunn: No differences | |
| **Summer-autumn**: | | | | | | |
| Population centres | Grass | 3 | H = 9.494 | 0.023 | Dunn:1 vs 4 | < 0.05 |
| | Mire | 3 | F = 10.067 | < 0.001 | Tukey:1 vs 4;<br>2 vs 4; 3 vs 4 | 0.001;<br>< 0.001; 0.002 |
| Buildings | Grass | 3 | H = 2.504 | 0.475 | - | |
| | Mire | 3 | F = 3.653 | 0.022 | Tukey: 1 vs 3 | 0.028 |
| Main roads | Grass | 3 | H = 3.434 | 0.329 | - | |
| | Mire | 3 | H = 8.903 | 0.031 | Dunn: 1 vs 2 | < 0.05 |

infrastructure types avoided were population centres, main roads, and single buildings or groups of buildings. These three types of human infrastructure affected home range selection in all seasons studied, and reindeer also avoided them at some level in their within-home-range selection. Although there were some differences in the pasture composition within different infrastructure buffers, we did not observe differences that could have explained adequately or clearly enough the reindeer avoidance of these areas in within-home-range selection.

Within and around population centres, many infrastructure types are clumped together, and the level of human activity is high. Therefore, reindeer strongly avoided population centres all year round when selecting their home range areas, and they also avoided such centres that were situated within the home range area, as was the case in the summer-autumn season. However, observed differences in the pasture composition within buffers during the summer-autumn season may indicate that pasture composition, as well as avoidance of human activity and infrastructure, could also have affected the range selection by reindeer. Because reindeer did not select winter home ranges near population centres, their selection with respect to population centres within winter home ranges could not be analyzed. The data simply indicate strong avoidance of population centres during winter, even within home range areas. Also, reindeer avoided buildings in all seasons when selecting their seasonal home ranges. In within-home-range selection, buildings were avoided at a distance of 400 m in both early winter and summer seasons. This avoidance probably arises from the fact that around buildings, the level of human activity and other disturbances (e.g., number of dogs) can also be high.

Roads are a common type of infrastructure in the landscape and have many ecological effects. Examples are mortality of animals caused by collisions with vehicles, changes in animal behaviour, alteration of the physical environment, and increased use of areas by humans (Trombulak and Frissell, 2000). These effects can also be seen when studying reindeer. Of the infrastructure types studied, main roads seem to have the highest relative impact on reindeer range use, as well as the usability value of the ranges, because they strongly affected both home range selection and within-home-range selection in all seasons. Roads also form a network, being more evenly distributed in the landscape than more concentrated human constructions such as population centres. Although reindeer avoid main roads, traffic still causes reindeer losses in the Ivalo district, primarily along the main road E75, which goes through the southern parts of the district (Fig. 1). Traffic accidents occur especially near the Saariselkä tourism centre in the early winter season (Kemppainen et al., 2003). At that time of year, reindeer migrate between pasture areas in small groups, and snow accumulation may prompt them to use roads as easy alternative routes. Roads may also attract reindeer especially in early winter, because sand and salt are used for anti-skid treatment (Kemppainen et al., 2003). However, it seems that female reindeer, which form the majority of the reindeer herd, are still predominantly avoiding the main roads both when selecting their home ranges and when using these ranges, especially during the early winter, when they graze relatively freely. During early winter, the GPS-collared reindeer avoided pasture areas located less than 1500 m from the main roads. Reindeer also avoided the immediate vicinity of the main roads when they grazed

TABLE 5. The distances (m) used for calculating the areas (as km$^2$ and % of the total land area) covered by different types of infrastructure. Data from buildings was in point format, so the average size of the buildings and their courtyard area was estimated. For roads and recreational routes, the distance is reported from the centre line and the coverage was calculated in both directions from that line.

| Infrastructure | Distance from the infrastructure feature, m | Length, km | Area covered, km$^2$ | Area covered, % |
|---|---|---|---|---|
| Population centres | area itself | | 9.9 | 0.38 |
| Buildings | 20 | | 0.4 | 0.02 |
| Main roads | 7.5 | 140 | 2.1 | 0.08 |
| Forest roads | 4 | 1070 | 8.5 | 0.33 |
| Snowmobile tracks | 0.75 | 191 | 0.3 | 0.01 |
| Skiing trails | 1 | 133 | 0.3 | 0.01 |
| Gold digging areas | area itself | | 9.0 | 0.35 |
| Total area covered | | | 29.9 | 1.2 |

within their home ranges during other seasons studied, but the avoidance zone was not as wide (100 m) as in early winter. The explanation for this could be both behavioural and nutritional: for example, in late April to early May, reindeer mobility increases in general, and at the same time, melting snow along the roadsides reveals the first growing green plants, which attract the animals.

In addition to population centres, buildings, and main roads, reindeer also avoided gold-digging areas during late winter and summer seasons when selecting their home range areas. Summer is the most active time for gold mining, which causes many kinds of disturbances for animals both in digging places and in nearby areas (people and mechanical movements, noise, dust, etc.). Additionally, gold mining is a major tourist attraction that brings extra traffic and other disturbance (e.g., people and dogs) to the mining area. Weir et al. (2007) also found that woodland caribou in Newfoundland responded to disturbance caused by gold mining in all seasons, although they were most affected during pre-calving and calving seasons. Snowmobile tracks during early and late winter and skiing trails in late winter also affected the selection of home range by reindeer. Snowmobile tracks were also highly avoided within the home range during late winter: reindeer mostly avoided areas closer than 1500 m to the tracks. However, range use by reindeer with respect to skiing trails within the late winter home ranges could not be analyzed because reindeer had already avoided them at the upper level of habitat selection, so that reindeer home ranges did not reach the skiing trail buffer areas. During late winter, which is the most active tourism season in Finnish Lapland, as in the Saariselkä area, all routes are intensively used. In late winter, when grazing conditions are most difficult, pregnant females are preparing for calving and may also avoid disturbed habitats in order to save energy (Kumpula et al., 2007). Other factors, like herd size (large herds allow humans closer than small ones) and the general level of anthropogenic disturbance in the area (the more people reindeer are exposed to, the less frightened they become, i.e., animals habituate) have been noted to affect the reindeer fright-and-flight behaviour towards off-road vehicles and humans moving on foot or on skis (Reimers and Colman, 2006). This behaviour has been studied for *Rangifer*, but only in wild reindeer and caribou. However, it has been shown that wild reindeer with domesticated origin react to humans moving on foot or skis at shorter distances compared to wild reindeer, which indicates that domestication has reduced the flight response of the animals (see e.g., review by Reimers and Colman, 2006). Also, it has been found that the flight distance of wild reindeer after disturbance by people on skis is longer than after exposure to snowmobiles (Reimers et al., 2003), indicating that reindeer see a human on skis as a bigger threat (hunter) than a motorized vehicle (Reimers and Colman, 2006).

The present analysis seems to indicate that forest roads have only minor impact on reindeer home range selection during early winter, and no impact in other seasons. Results also indicated that forest roads did not affect within-home-range selection at any season. Compared with an earlier study (Kumpula et al., 2007), this result is somewhat contradictory. In the earlier results, the class of forest roads was avoided in early winter home range selection and within-home-range selection, as well as in late winter home range selection. One reason for this difference could be methodological. In the present analysis, we used zones with the smallest buffer extending 100 m from both sides of the forest roads, while in the previous study only the area covered by forest roads was included. For measuring the potential disturbance effect of forest roads, a narrower buffer zone might be better suited. Also, forest roads are a common feature in the landscape (altogether 1070 km in the study area, covering 8.5 km$^2$) with a relatively even distribution (Table 5, Fig. 1), and therefore they are difficult to avoid. Thus, the effect of forest roads on the range selection by reindeer is probably a more complicated question that depends also on the season and the amount of traffic on these roads, and the type of traffic may also be important. In the southern parts of the herding district, for example, forest roads closed by snow accumulation are also used by herders on snowmobiles to provide supplementary feed for reindeer during late winter. Consequently, the possible avoidance of these roads is partly overruled because reindeer also gain food from the areas near roads. In this way, reindeer herding has adapted to use this type of infrastructure and at the same time reindeer may also have been habituated to use the areas near forest roads. However, habituation was not examined here because its study demands observations over time. Furthermore, if other land users, such as tourists

TABLE 6. Avoidance distances from infrastructure and potential areas affected by different types of infrastructure in home range selection and within-home-range selection by reindeer.

| Infrastructure | Home range selection: Avoidance distance, m | Home range selection: Potential area affected, % of the land area | Within-home-range selection: Avoidance distance, m | Within-home-range selection: Potential area affected, % of the land area |
|---|---|---|---|---|
| **Early winter**: | | | | |
| Population centres | 2500 | 5.2 | 2500[1] | 5.2 |
| Buildings | 1500 | 13.8 | 400 | 2.5 |
| Main roads | 1500 | 14.2 | 1500 | 14.2 |
| Forest roads[2] | 0 | 0 | 0 | 0 |
| Snowmobile tracks | 1500 | 13.3 | 0 | 0 |
| Skiing trails | 0 | 0 | 0 | 0 |
| Gold digging areas | 0 | 0 | 0 | 0 |
| Total area affected | | 27.5 (709.6 km$^2$) | | 16.9 (436.2 km$^2$) |
| **Late winter**: | | | | |
| Population centres | 2500 | 5.2 | 2500[1] | 5.2 |
| Buildings | 1500 | 13.8 | 0 | 0 |
| Main roads | 1500 | 14.2 | 100 | 1.0 |
| Forest roads | 0 | 0 | 0 | 0 |
| Snowmobile tracks | 1500 | 13.3 | 1500 | 13.3 |
| Skiing trails | 1500 | 8.3 | 1500[1] | 8.3 |
| Gold digging areas | 1500 | 11.9 | 0 | 0 |
| Total area affected | | 39.0 (1004.5 km$^2$) | | 20.3 (524.0 km$^2$) |
| **Summer-autumn**: | | | | |
| Population centres | 2500 | 5.2 | 2500 | 5.2 |
| Buildings | 1500 | 13.8 | 400 | 2.5 |
| Main roads | 1500 | 14.2 | 100 | 1.0 |
| Forest roads | 0 | 0 | 0 | 0 |
| Snowmobile tracks | 0 | 0 | 0 | 0 |
| Skiing trails | 0 | 0 | 0 | 0 |
| Gold digging areas | 1500 | 11.9 | 0 | 0 |
| Total area affected | | 30.7 (790.3 km$^2$) | | 7.2 (185.8 km$^2$) |

[1] The within-home-range selection could not have been tested in these cases because there were only a few reindeer whose home ranges reached the buffer areas of infrastructure; reindeer had strongly avoided these infrastructure types already when selecting the home range. Therefore, the greatest possible avoidance distances were determined for the calculations of the within-home-range selection as well.

[2] The selection of home range with respect to forest roads was non-random during early winter, but there were no significant differences in the use of the buffer areas in pairwise comparisons.

and dog sledges, use forest roads intensively in the winter season, this use probably affects the range selection by reindeer (see Kumpula et al., 2007).

Total land area directly covered by infrastructure within the Ivalo reindeer-herding district was approximately one percent. However, the potential area affected, i.e., the functional habitat loss due to reduced use, was much greater. The largest cumulative effects of infrastructure and human activity on reindeer range use were detected during the late winter season, when the potential affected area was 39% of the total study area in home range selection and 20% in within-home-range selection. The strongest avoidance of human disturbance corresponds well to that found in the similar study of woodland caribou in Canada conducted at the scale of within-home-range selection (Dyer et al., 2001). In that study, it was observed that the functional habitat loss was largest during late winter, but the possible habitat loss was found to be even larger (48% of the study area), probably because the woodland caribou is wild, in contrast to semi-domesticated reindeer. During late winter, reindeer are more sedentary than during other seasons and therefore also more dependent on fixed grazing (cratering) sites at optimal habitat types. For the reindeer grazing in difficult snow conditions and scanty lichen pastures, it is probably most important to try to balance the net energy budget (Kumpula et al., 2007). Therefore, avoidance of human disturbance probably increases towards late winter, since disturbance can cause substantial energy loss for reindeer through extra movements and digging work.

The smallest cumulative effects of infrastructure and human activity were measured in the summer-autumn season, when the potential area affected was 7.2% at the level of within-home-range selection. For home range selection, the smallest response was documented during the early winter and summer-autumn seasons, when the potential areas affected were 27.5% and 30.7% of the study area, respectively. During late spring and early summer, female reindeer seek tranquil areas for calving and grazing with the newborns (e.g., Dyer et al., 2001; Vistnes and Nellemann, 2001; Haskell et al., 2006; Weir et al., 2007). However, during late summer and autumn, the reindeer move continuously over wide areas, usually staying in the same place for only a short time while searching for food. During insect harassment, reindeer may also seek relief from the forest roads or other places near infrastructure (see Skarin et al., 2004). In addition, the landscape is much more covered by vegetation in summer than in winter. These facts probably reduce the disturbance effects in general and may explain the smaller potential areas affected during summer. Similarly, during early winter, reindeer are still able to move and find food relatively easily from many kinds of habitat, which is probably why reindeer are not so sensitive to disturbance in early winter, when disturbance is not as important for the energy budget as it is during late winter.

Habitat selection of animals is hierarchical (Johnson, 1980). It has been suggested that the factors that limit an individual's fitness also have hierarchical order, that is, they vary at different scales. Factors with greater potential to reduce fitness should be avoided at coarser temporal and spatial scales (e.g., within landscape), and less limiting factors, at finer scales (e.g., within seasonal home range). Influence of the limiting factor may continue to finer scales if its effects cannot be overcome at the coarsest scale where it has been encountered (Rettie and Messier, 2000). For example, in large ungulates, the avoidance of predators can be important at a larger scale, while forage may become a more important factor at a finer scale (Rettie and Messier, 2000; Dussault et al., 2005). The overall results of the two individual stages of compositional analysis seem to indicate that infrastructure and human disturbance are affecting the selection of seasonal home range areas by semi-domesticated reindeer more than they affect the use of areas within the home ranges. Thus, the avoidance of disturbance might be more important at the larger spatial scale than at the finer scale. Human disturbance might therefore be considered as a factor that greatly affects the availability of good pasture areas, and thus, the nutritional status and body condition of semi-domesticated reindeer, in an environment where predators cause only marginal losses (8–62 carcasses found annually in the study area during the study period). Also, Dyer et al. (2001) suspected that avoidance of human infrastructure by woodland caribou might be greater at a larger spatial scale than inside seasonal home ranges and therefore forms a serious challenge to the maintenance of this threatened caribou population in Alberta. The semi-domesticated reindeer populations in Finland are not facing the same threat as the caribou. But the loss of suitable and good pasture areas and the cumulative impacts of infrastructure development are serious problems for free-ranging semi-domesticated reindeer herding as well, and these factors must be taken into account when new land-use projects are planned in areas important for reindeer herding. Although semi-domesticated reindeer management has succeeded in adapting to infrastructure development in many ways, continuous adaptation is not easy, or even always possible. Besides nutritional aspects, good and suitable pasture areas also include an undisturbed environment. That is why reindeer herders greatly value peaceful grazing areas (see e.g., Kitti et al., 2006).

## ACKNOWLEDGEMENTS

We warmly thank Research Technician Jukka Siitari from FGFRI's Reindeer Research Station for his valuable contribution to the collection and analysis of the data. We would also like to thank the reindeer herders of the Ivalo reindeer-herding district, especially the (former) head, Viljo Huru, for enabling the GPS tracking of reindeer. Two anonymous reviewers gave numerous valuable comments to improve the manuscript, for which we are also thankful. GPS tracking was partly financed by the LUIAS Project (no. 52759) in the SUNARE research programme of the Finnish Academy. Marja Anttonen was personally supported by the EnviroNet graduate school and the Geography Graduate School funded by the Finnish Ministry of Education.

## REFERENCES

Aebischer, N.J., Robertson, P.A., and Kenward, R.E. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Aitchison, J. 1986. The statistical analysis of compositional data. London: Chapman and Hall.

Cameron, R.D., Reed, D.J., Dau, J.R., and Smith, W.T. 1992. Redistribution of calving caribou in response to oil field development on the Arctic Slope of Alaska. Arctic 45: 338–342.

Colman, J.E., Jacobsen, B.W., and Reimers, E. 2001. Summer response distances of Svalbard reindeer *Rangifer tarandus platyrhynchus* to provocation by humans on foot. Wildlife Biology 7:275–283.

Dussault, C., Ouellet, J.-P., Courtois, R., Huot, J., Breton, L., and Jolicoeur, H. 2005. Linking moose habitat selection to limiting factors. Ecography 28:619–628.

Dyer, S.J., O'Neill, J.P., Wasel, S.M., and Boutin, S. 2001. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management 65:531–542.

———. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. Canadian Journal of Zoology 80:839–845.

Haskell, S.P., Nielson, R.M., Ballard, W.B., Cronin, M.A., and McDonald, T.L. 2006. Dynamic responses of calving caribou to oilfields in northern Alaska. Arctic 59:179–190.

Helle, T., and Särkelä, M. 1993. The effects of outdoor recreation on range use by semi-domesticated reindeer. Scandinavian Journal of Forest Research 8:123–133.

Hooge, P.N., and Eichenlaub, B. 1997. Animal movement extension to ArcView ver. 1.1. Anchorage: Alaska Science Center, Biological Science Office, U.S. Geological Survey.

Jernsletten, J.-L.L., and Klokov, K. 2002. Sustainable reindeer husbandry. Tromsø, Norway: Centre for Saami Studies, University of Tromsø. 157 p.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, C.J., Boyce, M.S., Case, R.L., Cluff, H.D., Gau, R.J., Gunn, A., and Mulders, R. 2005. Cumulative effects of human development on Arctic wildlife. Wildlife Monographs 160. 36 p.

Kemppainen, J., Kettunen, J., and Nieminen, M. 2003. Porojen liikennekuolemat vuosina 1992–2002 [Reindeer traffic accidents during 1992–2002]. Kala- ja riistaraportteja [Game and Fisheries Reports] No. 293. Helsinki: Game and Fisheries Research. 19 p.

Kitti, H., Gunslay, N., and Forbes, B.C. 2006. Defining the quality of reindeer pastures: The perspectives of Sámi reindeer herders. In: Forbes, B.C., Bölter, M., Müller-Wille, L., Hukkinen, J., Müller, F., Gunslay, N., and Konstantinov, Y., eds. Reindeer management in northernmost Europe. Ecological Studies 184. Berlin: Springer-Verlag. 141–165.

Klein, D.R. 2000. Arctic grazing systems and industrial development: Can we minimize conflicts? Polar Research 19:91–98.

Kumpula, J. 2001. Productivity of the semi-domesticated reindeer (*Rangifer t. tarandus* L.) stock and carrying capacity of pastures in Finland during 1960–1990's. Acta Universitatis Ouluensis Vol. A 375. 44 p.

Kumpula, J., Colpaert, A., Anttonen, M., and Nieminen, M. 2004. Poronhoitoalueen pohjoisimman osan (13 paliskuntaa) talvilaidunten uusintainventointi vuosina 1999–2003 [The repeated reindeer pasture inventory in the northernmost part (13 districts) of the reindeer management area during 1999–2003; in Finnish with English abstract]. Kala- ja riistaraportteja No. 303. Kaamanen: Game and Fisheries Research. 39 p.

Kumpula, J., Colpaert, A., and 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.

Luhta, V. 1999. Inarin havumetsävyöhyke, luonnonolot ja käyttö [The coniferous forest zone of Inari, natural conditions and use]. Metsähallituksen metsätalouden julkaisuja [Forestry Publications of Metsähallitus–Forest and Park Service] No. 21. 121 p.

Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223–249.

Nellemann, C., and Cameron, R.D. 1996. Effects of petroleum development on terrain preferences of calving caribou. Arctic 49:23–28.

———. 1998. Cumulative impacts of an evolving oil-field complex on the distribution of calving caribou. Canadian Journal of Zoology 76:1425–1430.

Nellemann, C., Jordhøy, P., Støen, O.-G., and Strand, O. 2000. Cumulative impacts of tourist resorts on wild reindeer (*Rangifer tarandus tarandus*) during winter. Arctic 53:9–17.

Nellemann, C., Vistnes I., Jordhøy, P., and Strand, O. 2001. Winter distribution of wild reindeer in relation to power lines, roads and resorts. Biological Conservation 101:351–360.

Nellemann, C., Vistnes, I., Jordhøy, P., Strand, O., and Newton, A. 2003. Progressive impact of piecemeal infrastructure development on wild reindeer. Biological Conservation 113:307–317.

Pollard, R.H., Ballard, W.B., Noel, L.E., and Cronin, M.A. 1996. Summer distribution of caribou, *Rangifer tarandus granti*, in the area of Prudhoe Bay oil field, Alaska, 1990–1994. Canadian Field-Naturalist 110:659–674.

Reimers, E., and Colman, J.E. 2006. Reindeer and caribou (*Rangifer tarandus*) response towards human activity. Rangifer 26(2):55–71.

Reimers, E., Eftestøl, S., and Colman, J.E. 2003. Behavior responses of wild reindeer to direct provocation by a snowmobile or skier. Journal of Wildlife Management 67:747–754.

Reimers, E., Dahle, B., Eftestøl, S., Colman, J.E., and Gaare, E. 2007. Effects of a power line on migration and range use of wild reindeer. Biological Conservation 134:484–494.

Rettie, W.J., and Messier, F. 2000. Hierarchical habitat selection by woodland caribou: Its relationship to limiting factors. Ecography 23:466–478.

Schaefer, J.A., and Mahoney, S.P. 2007. Effects of progressive clearcut logging on Newfoundland caribou. Journal of Wildlife Management 71:1753–1757.

Skarin, A. 2006. Reindeer use of alpine summer habitats. Doctoral thesis, Faculty of Veterinary Medicine and Animal Science, Swedish University of Agricultural Sciences, Uppsala. Acta Universitatis Agriculturae Sueciae 73. 30 p.

———. 2007. Habitat use by semi-domesticated reindeer, estimated with pellet-group counts. Rangifer 27(2):121–132.

Skarin, A., Danell, Ö., Bergström, R., and Moen, J. 2004. Insect avoidance may override human disturbances in reindeer habitat selection. Rangifer 24(2):95–103.

Smith, K.G., Ficht, E.J., Hobson, D., Sorensen, T.C., and Hervieux, D. 2000. Winter distribution of woodland caribou in relation to clear-cut logging in west central Alberta. Canadian Journal of Zoology 78:1433–1440.

Smith, P.G. 2003. Compositional Analysis Excel tool user's guide, version 4.0. Available from the author (e-mail: pgsmith@aber1.fsnet.co.uk), Bettws Cottage, Bettws, Abergavenny, Monmouthshire, NP7 7LG, Wales, United Kingdom.

Trombulak, S.C., and Frissell, C.A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18–30, doi:10.1046/j.1523-1739.2000.99084.x.

UNEP. 2001. GLOBIO - Global methodology for mapping human impacts on the biosphere. In: Nellemann, C., Kullerud, L., Vistnes, I., Forbes, B.C., Husby, E., Kofinas, G.P., Kaltenborn, B.P., et al., eds. Nairobi, Kenya, UNEP/DEWA/TR.01-3. www.globio.info/downloads/218/globioreportlowres.pdf.

Vistnes, I. 2008. Impacts of human development and activity on reindeer and caribou habitat use. Doctoral thesis, Norwegian University of Life Sciences, Alta/Ås.

Vistnes, I., and Nellemann, C. 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. Journal of Wildlife Management 65:915–925.

———. 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., Jordhøy, P., and Strand, O. 2001. Wild reindeer: Impacts of progressive infrastructure development on distribution and range use. Polar Biology 24:531–537.

———. 2004. Effects of infrastructure on migration and range use of wild reindeer. Journal of Wildlife Management 68:101–108.

Weir, J.N., Mahoney, S.P., McLaren, B., and Ferguson, S.H. 2007. Effects of mine development on woodland caribou *Rangifer tarandus* distribution. Wildlife Biology 13:66–74, doi:10.2981/0909-6396(2007)13[66:EOMDOW]2.0.CO;2.

Weladji, R.B., and Forbes, B.C. 2002. Disturbance effects of human activities on *Rangifer tarandus* habitat: Implications for life history and population dynamics. Polar Geography 26:171–186.

Wolfe, S.A., Griffith, B., and Wolfe, C.A.G. 2000. Response of reindeer and caribou to human activities. Polar Research 19:63–73.