

# Space use by Eurasian lynx in relation to reindeer migration

Anna C. Danell, Henrik Andrén, Peter Segerström, and Robert Franzén

**Abstract:** Semi-domesticated reindeer (*Rangifer tarandus tarandus* (L., 1758)) is the primary prey of Eurasian lynx (*Lynx lynx* (L., 1758)) in northern Sweden. The reindeer migrate between winter range in the forest and summer range in the mountains, a distance of 100–150 km. We studied space use by Eurasian lynx in relation to seasonal fluctuations of their primary prey in northern Sweden. The seasonal activity range sizes for males and single females were not significantly different between the three periods of the year (December–April, May–July, and August–November). The activity range size for family groups (i.e., female with kittens) was significantly smaller during summer than during autumn and winter. The mean distance between the centre of an individual lynx's activity range in one season to the centre of the activity range in the season immediately following did not differ significantly between seasons; mean distances were 6.6 km for males, 7.3 km for single females, and 8.4 km for family groups. This is about one order of magnitude shorter than the distance between summer and winter ranges for reindeer (100–150 km). The grand mean overlap between a lynx's activity range in one season and the next season was more than 40%. Hence, Eurasian lynx in northern Sweden do not appear to move with the migrating semi-domesticated reindeer.

**Résumé :** Les rennes (*Rangifer tarandus tarandus* (L., 1758)) semi-domestiqués constituent les proies principales des lynx boréaux (*Lynx lynx* (L., 1758)) dans le nord de la Suède; ils migrent entre leur territoire d'hiver en forêt et leur territoire d'été en montagne, une distance de 100–150 km. Nous avons étudié l'utilisation de l'espace chez le lynx boréal en relation avec les fluctuations saisonnières de sa proie principale dans le nord de la Suède. Les aires d'activité saisonnières des mâles et des femelles seules ne diffèrent pas significativement durant les trois périodes de l'année (décembre–avril, mai–juillet et août–novembre). La taille des aires d'activité des groupes familiaux (c.-à-d. une femelle et ses petits) est significativement plus petite durant l'été que durant l'automne et l'hiver. La distance moyenne entre le centre de l'aire d'activité d'un lynx particulier en une saison donnée et le centre de son aire d'activité dans la saison qui suit immédiatement ne varie pas en fonction des saisons et est de 6,6 km chez les mâles, de 7,3 km chez les femelles seules et de 8,4 km chez les groupes familiaux. Cette distance est environ un ordre de grandeur plus courte que la distance entre les aires d'hiver et d'été des rennes (100–150 km). Le chevauchement moyen majeur entre l'aire d'activité d'un lynx à une saison et son aire d'activité à la saison suivante est de plus de 40 %. Le lynx boréal du nord de la Suède ne semble donc pas se déplacer pour suivre la migration de sa proie principale, le renne semi-domestiqué.

[Traduit par la Rédaction]

## Introduction

In an ecosystem with large territorial predators and migratory prey, the predators experience large variations in prey availability between seasons. Lions (*Panthera leo* (L., 1758)) in Serengeti, Kenya, are stationary, while blue wildebeest (*Connochaetes taurinus* (Burchell, 1823)), an important prey, are migratory (Scheel and Packer 1995; Thirgood et al. 2004). Similarly, in northwestern Alaska, USA, and in the Northwest Territories, Canada, the primary prey of gray wolves (*Canis lupus* L., 1758) are migratory caribou (*Ran-*

*gifer tarandus* (L., 1758)) for as long as they are present within the gray wolf territory (Kuyt 1972; Dale et al. 1995; Ballard et al. 1997). Different predator species have adopted different strategies to deal with these prey movements. While lions and some gray wolf populations remain as year-round residents and switch to alternative prey (Schaller 1972; Dale et al. 1995; Ballard et al. 1997), other gray wolf and some mountain lion (*Puma concolor* (L., 1758)) populations actually display seasonal movements and follow their prey (Forbes and Theberge 1996; Ballard et al. 1997; Pierce et al. 1999; Walton et al. 2001). Other species such as the spotted hyaena (*Crocuta crocuta* Erxleben, 1777) adopt a commuting system where packs cross each other's territories in pursuit of migratory herds (Hofer and East 1993).

In Sweden, Eurasian lynx (*Lynx lynx* (L., 1758)) are found in the northern two-thirds of the country and slightly <50% of the Swedish lynx population is found in the reindeer husbandry area, with migratory reindeer (Liberg and Andrén 2005). The prey preference of Eurasian lynx varies depending on region and availability. The lynx tend to prefer medium-sized ungulates whenever they are available (Jędrzejewski et al. 1993; Okarma et al. 1997; Aanes et al. 1998; Jobin et al. 2000). However, in areas where these

Received 7 July 2005. Accepted 13 February 2006. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 27 April 2006.

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species are lacking, lynx survive on small game such as hares (genus *Lepus* L., 1758) and tetranoids (Pulliainen 1981; Jędrzejewski et al. 1993). In southern Sweden, western roe deer (*Capreolus capreolus* L., 1758) is the major prey species (Haglund 1966; Liberg and Glöersen 1995), whereas in northern Sweden, where roe deer occur at either very low densities or are absent, semi-domesticated reindeer (*Rangifer tarandus tarandus* (L., 1758)) is the primary prey species that comprises up to 90% of the lynx diet (Haglund 1966; Pedersen et al. 1999).

Sámi reindeer husbandry areas cover approximately 40% of the total land area in Sweden, or 160 000 km<sup>2</sup>. On average, the total number of reindeer in Sweden has been 225 000, with cyclic 25–30 year fluctuations of  $\pm 25\%$  during the last 100 year (Statistiska centralbryån 1999). Semi-domesticated reindeer are part of an extensive transhumance herding practice. The reindeer are actively corralled and moved seasonally between winter and summer ranges. Activities in reindeer management follow the yearly cycle of events of the reindeer such as calving, rutting, and searching for food in seasonal ranges. Calving takes place in May on calving grounds in low-alpine areas. During the height of the summer, the reindeer are usually found in alpine areas above the treeline or in the adjacent subalpine birch forests. During the autumn and early winter, the reindeer are gathered and moved into the forested areas at lower altitudes, often 100–300 km away from the summer ranges, where they are herded during December through April (Björvall et al. 1990).

Thus, the primary prey of Eurasian lynx living within the reindeer husbandry area in Sweden migrate between summer and winter ranges, which are often far apart. Given that Eurasian lynx have been shown to be year-round residents of stable intra-sexual territories in more southern populations (Breitenmoser et al. 1993; Schmidt et al. 1997), this raises the question of whether lynx in northern Sweden change their range use in relation to their migrating primary prey, the semi-domesticated reindeer. Therefore, the aim of this study was to analyse if migratory reindeer affect space use by lynx. Previous studies of lynx home-range size in relation to prey density has shown an inverse relationship between lynx home-range size and roe deer density (Herfindal et al. 2005). Hence, if lynx respond to migrating reindeer, it would be expected that the activity range would be larger in winter in response to decreased density of the primary prey. The centroids of the activity ranges should move a similar distance as the reindeer, i.e., 100–150 km. If the lynx move with the reindeer, then the overlap between individual activity ranges should be small or nonexistent between seasons. In addition, the direction of movement of the centroids should be in the same direction as that of the reindeer, e.g., direction of movement from winter to summer and from southeast to northwest is approximately 135°.

Since the density of Eurasian lynx does not appear to vary with season, whereas the density of semi-domesticated reindeer does, it is expected that the availability of alternative prey will be higher in areas where lynx remain. Therefore, to determine the availability of alternative food resources, we also surveyed the density of alternative prey such as mountain hare (*Lepus timidus* L., 1758), ptarmigan (*Lagopus muta* (Montin, 1781)), and willow grouse (*Lagopus lagopus*

(L., 1758)) in the summer and winter ranges of reindeer. These species are important alternative prey in areas where medium-sized ungulates are absent (Pulliainen 1981; Jędrzejewski et al. 1993).

### Study area

The core study area in northernmost Sweden covers 10 000 km<sup>2</sup> in the county of Norrbotten, mainly between the two large river systems Lilla and Stora Luleälv, and extends from the town of Jokkmokk in the southeast (66°99'N, 17°41'E) to lake Akkajaure in the northwest (67°75'N, 16°50'E) (Fig. 1). The area encompasses Sarek, Padjelanta, and Stora Sjöfallet national parks, which form the core parts of the Lapponia world heritage area (Swedish Environmental Protection Agency 1998).

The climate has a strong continental influence with average temperatures of  $-10\text{ }^{\circ}\text{C}$  in January and  $13\text{ }^{\circ}\text{C}$  in July. Snow depth during winter exceeds 1 m. The altitudinal gradient is from 200 to 2000 m above sea level, with treeline occurring at 850 m. The southeastern part of the study area consists mainly of coniferous forest, with a mixture of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.), comprising 30% of the total area. Twelve percentage of the study area is covered by deciduous forest, mainly subalpine birch (genus *Betula* L.), 28% are heath and meadows, and 10% boulders and bedrock outcrops. Nine percentage of the total study area consists of water (lakes and rivers), 8% of wetlands, 2% of permanent snowfields and glaciers, and <1% of the study area is classified as cultivated land. Human settlement and infrastructural development are minimal in the area. Moose (*Alces alces* L., 1758) are found throughout the valleys and in the forested parts of the area. Brown bears (*Ursus arctos* L., 1758) and wolverines (*Gulo gulo* (L., 1758)) are abundant in the study area, whereas gray wolves are restricted to being occasional dispersers.

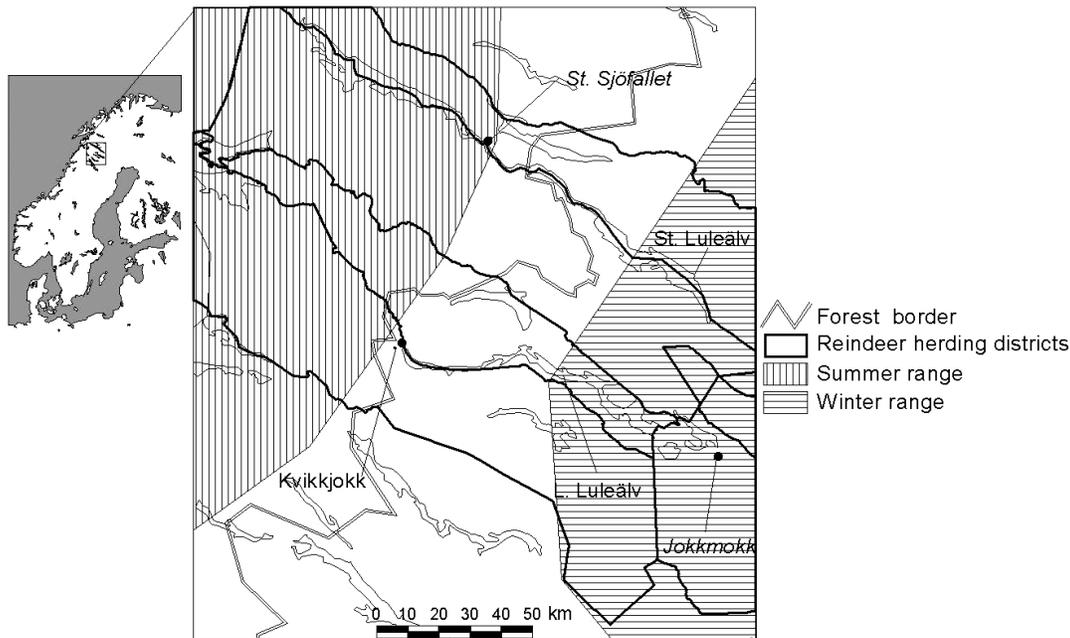
### Reindeer husbandry in the area

The study area constitutes parts of four Sámi reindeer herding districts (Tuorpon, Jåhkågasska, Sirges, and Sör-Kaitum). The year-round grazing area (used from May through November) for the four reindeer herding districts covers 17 607 km<sup>2</sup>, with 41% of this grazing area within our core study area. From the late 1980s to 2003, the total number of reindeer has fluctuated between 20 000 and 30 000 in these four reindeer herding districts (Statistiska centralbryån 1999; T. Raunistola, personal communication). Typically, the winter herd (after slaughter) is composed of a large proportion of adult females (70%), of which 75% are found to be at reproductive ages, a smaller number of calves (20%), and in general, few males (10%) (Statistiska centralbryån 1999). The harvest consists mainly of calves (approximately 70%), followed by old (non-reproductive) females, and some males.

### Reindeer migration

The general pattern of reindeer migrations within the study area is well documented in the land-use plans of the reindeer herding districts (Länsstyrelsen i Västerbotten 2000). The land-use plans show favoured areas at different times of the year, calving grounds and areas for corraling

**Fig. 1.** Study area showing the four herding districts and the winter and summer ranges of semi-domesticated reindeer (*Rangifer tarandus tarandus*) based on land-use maps. The double line delineates the approximate forest border and is based on vegetation maps of the area. Forested land is found to the southeast of the line and alpine areas to the northwest of the line.



and slaughter, in addition to the regular winter and summer ranges (Fig. 1), as well as yearly migration routes for the semi-domesticated reindeer. Empirical studies have also verified the land-use maps (Björvall et al. 1990).

## Methods

### Movement of Eurasian lynx

To live capture and equip adult lynx with VHF radio collars, darts containing a mixture of ketamine (5 mg/kg) and medetomidine (0.2 mg/kg; Kreeger et al. 1999) were fired from a helicopter. The handling scheme for the lynx has been examined by the Swedish Animal Welfare Agency and fulfils the ethical requirements for animal research. The lynx were radio-tracked at least 2–4 times per month, mostly by airplane. The winter period is a difficult period to perform radio-tracking because of the lack of daylight and the difficult weather conditions, which result in few attempts at obtaining positions that translate to few positions being recorded. Between aerial radio-tracking, each individual was located by taking single bearings from the ground when the opportunity arose, e.g., during other fieldwork. In addition, individuals were always found and located within their expected home range when attempts were made at obtaining their positions. The accuracy of the positions was determined to the nearest 100 m. To determine home ranges, 14 individuals (5 males and 9 females) were selected based on a minimum requirement of 6 positions for each seasonal period. The number of positions is too few to formally and accurately estimate home-range size; however, in the context of this study, the data are being used only to establish home-range location with respect to reindeer migration and to provide an index of seasonal space use in the area bounded by the available home-range locations (herewithin referred to as the activity range). The mean number of posi-

tions was 11 (range 6–39) in winter, 15 (range 8–102) in summer, and 34 (range 6–118) in autumn. For lynx individuals that were followed for several years, the average activity range was used for each seasonal period. The study was performed from 1993 to 2005, although the more intensive radio-tracking diminished after 1996 and only data from 1993 to 1998 were used for the lynx. Activity ranges consisting of 100% minimum convex polygons (MCPs) and centres of activity ranges for the different individuals were estimated using the animal movement extension for ArcView<sup>®</sup> version 3.3 (Environmental Systems Research Institute, Inc. 2002).

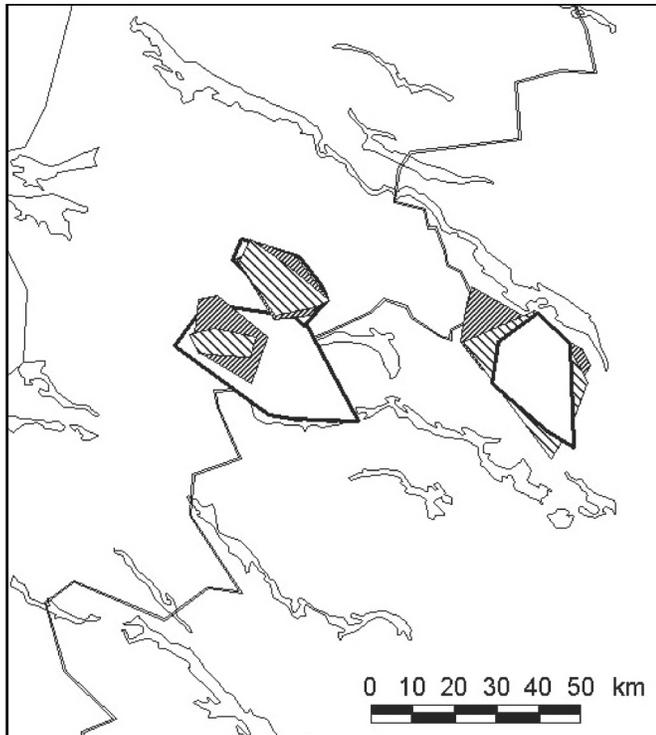
Based on reindeer herding activities during the year and on radio-tracked reindeer (Björvall et al. 1990), the year was divided into three periods: winter (December–April), summer (May–July), and autumn (August–November). The radio-collared lynx were divided into three categories: males, single females, and family groups. Females with juveniles present for at least 50% of the time during a period were classified as a family group for that period. Juvenile presence was determined by field observations. The distances and direction between the centres of the activity ranges between the three different periods were estimated. The direction was tested using Rayleigh's test (Zar 1996). Two measures of activity range overlap between periods (i.e., mean and largest values) were calculated. The overlap between activity ranges A and B is C, which is equal to  $A \cap B$ . The mean overlap (%) is equal to  $0.5(C/A + C/B)$ . The largest overlap is the largest value of  $C/A$  and  $C/B$ . Hence, the largest overlap range is somewhere between the mean overlap and the 100% overlap, where 100% indicates that one of the activity ranges is completely overlapping the other. Because we have very few positions for some individuals, we tested the effect of small sample size on the precision of the estimated centre of the activity range by

**Table 1.** Mean activity ranges (100% minimum convex polygons (MCPs); km<sup>2</sup>) of Eurasian lynx (*Lynx lynx*) during the three periods of the year.

	Period		
	Winter	Summer	Autumn
Male ( <i>n</i> = 5)	286 (140–461)	280 (112–488)	305 (116–552)
Female ( <i>n</i> = 4–6)*	203 (38–377)	256 (177–332)	166 (71–397)
Family group ( <i>n</i> = 6–9) <sup>†</sup>	320 (100–665)	68 (11–472)	127 (32–260)

**Note:** Values in parentheses are ranges.  
 \*The number of single females was 6 in winter (December–April), 4 in summer (May–July), and 6 in autumn (August–November).  
<sup>†</sup>The number of family groups was 6 in winter (December–April), 8 in summer (May–July), and 9 in autumn (August–November). The different sample sizes depended on whether females had young present, and therefore were classified as a family group.

**Fig. 2.** Example of seasonal activity ranges (100% minimum convex polygons (MCPs)) of three female Eurasian lynx (*Lynx lynx*) showing the range of overlap and size of the area available in the data set.



□ Dec.- Apr.    ▨ May - July    ▩ Aug.- Nov.

simulation. We sampled 6 positions 1000 times from data sets with more than 25 positions from a period, and compared the centre of the activity range for the entire data set with that for the sampled data sets.

**Alternative prey abundance**

Abundance of alternative prey, i.e., ptarmigan and willow grouse (pooled together) and mountain hare, was surveyed by faecal pellet counts (Lindström et al. 1994; Newey et al. 2003). The study area was divided into a grid consisting of 10 km × 10 km squares. The starting point of one 3 km equilateral triangle was randomly positioned within each square. Thirty-two of the triangles were located in the south-eastern coniferous forest part of the study area and 37 of the

triangles were located in the northwestern mountainous part. We surveyed 56 triangles in 1999 and 28 triangles in 2000, of which 15 triangles were surveyed in both years. Sixty equidistantly spaced plots of 10 m<sup>2</sup> were surveyed along the sides of the triangle, i.e., the distance between two plots was 150 m. The location of each plot was determined through pacing. Only faecal pellets judged to be from the preceding winter were counted. The level of degradation and the presence of leaf litter covering the faecal pellets were used to discriminate between old and new pellets. For each triangle a prey species index was calculated based on the proportion of the 10 m<sup>2</sup> plots containing faecal pellets of a particular species.

For the triangles surveyed in both 1999 and 2000, there was a strong significant correlation between the index for mountain hare in both years (*r* = 0.66, *df* = 13, *p* < 0.007), as well as between the index for ptarmigan – willow grouse in both years (*r* = 0.96, *df* = 13, *p* < 0.0001). Therefore, one index was calculated for mountain hare and another for ptarmigan – willow grouse based on both surveys and a mean index was calculated for the triangles that were surveyed in both years. The prey index was interpolated with the inter-distance weighting (IDW) method and 12 nearest neighbours over the entire area using the spatial analyst extension for ArcView<sup>®</sup> version 3.3 (Environmental Systems Research Institute, Inc. 2002).

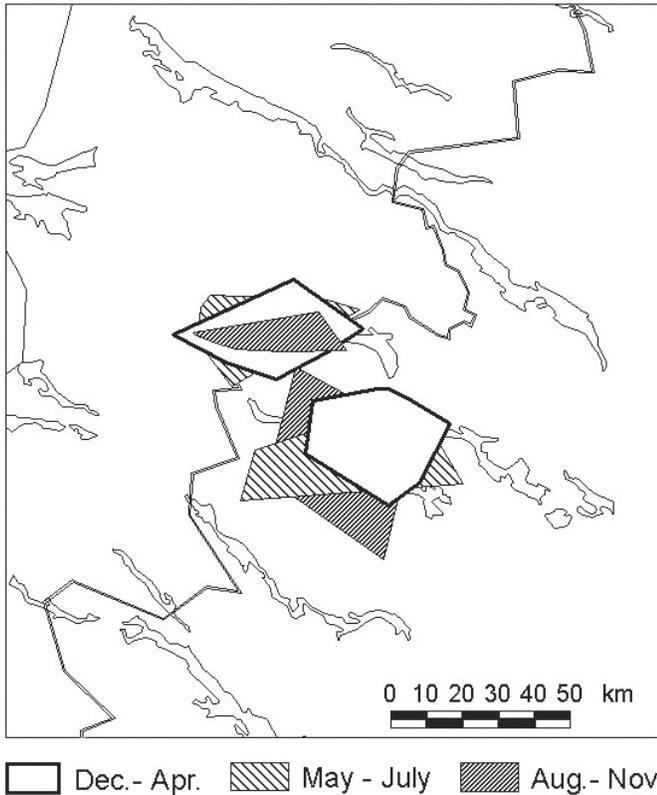
**Results**

**Activity ranges of Eurasian lynx**

There were no significant differences between the three periods in the activity range sizes for males (Friedman’s test,  $\chi^2 = 0.1$ , *n* = 5, *p* = 0.95) or for single females (Kruskal–Wallis test, *H* = 0.933, *n*<sub>1</sub> = 7, *n*<sub>2</sub> = 4, *n*<sub>3</sub> = 6, *p* = 0.62; Table 1, Figs. 2, 3). The grand means were 274 km<sup>2</sup> for males and 209 km<sup>2</sup> for females. However, the activity range size was significantly smaller (68 km<sup>2</sup>) for family groups during the summer period than during the autumn (127 km<sup>2</sup>) and winter (320 km<sup>2</sup>) periods (Kruskal–Wallis test, *H* = 10.151, *n*<sub>1</sub> = 6, *n*<sub>2</sub> = 9, *n*<sub>3</sub> = 8, *p* = 0.0062; Table 1).

There were no significant differences between the three periods in the distance between the centre of the activity range in each season to the centre of the activity range in the season immediately following for males (Friedman’s test,  $\chi^2 = 1.200$ , *n* = 5, *p* = 0.54), for single females (Kruskal–Wallis test, *H* = 2.279, *n*<sub>1</sub> = 7, *n*<sub>2</sub> = 4, *n*<sub>3</sub> = 6, *p* =

**Fig. 3.** Example of seasonal activity ranges (100% MCP) of two male Eurasian lynx showing the range of overlap and size of the area available in the data set.



0.31), or for family groups (Kruskal–Wallis test,  $H = 2.704$ ,  $n_1 = 6$ ,  $n_2 = 9$ ,  $n_3 = 8$ ,  $p = 0.25$ ). The grand means were 6.6 km for males, 7.3 km for females, and 8.4 km for family groups (Table 2).

The distance between the centre for the entire data set (number of positions >25) and the centre for the sample of 6 positions was  $4.4 \pm 1.9$  km (mean  $\pm$  SD; based on 7 independent simulations of 1000 samples each). Thus, the effects of small sample sizes on the estimated centre of activity were just slightly lower than the estimated distances between the centres of the activity range during different seasons (Table 2). However, the variation owing to small sample sizes was much smaller than the expected changes in centre of activity range if the lynx would have followed the reindeer herd (a minimum of 75 km, but more likely 100–150 km). As expected, the centres for the samples were not significantly different from a uniform circular distribution around the centre of the entire data set (Rayleigh's test,  $z = 0.042$ ,  $n = 7$ ,  $p > 0.50$ ).

The direction of movement between summer–autumn and autumn–winter were not significantly different from a uniform circular distribution (Rayleigh's test,  $z < 0.938$ ,  $p > 0.2$  in all cases). Between winter and summer the direction of movement was significantly different from a uniform circular distribution for single females (Rayleigh's test,  $z = 3.309$ ,  $n = 7$ ,  $p < 0.05$ ) and for family groups (Rayleigh's test,  $z = 5.976$ ,  $n = 6$ ,  $p < 0.001$ ), but not significantly different for males (Rayleigh's test,  $z = 1.803$ ,  $p > 0.1$ ). Mean direction of movement between winter and summer was  $111^\circ$

for single females and  $147^\circ$  for family groups, i.e., movements were from southeast to northwest (Table 3).

Furthermore, there were no significant differences between the three periods in overlap of the activity range of an individual on that individual's activity range from the previous season for males (Friedman's test,  $\chi^2 = 2.800$ ,  $n = 5$ ,  $p = 0.24$ ), for single females (Kruskal–Wallis test,  $H = 1.707$ ,  $n_1 = 7$ ,  $n_2 = 4$ ,  $n_3 = 6$ ,  $p = 0.42$ ), or for family groups (Kruskal–Wallis test,  $H = 278$ ,  $n_1 = 6$ ,  $n_2 = 9$ ,  $n_3 = 8$ ,  $p = 0.87$ ). The grand means in overlap were 53% for males, 50% for females, and 44% for family groups (Table 4). The grand means in largest overlap found were 72% for males, 64% for females, and 57% for family groups.

### Alternative prey

The index of hare density (Fig. 4) was significantly higher in the mountain habitat ( $0.073 \pm 0.012$ ; mean  $\pm$  SE) than in the coniferous forest habitat ( $0.045 \pm 0.009$ ) (Mann–Whitney  $U$  test,  $U = 212.5$ ,  $n_1 = 37$ ,  $n_2 = 32$ ,  $p = 0.03$ ). This would correspond to actual mean hare densities of about  $0.6/\text{km}^2$  (range 0–2.3/ $\text{km}^2$ ) in the mountains and  $0.3/\text{km}^2$  (range 0–1.6/ $\text{km}^2$ ) in the forest (based on faecal pellet production estimates from captive hares on natural diet observed for 1000 days; Åke Pehrson, personal communication). Similarly, the index of ptarmigan – willow grouse density (Fig. 5) was higher in the mountain habitat ( $0.107 \pm 0.091$ ) than in the forest habitat ( $0.042 \pm 0.066$ ) (Mann–Whitney  $U$  test,  $U = 257.0$ ,  $n_1 = 37$ ,  $n_2 = 32$ ,  $p < 0.0001$ ). Concurrent population census of ptarmigan – willow grouse densities in the same region have shown winter populations of 6–10 individuals/ $\text{km}^2$  (Hörnell-Willebrand 2005).

### Discussion

The distance between the main winter and summer ranges was  $>100$  km for the semi-domesticated reindeer (Björvall et al. 1990; Länsstyrelsen i Västerbotten 2000), while the activity ranges only changed marginally between seasons for most Eurasian lynx. Single females and family groups had mean directions of movement from winter to summer that differed from a uniform circular distribution (Fig. 6). The mean directions of  $111^\circ$  for single females and  $147^\circ$  for family groups (Table 3) are close to the expected direction of movement of reindeer ( $135^\circ$ ). However, the mean distance between the centre points of individual lynx were mostly  $<10$  km and the overlap was mostly  $>40\%$  between seasons. The reindeer in the same area moved 100–150 km and did not have overlapping ranges. Thus, the lynx in our study did not follow the reindeer as they migrated. There were two instances where lynx females with young, at the border between forest and mountain, moved the centre point of their activity ranges (9 and 13 km, respectively) into the more forested area during the winter, thus potentially reaching areas with more reindeer during the winter period. However, their seasonal activity ranges still overlapped by 35% and 21%, respectively. Individuals with their activity ranges farther into the alpine region are too far from the winter range of reindeer and, consequently, must sustain themselves through the winter by other means.

The autumn generally is a time when reindeer are spread out over larger areas. Reindeer, like caribou, start dispersing

**Table 2.** Mean distance (km) between centre points of activity ranges (100% MCP) of Eurasian lynx during the three periods.

	Period		
	Winter–summer	Summer–autumn	Autumn–winter
Male ( <i>n</i> = 5)	5.2 (4.1–6.5)	7.6 (0.3–14.1)	6.5 (1.9–17.1)
Female ( <i>n</i> = 4–6)*	6.5 (2.6–11.9)	5.1 (1.5–9.7)	10.0 (2.7–17.0)
Family group ( <i>n</i> = 6–9)†	11.9 (2.9–39.8)	5.0 (0.7–8.9)	11.0 (2.8–40.0)

**Note:** Values in parentheses are ranges.  
 \*The number of single females was 6 in winter (December–April), 4 in summer (May–July), and 6 in autumn (August–November).  
 †The number of family groups was 6 in winter (December–April), 8 in summer (May–July), and 9 in autumn (August–November). The different sample sizes depended on whether females had young present, and therefore were classified as a family group.

**Table 3.** Mean direction of movement (°) from the centroid of activity ranges of Eurasian lynx between the three periods.

	Period		
	Winter–summer	Summer–autumn	Autumn–winter
Male ( <i>n</i> = 5)	212 (135–303)	210 (67–298)	358 (62–356)
Female ( <i>n</i> = 4–6)*	111 (3–172)	36 (78–352)	280 (128–318)
Family group ( <i>n</i> = 6–9)†	147 (114–188)	288 (12–343)	1 (12–340)

**Note:** Values in parentheses are ranges.  
 \*The number of single females was 6 in winter (December–April), 4 in summer (May–July), and 6 in autumn (August–November).  
 †The number of family groups was 6 in winter (December–April), 8 in summer (May–July), and 9 in autumn (August–November). The different sample sizes depended on whether females had young present, and therefore were classified as a family group.

**Table 4.** Mean and largest overlap (100% MCP) in activity ranges of Eurasian lynx between the three periods.

	Period		
	Winter–summer	Summer–autumn	Autumn–winter
Male ( <i>n</i> = 5)			
Mean (range)	46.5 (24.0–59.0)	54.6 (30.0–68.0)	57.4 (17.0–77.0)
Largest (range)	71.0 (44.0–90.0)	70.0 (30.0–88.0)	76.0 (55.0–97.0)
Female ( <i>n</i> = 4–6)*			
Mean (range)	44.8 (5.0–70.0)	62.3 (38.0–80.0)	49.0 (10.0–82.0)
Largest (range)	60.0 (11.0–90.0)	64.0 (53.0–92.0)	68.0 (27.0–99.0)
Family group ( <i>n</i> = 6–9)†			
Mean (range)	40.5 (29.0–64.0)	40.8 (9.0–78.0)	37.4 (13.0–68.0)
Largest (range)	60.0 (30.0–92.0)	62.0 (21.0–95.0)	48.0 (22.0–70.0)

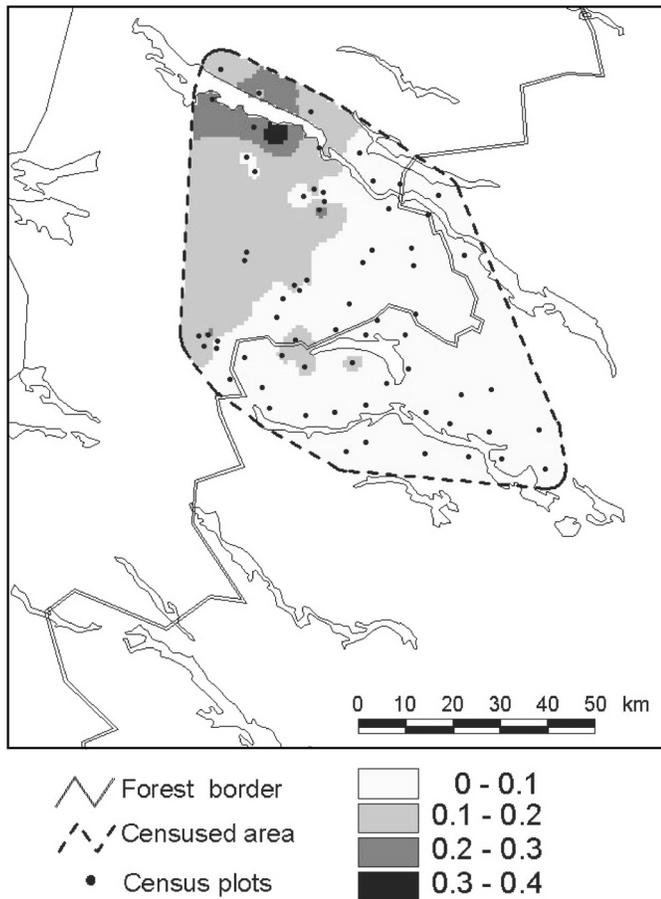
**Note:** Values in parentheses are ranges.  
 \*The number of single females was 6 in winter (December–April), 4 in summer (May–July), and 6 in autumn (August–November).  
 †The number of family groups was 6 in winter (December–April), 8 in summer (May–July), and 9 in autumn (August–November). The different sample sizes depended on whether females had young present, and therefore were classified as a family group.

shortly after the warm period, as soon as the insect pressure is released and as the quality of the grass deteriorates (Björvall et al. 1990; Danell and Nieminen 1997). Depending on the weather conditions each year, they may start their migration early. Inevitably, a small number of reindeer will remain in the mountainous region during the winter. However, this number is merely a fraction (1%–2%) of the larger primary population. The actual number of reindeer remaining in the mountainous region may vary from year to year based on the weather conditions during the time of the fall migration, efforts to corral and move animals to winter pastures, and disturbances that may occur in connection with the seasonal migration. However, there is no doubt that

the density of reindeer is substantially lower in alpine areas during winter (December–April) compared with other periods. A similar situation occurs in Alaska where the western Arctic caribou herd (WACH) migrates; a smaller number of caribou, as well as some resident moose, always remain in one place in Alaska (Ballard et al. 1997).

In modern times, some reindeer are transported with large lorries to the winter grazing areas. It could be argued that the lynx then would not be able to follow. However, the reindeer still make the initial migration from high-alpine areas to low-alpine areas on foot. If the lynx actually followed the reindeer, we should have seen an expanded activity range prior to the final migration. Despite having a migrat-

**Fig. 4.** Index of ptarmigan (*Lagopus muta*) – willow grouse (*Lagopus lagopus*) densities in the study area based on the proportion of plots with faecal pellets. The solid circles indicate the centre of each survey triangle and the broken line indicates the surveyed area.



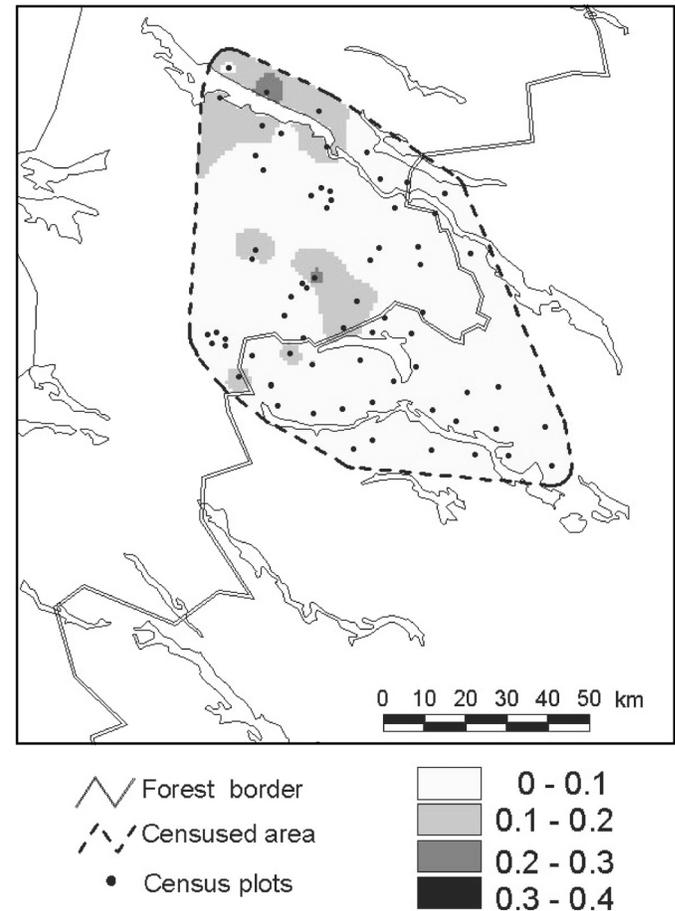
ing prey source, the lynx in our study showed a behavioural pattern similar to that of predators with a more constant access to their primary prey.

The differences in activity range size for lynx family groups in summer (May–July) compared with those in winter (December–April) and autumn (August–November) are most probably due to the limited mobility of the young. During the first month following birth, the lynx female only leaves her young for shorter periods of time before returning to the den (Reinhardt and Halle 1999). This results in females with young using a substantially smaller area during the summer months compared with single females.

At low cervid densities (<0.5 individuals/km<sup>2</sup>), lynx have been reported to switch to alternative prey, often small mammals or birds (Jędrzejewska and Jędrzejewski 1998). The proportion of hares in the lynx diet has been shown to increase in areas of Sweden when roe deer densities have decreased from 1.12 to 0.48 individuals/km<sup>2</sup> (Liberg and Glöersen 2000).

The widely studied Canadian lynx (*Lynx canadensis* Kerr, 1792) feed primarily on smaller prey such as snowshoe hare (*Lepus americanus* Erxleben, 1777), red squirrel (*Tamiasciurus hudsonicus* Erxleben, 1777), and other small mammals and birds (Krebs et al. 2001). Eurasian lynx in central

**Fig. 5.** Index of mountain hare (*Lepus timidus*) densities in the study area based on the proportion of plots with faecal pellets. The solid circles indicate the centre of each survey triangle and the broken line indicates the surveyed area.

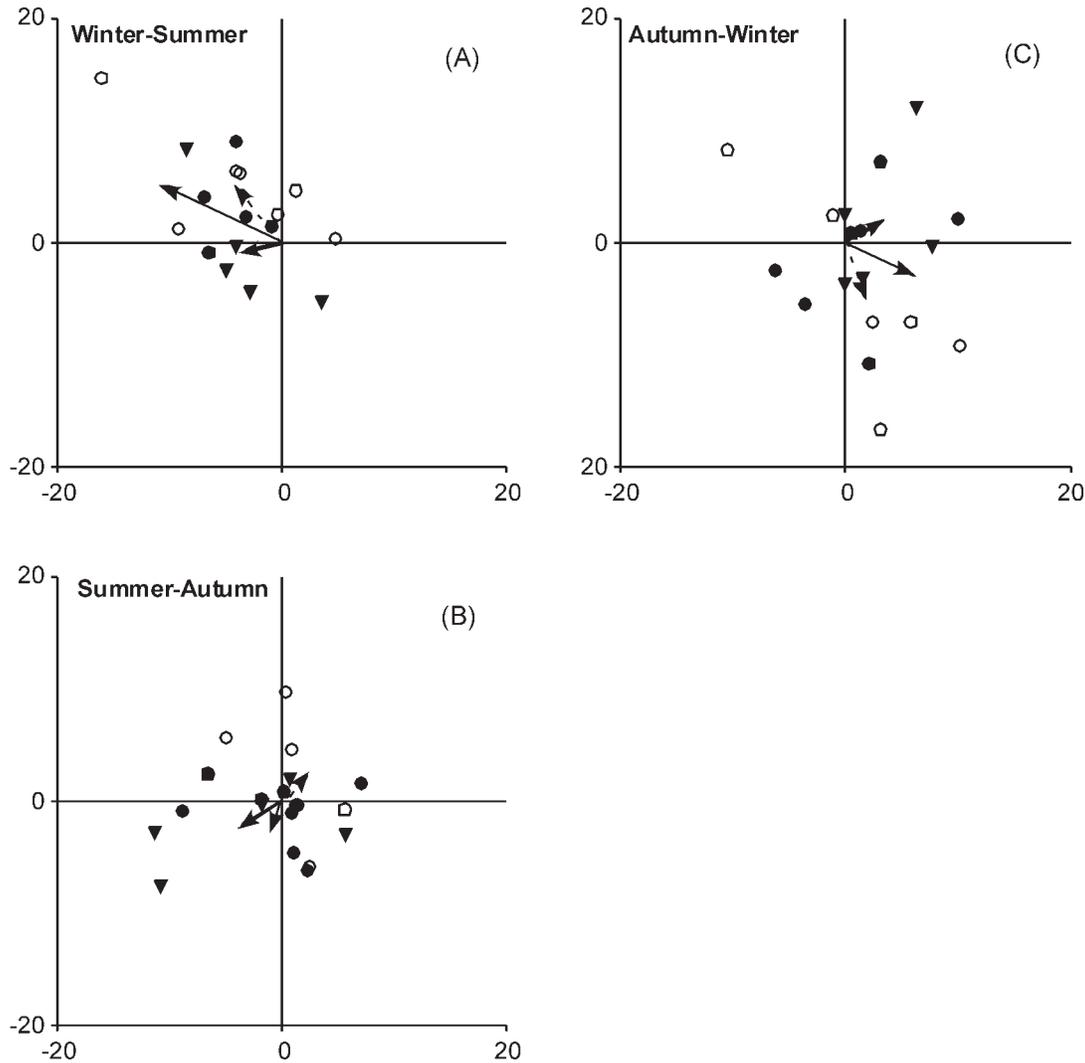


Norway inhabit both lowland and more alpine habitat. Roe deer is the primary prey in the lowlands, while the Eurasian lynx rely on semi-domesticated reindeer and free-ranging sheep (*Ovis arie* L., 1758) as food resources in the more alpine regions. Eurasian lynx, however, have shown a preference for lowland habitats, which probably reflects the need for a reliable food resource (Sunde et al. 2000).

Our study showed that there were significantly higher densities of alternative prey species (mountain hare and ptarmigan – willow grouse) in the mountain region (i.e., the summer range of reindeer) than in the coniferous forest (i.e., the winter range of reindeer). Thus, the Eurasian lynx that remain in the mountains during the winter may increase their hunting frequency for the more abundant alternative prey species such as mountain hare and ptarmigan – willow grouse.

This shift to alternate prey species is similar to that seen in gray wolves in North America and lions in the Serengeti that rely on alternative prey during times when their primary prey is absent or scarce. In northwest Alaska, barren-ground caribou (*Rangifer tarandus granti* J.A. Allen 1902) is the primary prey of gray wolves as long as they are present within the gray wolf territory (Dale et al. 1995; Ballard et al. 1997). When the caribou herd migrates to winter grounds, densities of caribou within the gray wolf territories

**Fig. 6.** Movements based on changes in distance (km) and direction (km) of the centre of activity ranges of Eurasian lynx between seasons (*a*, winter–summer; *b*, summer–autumn; *c*, autumn–winter) for the different lynx categories: single females (open circles, dashed arrow), family groups (solid circles, thin arrow), and single males (solid triangles, thick arrow).



drop, resulting in gray wolves having to switch to resident moose and other alternative prey species for food. Territorial lions in the Serengeti have shown no tendency to change their home ranges as the wildebeest migrate away from an area. Instead, the lions switch to other prey species. Lion prides living in the plains will increase their hunting frequency of locally more abundant species such as Burchell's zebras (*Equus burchellii* (Gray, 1824)) or Thomson gazelles (*Gazella thomsoni* Günther, 1884), while woodland prides will rely on the resident African buffalo (*Syncerus caffer* Sparrman, 1779) population (Scheel and Packer 1995).

Although Eurasian lynx in our study may include small mammals in their diet, the densities of mountain hare and ptarmigan – willow grouse found within our study area were much lower than those found in North America. The Kluane project, for example, reported snowshoe hare densities of roughly 10–150/km<sup>2</sup> and spruce grouse densities of 10–40/km<sup>2</sup> (Krebs et al. 2001). Densities of mountain hare, based on our faecal pellet counts, ranged between 0 and 2.3/km<sup>2</sup>, with a mean density of 0.5/km<sup>2</sup>. Likewise ptarmigan – willow grouse densities were about 6–10

adults/km<sup>2</sup> (Hörnell-Willebrand 2005). Previous studies have shown that the amplitude between minimum and maximum mountain hare densities is about 2 (Lindström et al. 1994). The fluctuations in density of willow grouse in the same area as our study had an amplitude of about 3 (Hörnell-Willebrand 2005). These facts indicate that the density, as well as the fluctuations in density, is much higher in North America than in Scandinavia.

On the other hand, the Eurasian lynx in our study area may not have been completely dependent on alternative prey, as there were also a number of reindeer left in the mountains during the winter period. However, this is only a small fraction of the reindeer herd. These reindeer may not have been found during corraling and, thus, will serve as prey for the lynx during the winter. It is nevertheless difficult to get an accurate count from the reindeer herding communities of how many reindeers actually remain in the mountains during different years. The numbers vary greatly and depend on several factors such as weather conditions, the successes in gathering the animals before moving, and the feeding possibilities for reindeer remaining in the mountains.

In addition to affecting the space used by the Eurasian lynx, the migrating prey might also have an effect on other aspects of the lynx's life history. Low prey densities or greatly varying prey densities could have a negative effect on reproductive success and (or) survival of the lynx. A previous study documented higher reproductive success of lynx in south-central Sweden compared with those of lynx in northern Sweden (Andrén et al. 2002).

Although reindeer distribution within the study area appears clustered in time and space, the roe deer in south-central Sweden is much more evenly distributed. Assuming that an average of 25 000 reindeer would have an even distribution in the year-round grazing area of the four herding districts, it would equal a density of 1.4/km<sup>2</sup>. The mass of a reindeer in a net herd in the early-winter range is between 30 and 80 kg, with a mean mass of 60–65 kg (results from a herd simulation program; Ö. Danell, personal communication). In central Sweden, the density of roe deer is 3–4/km<sup>2</sup>. During winter, the mass of adult roe deer in central Sweden varies between 20 and 30 kg (Aanes et al. 1998), with a mean of 23.3 kg (based on live masses of 409 individuals; P. Grängstedt, personal communication). The total available prey resource is roughly the same within the study area as it is in south-central Sweden, but whereas lynx in south-central Sweden have fairly regular access to its prey, lynx in our study area experience larger variations in prey density. Eurasian lynx density is higher in south-central Sweden (0.01–0.22/km<sup>2</sup>) than in northern Sweden (0.002–0.007/km<sup>2</sup>) (Liberg and Glöersen 2000; Liberg and Andrén 2005; Norrbotten county board, personal communication). Thus, the total available prey resource per predator might actually be higher in northern Sweden than in south-central Sweden. The lower reproductive rate in our study area compared with those in south-central Sweden is possibly an indication of the cost of having migrating prey or large seasonal variation in prey availability. This is similar to the findings of Ballard et al. (1997), who pointed out that gray wolves living within the migratory range of the western Arctic caribou herd existed at a lower density than predicted by mean prey densities.

## Acknowledgements

We thank the Swedish Environmental Protection Agency, the World Wide Fund for Nature (Sweden), the local government of Norrbotten, and the private foundation Olle och Signhild Engkvists stiftelse for their financial contribution to this project. We also thank Tom Wiklund, Linn Svensson, Andreas Norin, Elisabeth Vannar, Kent Sköld, Mona Hansers, Per Ahlqvist, Lennart Åstot, David Åstot, and Leif Länta for invaluable help in collecting field data, and J.-O. Helldin, John Linnell, and Jens Persson for invaluable input on earlier stages of the manuscript.

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