Home ranges of mountain hares Lepus timidus in boreal forests of Finland

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Home ranges of mountain hares *Lepus timidus* were studied in boreal forests in Finland and compared to those on the British Isles and in Sweden. During 1998-2001 we radio-tracked 22 hares. Mean yearly home range size was 206 ha. Home ranges were largest in late winter-spring (mean: 202 ha) and smallest in autumn (mean: 71 ha). Home ranges were rather stationary, and only minor shifts in home range locations occurred between seasons. The hares used, however, partly different core areas in different seasons. Home ranges were much larger in the boreal forests of Finland, where the climate is cold, than in the moorlands and grasslands of the British Isles, where the climate is much milder. Home ranges in Finland were similar in size to those in the boreal forests of Sweden. In Finland and Sweden, winters are harsh, the growing season for plants short and the field layer vegetation is covered by snow from November until late April. The large home ranges in the boreal forests are probably mainly due to the low food availability in this environment.

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In Europe, the natural distribution of the mountain hare *Lepus timidus* covers Fennoscandia, the Baltic states, northeast Poland, Belarus and northern Russia. The species also occurs in Scotland, Ireland and the Alps as a glacial relict (Sulkava 1999). Mountain hares live in various habitats, including heather moor, alpine grassland, pastures, shrublands, bogs, tundra and boreal and mixed forests (Angerbjörn & Flux 1995). In Finland, the mountain hare lives in rather unproductive boreal forest and bogs, where the climate is harsh, winters are long and the snow cover thick, and the growing season is short. Furthermore, most young deciduous trees are cleared from the heavily managed forests.

Home ranges of the mountain hare have been studied in heather moorland in the uplands of Scotland (*L. t. scoticus*; Flux 1970, Hewson 1965, Hewson & Hinge 1990, Hulbert et al. 1996a) and in the lowland pastures and grasslands of Ireland (*L. t. hibernicus*; Wolfe & Hayden 1996). Only few home range studies of the mountain hare *L. t. timidus* have been done in the boreal forests of northern Europe, i.e. the main distribution area of the species in Europe (Seiskari 1957, Olsson 1997,

Dahl & Willebrand in press). Knowledge of home ranges is, however, essential for understanding the habitat use of hares. Information about the habitat use is needed, e.g. when planning forestry and game management.

Our radio-tracking study is part of a larger project planned to evaluate the population biology of the mountain hare in Finland, and to obtain knowledge that can be applied in forest and game management. The aim of our paper was to examine the home ranges of mountain hares in different seasons in a managed boreal forest in Finland. Habitat use within home ranges is presented in another paper. We also compare the results of home range sizes with results published from the British Isles and Sweden.

Material and methods

Study areas

Mountain hares were radio-tracked in two areas in Finland during 1998-2001: around Evo Game Research Station, southern Finland (61°14'N, 25°10'E) and near the city of Oulu (Sanginjoki), northern Finland (65°01'N, 25°50'E). The southern area covers 20 km² and is mainly coniferous and mixed forest with clear-cuts, small swamps and small lakes and streams. Much of the area is unproductive barren heath. The northern area covers 15 km² and mainly consists of mixed forest and pine heath with some small lakes. Forests in both study areas are managed, and there are also clear-cuts and plantations. Many small timber roads run through both areas, facilitating radio-tracking. Hare hunting was not allowed in the northern area during the study, but hares were occasionally hunted in the southern area.

Mean yearly temperature is 3.4°C in the southern and 2.1°C in the northern study area (www.worldclimate. com). The coldest month is January with the average temperature of -9.3°C in the southern and -11.8°C in the northern area. The warmest month is July with a mean temperature of 15.7°C in both areas. The permanent snow cover lasts from late November or December until late April in the southern area and from late November until late April in the northern area. The growing season for plants starts in the beginning of May and ends during the second week of October in the southern area. In the northern area, the growing season lasts from the first week of May to the first week of October. Thus, the length of the growing season is about 162 days in the southern area and 150 days in the northern area (Finnish Meteorological Institute 2004).

Temperature data are also given for Scotland, Ireland and Sweden (www. worldclimate.com; see Table 4).

The annual mean temperature and the mean temperatures for late winter-spring (March-April) and autumn (October-November) are here considered as rough estimates of the plant growing season, because the temperatures in spring and autumn mainly determine the onset and end of the growing season. For instance in Finland, there is a strong positive correlation between the annual mean temperature and the length of the growing season (r = 0.97, P = 0.002, N = 6). The length of the growing season is one factor, among others, affecting primary production.

Radio-tracking

Mountain hares were captured in March and April using baited wire traps. The hares were ear-tagged and fitted with transmitter collars (Televilt, 230 MHz, weight 52 g). Transmitter life was about one year. Hares were also sexed and weighed. Because hares were captured in March and April, all of them were > 6 months old. After capturing, the hares were released within few hours. We radio-tracked 11 hares (eight males and three females) in Evo between March 1998 and December 2000, and 11 (six males and five females) in Oulu between March 1999 and April 2001.

Hares were located from a vehicle with a Yagi-type antenna with five elements that could be lifted up to 4 m above ground. Bearings were taken from at least two points. The angles between the bearings were as near to 90° as possible and the time interval < 5 minutes. The distance between the transmitter and receiver was < 1 km. Data were collected in two ways: 1) using 'the point method': hares were located several times a week at different times of day and night, and 2) using 'intensive tracking nights': hares were located at 15-minute intervals during whole nights (from 17:00 to about 09:00) until the hares settled at their day lairs.

Home range calculations

When testing mean location error, one person walked in the woods with a GPS-instrument and a radio transmitter (made for hares) imitating hare movements, and others located that person every 15 minutes in a way similar to the way used to locate hares. The test revealed that the home range sizes calculated on the basis of true (GPS) locations and radio-fixes did not differ significantly (P = 0.459; for details of the test see Kauhala & Tiilikainen 2002).

We calculated home range sizes using both the locations from the intensive tracking nights and the data collected using the point method. Because the day resting places were within the night ranges of hares, both day and night fixes were included in home range calcula-

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tions. Although successive locations from the intensive tracking periods may not be independent, they can be used in home range calculations, if there are several tracking nights per home range (Smith et al. 1981). Furthermore, Rooney et al. (1998) found that the correct strategy for estimation of home range size would be repeated use of as short a sampling interval as possible over an extended period of time. Since no fixes in an animal's home range are completely independent from any other, one should not be overconcerned with eliminating autocorrelation from the data (Rooney et al. 1998).

Home ranges were calculated using the fixed Kernel method. To exclude the worst 'outliers' and location errors, we defined total home range as the 95% Kernel home range. We also calculated the 'core area'; it was determined individually from the utilisation distribution curves (Fig. 1). Also the overlap between seasonal home ranges of each individual was calculated. We used the software Ranges V (Kenward & Hodder 1996).

When calculating the seasonal home ranges, we divided the data into four seasons: late winter-spring (March-May), summer (June-August), autumn (September-November) and mid-winter (December-February). Of the 22 hares, 12 were still alive nine months after they had been fitted with a radio collar, and could thus be radio-tracked for three seasons, i.e. from March to the end of November. Data for the whole year were obtained for only six hares, because the hares were trapped in March-April and most of them died or disappeared before the end of the year.

Statistical tests

Accuracy of home range estimates is closely linked to the number of radio locations (e.g. Jennrich & Turner

Figure 2. Total home ranges (95% Kernel; A) and core areas (N = 54; B) of the male (●, ■) and female (○, □) mountain hares radio-tracked in the Evo and Oulu study areas in Finland between late winter-spring 1998 and winter 2001.

1969). When testing the variation in home range sizes between years, areas, sexes and seasons (ANOVA), we therefore used the number of locations as a covariate. We first tested the significance of each factor using ANOVA. We then, step by step, excluded the factor that was least significant and repeated the analysis until only significant factor(s) was/were left and calculated the
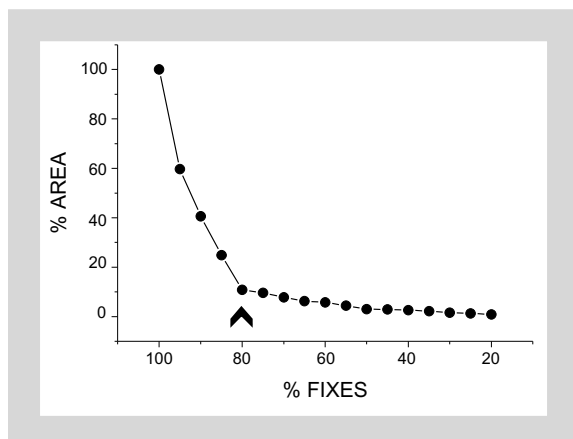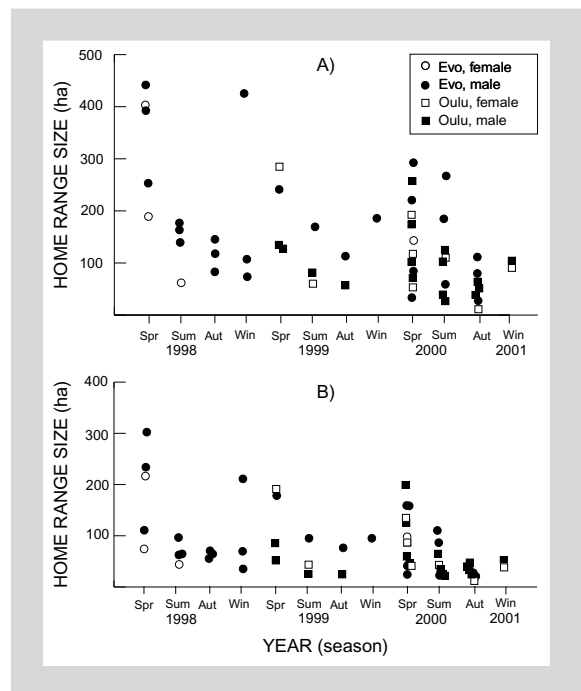
Figure 1. Example of a utilisation distribution curve of a radio-tracked mountain hare. In this case the core area of the home range includes 80% of the fixes (arrow).

Table 1. Results of ANOVA when testing the effect of different factors on mountain hare home range size for 95% Kernel home ranges and core areas, respectively.

Source	df	F-ratio	P
95% Kernel home ranges			
Area	1	1.88	0.177
Sex	1	0.33	0.566
Season	3	6.73	0.001
Year	3	1.65	0.192
Error	45		
Core areas			
Area	1	1.46	0.233
Sex	1	0.19	0.662
Season	3	8.27	< 0.001
Year	3	1.42	0.250
Error	45		

Table 2. Mean home range sizes (in ha; ± SD) of mountain hares in different seasons and proportion of core areas of the total (95% Kernel) home ranges. Friedman two-way analysis of variance was calculated for six and 12 cases: four seasonal home ranges (late winter-spring, summer, autumn, mid-winter) could be calculated for six hares, while three seasonal home ranges (late winter-spring, summer, autumn) could be calculated for 12 hares. N = number of locations per home range. Data were obtained using radio-tracking between March 1998 and April 2001.

Home range	Late winter-spring	Summer	Autumn	Winter	Friedman test statistic		P	
					6 cases	12 cases	6 cases	12 cases
Total home range	202 ± 115.8	118 ± 65.9	71.0 ± 38.5	166 ± 130.4	14.00	18.50	0.003	< 0.001
Core area	122 ± 75.5	55 ± 30.6	37.0 ± 23.4	83 ± 66.6	11.85	16.63	0.008	< 0.001
Core area proportion	0.60	0.48	0.53	0.49				
Mean N	80.9	85.0	98.4	71.3				

final models. We also used also Friedman two-way analysis of variance and paired t-test to test the differences between seasonal home range sizes. The level of significance was set at 0.05.

Results

The yearly home range size varied between 91 and 445 ha, the mean size being 206 ha (SD = 107.5, N = 12; including the hares which were radio tracked for at least nine months). We calculated the size of 54 seasonal home ranges: 21 for late winter-spring, 15 for summer, 12 for autumn and six for mid-winter (Fig. 2). No differences in home range size existed between years, areas

or sexes (Table 1). After excluding the least significant factor step by step, we got the final models with only season as a significant factor (95% Kernel home range: $r^2 = 0.42$, F = 8.66, df = 3,50, P < 0.001; core area: $r^2 = 0.48$, F = 11.28, df = 3,50, P < 0.001). We also tested the effects of sex, area and year on home range size,

Table 3. Results of paired t-tests showing seasonal differences in total home range size and core areas of mountain hares radio-tracked in Finland during 1998-2001.

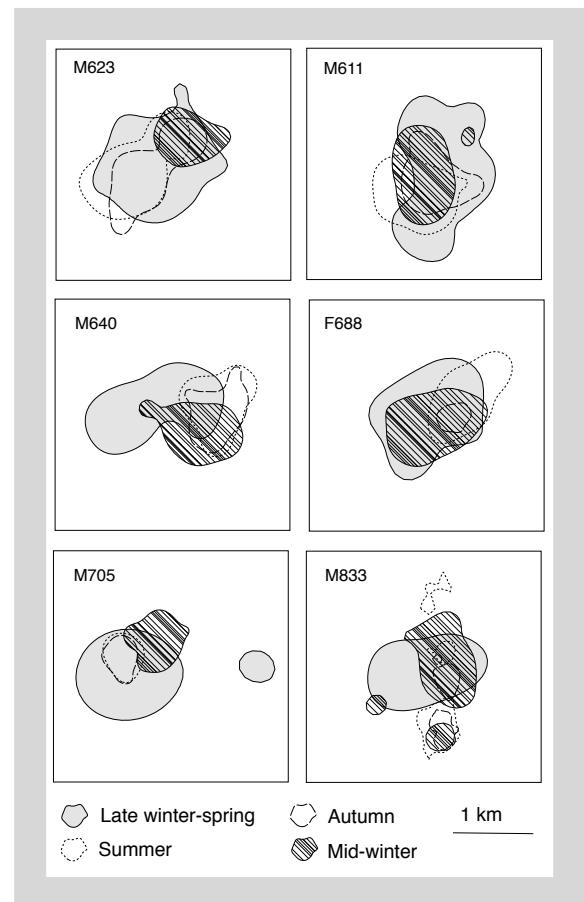|	Summer	Autumn	Mid-winter
Total home ranges			
Late winter-spring	t = 3.37	4.84	3.41
	df = 14	11	5
	P = 0.005	0.001	0.019
Summer		t = 3.46	0.39
		df =11	5
		P = 0.005	0.715
Autumn			t = 1.35
			df = 5
			p = 0.234
Core areas			
Late winter-spring	t = 3.89	4.52	7.26
	df = 14	11	5
	P = 0.002	0.001	0.001
Summer		t = 2.65	0.92
		df =11	5
		P = 0.023	0.400
Autumn			t = 1.18
			df = 5
			P = 0.290

Figure 3. Overlap between seasonal core areas of six (five males and one female) mountain hares which were radio-tracked for 12 months. Data were collected in Finland during 1998-2001, and the home ranges were calculated using the fixed Kernel method.

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using only the data for March-May (largest sample) to exclude the effect of season, but did not get significant models (95% Kernel home range: F = 1.68, df = 9,11, P = 0.206; core area: F = 1.11, df = 9,11, P = 0.430). Therefore we pooled the data for both areas, sexes and all years when seasonal variation in home range size was tested in more detail.

Home ranges were largest in late winter-spring and smallest in autumn. Mid-winter home ranges did not differ significantly from summer and autumn home ranges (see Fig. 2, Tables 2 and 3).

The mean core area included 81% of the locations (range: 70-90%) and comprised 54% of the range area, i.e. the hares spent 81% of their time in an area that was, on average, 54% of the total home range. Seasonal home ranges of each hare overlapped largely (mean for total home ranges = 56%). Seasonal core areas of each hare overlapped 37-59% (mean: 50%; Fig. 3).

Discussion

Mean yearly home range size of the mountain hares in our study was 206 ha. Thus, home ranges in Finland seem to be much larger than home ranges in Scotland or Ireland and about the same size as those in Sweden (Table 4). The climate in Scotland and Ireland is mild (high mean temperatures), the snow covers the earth only for about two months (in Scotland) and spring comes early (Thirgood & Hewson 1987). This means a long growing season for plants and, probably, abundant food available for hares. In Finland, the ground is covered by snow for 5-6 months, the mean annual temperature is low, the growing season short and food availability apparently lower than further south. Boutin (1984) showed experimentally that home range size in lagomorphs is usually negatively correlated with the abundance of food. Boutin (1990) also reviewed other studies and concluded that in terrestrial vertebrates animals receiving supplemental food usually had smaller home ranges than control animals. Hulbert et al. (1996a) found that home range size in Scotland varied according to habitat and season; there was a negative correlation between home range size and the available green biomass of grass. These findings support the conclusion that a severe climate with a short growing season, a thick long-lasting snow cover in winter and consequently, low food availability for hares may be the main reasons for the large home ranges in Finland as compared to those in the British Isles.

Furthermore, mountain hares have distinct daytime resting areas and smaller nighttime feeding areas in Scotland (Flux 1970, Hulbert et al. 1996a). In Finland, the day lairs were within the night ranges. Therefore one should actually compare Finnish home ranges to the night ranges in Scotland and Ireland (see Table 4), which makes the difference between the geographical areas even greater.

In managed boreal forests of Sweden, home ranges of mountain hares seem to be about as large as in Finland (Olsson 1997, Dahl & Willebrand in press). This was expected, because the climate and the structure of forests are very similar in Sweden and Finland. Also Seiskari (1957) found large home ranges (up to 310 ha) in a boreal forest near our southern study site. His estimate was based on snow tracking of hares in winter.

Body size of a mammal may also affect the home range size, because larger animals need more food and energy than smaller ones. Home ranges of mountain hares are indeed largest in northern Europe, where hares are also largest; the mean body weight of *L. t. timidus* in Fennoscandia is 3,438 g, of *L. t. hibernicus* in Ireland 3,190 g, and of *L. t. scoticus* in Scotland 2,750 g. The skull lengths are 94.8 mm, 93.3 mm and 89.2 mm for *L. t. timidus*, *hibernicus* and *scoticus*, respectively (Angerbjörn & Flux 1995). The difference in body size between geographical areas is not, however, very large, and probably cannot explain in itself the great difference in observed home range sizes. But the difference in body size together with the difference in climate, plant productivity and food availability may well explain the observed variation in home range size; the large hares in the rather unproductive taiga with long-lasting snow cover need large home ranges compared to the small hares in the more productive environments of the British Isles. Furthermore, because of the cold winters in the northern areas, hares need more energy to maintain their body temperature.

Seasonal variation in home range size was evident in Finland, home ranges being largest in late winter-spring and smallest in autumn. Hewson & Hinge (1990) and Rao et al. (2003) in Scotland and Wolfe & Hayden (1996) in Ireland did not find significant seasonal differences in home range size. Hulbert et al. (1996a), on the other hand, found differences in home range size according to habitat and season; seasonal variation was large in moorland hares, i.e. in an unproductive environment. In more productive pastures and forests seasonal variation was slight. Also in the boreal forests of Sweden home ranges seem to be smallest in summer and autumn (Dahl & Willebrand in press).

Food scarcity may explain the large home ranges in late winter and spring in northern boreal forests. In Finland, the snow melts during April (the snow depth at

Table 4. Data on home range sizes of mountain hares from northeast Scotland, Ireland, Sweden and Finland. Climate data were obtained from www.worldclimate.com and included temperature data for Braemar, 57°N, 3.40°W, 339 m a.s.l. in northeast Scotland, Rosslare, 52.25°N, 6.30°W, 23 m a.s.l. in Ireland, and Umeå, 63.80°N, 20.20°E, 7 m a.s.l. in Sweden. F = female, M = male.

Area/habitat	Home range size (ha)	Reference/method	Year	Jan	Mar	Apr	Oct	Nov
NE Scotland:								
Heather moor, Heather moor with trees, Grassland-mire	mean in summer: 10.3 / mean in winter: 9.6	Rao et al. 2003, radio-tracking	6.3	1.0	2.4	4.9	6.6	3.3
Moorland Pasture Forest	mean total: 17.3 / mean total: 7.3 / mean total: 10.4	Hulbert et al. 1996a, radio-tracking	6.3	1.0	2.4	4.9	6.6	3.3
Heather moor, Pastures	mean total: 89 (F),113 (M) / mean night: 16 (F), 21 (M) / breeding season: 75 (M), 69 (F) / post-breeding season: 54 (M), 66 (F)	Hewson and Hinge 1990, radio-tracking	6.3	1.0	2.4	4.9	6.6	3.3
Heather moor	winter range, night: up to 50 / breeding season, day: 13.7 (M), 3.7 (F)	Flux 1970, sightings of marked hares	6.3	1.0	2.4	4.9	6.6	3.3
Ireland:								
Grassland, Salt marsh	mean total: 22 (F), 50 (M) / range total: 12-70 / mean night: 14 (F), 33 (M) / range night: 5-43	Wolfe & Hayden 1996, radio-tracking	10.2	6.0	7.0	8.3	11.5	8.4
Sweden:								
Boreal forest	range: 200-1300, May	Olsson 1997, radio tracking	2.8	-10.1	-3.8	1.4	4.3	-2.0
Boreal forest	yearly range: 26-806 / yearly mean: 66 (F), 219 (M)	Dahl & Willebrand in press, radio-tracking	2.8	-10.1	-3.8	1.4	4.3	-2.0
Finland:								
Boreal forest	winter: up to 310	Seiskari 1957, snow-tracking	3.6	-10.4	-3.5	2.1	4.6	-1.2
Boreal forest	yearly mean: 206, range: 91-445 / breeding season: 202, autumn: 71	present study, Evo: radio-tracking / present study, Oulu: radio-tracking	3.6 / 2.1	-10.4 / -11.8	-3.5 / -6.0	2.1 / 0.7	4.6 / 3.6	-1.2 / -2.3

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Evo during the latter half of March is on average 37 cm; weather data collected at the Evo Game Research Station). The field layer vegetation is thus under snow until late April or even early May, and in early May there is very little green grass available. During the summer, the amount of green forage increases and therefore home ranges can be smaller. The hares also used partly different core areas in different seasons, indicating that the best foraging areas may differ between seasons. In summer, the hares are mainly grazers, using different foraging areas than in winter when they are browsers of mainly deciduous trees and shrubs (Flux 1970, Hulbert et al. 1996b). The onset of the breeding season in spring may also cause an increase in the size of home ranges; in spring especially males may cross larger areas searching for females (Hewson & Hinge 1990, Dahl & Willebrand in press). The food demands of females also increase during the nursing period, which may also result in a need for larger home ranges in spring.

Conclusions

Mountain hares have larger home ranges in northern boreal forests than in Scotland and Ireland. In the northern taiga forests the climate is harsh, winters are cold and the snow cover lasts for a long time, and the growing season is short. Consequently, less food is available to hares than in the milder environment of the British Isles. Hares in northern Europe are larger than those on the British Isles, which may also affect the size of their home ranges. Seasonal variation in home range size is evident in harsh environments, but is lacking in more productive areas. Seasonal variation in home range size is probably due to differences in food availability and the breeding cycle of hares. Although the total home ranges were rather stationary in Finland, the hares used partly different core areas in different seasons, probably indicating that their favourite foraging areas differ between seasons.

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