Natal dispersal, adult home ranges and site fidelity of mountain hares Lepus timidus in the boreal forest of Sweden

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Using radio-telemetry we investigated natal dispersal, adult home ranges and site fidelity of mountain hares *Lepus timidus* in northern Sweden. We captured 48 leverets from 20 litters while these were still suckling and radio-tracked them for up to 37 months. Leverets showed limited dispersal; < ⅓ moved far enough to leave the home range of an average adult female. We radio-collared and tracked 73 adult hares to determine annual and seasonal home ranges along with site fidelity. Males had significantly larger annual and winter-spring home ranges than did females. Both sexes, and especially males, had significantly larger home ranges during winter-spring than during summer-autumn. Adults showed strong site fidelity. None of the adults dispersed from an established home range even though some long-distance excursions were recorded, especially for the males during the breeding season in spring. Limited natal dispersal and a high degree of adult site fidelity suggest that dispersal of mountain hares, as juveniles or as adults, occurs at a low rate in the boreal forest during prevailing conditions, i.e. during low densities and in a continuous population. We conclude that the mountain hare seems to be a philopatric species compared with other small game species in the same ecosystem.

Key words: Exploratory movement, fixed kernel, Lepus timidus, leveret, MCP, mountain hare

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The importance of spatial dynamics in management and conservation of wildlife has received increased attention in recent years (e.g. Sutherland et al. 2000, Clobert et al. 2001). Movements have the potential of buffering local variations in population numbers, and buffer zones could be used as simple means to reduce risks of potential overharvest as suggested by Willebrand & Hörnell (2001) for willow grouse *Lagopus lagopus*. At the population level, dispersal is arguably the most important movement an animal makes, because it moves individuals from one area to another. Seasonal movements can create large temporal changes in abundance, even in species that would not normally be considered migratory, but do not move animals between populations (Begon et al. 1996, Clobert et al. 2001). Natal dispersal was defined by Greenwood (1980) as dispersal from the birth site to

that of first reproduction or potential reproduction, and is often the only long-distance movement an animal will make (Dice & Howard 1951, Sutherland et al. 2000, Engen et al. 2002). Information on both natal dispersal rate and distance moved is needed to understand the effect of dispersal on population dynamics (Pulliam et al. 1992, Schumaker 1996), but such detailed information is known only for a limited number of species (Sutherland et al. 2000). Despite its importance only one previous study has been published on natal dispersal of any hare species, viz. the snowshoe hare *Lepus americanus*, tracking leverets from suckling until they had established adult home ranges (Gillis & Krebs 1999). Breeding dispersal, i.e. the subsequent movements of adults after their first reproduction (Greenwood & Harvey 1982), usually occurs at lower frequency than natal dispersal, but can be important for the lifetime reproductive success of individuals (Clutton-Brock 1988, Newton 1989). Although not within the scope of this paper, dispersal also has important consequences for population genetics (Aars & Ims 2000).

Home-range size can be used to determine the spatial scale to which dispersal distances should be weighted. Annual home-range sizes (MCP) are well known for the mountain hare *Lepus timidus* in Scotland, e.g., Hewson & Hinge (1990) found home ranges to be 113 ha and 89 ha for males and females, respectively. In Scandinavia, however, only a few limited studies have investigated home-range size, and none of them followed the hares for a whole year (Seiskari 1957, Olsson 1997).

The mountain hare is one of Sweden's most popular game species due to its extensive range; 40,000-200,000 have been bagged annually during the last 25 years. Several studies using bag data have pooled the mountain hare with capercaillie *Tetrao urogallus* and black grouse *T. tetrix* in a coherent group of small game showing similar patterns of population dynamics (Hörnfeldt 1978, Small et al. 1993). In Sweden, the synchronous fluctuation of the small game community in the boreal forest is attributed to the alternative prey hypothesis, where predators act as a link to the microtine 3-4 year cycle (Marcström et al. 1988, 1989, Lindström et al. 1994). It should be noted, however, that the periodicity and degree of synchrony may vary in different parts of Scandinavia and the former Soviet Union (Labutin 1960, Lindén 1988). Still, it is doubtful if bag data can be used to resolve any detailed pattern of mountain hare population dynamics at a local scale.

In this study we measured natal dispersal, and annual/seasonal home ranges of adult mountain hares in the boreal forest of northern Sweden. We also investigated the site fidelity of adult individuals. The aim of our study was to develop an understanding of the dispersal of the mountain hare in the boreal forest. That is, the way animals displace themselves over the landscape, both as juveniles and as breeding adults.

Material and methods

Study area
The 100-km² large study area was situated in the boreal region of northern Sweden (64°20'N, 20°10'E). The area is dominated by intensively managed coniferous forest (Ball et al. 2000). The climate is continental with cold winters (-11°C in January) and moderately warm summers (15°C in July). The altitude ranges within 90-186 m. a.s.l. Annual precipitation ranges within 600-800 mm, and the ground is usually covered with snow from November to April. The mountain hare forms a continuous population all over the boreal forest of Sweden. However, population densities are substantially lower than for snowshoe hares in the boreal forest of North America (Keith 1981, Lindlöf & Lemnell 1981).

Capture and instrumentation
Adult hares were trapped in spring (February-April) using spring-loaded bow nets (Marcström et al. 1989). The traps were baited with hay, aspen twigs and salt blocks, and were checked in the early morning and late evening. All hares captured in spring were classified as adults, because it is difficult to distinguish between adults and leverets after the age of 6-7 months (Bray et al. 2002). Individuals born the previous summer were at least seven months old at the beginning of each trapping season, because in the study area the last litter is normally born in early July. The adult hares were tagged with radio-collars equipped with mortality sensors (Biotrack, UK and AWM, US).

Leverets were caught on sight during summer (May-July) with hand-nets or long-nets. Leverets were equipped with small (3 g or 10 g) transmitters (Holohil, Canada), mounted around the neck with elastic collars. None of the leverets carried transmitters weighing > 3% of their body weight. Tagging did not affect the leverets' weight development compared with captive leverets, for which the daily weight increase was found to be close to 30 g (Pehrson & Lindlöf 1984). The median daily weight gain for 22 recaptured individuals in our study was 30.0 g (interquartile range = 28-33).

During 1997-2001, we captured 73 adult mountain hares (29% females and 71% males) and 48 leverets (58% females and 42% males). Leverets were caught from 20 separate litters; 13 from the first and seven from

310

the second litter period. Number of individuals caught from each litter ranged from one to five. On average, 2.17 (SD = 1.34) leverets were caught from litters of the first litter period and 3.00 (SD = 1.15) from the second period. Four leverets were classified as being ≤ 10 days old at time of capture, 39 as being 11-30 days old and five as being 31-56 days old.

All handling of animals in the study followed the principles and guidelines set out by the Swedish National Board for Laboratory Animals.

Dispersal of leverets

Leverets were followed from capture (as young as four days of age) to a maximum of 37 months of age for one individual, and six individuals were followed past the start of their first breeding season. Positions of radio-collared study animals were collected daily for the first month after birth using triangulation and a hand held Global Positioning System (GPS). Thereafter positions were obtained on average (± SE) every 4.1 ± 0.31 days (N = 33 individuals) for individuals up to 100 days of age, and further every 8.0 ± 0.95 (N = 12) and 20.2 ± 10.2 (N = 9) days for individuals 100-180 and > 180 days of age, respectively.

Suckling site locations, i.e. a distinct confined plot where each litter was fed by their mother, were determined by intense monitoring of females feeding their young. Distance to the suckling site was calculated for all positions of each radio-collared leveret. Mean distance for every 10-day period was calculated for each leveret from birth until death, or up to 180 days of age for the individuals that survived that long (N = 8). The average of individual mean 10-day values was calculated for each sex and litter period. Birth dates were estimated from growth curves of captive leverets (Pehrson & Lindlöf 1984).

Individuals were defined to show natal exploratory movements the day they were found at a substantial distance (50-150 m) from their suckling site. This was readily apparent, because the leverets showed very local movement patterns during their first weeks of life. We defined an exploratory phase as the period of comparatively long movements, including regular returns to their suckling site. Later the movements gradually decreased and the leverets rarely returned to their suckling site, and we defined this as the time when the juvenile home range
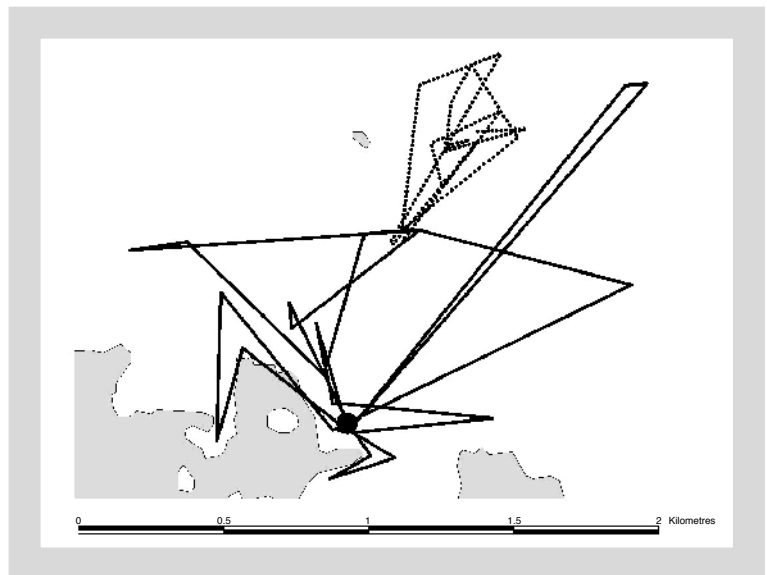

Figure 1. Early movements of a typical leveret. A natal exploratory phase was defined in time as the time from when first found substantially away from their suckling site to establishing a juvenile home range. Large dot shows < 30 days (suckling site), solid line 31-70 days (exploratory phase) and dotted line 71-90 days (juvenile home range established).

was established (Fig. 1). This home range usually overlapped the presumed home range of their mother. Leverets with a home range that apparently did not overlap the home range of its mother were defined as true natal dispersers.

Home-range analysis and fidelity of adult hares

We calculated home-range sizes of adults to obtain a threshold limit outside which hares were considered to have dispersed (natal or breeding dispersal). Locations were estimated by triangulation as outlined by Kenward (1987) using a hand-held 3-element Yagi antenna. Two different methods of home-range estimation were used: the fixed kernel method (95% and 50%) for both annual and seasonal estimates (Worton 1989), and the 100% Minimum Convex Polygon (MCP; Mohr 1947) for annual home-range estimates only. The fixed kernel estimate was used because it has been proven to be one of the most reliable estimators of animals' true range use (Seaman & Powell 1996). A smoothing factor of 0.71 was chosen for all kernel estimates, based on Kenward's (2001) suggestion that a global smoothing parameter should be used to compare home ranges. The choice of factor was done by first allowing Ranges 6 (Anatrack Ltd., UK) to allocate individual specific smoothing parameters based on least-square cross validation. We then ran a second analysis and manually specified a global smoothing function calculated as the median smoothing parameter from the first analysis. The MCP method

has been criticised, because it incorporates large unused areas and does not make use of other than the outermost fixes. We still chose to include it, because it is considered the only valid method for comparing the results with those of other studies (Harris et al. 1990).

Data from adults that survived > 1 year, with a sufficient number of positions evenly distributed over a whole year, were used for annual home-range analysis. Seasonal home ranges were estimated separately for adults during four biologically important time periods that could influence their ranging behaviour, i.e. spring (March-May, breeding and moulting), summer (June-August, suckling period), autumn (September-November, moulting), and winter (December-February, snow cover and fully moulted). Within these periods, individuals were followed intensively for 10-15 days, sampling 1-2 discontinuous night positions and one day position per 24 hours. All positions used for kernel estimates were separated by at least three hours (seasonal) or four days (annual) in time to enable the individuals to move through their entire home range between consecutive sampling occasions, thus minimising the risk of spatial autocorrelation. Schoener's ratio was calculated for all individuals in both the seasonal and annual kernel data for detection of discriminating autocorrelation (Schoener 1981, Swihart & Slade 1985). All available fixes were used for the annual MCP estimates, including seasonal fixes, because this method is not biased by autocorrelated data (Cresswell & Smith 1992).

Maximum distance ever moved from the arithmetic mean of all positions of each adult followed for at least six months was used as a measure of site fidelity. These distances were compared with twice the average maximum distance between the centre and the edge of annual MCP home ranges.

Data analyses

Ranges 6 (Anatrack Ltd., UK) was used for home-range estimation, ArcView GIS 3.2a (ESRI, USA) and Animal Movement (Hooge & Eichenlaub 2000) were used for analyses of site fidelity and natal dispersal, and SAS v. 8.02 (SAS, USA) was used for statistical analysis.

Annual home ranges were pooled over years, because we could not detect any between-year differences in home-range size. We were unable to check

for an asymptote in number of fixes in home-range calculations, as reviewed by Harris et al. (1990), because it is difficult to establish an asymptote for a non-territorial generalist herbivore like the mountain hare. To determine which minimum number of fixes to use, we performed a regression analysis to find a cut-off point where there was no positive correlation between home-range size and number of fixes. Mean values along with range are used to present natal movements and adult home ranges, as it was considered most informative. Non-parametric tests were used due to small sample sizes (number of individuals) or extreme outliers. A non-parametric equivalent to the two-way GLM, the Scheirer-Ray-Hare test (Scheirer et al. 1976), was used to test the significance of differences between seasons and sexes in the 95% seasonal home-range data, because the data did not fulfill the criteria for a parametric test. When pooled seasons contained the same individual, the mean value of the individual's home ranges was used to avoid pseudo-replication.

Results

Exploratory movements and dispersal of leverets

The suckling sites were always confined to a small area; the females fed their young at the same spot every night. On no account were these sites observed to be larger
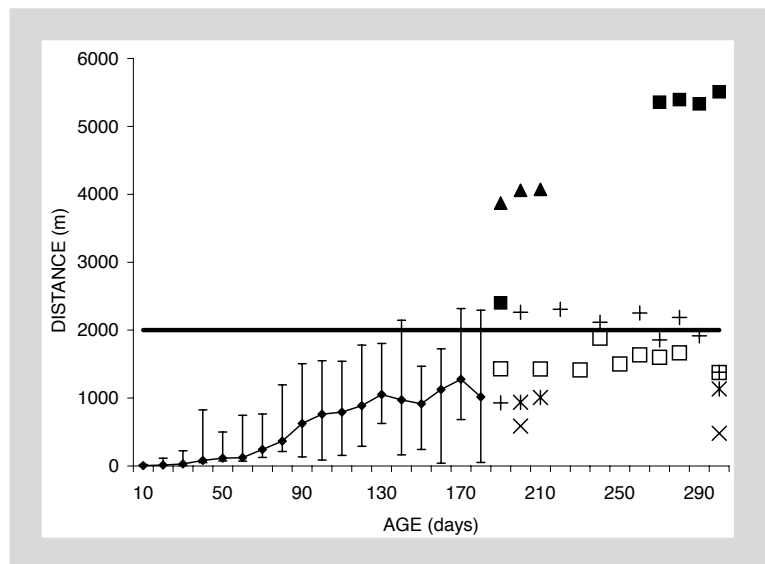
Figure 2. Dispersal distances (in m) of leverets expressed as mean and range for < 180 days, after which individual distances are given (N = 6). Filled triangles are a male, all other individual symbols represent females. One female (filled squares) was lost from day 187 until she was found again day 270. The horizontal reference line is twice the average maximum distance between the centre and the edge of annual female MCP home ranges.

than 4 m². Leverets started their exploratory phase when 17-83 days of age (median = 43, N = 24), and there was no difference between litters from different litter periods or between sexes (Wilcoxon two-sample test; litter: Z = 0.62, N = 24, P = 0.54; and sex: Z = 0.46, N = 24, P = 0.64). Movement distances away from their suckling site increased gradually with age (Fig. 2). Most leverets occasionally returned to their suckling site up to the age of 100 days. By 100 days of age all of the individuals surviving up to 180 days or more (N = 8) had settled in what would become their juvenile home range.

Mean distance moved was 762 m (range: 43-1,507 m; N = 11) at the age of 100 days and did not differ between sexes or litter periods (Wilcoxon two-sample test; sex: Z = 0.64, N = 11, P = 0.53; and litter: Z = 1.4, N = 11, P = 0.16). Mean distance continued to increase somewhat between 100 and 180 days, which was explained by formation and expansion of juvenile home ranges (see Fig. 2).

Mean distance moved at the age 180 days was 1,016 m (range: 10-2,252 m; N = 8). Only seven leverets survived beyond 180 days. Four of these, all females, kept their juvenile home ranges inside their forthcoming adult ranging area for as long as they were followed (range: 332-1,165 days), with a mean distance moved from their suckling site of 1,677 m (range: 1,490-1,939 m) over 100-1,165 days. None of these four were ever recorded > 2,832 m from their suckling site, or > 1,393 m from their mean centre of all fixes from the age of 100 days and onwards. One male was shot 1,815 m from his birth place at the age of 913 days, after his radio-transmitter had failed at the age of 180 days.

Of the seven leverets, two, one male and one female, moved again at a later stage, at the ages of 188 and 186 days, respectively. By that time, they left the juvenile home ranges they had used the previous three months, after leaving their suckling sites, and moved 4.5 and 5.5 km from their suckling sites (see Fig. 2). The male was killed one month after his second long movement started. The female was temporarily lost at the onset of her second movement; once found again in an established

home range, she remained there until the transmitter battery died 351 days after her birth. Six of the leverets were thus followed into or past their first breeding season, after which the breeding dispersal of adults was studied.

Annual home-range sizes and fidelity of adults

All individuals with at least 19 positions evenly distributed over one whole year (17 males, 11 females) were used for annual home-range analysis. Size of home ranges appeared to be saturated at about 20 fixes, and increasing the number of fixes (range: 19-111 for MCP and 19-45 for kernel) did not significantly increase home-range areas (range: 40-631 ha for MCP and 26-806 ha for kernel; r = 0.20 and r = 0.08, respectively). The mean Schoener's ratio was 1.41 ± 0.39 (SD) for the annual kernel data (N = 28), which we considered acceptable in accordance with Kenward (2001).

Mean MCP sizes (mean and range) were 280 ha (86-631) for males and 116 ha (40-315) for females. Male and female home ranges differed significantly both for the MCP (Wilcoxon two-sample test: Z = 3.01, N = 28, P = 0.003) and the 95% fixed kernel estimate (Wilcoxon two-sample test: Z = 3.76, N = 28, P = 0.002; Table 1). The kernel home-range sizes decreased steeply as the outermost positions were eliminated, however, the difference for 50% fixed kernel home-range size between sexes was still highly significant (Wilcoxon two-sample test: Z = 3.67, N = 28, P = 0.0002; see Table 1).

We followed 46 adult hares (33 males and 13 females) to investigate site fidelity. Of these, 16 were followed for more than six months, 20 for more than one year, nine for more than two years and one for more than three years. None of the 46 individuals ever remained for a longer period outside their established home range even though some temporary long-distance movements were found. The most extreme was one male once found 4,775 m from his home range centre in spring. Annual MCP home ranges corresponded to average maximum distances between the arithmetic centre and the edge of 1,680 m for males and 1,000 m for females. Using twice these distances as measures of extreme outliers, i.e. exploratory movements, we found that only three (9%)

Table 1. Annual and seasonal fixed kernel home range sizes (95% and 50% cores; in ha) of adult mountain hares, expressed as mean with N and range given in parentheses. See text for differences between groups.

Season	Fixed kernel home range size							
	Males 95%		Males 50%		Females 95%		Females 50%	
Annual	219	(17, 57-806)	42	(17, 14-95)	66	(11, 26-151)	14	(11, 6-28)
Winter	92	(6, 59-153)	23	(6, 15-31)	47	(3, 7-93)	6	(3, 1-10)
Spring	123	(6, 78-290)	29	(6, 16-76)	68	(7, 33-93)	18	(7, 7-42)
Summer	66	(7, 18-159)	10	(7, 5-16)	40	(7, 8-69)	9	(7, 1-16)
Autumn	39	(8, 16-61)	9	(8, 2-15)	23	(5, 7-45)	5	(5, 2-10)

of the males and one (8 %) of the females were ever recorded outside these boundaries.

Seasonal home-range sizes

We sampled 49 seasonal home ranges during five years and found no correlation between number of fixes (range: 22-33) and home-range sizes (range: 7-290 ha; $r = 0.02$). Schoeners ratio was (mean ± SD) 1.21 ± 0.44.

The Scheirer-Ray-Hare test ($F = 23.5$, df = 7, $P < 0.002$) showed that both sex ($P = 0.013$) and season ($P < 0.001$) had a significant affect on home-range size, although there was no significant interaction between the two factors ($P = 0.928$). A Duncan multiple range test ($P = 0.05$) grouped the seasons in two groups: winter-spring and summer-autumn. A sex difference in home-range size was found in the winter-spring season (Wilcoxon two-sample test: $Z = 2.05$, $N = 21$, $P = 0.043$), but not in the summer-autumn season (Wilcoxon two-sample test: $Z = 1.46$, $N = 17$, $P = 0.145$; see Table 1).

Discussion

Suckling sites were important reference points for the litters, because the females always used one particular site throughout the suckling period of a litter. The females never moved or deserted their young even when disturbed, e.g. by capture efforts during suckling. Approximately 20 minutes after being disturbed the litter gathered again and the mother returned to continue feeding. One female was observed using the same site for two consecutive litters. No third litter period was observed during the study, which conforms to expectations at this latitude (Myrberget 1983). The suckling sites were typically characterised by lush vegetation, probably of good nutritional value.

It is difficult to suggest any factor that determined the onset of the exploratory phase, and there was a large variation in the age when leverets started to leave their suckling site to explore the surroundings. Even though they had started exploring, it was not uncommon that they returned 2-3 days later to suckle. It was always the young that chose not to return to the suckling site, as the females continued showing up on their sites 2-3 days after the last leveret stopped returning. The distribution of distances shows that most leverets moved < 2 km. Only two leverets truly dispersed, and both in a second distinct movement at similar ages (186 and 188 days of age) even though they came from different litter periods. This second movement is comparable to observations on grouse species (Schroeder 1986, Willebrand

1988, Smith 1997). It seems to be the onset of spring that triggers this second movement in grouse, whereas the hares in our study moved in the winter period (November and January) long before spring and the first breeding period in late February - early March. Although the sample size is small, it is obvious that both males and females can disperse well away from their mothers' home ranges, however, most of them chose not to do so. In addition, adult males can show long-distance excursions in spring and all leverets, including the dispersers, were within the range of such breeding excursion movements.

Males did not move further during their exploratory phase than females, which is inconsistent with the general mammalian pattern (Greenwood 1980, Sutherland et al. 2000). The rate and distances of natal dispersal observed in our study are comparable with those of other herbivores of similar sizes, usually showing a left skewness with a few outliers that move longer distances (Sutherland et al. 2000). Onset of dispersal and dispersal distances for snowshoe hares reported by Gillis & Krebs (1999) are similar to our findings. The extreme distances of up to 200 km reported for the mountain hare by Sutherland et al. (2000) refer to Angerbjörn & Flux (1995), who reported results from released hares that had been bred in captivity.

We were unable to differentiate between juveniles and adults caught in late winter and early spring, but in other studies the proportion of juveniles in winter ranged within 47-84% (Angerbjörn & Flux 1995). Because we never observed any dispersal in our group of hares, we suggest that breeding dispersal is almost non-existent, even though some long-distance excursions were recorded. These excursions were mostly made by males in late winter and spring, presumably to locate females for mating. Of the males and females followed over one year, 80 and 23%, respectively, made their longest movement from their arithmetic mean centre during late winter or spring. The rest of the individuals had their longest movement spread evenly over other parts of the year. All of the individuals that were found far away from their normal range were checked within a few days and had always returned by then. We conclude that most leverets did not show true natal dispersal according to our definition; neither did we observe any breeding dispersal. Even the leverets that were classified as true natal dispersers were within the range of their parents when compared to the distance of occasional exploratory movements recorded for adults.

It can be expected that most hares could find increased quality and quantity of food and cover by relocating to new areas, but we never observed such shifts. Adult dis-

persal has not been observed in woodland grouse, the other dominating small herbivore of this boreal system (Willebrand 1988, Smith 1997) either. We suspect that the gain in food and/or cover does not compensate for the loss of knowledge about secure sites and escape routes in an established home range. Thus previous knowledge of an area can be an important habitat quality.

Adult home-range sizes in our study are comparable to those of other studies in Scandinavia (Seiskari 1957, Olsson 1997), but larger than those reported from Scotland (Hewson & Hinge 1990, Hulbert et al. 1996, Rao et al. 2003) and Ireland (Wolfe & Hayden 1996). Adult males had significantly larger annual home ranges than did females, which was due to larger winter-spring home ranges. Both sexes had larger winter-spring than summer-autumn home ranges, as expected from increased activity during the breeding season. We found no difference in summer-autumn home ranges between males and females. Consecutive seasonal home ranges of individual animals showed a limited overlap, suggesting that the hares adjusted their habitat use according to seasonal conditions. Common core areas were often used between seasons, however, and it is possible that they contained some important patches of food or cover that was incorporated in the individuals' home range throughout their life; this is being investigated in an ongoing study.

The apparently limited rate of natal dispersal and lack of breeding dispersal in the mountain hare suggest that population dynamics should show strong local characteristics, even more local characteristics than the grouse in the same small-game community, where especially females move longer and at a higher rate (Willebrand 1988, Smith 1997, Warren & Baines 2002). Thus, we anticipate that small-game management actions in the boreal forest, such as reducing red fox *Vulpes vulpes* in an area (Marcström et al. 1989), would induce a stronger local increase in mountain hare density than in capercaillie and black grouse. The short movements, low rate of true natal dispersal, and strong site fidelity observed in our study may not apply to populations in less homogenous habitats, e.g. the fragmented agricultural/forest landscape in mid-Sweden. It is also possible that the rate of natal dispersal would increase with higher densities as has been suggested by Boutin et al. (1985) for snowshoe hares. However, the readily observed malnutrition of snowshoe hares during density peaks has never been observed for the mountain hare in the boreal forest.

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