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The effects of sex and season on home range in European hedgehogs at the northern edge of the species range

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Limited data exist on ecology of European hedgehog (*Erinaceus europaeus*) at the northern edge of the species' range. In our study, spatial analysis using radio-tracking data from Finland showed that sex and season had significant effects on the home-range size of hedgehogs. Although males were heavier than females, body weight had no effect on home-range size. Total home ranges (male 98, female 55 ha) were larger than those in southern areas. Thus, male home ranges were larger than those of females during the mating (male 72, female 21 ha) and post-mating seasons (male 48, female 20 ha), but the differences were small and reversed before hibernation (male 17, female 29 ha). Home ranges of individuals of both sexes overlapped, but females shared core areas with other females only during the mating season. Our results imply possible differences in hedgehog ecology probably due to a less productive and harsh northern habitat.

Introduction

Home range is the area over which an animal or group of animals normally travels and searches for food (Burt 1943). Thus, home-range size is an important biological parameter reflecting aspects such as sex, reproductive strategy, body weight, diet, food availability and shelter seeking (Clutton-Brock & Harvey 1978, Fisher & Lara 1999, Fisher & Owens 2000). In many mammalian species, males have larger home ranges than females (e.g. Kristiansson 1984, Dahle & Swenson 2003, Taulman & Smith 2004). Social organization and mating systems are intimately associated with spacing behaviour and thus, sex-specific home ranges can be interpreted as features of reproductive strategies (Gaulin & Fitzgerald 1988, 1989, Steinmann *et al*. 2005). In species with promiscuous and polygynous mating systems, home ranges of females are expected to depend mostly on the availability and spatial distribution of food, whereas male home-range size is mostly influenced by two limiting resources: receptive females and food (Clutton-Brock 1989, Gehrt & Fritzell 1998). Nutrition influences home-range size through size-dependent metabolic rate and habitat productivity (McNab 1963). Mammals that live in less productive habitats (e.g. arid areas, high latitudes) or utilize patchily distributed food resources have larger home ranges as they have to move over greater distances to find adequate food (Harestad & Bunnell 1979, Damuth 1981, Dahle & Swenson 2003).

The western European hedgehog (*Erinaceus europaeus*) is a hibernating insectivore with a fairly wide geographical distribution, occurring in a wide variety of climatic conditions. This species has a solitary life-style, is nocturnal, and has a promiscuous mating system i.e., both sexes court multiple partners (Reeve 1994, Jackson 2006, Moran *et al*. 2009). Males take no part in parental care and the young disperse soon after being weaned (Reeve 1994, Jackson 2006). Sex significantly influences home-range size in hedgehogs: males have larger home ranges (Reeve 1982, Kristiansson 1984, Riber 2006). Hedgehogs are not territorial, and home ranges often overlap with individuals of the opposing or same sex (Boitani & Reggiani 1984, Kristiansson 1984, Riber 2006), although there are a few divergent observations (Berthoud 1978, Karaseva *et al*. 1979).

Hedgehogs in Finland live at the northernmost limit of their distribution range. The Finnish population of hedgehogs is a result of intentional introductions that were carried out > 100 years ago (Kristiansson 1981). The hedgehog was actively introduced into new areas by man due to the assumption that it kills snakes and rats (Kristoffersson *et al*. 1966). Harsh boreal winters and a reduced supply of macro-invertebrates impose limits on food availability (Kristiansson 1981). It has been suggested that hedgehogs from different areas are physiologically adapted to the prevalent environmental conditions (Kristoffersson & Soivio 1967). Behaviour can also vary geographically within species (Lacki *et al*. 2010), highlighting the need for regional studies examining the minimum requirements and preference for each species. A significant decline in hedgehogs has been evidenced in recent years (Hof 2009) and knowledge of how species use the space available to them, especially in their northern part of the distribution range, may aid their conservation in the future. Data on the ecology of the hedgehog in northern Europe is scarce (Kristiansson 1984, Jensen 2004, Riber 2006). Specifically, information on the spatial ecology of hedgehogs in the northernmost parts of its range has not been reported. Previous studies have focused primarily on distribution (Kristoffersson *et al*. 1966, Kristiansson 1981, Terhivuo 1990) and hibernation physiology (Kristoffersson & Soivio 1964, 1967, Soivio & Kristoffersson 1974) of hedgehogs, as well as on the metal, arsenic and selenium concentrations (Rautio *et al*. 2010) in hedgehogs.

In the present study, we examined hedgehog spatial ecology based on space-use patterns during the active period from spring to autumn in an urban environment in eastern Finland. Our specific aims were to study: (1) the effect of sex, season and body weight on home-range size, (2) the effect of sex and season on home-range overlap between individuals and between seasons within individuals, (3) the shift of the home-range centre, and (4) the effect of sex and period on body weight in hedgehogs over two active periods.

Material and methods

Study area

The study was conducted in the town of Joensuu (63°N, 29°E) in eastern Finland, a medium-sized town with a population of 73 000. The study area (7.2 km^2) included the university campus area, the town centre, and the surrounding urban and small-scale garden areas. The study took place between spring 2004 and early summer 2006. The ground was covered with snow for about five months (end of November to end of April), with average snow depth being 36 cm (range 21–70 cm) in January.

Radio tracking

Twenty-five adult hedgehogs were captured by hand or in wooden mink-traps and anaesthetized (Domitor and Butarphenol Tartrate 1:1, Antisedan). Before tagging, hedgehogs were weighed, sexed, marked with uniquely numbered plastic ear tags (Dalton mini tag, UK) and checked for injuries. The transmitters (Biotrack, UK, model TW-3, 230 MHz, battery life approx. 12–13 months, weight 10–15 g (1.65% of average total body weight) were glued with acrylic resin (Unifast trad, GC Europe N.V., Belgium) directly to a mid-dorsal patch of clipped spines (*see* Morris 1988). Sexual maturity was determined based on body weight, size, and capture date. Hedgehogs reach sexual maturity in the second year of life, after their first winter hibernation (Allanson 1934, Deanesly 1934). Juveniles (from birth to first hibernation) are weaned in the end of July (average weaning time 38–44 days, Reeve 1994) and are distinguishable from adults (juvenile weight 200–235 g at around 40 days, Reeve 1994). Tagged hedgehogs (males $n = 13$, females $n = 12$) weighed between 568 and 1330 grams and were all designated as sexually mature (individuals, that had hibernated at least once).

Study animals were tracked using radio receivers (AOR8000, AOR Ltd., Tokyo, Japan) and H-shaped directional antennas. Hedgehogs carried transmitters from four days to > 1 year (Appendix 1). Active hedgehogs were radio-tracked between April and October. Eleven hedgehogs (female $n = 5$, male $n = 6$) hibernated with the transmitters.

Tracking was initiated before hedgehogs emerged in the evening and terminated after the last individuals retreated into the day nests the following morning (approximately 18:00–20:00 to 05:00–09:00). The majority of the locations (99.5%) were determined between 19:00 and 07:00. When possible, locations were taken every two hours. Hedgehogs were typically tracked from a distance of ≤ 30 m and animals were often visually observed. Research was done according to the regulations of the University of Joensuu Ethical Commission on Animal Experiments. A license to catch hedgehogs in the field was granted by the North Karelia Environment Centre.

Home range calculations

Although successive locations may not have been independent, we used them for home-range calculations because we had several tracking nights per home range (Smith *et al.* 1981), and because the interval between the locations was relatively constant (De Solla *et al.* 1999). Based on previous studies, auto-correlation in telemetry data is not problematic as long as the study has short sampling intervals over an extended period (Rooney *et al.* 1998). Nest locations as well as other inactive locations were not included in the calculation of home-range size because we studied hedgehogs' active home-range use. A minimum convex polygon 100% and Kernel 95% incremental analysis were used to show when the home-ranges reached an asymptote (Kenward 2001).

Home-range sizes of the active period of hedgehogs (April–September for males and May–October for females) as well as separate home-range sizes for the three seasons were calculated. Seasons corresponded to the phases of hedgehog breeding behaviour (Kristiansson 1984, Reeve 1994) and were also based on our observations during the field studies (mating season: 1 May–15 June, post-mating season: 16 June–31 July and pre-hibernation season: 1 August–15 September; *see* later the division of active period into three two-month periods for body weight data).

Location data (Finnish KKJ27 grid) were analyzed with the programs Ranges8 (Anatrack Ltd., Wareham, UK; Kenward *et al.* 2008), ArcGIS 9 (ESRI Inc., Redlands, CA) and Quantum GIS 1.7.1 (Quantum GIS Development Team 2012). Home ranges were estimated using the fixed Kernel method with the reference smoothing parameter (1.0). The 95% kernel (K95) was considered to represent the total home range (5% of the outermost locations including location errors and occasional trips outside the frequently used home range were eliminated). Core areas (areas of intensive use) were estimated by 50% kernel (K50) home ranges, which give the area where the animal spends 50% of its time. Minimum Convex Polygons (100%) (MCP100) were also calculated. Despite the fact that MCP100 overestimates home-range size because of the outliers and inclusion of areas never visited by individuals (White & Garrot 1990), it enables better comparison with previous hedgehog home-range studies in which MCP100 had often been used (Reeve 1982, Boitani & Reggiani 1984, Kristiansson 1984, Riber 2006, Haigh 2011).

Overlap analysis, which gives the percentage overlap between each pair of home ranges, was also conducted. Overlap of home ranges (K95, K50 and MCP100) was studied within (FF, MM) and between sexes (FM, MF) and only home ranges that overlapped were included. Overlap of home ranges among the three seasons (mating, post-mating and pre-hibernation) for each individual was also calculated. The home-range centre shift for each individual was estimated by measuring the distance between centres of K50 (kernel centre) in the three seasons using the interlocation measures in the Ranges8 software.

Body weight change

To study body weight change during the active period, tracked hedgehogs ($n = 25$) were weighed approximately every two weeks or when possible to avoid excessive disturbance. Weight data on ear-tagged, free-living hedgehogs in the study area (female $n = 77$ and male $n = 82$, weighed at least once during the active period) were also included. Juveniles (individuals < 500 g from July to the end of the active period) were excluded from analyses. Thus, all individuals included had hibernated at least once. For body-weight analysis, the active period was grouped into three two-month periods: April–May, June–July, and August–September.

Statistical analyses

Linear mixed-effects models were used to assess factors explaining the hedgehog home-range size, home-range overlap and body weight. We developed three linear mixed-effect models to test whether the number of locations recorded per animal per season influenced K50, K95 and MCP100. An individual was included as a random factor in the analyses. Prior to analyses, K95 and MCP100 were sqrt(x + 0.5)-transformed, and K50 and the number of locations (covariate) recorded per animal were log(x + 1)-transformed to meet the assumptions of normality. Range size was modeled as a function of sex, season (fixed effects) and their interaction. In these models, the weight of radio-tracked individuals per season was included as a covariate (log(x + 1)-transformed) and the individual as a random factor.

Percent overlap in home ranges (K95, MCP100) with neighbouring individuals was modeled using the sex of the neighbour, season and their interaction as fixed effects, and the individual as a random effect. Before analyses, percent overlap (P) was arcsine-transformed ($\sin^{-1}\sqrt{0.01P}$). We conducted analyses separately for males and females. Due to the low number of female-female and male-male overlaps, it was impossible to model the percent overlap of K50. Body weight (radio-tracked and ear-tagged free-living hedgehogs) was modeled as a function of sex, period and their interaction as fixed effects and the individual as a random effect. Prior to the analysis, body weight was sqrt(x + 0.5)-transformed. All statistical analyses were performed with R 2.15.0. (R Development Core Team 2012). Transformations were used to meet the assumptions of normality.

Results

Home-range size

Incremental analysis showed that less than 30 locations would be enough for reliable home-range determination. However, we chose a slightly more conservative approach and required a minimum of 30 locations to analyze home ranges per season (*see* Kenward 2001). Of the 25 radio-tracked hedgehogs, a sufficient number of locations for an estimate of home-range size was obtained for 21 individuals (10 females and 11 males; Appendix 1). The number of locations (mean ± SE) per night per animal was 4.3 ± 0.2 and tracking period (mean ± SE) per animal was 50 ± 7 nights (Appendix 1). As two hedgehogs were tracked for less than one week and two hedgehogs had too few locations per season, these individuals were excluded from the analyses. The number of locations recorded per animal per season was not positively related to MCP100 (Linear mixed-effect model: slope = 3.503, SE = 1.688, df = 19, $t = 2.075$, $p = 0.052$), K50 (slope = 0.211, SE = 0.269, df = 19, $t = 0.784$, $p = 0.443$) or K95 (slope = 1.624, SE = 1.681, df = 19, $t = 0.966$, $p = 0.346$).

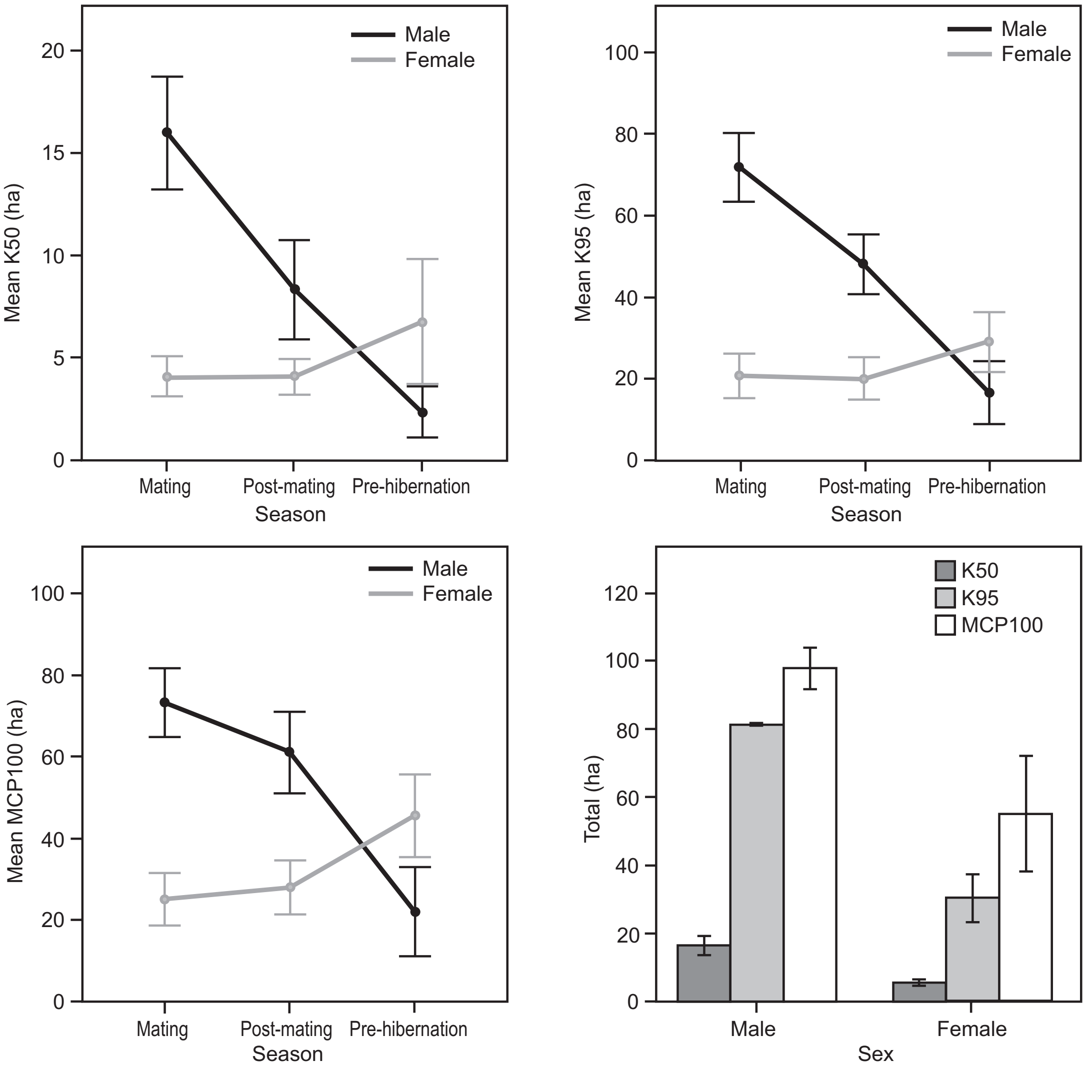

Fig. 1. Home-range sizes (± SE) of hedgehogs in different seasons, and home-range size of the active period. The number of individuals and the mean number of locations per home range (± SE): Male: mating season; *n* = 7, locations = 96 ± 12; post-mating season; *n* = 6, locations = 115 ± 16; pre-hibernation season; *n* = 5, locations = 66 ± 11; total home range; *n* = 4, locations = 266 ± 29 and female: mating season; *n* = 8, locations = 101 ± 17; post-mating season; *n* = 6, locations = 136 ± 15; pre-hibernation season; *n* = 6, locations = 120 ± 18 (31–148), total home range; *n* = 3, locations = 396 ± 16.

The home-range sizes (± SE) of males in an active period (K95: 81.6 ± 0.2 ha, MCP100: 97.9 ± 6.1 ha) were more than double that of females (30.3 ± 7.0 ha, 55.2 ± 17.1) (Fig. 1 and Table 1). Female home-range size remained rather similar until the pre-hibernation season when it increased while male home-range size decreased throughout the active period (Figs. 1a–c and 2, Table 2). Sex, season and their interaction had a significant effect on the size of K50, K95 and MCP100, while body weight did not have a significant effect on home-range size (Table 2).

We excluded the possibility that the number of locations from each individual confounds the results observed by including the number of locations as an additional explanatory variable to the full models reported above and examined the change in Akaike's Information Criterion (AIC) and model parameters. AIC increased > 1.8 after the number of locations recorded was added to

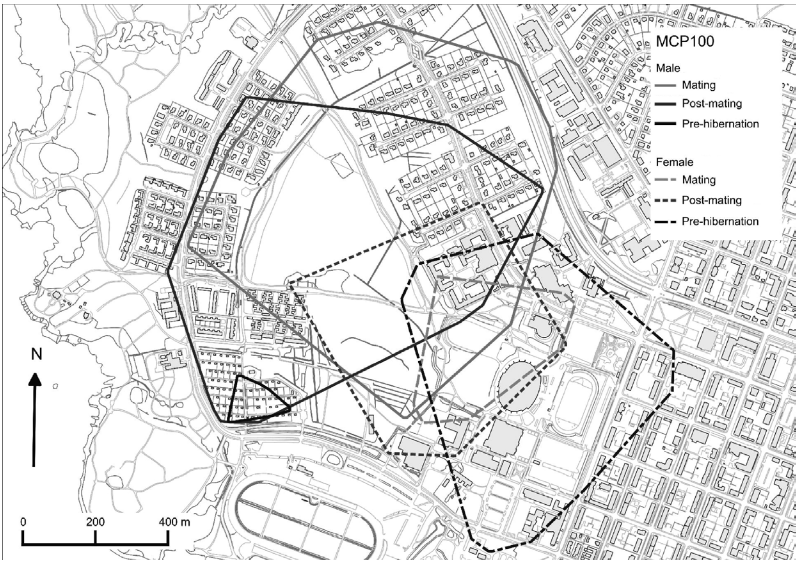

Fig. 2. Examples of the home ranges (MCP100) of male and female hedgehogs during different seasons.

the K50 and K95 models. There was no change in the significance of fixed-effect coefficients, and the effect of the number of locations remained non-significant. AIC remained approximately the same (change < 0.4) after the number of recorded locations was included in the MCP100 models, but similarly there was no change in the significance of fixed-effect coefficients and the number of locations remained non-significant.

Home-range overlap

The number of animals of both sexes overlapping in their core area (K50) with another individual or individuals was very low (Fig. 3), which made it impossible to model the percent overlap for both males and females. In fact, no female-female (FF) core areas overlapped during the post-mating and pre-hibernation seasons,

Table 1. Summary of hedgehog home-range area estimates (ha, mean ± SD). The method in all studies was radio tracking (MCP100) and only studies with a long tracking period are included. HR = home-range estimate, – = unknown, value was not reported in the study.

Sex	HR ± SD	Range	*n*	Tracking period	Study area	Study
♂	32 ± 8.9	15.5–41.5	6	Seasonal range area	(51°N, 00°W) golf course	Reeve (1982)
♀	10 ± 2.2	5.5–12.0	7		surrounded by private gardens	
♂	46.5 ± 15.8	25.0–67.7	5	114 nights	(55°N, 13°E) abandoned	Kristiansson
♀	19.7 ± 8.4	8.1–29.5	6		farmland	(1984)
♂	57.13 ± 36.6	5.5–102.5	9	March 1980 to	(42°N, 11°E) Mediterranean	Boitani &
♀	29.08 ± 20.08	10.0–56.2	5	July 1981	*maquis* region	Reggiani (1984)
♂	96 ± 24	–	4	Between May	(56°N, 10°E) mixture of arable	Riber (2006)
♀	26 ± 15	–	4	and July	land, forests and grassland	
♂	56.0 ± 0.67*	–	4	June 2008	(51°N, 8°W) rural area	Haigh (2011)
♀	16.5 ± 0.49*	–	3	to June 2010		
♂	97.9 ± 6.1	88.3–111.2	4	May 2004	(63°N, 29°E) urban area	Present study
♀	55.2 ± 17.1	23.6–82.2	3	to June 2006		

* SE.

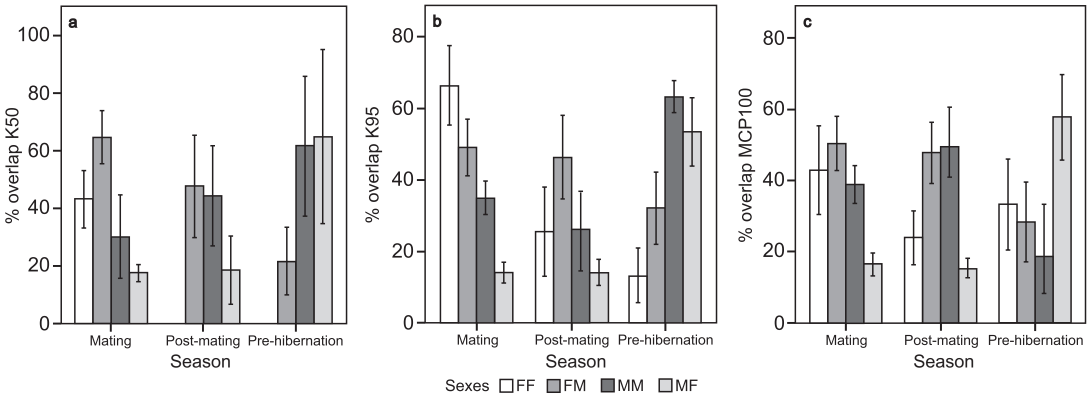

Fig. 3. Home-range overlaps (mean ± SE) over different seasons. FF = female with another female, FM = female with male, MM = male with male and MF = male with female. Numbers of hedgehogs with overlapping home ranges are given in Appendix 2.

Table 2. Results of linear mixed-effects models describing how sex, season, sex × season interaction and weight explain home-range size in hedgehogs. K95 and MCP100 were sqrt(x + 0.5) and K50 and weight were log(x + 1) transformed.

	Coefficient	SE	df	*t*	*p*
K50					
Fixed effects					
Intercept	1.025	1.877	19	0.546	0.592
Sex	–0.524	0.135	19	–3.886	0.001
Season: mating *vs.* post-mating	–0.338	0.160	11	–2.111	0.058
Season: mating *vs.* pre-hibernation	–0.874	0.208	11	–4.202	0.002
Sex × season: mating *vs.* post-mating	0.360	0.194	11	1.860	0.090
Sex × season: mating *vs.* pre-hibernation	0.952	0.230	11	4.139	0.002
Weight	0.055	0.650	11	0.084	0.935
Random effects					
Individual (SD = 0.200)					
K95					
Fixed effects					
Intercept	11.410	10.894	19	1.047	0.308
Sex	–4.196	0.770	19	–5.449	< 0.001
Season: mating *vs.* post-mating	–1.869	0.964	11	–1.939	0.079
Season: mating *vs.* pre-hibernation	–4.559	1.247	11	–3.657	0.004
Sex × season: mating *vs.* post-mating	1.889	1.188	11	1.590	0.140
Sex × season: mating *vs.* pre-hibernation	5.519	1.403	11	3.934	0.002
Weight	–1.028	3.769	11	–0.273	0.790
Random effects					
Individual (SD = 0.958)					
MCP100, Fixed effects					
Intercept	8.291	12.218	19	0.679	0.506
Sex	–3.903	0.869	19	–4.491	< 0.001
Season: mating *vs.* post-mating	–1.190	1.107	11	–1.075	0.305
Season: mating *vs.* pre-hibernation	–3.836	1.426	11	–2.690	0.021
Sex × season: mating *vs.* post-mating	1.805	1.379	11	1.308	0.217
Sex × season: mating *vs.* pre-hibernation	5.845	1.621	11	3.607	0.004
Weight	0.065	4.223	11	0.015	0.988
Random effects					
Individual (SD = 0.955)					

although the core area of females overlapped with some males during the same season (FM) (Fig. 3). During the mating season, the K50s overlapped more often with the opposite sex (K50 overlap frequencies FF and MM (male-male) = 10, FM and MF (male-female) = 18 including K50 overlaps with one or two individuals, the number of individuals with overlapping home range: female *n* = 7, male *n* = 5). A core area rarely overlapped with the same sex, but more frequently overlapped with the opposite sex during the post-mating season (K50 overlap frequencies MM = 2, FM and MF = 8 including K50 overlaps with one or two individuals: female *n* = 3, male *n* = 4) and during pre-hibernation season (K50 overlap frequencies MM = 2, FM and MF = 6 including K50 overlaps with one or two individuals: female *n* = 2, male *n* = 3).

Among females, the difference in K95 range overlap was significantly lower during the pre-hibernation season than during the mating season (Table 3 and Fig. 3b). None of the factors significantly explained the percent overlap of MCP100 in females (Table 3 and Fig. 3c). Among males, the percent overlap in K95 was explained by the sex of the neighbour, as percent overlap with other males (MM) was larger than with females (MF) (Fig. 3b and Table 3). The percent MCP100 overlap with other males (MM) was larger than with females (MF) during the mating and post-mating seasons, but the difference was reversed in the pre-hibernation season (Fig. 3c and Table 3).

Large differences in the percent overlap of K50, K95 and MCP100 between mating and pre-hibernation, and pre-hibernation and post-mating seasons suggest that locations and centres of home ranges could have shifted markedly (Table 4 and Fig. 2). This was further inspected by calculating the shifts in home-range centres (Table 5). The location of home-range core areas (K50) was quite stable in females, while larger shifts in home-range centre were observed in males, although no statistical testing was possible due to the low number of observations.

All radio-tracked hedgehogs used food sources intentionally or unintentionally provided by humans as supplements to their diet. The exact number of feeding grounds (food provided intentionally) in the study area or the times when hedgehogs visited the feeding grounds are not known because the feeding grounds were mainly in private residential gardens where movement was often restricted.

Body weight change

The mean ± SE body weight of males (858 ± 17 g, number of individuals = 95, mean ± SE number of weighings per individual 2.1 ± 0.2, range = 1–10 times) was significantly higher than that of females (757 ± 12 g, number of individuals = 89, mean number of weighings per individual 1.7 ± 0.2, range = 1–12) (Fig. 4 and Table 6). Period had a significant effect on body weight (Table 6), and there was a significant interaction between sex and period (Fig. 4 and Table 6). The mean body weights (± SE, range, *n*) for males and females in April–May were: male 755 ± 15 g, 312–1150, *n* = 57; female 667 ± 21 g, 360–915, *n* = 34; June–July: male 900 ± 27 g, 540–1555, *n* = 44; female 794 ± 15 g, 431–1092, *n* = 53 and August–September: male 1117 ± 48 g, 510–1547, *n* = 24; female 790 ± 28 g, 500–1240, *n* = 29. Females were slightly heavier than males during pregnancy in June (Fig. 4).

Male hedgehogs hibernated from August/September until April and females from September/October until May. The mean ± SE body weights prior to hibernation of radio-tracked males and females were 1286 ± 127 g (*n* = 5) and 958 ± 40 g (*n* = 4), respectively. After hibernation, the mean body weights of males and females were 924 ± 60 g and 686 ± 26 g, respectively. Thus, average weight loss during hibernation was 28% for both sexes.

Discussion

This study shows that the average home range of hedgehogs in northern latitudes is larger than that of hedgehogs living in more southern areas (Table 1). In our study area (63°N), the growing season is very short (150–175 days) (Tveito *et al*. 2001) compared with that in the more southern areas where hedgehog home ranges had been studied previously (southern Sweden 175–200 days, Denmark 200–225 days and southern Europe > 225 days: Rötzer & Chmielewski 2001, Tveito *et al.* 2001). During the short active period (< 5 months), hedgehogs have to build up body stores for hibernation. Our results are consistent with the observations that increasing latitude (> 50°N) is broadly associated with decreasing primary productivity (NPP) (Huston & Wolverton 2009), and mammals living in less productive habitats are predicted to have larger home ranges to meet their energy requirements (Harestad & Bunnell 1979, Dahle & Swenson 2003). Temperate zones offer longer growing seasons, and food availability is high for a longer period (Huston & Wolverton 2009, Hails 1982)

Table 3. Results of the linear mixed-effects models describing how the sex of the neighbour, the season and their interaction explain home-range overlaps in hedgehogs. Full models are represented. K95 and MCP100 overlap percents were arcsine-transformed.

	Coefficient	SE	df	*t*	*p*
K95: Females					
Fixed effects					
Intercept	0.967	0.177	35	5.470	< 0.001
Sex	–0.133	0.192	35	–0.691	0.494
Season: mating *vs.* post-mating	–0.378	0.342	35	–1.106	0.277
Season: mating *vs.* pre-hibernation	–0.668	0.271	35	–2.470	0.019
Sex × season: mating *vs.* post-mating	0.346	0.376	35	0.921	0.364
Sex × season: mating *vs.* pre-hibernation	0.390	0.350	35	1.116	0.272
Random effects					
Individual (SD = 0.129)					
K95: Males					
Fixed effects					
Intercept	0.618	0.056	49	10.992	< 0.001
Sex	–0.276	0.076	49	–3.643	< 0.001
Season: mating *vs.* post-mating	–0.146	0.101	49	–1.440	0.156
Season: mating *vs.* pre-hibernation	0.301	0.178	49	1.690	0.097
Sex × season: mating *vs.* post-mating	0.157	0.136	49	0.153	0.255
Sex × season: mating *vs.* pre-hibernation	0.174	0.214	49	0.813	0.420
Random effects					
Individual (SD = < 0.001)					
MCP100: Females					
Fixed effects					
Intercept	0.712	0.152	43	4.671	< 0.001
Sex	0.162	0.164	43	0.992	0.327
Season: mating *vs.* post-mating	–0.113	0.316	43	–0.357	0.723
Season: mating *vs.* pre-hibernation	–0.014	0.215	43	–0.066	0.947
Sex × season: mating *vs.* post-mating	0.050	0.346	43	0.145	0.885
Sex × season: mating *vs.* pre-hibernation	0.353	0.281	43	1.256	0.216
Random effects					
Individual (SD = 0.153)					
MCP100: Males					
Fixed effects					
Intercept	0.685	0.065	55	10.573	< 0.001
Sex	–0.294	0.079	55	–3.731	< 0.001
Season: mating *vs.* post-mating	0.108	0.107	55	1.016	0.314
Season: mating *vs.* pre-hibernation	–0.302	0.141	55	–2.140	0.037
Sex × season: mating *vs.* post-mating	–0.099	0.139	55	–0.714	0.479
Sex × season: mating *vs.* pre-hibernation	0.809	0.175	55	4.618	< 0.001
Random effects					
Individual (SD = 0.067)					

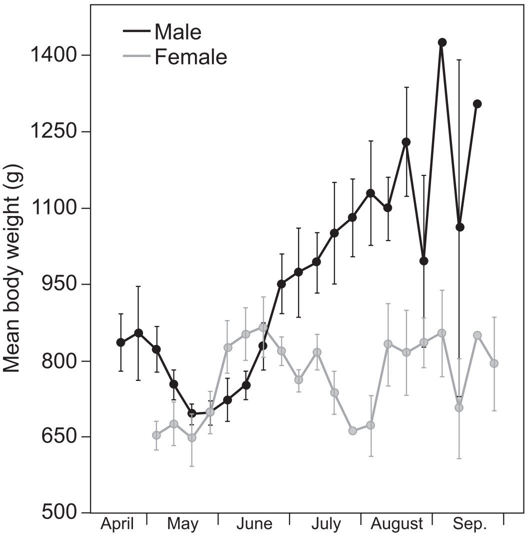

Fig. 4. Changes in body weight (± SE) during active period of hedgehogs (the number of weighings per dot in males varied between 1 and 32 and in females between 1 and 17).

thus enabling, for example, second litters for hedgehogs (Reeve 1994). Body weight did not affect home-range size in this study, although an increase in range size with increasing body weight was found in an earlier study (Dowding 2007).

On average, the estimated male home-range size was larger than that of females, which is in accordance with several previous studies (Table 1). In our study area, the mating season lasted for only four to five weeks, whereas in southern Sweden the mating season lasts for two months (Kristiansson 1981) and in Britain for up to four months (Jackson 2006). Our results, and those of the previous studies, suggest that during the short mating season males can increase fitness by roaming over large areas to consort with as many females as possible but movements clearly decline in the post-mating season (Boitani & Reggiani 1984, Kristiansson 1984, Clutton-Brock 1989).

A promiscuous mating system in hedgehogs (Reeve 1994, Jackson 2006, Moran *et al*. 2009) is consistent with the frequent overlap of home ranges found in the present study. Each individual's home range overlapped with those of several members of the opposite sex, which is expected in mammal species with a promiscuous mating system (Steinmann *et al*. 2005, Blondel *et al*. 2009). Males' home ranges overlapped more with each other, which is explained by their larger home ranges, especially during mating season. However, male spatial organization is probably mostly affected by female space use, because a male's reproductive success is dependent on the number of mates it can find and defend (Clutton-Brock 1989, Gehrt & Fritzell 1998). In solitary and promiscuous hedgehogs, receptive females are widely dispersed because of patchy

Table 4. Percent overlap of home-range locations within each individual between different seasons (mean ± SE). *n* = hedgehogs compared in each season.

	K50	*n*	K95	*n*	MCP100	*n*
Males: Season						
Mating *vs*. post-mating	31.8 ± 11.8	4	51.9 ± 12.2	4	73.5 ± 9.7	4
Post-mating *vs*. mating	47.8 ± 20.6	4	63.7 ± 4.6	4	71.8 ± 7.5	4
Mating *vs*. pre-hibernation	0.2 ± 0.2	4	9.0 ± 4.3	4	10.7 ± 3.8	4
Pre-hibernation *vs*. mating	17.5 ± 17.5	4	58.6 ± 23.7	4	55.4 ± 24.7	4
Post-mating *vs*. pre-hibernation	4.5 ± 3.2	2	14.0 ± 11.0	2	11.3 ± 9.1	2
Pre-hibernation *vs*. post-mating	65.8 ± 34.0	2	86.8 ± 13.2	2	87.9 ± 10.3	2
Females: Season						
Mating *vs*. post-mating	44.0 ± 10.7	7	66.1 ± 7.1	7	71.5 ± 7.0	7
Post-mating *vs*. mating	37.7 ± 6.8	7	66.6 ± 5.3	7	67.6 ± 9.3	7
Mating *vs*. pre-hibernation	38.1 ± 17.9	4	81.5 ± 9.5	4	95.2 ± 3.4	4
Pre-hibernation *vs*. mating	29.4 ± 18.6	4	45.6 ± 12.2	4	30.9 ± 7.7	4
Post-mating *vs*. pre-hibernation	18.5 ± 13.8	4	65.4 ± 7.2	4	70.0 ± 7.2	4
Pre-hibernation *vs*. post-mating	20.5 ± 18.1	4	39.1 ± 3.1	4	35.7 ± 7.3	4

food resources (Kristiansson 1984). This makes it difficult for males to predict the location of a female and follow and guard her.

Based on observations during radio tracking, many hedgehogs in our study area used food sources provided unintentionally or intentionally by humans as supplements to their diet. Food addition significantly changes the spatial pattern of hedgehogs' habitat use and individuals alter their searching behaviour, and learn an association between food and visual stimuli (Cassini & Krebs 1994). Furthermore, in the present study, male home-range size reduced drastically in pre-hibernation season, which could be partially related to regular supplementary feeding. However, hedgehogs do not seem to become over-dependent on supplementary food and they use it only as a supplement to their natural diets (Morris 1985, Hubert *et al*. 2011). Males also shifted the centre of the core area of their home ranges more than females during the active period (although the significance was not tested due to the low number of observations) suggesting that the breeding area in the mating season and the main foraging areas in the pre-hibernation season are located in separate areas. This could mean that the location of optimum foraging areas varies seasonally (Rühe & Hohmann 2004, Haigh 2011). In urban areas, vegetation growth and human activities can differ over the course of the active period, which can bring about distinct seasonal landscape changes, and affect the availability of resources and ease of locomotion for many of its inhabitants (Rühe & Hohmann 2004).

Among females, the changes in home-range size during the active period were smaller than among males. The core area of the home range was the smallest during nursing in post-mating season. Limited home ranges during lactation have also been observed in other small mammals (Koskela *et al*. 1997, Henry *et al*. 2002). In the beginning of the pre-hibernation season, female home-range size increased potentially due to more active food searching to accumulate fat reserves for winter. Although our results support the findings of earlier work, showing non-territoriality in hedgehogs (Reeve 1982, Boitani & Reggiani 1984, Riber 2006), we found that females tend to be more exclusive in their space use than males. Particularly interesting was the lack of the female-female core area overlaps

Table 5. The distance (m) between centres of K50 between three seasons.

	Males			Females		
	Mean ± SE	Range	*n*	Mean ± SE	Range	*n*
Mating–post-mating	380 ± 186	42–1066	4	116 ± 34	11–255	8
Post-mating–pre-hibernation	226 ± 13	213–238	2	240 ± 59	66–317	4
Mating–pre-hibernation	581 ± 169	321–1066	4	182 ± 63	8–313	4
Overall	429 ± 102	42–1066		164 ± 29	8–317	

Table 6. Results of the linear mixed-effects model describing how sex, periods and their interaction explain weight (sqrt(x + 0.5)-transformed) during a hedgehog's active period.

	Coefficient	SE	df	*t*	*p*
Fixed effects					
Intercept	26.674	0.341	185	78.213	< 0.001
Sex	–1.256	0.539	185	–2.329	0.021
Period: April–May *vs*. June–July	2.852	0.390	185	7.304	< 0.001
Period: April–May *vs*. August–September	5.798	0.541	185	10.722	< 0.001
Sex × period: April–May *vs*. June–July	–0.721	0.580	185	–1.242	0.216
Sex × period: April–May *vs*. August–September	–3.152	0.736	185	–4.282	< 0.001
Random effects					
Individual (SD = 2.328)					

during the post-mating and pre-hibernation seasons. Also the percent overlap of K95 in females decreased towards the pre-hibernation season. Additionally, in previous studies it was found that the ranges of female hedgehogs did not overlap, or overlapped only very slightly (Karaseva *et al*. 1979, Riber 2006, Haigh 2011). In Switzerland, Berthoud (1978) found that female hedgehogs had territories that were contiguous but did not overlap. However, no marking behaviour was observed and the frequent movements into other individuals' territories did not elicit aggressive responses. Exclusive space use by female hedgehogs does not seem to rise from an active defence of territory but is rather due to avoidance of same-sex individuals (Morris 1969). A high degree of mutually exclusive use of space has been widely documented in small-mammal females (e.g. Ostfeld 1990, Wolff 1993, Steinmann *et al*. 2005, Blondel *et al*. 2009). During nursing, female hedgehogs stay close to the breeding nests and thus the core areas do not overlap with those of other females. However, after weaning females' non-overlapping core areas may be a mechanism to ensure food availability by avoiding the use of the same area with others. In the present study, home-range core areas were quite stationary suggesting that females search for food in the same area during their whole active period.

Our study confirms that hedgehogs in northern Europe seem to be slightly larger than hedgehogs at more southern latitudes (Boitani & Reggiani 1984, Parkes 1975, Kristiansson 1984, Reeve 1994). We also found evidence of sexual dimorphism in hedgehog body mass. Haigh *et al*. (2012) recently reported that males were significantly heavier during their active period, whereas earlier studies had not considered the difference significant (Kristiansson 1984, Reeve 1994). In the current study, the difference in body mass between sexes was greatest during August–September. The degree of weight loss during hibernation (here 28%) was in accordance with former studies in northern Europe (20%–40%) (Kristoffersson & Suomalainen 1964, Kristiansson 1984). In more southern areas, where the hibernation period is shorter, the recorded weight loss in females was 15%–38% and only 3%–6% in males (Haigh *et al*. 2012). The weight fluctuations of both sexes were in accordance with earlier studies (Kristiansson 1984, Reeve 1994). Kristiansson (1984) reported that the average body weight of adult males decreased from May (955 g) to June (870 g), but increased considerably from June to September (870–1410 g). During pregnancy, females' weight increased, but decreased during nursing, and increased again before hibernation (Kristiansson 1984, present study). In our study area, males emerged from hibernation as early as April when there was still snow. In terms of energy supply, hedgehog males face the hardest strain during the mating season (Tähti 1978, Kristiansson 1984) and lose weight during this time (Kristiansson 1984). During mating season, foraging activities are limited and males can sustain periods of short-term starvation (Kristiansson 1984). Especially in the northern areas, a good body condition improves survival through the long hibernation period (Reeve 1994, Morris 1984) and survival through the mating season (Kristiansson 1984). Generally promiscuous species tend to show little or no sexual size dimorphism (Heske & Ostfeld 1990) and therefore, hedgehogs seem to be an exception to typical promiscuous mating systems. In hedgehogs, like in several mammals (e.g. Kristiansson 1984, Poole 1989, Sandell 1989), body weight may have a major effect on male mating success as it influences other factors like range size and searching abilities.

Conclusions

Home ranges of boreal hedgehogs are larger than those of hedgehogs living at more southern latitudes. In addition, sex and season had major effects on home-range size of hedgehogs. The mating season is clearly shorter in Finland than in more southern areas. Males may have compensated for the short mating season by trying to reach as many females as possible by maximizing their home-range area. After the mating season, home-range size of males declined and, in the pre-hibernation season, the home ranges of both sexes were almost of the same size. Although hedgehogs are not territorial, we found an interesting pattern with low female-female core-area overlap, suggesting that females avoid other females to ensure their own food availability. Males' home ranges overlapped more often with males than with females probably due to their large home ranges. This also suggests that space use by males is more flexible than by females. It is likely that food availability and parental care among females and reproductive success among males affect home range sizes and spatial organization. Behavioural patterns can be explained by the promiscuous mating system of hedgehogs. The results of this study are particularly valuable because long study period enabled us to observe the changes in spatial ecology of hedgehogs during their active period for the first time at the northern edge of the hedgehog's distribution range.

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References

Allanson, M. 1934: The reproductive processes of certain mammals. VII. Seasonal variation in the reproductive organs of the male hedgehog. — *Philosophical transactions of the Royal Society London B* 223: 277–303.

Berthoud, G. 1978: Note préliminaire sur les déplacements du hérisson Européen (*Erinaceus europaeus* L.). — *La Terre et la Vie* 32: 73–82.

Blondel, D. V., Pino, J. & Phelps, S. M. 2009: Space use and social structure of long-tailed singing mouse (*Scotinomys xerampelinus*). — *Journal of Mammalogy* 90: 715–723.

Boitani, L. & Reggiani, G. 1984: Movements and activity patterns of hedgehogs (*Erinaceus europaeus*) in Mediterranean coastal habitats. — *Zeitschrift für Säugetierkunde* 49: 193–206.

Burt, W. H. 1943: Territoriality and home range concepts as applied to mammals. — *Journal of Mammalogy* 24: 346–352.

Cassini, M. H. & Krebs, J. R. 1994: Behavioural responses to food addition by hedgehogs. — *Ecography* 17: 289–296.

Clutton-Brock, T. H. & Harvey, P. H. 1978: Mammals, resources and reproductive strategies. — *Nature* 273: 191–195.

Clutton-Brock, T. H. 1989: Mammalian mating systems. — *Proceedings of the Royal Society of London B* 236: 339–372.

Dahle, B. & Swenson, J. E. 2003: Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. — *Journal of Zoology* 260: 329–335.

Damuth, J. 1981: Home range, home range overlap, and species energy use among herbivorous mammals. — *Biological Journal of the Linnean Society* 15: 185–193.

Deanesly, R. 1934: The reproductive processes of certain mammals. Part VI. The reproductive cycle of the female hedgehog. — *Philosophical transactions of the Royal Society London B* 223: 239–276.

De Solla, S. R., Bonduriansky, R. & Brooks, R. J. 1999: Eliminating autocorrelation reduces biological relevance of home range estimates. — *Journal of Animal Ecology* 68: 221–234.

Dowding, C. V. 2007: *An investigation of factors relating to the perceived decline of European hedgehogs (Erinaceus europaeus) in Britain*. — Ph.D. thesis, University of Bristol, Bristol.

Fisher, D. O. & Lara, M. C. 1999: Effects of body size and home range on access to mates and paternity in male bridled nailtail wallabies. — *Animal Behaviour* 58: 121–130.

Fisher, D. O. & Owens, I. P. F. 2000: Female home range size and the evolution of social organization in macropod marsupials. — *Journal of Animal Ecology* 69: 1083–1098.

Gaulin, S. J. & Fitzgerald, R. W. 1988: Home-range size as a predictor of mating system in *Microtus*. — *Journal on Mammalogy* 69: 311–319.

Gaulin, S. J. & Fitzgerald, R. W. 1989: Sexual selection for spatial-learning ability. — *Animal Behaviour* 37: 322–331.

Gehrt, S. D. & Fritzell, E. K. 1998: Resource distribution, female home range dispersion and male spatial interactions: group structure in a solitary carnivore. — *Animal Behaviour* 55: 1211–1227.

Haigh, A. 2011: *The ecology of the European hedgehog (Erinaceus europaeus) in rural Ireland*. — Ph.D. thesis, University College Cork, Cork.

Haigh, A., O'Riordan, R. M. & Butler, F. 2012: Nesting behaviour and seasonal body mass changes in a rural Irish population of the Western hedgehog (*Erinaceus europaeus*). — *Acta Theriologica* 57: 321–331.

Hails, C. J. 1982: A comparison of tropical and temperate aerial insect abundance. — *Biotropica* 14: 310–313.

Harestad, A. S. & Bunnell, F. L. 1979: Home range and body weight — a reevaluation. — *Ecology* 60: 389–402.

Henry, M., Thomas, D. W., Vaudry, R. & Carrier, M. 2002: Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). — *Journal of Mammalogy* 83: 767–774.

Heske, E. J. & Ostfeld, R. S. 1990: Sexual dimorphism in size, relative size of testes, and mating systems in

North American voles. — *Journal of Mammalogy* 71: 510–519.

Hof, A. 2009: *A study of the current status of the hedgehog (Erinaceus europaeus) and its decline in Great Britain since 1960*. — Ph.D. thesis, University of London, London.

Hubert, P., Julliard, R., Biagianti, S. & Poulle, M.-L. 2011: Ecological factors driving the higher hedgehog (*Erinaceus europaeus*) density in an urban area compared to the adjacent rural area. — *Landscape and Urban Planning* 103: 34–43.

Huston, M. A. & Wolverton, S. 2009: The global distribution of net primary production: resolving the paradox. — *Ecological Monographs* 79: 343–377.

Jackson, D. B. 2006: The breeding biology of introduced hedgehogs (*Erinaceus europaeus*) on a Scottish Island: lessons for population control and bird conservation. — *Journal of Zoology* 268: 303–314.

Jensen, A. B. 2004: Overwintering of European hedgehogs *Erinaceus europaeus* in a Danish rural area. — *Acta Theriologica* 49: 145–155.

Karaseva, E. V., Gotfrid, A. B. & Dubinina, N. V. 1979: The way of life of European hedgehog (*Erinaceus europaeus*) and their role in the natural focus of leptospirosis in the Yaroslavl district by the observations over marked individuals. — *Zoologicheskii Zhurnal* 58: 705–715. [In Russian with English summary].

Kenward, R. E. 2001: *A manual for wildlife radio tagging*. — Academic Press, London.

Kenward, R. E., Walls, S. S., South, A. B. & Casey, N. M. 2008: *Ranges 8: For the analysis of tracking and location data*. — Anatrack Ltd., Wareham, UK, online manual available at http://www.anatrack.com/ranges_home.php.

Koskela, E., Mappes, T. & Ylönen, H. 1997: Territorial behaviour and reproductive success of bank vole *Clethrionomys glareolus* females. — *Journal of Animal Ecology* 66: 341–349.

Kristiansson, H. 1981: Distribution of the European hedgehog (*Erinaceus europaeus* L.) in Sweden and Finland. — *Annales Zoologici Fennici* 18: 115–119.

Kristiansson, H. 1984: *Ecology of a hedgehog Erinaceus europaeus population in southern Sweden*. — Ph.D. thesis, University of Lund, Lund.

Kristoffersson, R. & Soivio, A. 1964: Hibernation of the hedgehog (*Erinaceus europaeus* L.). The periodicity of hibernation of undisturbed animals during the winter in a constant ambient temperature. — *Annales Academiae Scientiarum Fennicae Series* (A IV) 80: 1–22.

Kristoffersson, R. & Soivio, A. 1967: A comparative long-term study of hibernation in Finnish and German hedgehogs in a constant ambient temperature. — *Annales Academiae Scientiarum Fennicae, Series A IV: Biologica* 122: 1–23.

Kristoffersson, R. & Suomalainen, P. 1964: Studies on the physiology of the hibernating hedgehog. 2. Changes of body weight of hibernating and non-hibernating animals. — *Annales Academiae Scientiarum Fennicae, Series A IV: Biologica* 76: 1–11.

Kristoffersson, R., Soivio, A. & Suomalainen, P. 1966: The distribution of the hedgehog (*Erinaceus europaeus* L.) in Finland in 1964–1965. — *Annales Academiae Scientiarum Fennicae, Series A IV: Biologica* 102: 1–12.

Lacki, M. J., Baker, M. D. & Johnson, J. S. 2010: Geographic variation in roost-site selection of long-legged myotis in the Pacific Northwest. — *Journal of Wildlife Management* 74: 1218–1228.

McNab, B. K. 1963: Bioenergetics and the determination of home range size. — *American Naturalist* 97: 133–140.

Moran, S., Turner, P. D. & Reilly, C. O. 2009: Multiple paternity in the European hedgehog. — *Journal of Zoology* 278: 349–353.

Morris, P. A. 1969: *Some aspects of the ecology of the hedgehogs (Erinaceus europaeus)*. — Ph.D. thesis, University of London, London.

Morris, P. A. 1984: An estimate of the minimum body weight necessary for hedgehogs (*Erinaceus europaeus*) to survive hibernation. — *Journal of Zoology* 203: 291–294.

Morris, P. A. 1985: The effects of supplementary feeding on movements of hedgehogs (*Erinaceus europaeus*). — *Mammal Review* 15: 23–33.

Morris, P. A. 1988: A study of home range and movements in the hedgehog (*Erinaceus europaeus*). — *Journal of Zoology* 214: 433–449.

Ostfeld, R. S. 1990: The ecology of territoriality in small mammals. — *Trends in Ecology and Evolution* 5: 411–414.

Parkes, J. 1975: Some aspects of the biology of the hedgehog (*Erinaceus europaeus* L.) in the Manawatu, New Zealand. — *New Zealand Journal of Zoology* 2: 463–472.

Poole, J. 1989: Mate guarding, reproductive success and female choice in African elephants. — *Animal Behaviour* 37: 842–849.

Quantum GIS Development Team 2012: *Quantum GIS Geographic Information System*. — Open Source Geospatial Foundation Project [available at http://qgis.osgeo.org].

R Development Core Team 2012: *R: A language and environment for statistical computing*. — R Foundation for Statistical Computing, Vienna, Austria [available at http://www.R-project.org/].

Rautio, A., Kunnasranta, M., Valtonen, A., Ikonen, M., Hyvärinen, H., Holopainen, I. J. & Kukkonen, J. V. K. 2010: Sex, age, and tissue specific accumulation of eight metals, arsenic, and selenium in the European hedgehog (*Erinaceus europaeus*). — *Archives of Environmental Contamination and Toxicology* 59: 642–651.

Reeve, N. J. 1982: The home range of the hedgehog as revealed by a radio tracking study. — *Symposia of the Zoological Society of London* 49: 207–230.

Reeve, N. 1994: *Hedgehogs*. — Academic Press, London.

Riber, A. B. 2006: Habitat use and behaviour of European hedgehog *Erinaceus euroapeus* in a Danish rural area. — *Acta Theriologica* 51: 363–371.

Rooney, S. M., Wolfe, A. & Hayden, T. J. 1998: Autocorrelated data in telemetry studies: time to independence and the problem to behavioural effects. — *Mammal Review* 28: 89–98.

Rühe, F. & Hohmann, U. 2004: Seasonal locomotion and home-range characteristics of European hares (*Lepus europaeus*) in an arable region in central Germany. — *European Journal of Wildlife Research* 50: 101–111.

Rötzer, T. & Chmielewski, F.-M. 2001: Phenological maps of Europe. — *Climate Research* 18: 249–257.

Sandell, M. 1989: The mating tactics and spacing patterns of solitary carnivores. — In: Gittleman, J. L. (ed.), *Carnivore behavior, ecology and evolution* 1: 164–182. Cornell University Press, New York.

Smith, G. J., Cary, J. R. & Rongstad, O. J. 1981: Sampling strategies for radio-tracking coyotes. — *Wildlife Society Bulletin* 9: 88–93.

Soivio, A. & Kristoffersson, R. 1974: Changes in plasma main inorganic ion concentrations during the hibernation cycle in the hedgehog (*Erinaceus europaeus* L.). — *Annales Zooligici Fennici* 11: 131–134.

Steinmann, A. R., Priotto, J. W., Castillo, E. A. & Polop, J. J. 2005: Size and overlap of home range in *Calomys musculinus* (Muridae: Sigmodontinae). — *Acta Theriologica* 50: 197–206.

Taulman, J. F. & Smith, K. G. 2004: Home range and habitat selection of southern flying squirrel in fragmented forests. — *Mammalian Biology* 69: 11–27.

Terhivuo, J. 1990: Distribution and vernal awakening of the hedgehog (*Erinaceus europaeus* L.) in Finland in 1983. — *Memoranda Societatis pro Fauna et Flora Fennica* 66: 81–90.

Tveito, O. E., Førland, E. J., Alexandersson, H., Drebs, A., Jónsson, T. Tuomenvirta, E. & Vaarby-Laursen, E. 2001: *Nordic climate maps*. — DNMI-Report 06/01, Klima.

Tähti, H. 1978: Seasonal differences in O_2 consumption and respiratory quotient in a hibernator (*Erinaceus europaeus* L.). — *Annales Zoologici Fennici* 15: 69–75.

White, G. C. & Garrott, R. A. 1990: *Analysis of radio-tracking data*. — Academic Press, New York.

Wolff, J. O. 1993: Why are female small mammals territorial? — *Oikos* 68: 364–370.

Appendix 1. Details of tracked hedgehogs; (M = Mating, P = Post-mating, Pre = Pre-hibernation, Total = active period), whether the hedgehog hibernated with a transmitter or not. F5, F9, M24 and M25 were not included in home-range calculations. – = Not enough locations (< 30) to calculate home range or individual was not tracked during that season.

ID	Sex	Total nights	Mean locations per night	Total tracking period	Number of locations per home-range estimate					Hibernation	Status
					Year	M	P	Pre	Tot.		
F1	♀	33	5.7	27.VII.05–1.VI.06	2005	–	–	139	–	Y	Transmitter failure
F2	♀	137	4.9	5.VI.04–18.VII.05	2004	36	186	145	367	Y	Transmitter was lost
					2005	194	104	–	–	N	
F3	♀	35	4.9	1.VI.–27.VII.05	2005	47	123	–	–	N	Dead: cachexy
F4	♀	60	4.5	6.V.–22.VII.05	2005	155	117	–	–	N	Dead: traffic victim
F5	♀	12	3.3	18.VIII.05–12.V.06	–	–	–	–	–	Y	Dead: pneumonia and peritonitis
F6	♀	72	4.9	3.VIII.04–6.VII.05	2004	–	–	148	–	Y	Transmitter was lost
					2005	113	–	–	–		
F7	♀	80	5.6	19.V.05–1.VI.06	2005	123	164	133	420	Y	Transmitter was removed
F8	♀	95	4.2	19.V.–4.10.04	2004	69	175	124	402	N	Transmitter was lost
F9	♀	9	4.9	27.VII.–10.VIII.04	–	–	–	–	–	N	Dead: cachexy
F10	♀	39	2.6	14.V.–22.VI.04	2004	79	–	–	–	N	Transmitter failure
F11	♀	47	3.8	13.V.–17.VII.04	2004	97	80	–	–	N	Dead: cause of death unknown
F12	♀	7	4.4	30.VIII.–9.IX.04	2004	–	–	31	–	N	Dead: traffic victim
M13	♂	25	4.8	27.VII.05–5.VI.06	2005	–	–	65	–	Y	Transmitter was removed
					2006	35	–	–	–		
M14	♂	101	3.8	12.V.04–25.V.05	2004	99	154	43	296	Y	Dead: gangerous cellulitis in the feet
					2005	77	–	–	–	N	
M15	♂	73	2.6	12.V.04–3.V.05	2004	87	85	–	178	Y	Dead: traffic victim
M16	♂	96	3.4	13.V.04–27.V.05	2004	88	160	47	295	Y	Dead: gangerous cellulitis in the feet
M17	♂	47	3.9	22.VII.04–9.V.05	2004	–	–	105	–	Y	Dead: traffic victim
M18	♂	61	4.8	12.V.–5.VIII.05	2005	150	133	–	295	N	Transmitter was lost
M19	♂	28	4.6	7.V.–8.VI.05	2005	130	–	–	–	N	Dead: gangerous cellulitis in the feet
M20	♂	21	5.1	9.VI.–18.VII.05	2005	–	93	–	–	N	Transmitter was lost
M21	♂	18	4.9	12.VII.–29.IX.05	2005	–	63	–	–	N	Dead: parasitic enteritis
M22	♂	33	3.7	22.VIII.05–31.VII.06	2005	–	–	70	–	Y	Transmitter was removed
M23	♂	29	3.6	9.V.–15.VI.04	2004	105	–	–	–	N	Dead: pneumonia
M24	♂	2	–	11.VIII.–16.VIII.05	–	–	–	–	–	N	Dead: traffic victim
M25	♂	3	–	12.VII.–15.VII.05	–	–	–	–	–	N	Transmitter failure

Appendix 2. Number of pairs (FF, FM, MM or MF) of overlapping home ranges (K50, K95, MCP100)/number of hedgehogs overlapping in their home ranges with another individual or individuals.

Season	Home range	FF	FM	MM	MF
Mating	K50	6/6	9/12	4/3	9/12
	K95	6/6	22/13	18/6	22/13
	MCP100	6/8	22/13	18/6	22/13
Post-mating	K50	0/0	4/7	2/2	4/7
	K95	2/2	10/10	8/5	10/10
	MCP100	2/2	12/11	8/5	12/11
Pre-hibernation	K50	0/0	3/5	2/2	3/5
	K95	4/3	5/8	2/2	5/8
	MCP100	6/3	7/10	4/4	7/10