Life and Death of the Mountain Hare in the Boreal Forest of Sweden

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Abstract

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The mountain hare (Lepus timidus) is historically one of Sweden's most appreciated game species. Nevertheless, little is known about how the mountain hare lives its life, especially in its main habitat, the boreal forest. This is probably due to the challenges involved in studying an animal with a low population density and solitary life style.

The main objective of this thesis was to estimate several basic, and so far unknown, demographic parameters of relevance to the population dynamics of the mountain hare. The thesis is based on data from captured and radio-marked wild hares (73 adults and 48 leverets). In addition, one study also includes data from 65 released captive-reared leverets.

Leveret survival was low. From two weeks of age they exposed themselves and became easy targets for a wide range of predators. Once they had established a home range their survival became comparable to that of adult hares. Adult hares showed high annual survival rates. The lowest seasonal survival was found in males during the mating season in spring. Predation, especially by the red fox, is the main cause of mortality for both leverets and adult mountain hares. Mountain hare survival was synchronized with the abundance of small rodents; as vole density decreased, hare mortality increased. My results suggest, in accordance with other studies, that mountain hare population dynamics in the boreal forest of Sweden are driven by predation as suggested by the alternative prey hypothesis. Even though the hares had large home ranges, the species may still show very local population dynamic patterns. During the study, none of the adults moved from their initial home range, and only a small proportion of the leverets clearly dispersed from their birth place. An individual's contribution to coming generations will thus mainly be made in the area where it was born.

I suggest that the hare's accumulated experience of an area, rather than physical resources, may explain the adult hares' annually sedentary behaviour and, in effect, their high survival rate. Within this "area of experience", however, the hares tracked changing physical resource availability between seasons.

Keywords: Lepus timidus, survival, mortality, home range, dispersal, habitat, resource selection, population dynamics.

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Appendix

Papers I-V

I base my thesis on the following papers, which I refer to by their Roman numerals.

I. Dahl, F. & Willebrand, T. Survival rates and mortality causes of the mountain hare (*Lepus timidus*) in the boreal forest of Sweden. (Manuscript).

II. Survival rates and mortality causes of captive-reared mountain hares (*Lepus timidus*) released in different geographical areas in Sweden (Manuscript).

III. Dahl, F. Rest site characteristics and flushing distances of the mountain hare (*Lepus timidus*) in the boreal forest. (Manuscript).

IV. Dahl, F. and Willebrand, T. Natal dispersal, adult home ranges and site fidelity of mountain hares (*Lepus timidus*) in the boreal forest of Sweden. (Accepted for publication in *Wildlife Biology*).

V. Dahl, F. Distinct seasonal habitat selection by annually sedentary mountain hares (*Lepus timidus*) in the boreal forest of Sweden. (Accepted for publication in *European Journal of Wildlife Research*).

Papers IV and V are reproduced with kind permission from the publishers of the journals concerned.

Introduction

Hares are found in most of North America and nearly the entire old world, including Africa and are divided into approximately 29 species (Flux & Angermann, 1990). The mountain hare (*Lepus timidus*) is an arctic/sub-arctic species continuously distributed in the Eurasian taiga and tundra belt, with isolated populations in Ireland, Scotland, the European Alps and Japan (Flux & Angermann, 1990; Angerbjorn & Flux, 1995). It belongs to a circumpolar species complex, and is replaced by (*L. othus*) in Beringa and (*L. arcticus*) in North America and northern Greenland (Best & Henry 1994a; Best & Henry 1994b; Angerbjorn & Flux, 1995). The mountain hare is the only native hare species in Sweden, and is considered an important game species. It probably re-colonized the country approximately 12,000 years ago after the ice cover from the last ice age disappeared (Bergengren, 1969; Liljegren & Lageras, 1993), and is now distributed throughout all of Sweden, except for the southern part of our most southern county, Skane (Pehrson, Jansson & Helldin, 2002). In mid- and southern Sweden the mountain hare is sympatric and interbreeds with the introduced brown hare (*Lepus europaeus*) (Thulin, 2000), which occurs in the southern half of the country along the east coast, but is absent in the northern, more homogenous, boreal forest landscape (Pehrson, Jansson & Helldin, 2002).

The mountain hare

We have reasonably good knowledge of basic biology of the mountain hare, mainly from studies on dead (i.e. shot) or captive animals (*e.g.* Hoglund, 1957; Hewson, 1968; Flux, 1970; Hewson, 1970; Pehrson, 1981; Pehrson & Lindlof, 1984). The mountain hare has a promiscuous breeding strategy with a gestation time of approximately 50 days, followed by a new conception within hours after the litter is born (Hoglund, 1957). They typically give birth to two litters in northern Scandinavia and three in the south (Hoglund, 1957; Myrberget, 1990; Broseth & Pedersen, 2000). Mountain hare females give birth to 3-6 young per year (Flux, 1970; Hewson, 1976; Pehrson & Lindlof, 1984; Naumov, 1947; Naumov, 1960), and Hoglund (1957) found that on average 2.15 leverets were born in the first litter and 3.24 in the second. Hares in general differ from the other lagomorphs (jackrabbits, true rabbits and pikas) by giving birth to fully furred leverets, born with their eyes open and ready to move within minutes (Corbet, 1983). Leverets of captive-reared mountain hare females fed natural food weigh 108.5g at birth (Pehrson & Lindlof, 1984), and are dependent on milk from their mother for about 10 days (Flux, 1970). They start consuming vegetative food around the same age (Barikmo & Pedersen, 1997; Paper IV). The mountain hare is a generalist herbivore that can survive on low quality food if necessary due to its well adapted appendix (Pehrson, 1981; Pehrson, 1983; Pehrson, 1990; Hulbert, Iason & Mayes, 2001). In summer, mountain hares prefer grasses and herbaceous plants with high nutrient content, while in winter deciduous bushes (mainly birches (*Betula* spp.), rowan (*Sorbus* spp.) and willows (*Salix* spp.) dominate the hare's diet (Angerbjorn & Flux, 1995). Bilberry (*Vaccinium myrtillus*) is considered important during spring, late autumn and winters with poor snow cover (Pehrson, 1981; Barikmo & Pedersen, 1997).

The mountain hare is non-territorial and individual home ranges overlap each other (Flux, 1970; Hewson, 1976; Hewson & Hinge, 1990). Minimum convex polygon home range sizes, which can be compared between studies, have been estimated in the range of 15-89 ha for females and 20-113 ha for males in Great Britain (Hewson & Hinge, 1990; Hulbert *et al.*, 1996; Wolfe & Hayden, 1996; Rao *et al.*, 2003). Only a few limited studies have estimated home range sizes in Scandinavia; Seiskari (1957) estimated mean spring ranges for two individuals to 188 ha, Barikmo & Pedersen (1997) refer to a study investigating winter (80 ha) and spring (152 ha) home ranges of four individuals, while Lindlof (1987) gives a rough annual estimate of 200 ha in Sweden. Dispersal rates and distances have never been reported for the mountain hare in Scandinavia, even though such information may be very important for understanding hare population dynamics. On the Swedish mainland annual survival has been estimated to 0.34 in one previous study (Lindlof & Lemnell, 1981). Lemnell & Lindlof (1982) further estimated monthly summer survival of wild adults to 0.93, while captive-reared and released hares had a monthly survival rate as low as 0.18. Marcstrom *et al.* (1989) report annual adult survival rates of 0.52 and 0.64 for two islands in the north of the Gulf of Bothnia. Angerbjorn (1989) estimated annual survival rates of between 0.14 and 0.86 for five islands of the south coast of Sweden. In addition Angerbjorn (1986) gives an approximate estimate on juvenile survival from birth until next spring of 0.3. Annual adult survival in Scotland has been investigated more closely and ranges from 0.06-0.44 (Flux, 1970; Hewson, 1965; Hewson, 1976), with the highest mortality occurring from February to May (Flux, 1970). Juvenile survival, excluding the first six weeks after birth, range from 0.06-0.30 (Hewson, 1965; Hewson, 1976).

Prevailing hypothesis in hare population dynamics

All natural populations can be assumed to fluctuate, at least to some extent, due to environmental stochasticity (Turchin, 2003). Some population fluctuations are thought to be regulated around an equilibrium density, while others are not (Royama, 1992, Sinclair, 1989). The fluctuations may also have a cyclic pattern, *i.e.* a statistically significant periodicity (Berryman, 2002). The reasons for the fluctuations, other than stochasticity, may differ widely between species or even between populations. Basically, births, deaths, immigration and emigration determine the density of any animal population (Begon, Harper & Townsend, 1990). These four parameters are however influenced by a number of factors which decide how stable the density is over time. Each species has its own intrinsic “setting”, *i.e.* life-history traits, which lays the boundaries for *e.g.* how many offspring a female can produce, and thereby also how fast the population can grow, during different outer conditions (Begon, Harper & Townsend, 1990). Animals also interact, both within (*e.g.* social interactions, resource depletion) and between (*e.g.* predation, resource competition) species, which may affect both their survival and their movement to or from an area (Sutherland, 1996).

The best known population dynamic system of any lagomorph is the 10-year cyclic pattern of the snowshoe hare (*Lepus americanus*) - lynx (*Lynx lynx canadensis*) system in North America, first described by Elton (1927). Lloyd Keith and co-workers were the first to monitor the snowshoe hare in closer detail and to describe the machinery driving changes in hare numbers (*e.g.* Cary and Keith, 1979; Keith, 1981; Keith *et al.*, 1984). They found that declines in hares were initiated by winter food shortages during peek years in hare density (up to 3,100 hares per km2; Keith & Windberg, 1978) and exacerbated by predator numerical responses lagging behind hare numbers by 1-2 years (Keith, 1974; Vaughan & Keith, 1981; Keith, 1983). When the hares become scarce, predators decline in density and the vegetation recovers, where after hares can start increasing again. Food resources have been found to limit mountain hare density in winter on Swedish west-coast islands where densities can reach >300 hares per km^2 (Angerbjorn, 1981). The habitat on these islands are, however, more similar to the heather dominated Scottish highlands than the Swedish mainland, which means that in years with deep snow cover the food resources will become largely unavailable to the hares. In a feeding trial on captive hares, Pehrson & Lindlof (1984) found that leveret birth weights were significantly higher if the females were fed high quality food in winter. Such effects in early development are likely to have significant demographic consequences in, for example, agricultural landscapes with crop rotation. Food limitation is however unlikely to limit the low density mainland population in Sweden, estimated to 3.3 hares per km^2 by Lindlof and Lemnell (1981). In addition, there are no reports of malnutrition for the mountain hare in the Scandinavian boreal forest on the mainland where the food resources are plentiful.

Krebs and co-workers tested Keith's food hypothesis in two large scale experiments (Krebs *et al.*, 1995; Krebs, Boutin & Boonstra, 2001; Krebs *et al.* 2001; Boutin *et al.*, 2002). They advocate, contradictory to Keith (1983), that food shortage is not involved in initiating the decline phase of snowshoe hares (Krebs *et al.* 1995, Boutin *et al.* 2002). Instead they found predation to be the initiating factor, especially the predation caused by red squirrels (*Tamiasciurus hudsonicus*) and arctic ground squirrels (*Spermophilus parryii*) (Krebs *et al.* 1995, Boutin *et al.*, 2002). Squirrel and ground squirrel predation on young (less than two weeks old) leverets can lead to extremely high mortality (50%) during peak years, thereby making it possible for the overall predator community to halt the increase phase (Odonaghue 1994, Boutin *et al.*, 2002). Predation is also considered to be the main factor limiting the mountain hare density in Scandinavia, and the red fox is believed to be the main predator (Lemnell & Lindlof, 1982; Marcstrom *et al.*, 1989; Lindstrom *et al.*, 1994). The mountain hares in Scandinavia show regular fluctuations in density, which in several studies have been found to be synchronized to the 3 to 4-year cyclic pattern of small rodents according to the alternative prey hypothesis (Lack, 1954; Hornfeldt, 1978; Marcstrom *et al.*, 1989; Lindstrom *et al.*, 1994; Smedshaug *et al.*, 1999). The alternative prey hypothesis (Siivonen, 1948; Hagen, 1952; Lack 1954), suggests that generalist predators prey almost exclusively on voles when they are abundant, but as vole numbers decline the predators switch to preying on alternative prey instead (*i.e.* small game such as hares and grouse) until vole numbers have increased again.

Although not a strong candidate for driving the mountain hares cyclic pattern in Scandinavia (Hornfeldt, 1978), parasites are suggested to be important elsewhere. Naumov (1947, 1960), for example, argued that parasites are a major component in explaining regular/cyclic fluctuations in mountain hare numbers throughout large areas of Russia. Similar systems have been found in Scotland, where red grouse cycles seem to be driven by parasites (Hudson, Dobson & Newborn, 1998, 2002). Parasites have also been found to reduce body condition and fecundity of female mountain hares in Scotland, and are suspected to play an important role in their population dynamics (Newey, Thirgood & Hudson, 2004; Newey & Thirgood, 2004; Newey *et al.*, 2005). Diseases have been found to cause occasional severe population declines in Sweden. In the 1960's an outbreak of tularaemia in Sweden was probably responsible for the reduced harvest from 140,000 to 75,000 animals in one year (Hornfeldt, 1978). Although largely unexplored, parasites and diseases are, however, unlikely to drive the cyclic density pattern of the mountain hare on mainland Sweden. Hare densities are generally very low compared to Scottish highland populations where up to 245 hares can be found per km^2 (Watson & Hewson, 1973; Watson *et al.*, 1973; Newey, 2005). The low densities combined with cold winters and prolonged snow cover typical of Fennoscandia may be expected to reduce parasite density and transmission rates (Newey, 2005).

Concerns for management

The mountain hare has, at least for the last 65 years, been one of Sweden's most appreciated game species. Only a few mammalian species, such as the moose (*Alces alces*) and the roe deer (*Capreolus capreolus*), have occasionally exceeded the mountain hare in annual bag, mainly due to drastic increases in their population numbers indirectly caused by man (Ericson, 1999; Kjellander, 2000). Between 40,000 and 200,000 mountain hares have been bagged annually from 1939 until present. The recreational contribution of the mountain hare hunt is, however, likely to be much more important to the hunters than the number of animals bagged. Among the specialized hare hunters, 74% spend more than 20 days per year on their favourite game, while only 30% of the hunters specialised on moose and 35% of the grouse (*Tetraonidae*) hunters do the same (Unpublished data). In spite of the large interest in the species, surprisingly little is known about how the mountain hare lives its life. It is difficult to study any wild animal with a low population density and a solitary life style, and the mountain hare in the boreal forest is such an organism.

The population dynamics of mountain hares in Scandinavia is relatively well understood for confined islands (*i.e.* closed populations with limited dispersal in or out), thanks to several successful projects (Angerbjorn, 1986; Marcstrom *et al.*, 1989). From bag data, much has also been learnt regarding the population dynamic pattern on the mainland, such as the mountain hare's role as an alternative prey to small rodents (Hornfeldt, 1978; Angelstam, Lindstrom & Widén, 1985; Lindstrom *et al.*, 1994, Smedshaug *et al.*, 1999). Bag data are, however, unlikely to ever resolve the population dynamic pattern in any detail (Paper I). Consequently, although being one of Sweden's most appreciated game species, there are still large gaps in our knowledge of many basic parameters influencing mountain hare population dynamics, especially in the boreal forest of mainland Scandinavia. Some parameters, *e.g.* age specific survival, adult mortality causes and home range sizes, are known to some extent, while others, *e.g.* mortality causes in pre-weaning leverets, dispersal rates and dispersal distances, are largely unknown for the species. All such estimates are of uttermost importance for a sound future management of the mountain hare and are addressed more closely in this thesis.

Objectives

The main objective of this thesis is to estimate several basic, and so far unknown, parameters which are likely to be relevant for the population dynamics of the mountain hare in the boreal forest of Sweden, where it exists naturally and without interference by the brown hare. By putting these estimates into context I also aim to enhance our understanding of the population dynamics of the species in more general terms. More specifically my objectives in paper I-V were the following:

Paper I - To estimate survival rates and mortality causes of leverets as well as of adult mountain hares in my main study area in the boreal forest of northern Sweden.

Paper II - To compare survival rates and mortality causes of captive-reared mountain hares released in three different parts of Sweden. In addition, I calculate rates of movements to find out if released hares behave differently in the different areas. In one of the areas I also compare survival rates, rates of movement and day-rest cover of the released hares to that of wild adult hares.

Paper III - To determine if the mountain hare in the boreal forest select for any specific habitat when selecting day-rest site, and if the rest sites chosen by hares have denser cover than what could be expected by chance. In addition I also investigate which factors are influencing the distances at which the hares flush from their rest sites.

Paper IV - To develop an understanding of the dispersal pattern of the mountain hare in the boreal forest, that is, the way animals displace themselves over the landscape, both as leverets and as breeding adults. In this study I further estimate seasonal and annual home ranges of adults.

Paper V - To determine how far apart consecutive annual and seasonal home ranges of the same individual are situated, how much they overlap each other, and if habitat preference can explain the high site fidelity observed in paper IV.

Material and methods

Study areas

The approximately 100 km^2 large main study area, Kroksjö (64°20´N, 20°10´E), is situated within the middle boreal forest region of northern Sweden (Ahti, Hamet-Ahti & Jalas, 1968) (Figure 1). The area is dominated by coniferous forest intensively managed for timber production. A few human settlements occur within the area, where small patches of land are used for agricultural production (<1% of the total area). The climate is continental, with moderately warm summers (mean; 14 °C in July) and cold winters (mean; – 12 °C in January). The ground is usually covered with snow from November to April. Two other smaller study areas (<10km^2) were used in one of the studies (Paper II). One of these, Boda (61°30´N, 16°50´E) is also situated in the boreal forest region of northern Sweden (Figure 1), and has similar landscape- and climatic characteristics as the main area. The other area, Mark (57°30´N, 12°50´E), lie in the more fragmented agricultural-forest landscape of southern Sweden (Figure 1). The climate in this part of the country is generally warmer (mean; 16 °C in July and mean; – 2 °C in January), with a snow cover from December-March.

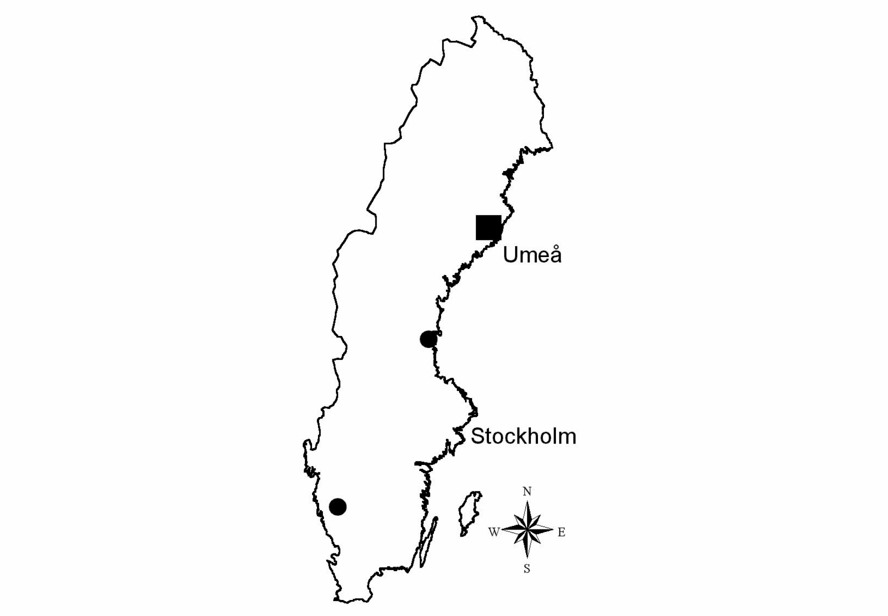

Figure 1. The main study area (Kroksjö), 30 km NW of Umeå in northern Sweden, and the two additional sites in mid-Sweden (Boda) and in southern Sweden (Mark).

Methods

My studies are based on individually marked adult and juvenile mountain hares. Seventy-three wild adult mountain-hares (29% females and 71% males) and 48 wild leverets (58% females and 42% males) were captured and radio-marked from 1997–2001 (Paper I, IV). In addition, 65 captive-reared leverets (65% females and 35% males) between 5 and 7 weeks of age were radio-marked and released from 1996-1997 (Paper II).

I trapped wild adult hares in spring (February–April) using spring-loaded bow nets (Marcstrom *et al.*, 1989), and tagged them with radio-collars equipped with mortality sensors (Biotrack, UK and AWM, US). I captured wild leverets on sight during summer (May–July) with hand-nets or long-nets (Paper I, IV). Leverets were equipped with small (3 g or 10 g) transmitters (Holohil, Canada), mounted around the neck with elastic collars (Paper I, IV). I monitored all individuals regularly by triangulation as outlined by Kenward (1987), to obtain data on dispersal patterns (Paper IV), site fidelity (Paper V), home ranges (Paper IV), survival (Paper I, II) and mortality causes (Paper I, II). When a mortality signal was detected I investigated the site as soon as possible to determine the cause of death (Paper I, II). For the captive-reared and released hares, I estimated survival rates and mortality causes as for the wild hares (Paper II). I further compared captive-reared hares movement patterns and rest site characteristics to wild adult hares (Paper II).

To obtain flushing distances and rest site characteristics (Paper III) I flushed 38 radio-tagged hares from their rest sites 131 times in total. All flushing of hares was done during daylight from May to December, when the hares lay at day-rest according to the sensors in their radio-collars (Paper III). Classified satellite images were used to extract vegetation data for resource selection analyses (Paper V).

Results and discussion

In paper I, we found a distinct annual pattern between the most abundant small rodent (field vole (*Microtus agrestis*)) index (Hornfeldt, 2004; Hornfeldt 2005), and the survival of both adult mountain hares and leverets (Figure 2). As voles increased, the survival of mountain hares improved. Vole indices can thus be seen as a good predictor of mountain hare survival (Paper I). This finding at least partly supports previous studies (*e.g.* Hornfeldt, 1978; Angelstam, Lindstrom & Widén, 1984, 1985; Marcstrom *et al.*, 1989; Lindstrom *et al.*, 1994) suggesting that hare and vole density are synchronized. The next step is to work out what causes this pattern and resolve if, which and when predators may have a large impact on the mountain hare population, as suggested by Hornfeldt (1978), Marcstrom *et al.* (1989) and Lindstrom *et al.* (1994).

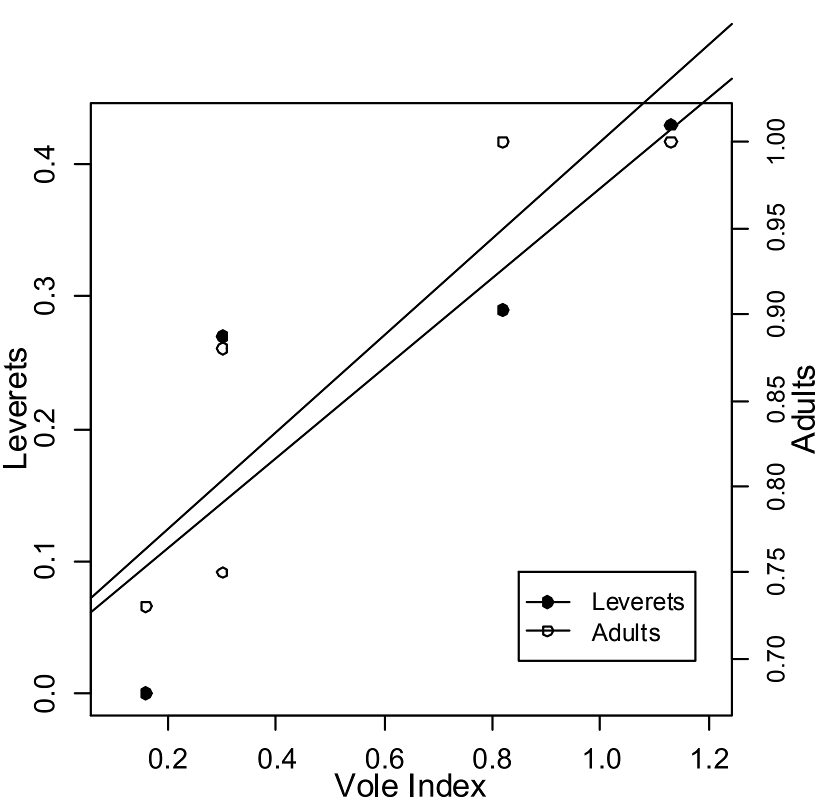

Figure 2. Relationship between field vole (*Microtus agrestis*) index (animals captured per 100 trap nights in autumn) and mountain hare survival, in northern Sweden (Paper I). Adult estimates refer to summer-autumn (June 1-Oct 31) survival from 1997-2001 when hunting are excluded from the analysis, while leveret survival was estimated as proportion of radio marked leverets surviving past 100 days of age from 1998-2001.

Survival

Although the leveret survival was synchronized with the changes in vole abundance, their survival were very low throughout the investigated years. Pooled together over all four years 85% died in the period from 14 days of age to their first breeding season the following spring (80% if hunting mortality was excluded) (Paper I). Survival between 14 and 100 days of age ranged between 0% and 43 % over four years, or 24% if pooled together (Paper I). Compared to snowshoe hares, this is a low survival rate of leverets. During peek years, however, survival rates of snowshoe hare leverets are extremely low, 50% mortality within the first 14 days from birth, mainly due to squirrel and ground squirrel predation. This concentrated high mortality rate is of great importance as it initiates the decline phase in the snowshoe hare's 10-year cyclic pattern (Boutin *et al.*, 2002)

It was impossible to give a reliable Kaplan-Meier survival estimate for mountain hare leverets during their first 14 days since the sample size was to low (Paper I; Pollock *et al.*, 1989). Seventeen leverets were nonetheless captured between 5 and 14 days of age, and the first death occurred 12 days from birth. Further, the number of leverets captured from each litter lay close to the numbers born in each litter-period according to Hoglund (1957), indicating that few leverets died in each litter before being captured. Mean litter ages at capture, for the first and the second litter-period respectively, was 13 and 17 days, and on average 2.17 and 3.00 leverets were captured (Paper I). Hoglund (1957) recorded 2.15 and 3.24 leverets born in these litter-periods. The heavy mortality of mountain hare leverets does not seem to concur with a high initial predation rate as for snowshoe hare leverets during peek years (Odonoghue, 1994; Paper IV), but may instead start with the shift in movement activity described below. No differences were found in survival between sexes, litter periods or sub-areas (one recreational area with summer residences where domestic cats were common, and one forest area) for the leverets.

Annual adult survival over five consecutive years ranged between 42% and 88% (Figure 3). This survival rate is high compared to the 34% survival rate estimated in the southern extent of the boreal forest in Sweden (Lindlof & Lemnell, 1981). It is also high compared to survival estimates of mountain hare populations in Scotland which range from 6-44% (Flux, 1970; Hewson, 1965; Hewson, 1976), but comparable with the survival of 52% and 64% found on two islands in the northern Gulf of Bothnia (Marcstrom *et al.*, 1989). Adult mountain hares in the northern boreal forest thus seem to have a high annual survival compared to more southern populations.

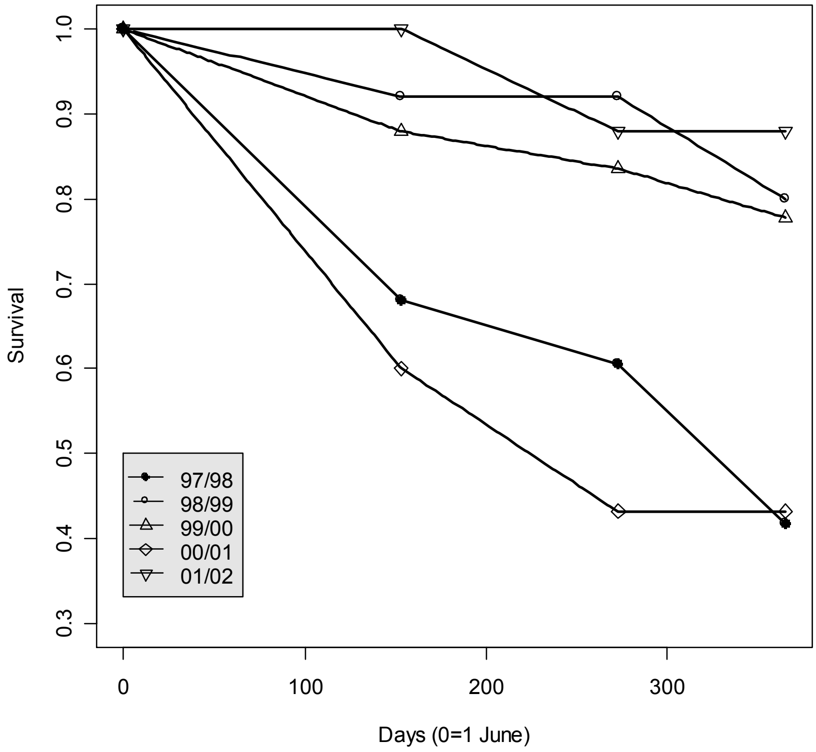

Figure 3. Annual adult survival (sexes pooled) from June 1 to last of May (1997-2002).

Seen on an annual basis, females had a significantly higher survival than males. This pattern was evident during the winter and spring seasons, while there was no significant difference in survival in the summer-autumn period (Table 1, Paper I). This is contradictory to survival of brown hares, where males had better survival than females (Marboutin & Hansen, 1998). Adult males had their lowest monthly survival in spring, while both sexes had a very high survival during winter (Table 1). Comparisons over the hunting season (1 September - last of February), excluding all mortality causes other than hunting, revealed no difference in hunting mortality between males (85%) and females (88%) (Paper I).

Table 1. *Seasonal and annual survival estimates (Se) and 95% confidence intervals (CI) for adult male and female mountain hares, pooled over years (1997-2002). The summer - autumn season incorporates dates from June 1 - Oct 31, winter from Nov 1 - last of Feb, and spring from March 1 - May 31.*

Hunting mortality	Sex	Summer - Autumn		Winter		Spring		Annual	
		Se	95% CI	Se	95% CI	Se	95% CI	Se	95% CI
Incl.	Males	0.76	0.64-0.88	0.84	0.71-0.96	0.78	0.68-0.88	0.50	0.37-0.63
Incl.	Females	0.77	0.62-0.93	1.00	1.00-1.00	0.94	0.86-1.02	0.73	0.55-0.90
Excl.	Males	0.82	0.71-0.93	0.92	0.82-1.01	0.78	0.68-0.88	0.59	0.45-0.73
Excl.	Females	0.88	0.75-1.01	1.00	1.00-1.00	0.94	0.86-1.02	0.83	0.67-0.89

Mortality causes

There was a significant difference between adult and leveret mortality causes, where a wider range of predators preyed upon leverets than on adult hares (Table 2). Domestic cats made a large impact on leveret survival in the recreational area, while goshawk was an important predator in the forest area (Paper I). Predation was the most important cause of death in general, accounting for 80% of the leveret mortality and 63% of the adult mortality. The red fox was the foremost predator and accounted for 40% of the total mortality (Table 2). There was no difference in mortality causes between sexes for either adults or leverets (Paper I). Predators, mainly foxes, killed a larger proportion of the radio-tagged adult population during vole lows (19 % and 24 % respectively) than during other years (13 %, 10 % and 11 %). Seventy-five percent of the marked leverets were killed by predators before they were 100 days old in year 2000, while 73% in 1999, 57% in 1998 and 44 % in 2001.

Table 2. *Mortality causes of mountain hare leverets and adult hares presented as percentage and number (in brackets) killed. Leverets were monitored from earliest five days of age until the start of their first mating season (302 or 254 days from birth depending on litter-period), and are divided into two groups; one representing a recreational area with summer residences(rec.) and the other a forest area (for.).*

Hare group	Fox	Cat	Goshawk	Other or unknown predator	Disease / accident	Hunting	Sum
Adults	47.6 (20)	0.0 (0)	11.9 (5)	4.8 (2)	11.9 (5)	23.8 (10)	100.0 (42)
Leverets (rec.)	26.7 (4)	46.7 (7)	0.0 (0)	6.6 (1)	20.0 (3)	0.0 (0)	100.0 (15)
Leverets (for.)	33.3 (7)	0.0 (0)	28.6 (6)	14.3 (3)	14.3 (3)	9.5 (2)	100.0 (21)
All groups	39.7 (31)	9.0 (7)	14.1 (11)	7.7 (6)	14.1 (11)	15.4 (12)	100.0 (78)

Adult home ranges

In paper IV we estimated annual 100% minimum convex polygon (MCP) home ranges to be able to compare our estimates with other studies. Our home range estimates were large, on average 280 ha and 116 ha for males and females respectively, compared to mountain hare populations in Scotland (20-113 ha for males and 15-89 ha for females; Hewson & Hinge, 1990; Hulbert *et al*., 1996; Wolfe & Hayden, 1996; Rao *et al*., 2003), but comparable to the one estimate previously reported from Scandinavia (Lindlof, 1987). Varying habitat and population density could be likely explanations for the large differences in home range size for the mountain hare in different parts of Europe. Hulbert *et al*. (1996), for example, found that mountain hares on Scottish moorlands had larger home ranges than forest or pasture dwelling hares, and Boutin *et al*. (1985) reported smaller home ranges for snowshoe hares at high compared to low population densities.

In our study, males always had larger seasonal home ranges than females, and this was especially obvious in spring during the breeding season (Paper IV, Table 3). This is similar to what has previously been found in Norway (Barikmo & Pedersen, 1997), and is probably connected to the mountain hares promiscuous mating system where the males try to locate as many females as possible for mating. Even though such occasional movements, as far as five km outside their normal home range were common in spring, they always returned back within days and thus showed high fidelity to their home range (Paper IV).

Table 3. *Annual and seasonal fixed kernel home range sizes (95% and 50% cores) of adult mountain hares in hectares. Mean values shown with, n and range in brackets.*

Group	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)

Individual hares always kept parts of their previous home range, both between years and between seasons, although the seasonal overlap was smaller, indicating that hares show a more pronounced change of areas between seasons than between years (paper V). The seasonal habitat selection was very distinct; the hares were tracking changing resource availability between seasons. In winter, deciduous forests and old infields (where twig browse can be found above the snow cover) were preferred, while in spring, mixed forests and spruce forests (correlated to the occurrence of bilberry *Vaccinium myrtillus*) were overrepresented (Pehrson, 1981; Barikmo & Pedersen, 1997; Paper V; Unpublished data). The annual selection was difficult to interpret as it mixed the seasonal patterns and consequently seems to be merely an artefact from the more important seasonal selection. I therefore caution that results from habitat selection studies based on annual home ranges that are estimated from animals in seasonally differing environments should be treated with care.

Dispersal

In paper IV we investigated dispersal distances and dispersal rates of both leverets (natal dispersal) and adult mountain hares (breeding dispersal). Most leverets remained close to their mother, *i.e.* overlapping their mothers anticipated home range (2 annual female home range radii from their birth place) with their own home range after settling down (Paper IV). A minor proportion, two of seven, did disperse according to our definition of true natal dispersers as they did not have contact with their mothers anticipated home range after establishing their own home range (Figure 4).

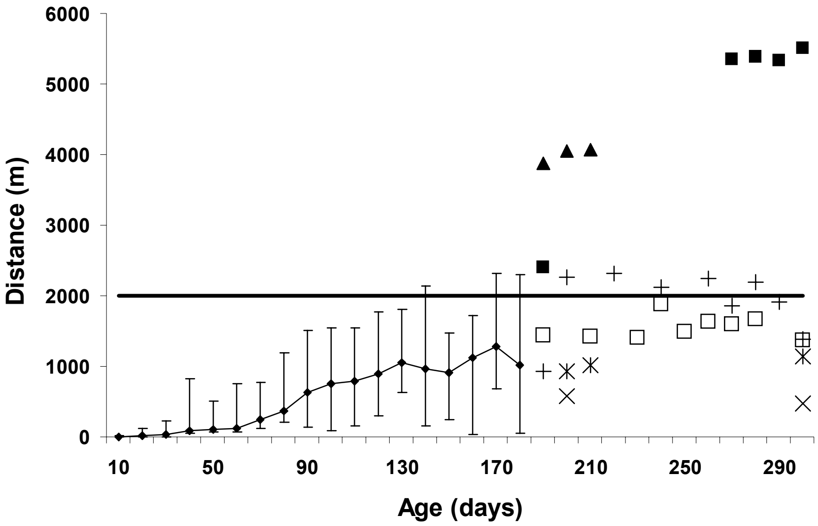

Figure 4. Dispersal distances of leverets (mean and range up to 180 days, thereafter individual distances, n=6). Filled triangles represent a male, all other individual symbols represent females. One female (filled squares) temporarily disappeared from day 187 until she was found again day 270. The horizontal reference line is twice the average maximum distance between the centre and the edge of annual female MCP home ranges. One male, not shown in the figure was shot 1,815 m from his birth place after 913 days, following radio-transmitter failure at an age of 180 days.

Our definition of a true natal disperser may, however, be challenged, since some adult males made long distance excursions during the breeding season (Paper IV). By doing so, they could reach both their own birth place if they were “dispersers”, or dispersing members of their family if they were non-dispersers. The rate and distances of natal dispersal observed in this study are comparable to that of other herbivores of similar sizes, usually showing a left skewness with a few outliers that move longer distances (Sutherland *et al.*, 2000). The onset of dispersal and dispersal distances for snowshoe hares reported by Gillis & Krebs (1999) are similar to our findings. Although few leverets dispersed, we have evidence that both sexes can do so; both a male (from the first litter-period) and a female (from the second litter-period) established their home ranges far from their mothers during our study (Figure 4).

Even though occasional long distance movements occurred among adults, especially by males during the breeding season, we found no evidence of any breeding dispersal (Paper IV). None out of 46 adults, followed at least six months and up to over three years, ever permanently moved from the home range where they were initially captured (Paper IV). We concluded that mountain hares in the boreal forest of Sweden have the capability to move long distances from where they were born, both as leverets and as adults, but few leverets and none of the adults choose to do so.

Is adult experience the key to high survival?

There was a large difference in survival between leverets and adults, and resolving the reason for this may provide important insights for a successful future management of the species. The high mortality of leverets, starting at 12 days of age, coincided in time with when the leverets became more active. At this age they started feeding on vegetation and playing during daytime inside their natal area (within 100 m of their suckling site), and thereby also became exposed to greater danger (Paper I, IV). The leverets were, however, still suckling at this time and stayed inside their natal area for approximately one month after birth. After that they started exploring the surroundings outside their natal area in search of a future home range (paper IV). This is also a very dangerous period, as shown by their mortality rate (Figure 5), but after approximately 80-100 days from birth, when the leverets had established a home range of their own (Paper IV), the mortality rate could no longer be distinguished from the adults (paper I).

The survival of captive-reared and released mountain hare leverets (0.14, 140 days after release) is similar to that of wild leverets (0.20, at 154 days of age), although their initial survival patterns differ (Figure 5, Paper I, II). There was no specific age at which the wild leverets started their movement phase, it varied from 17-83 days between individuals (Paper IV). While wild leverets could chose when to start feeding vegetative food and exploring their neighbourhood for a home range, the captive-reared hares were already at least five weeks of age when let out (Paper II). Consequently, as soon as they touched the ground, most of them started their movement phase and died at a very fast rate directly after being released (Figure 2). Predation was, as for wild hares, also the main cause of death for the captive-reared hares (Paper II). A disadvantage which is common to both wild leverets and captive-reared and released hares and is likely to be responsible for their equally low survival in the end, is their lack of experience. This may, for example, result in a bad choice of day-rest cover as shown for the released hares when compared to wild adults in the same area (Paper II). Sievert & Keith (1985) found that snowshoe hares (*Lepus americanus*) that were moved to a similar physical habitat outside their home range had higher predation rate than did residents. In addition, both wild and captive-reared leverets' physical weakness during their movement phases (*i.e.* small size and/or their incapability to outrun a predator if found) is likely to have a negative impact on survival. A wide range of predators, including domestic cats, American mink (*Mustela vision*) and goshawks (*Accepiter gentilis*), are capable of killing such a small and/or clumsy prey, and if given the opportunity they will undoubtedly do so as shown in Paper I and II.

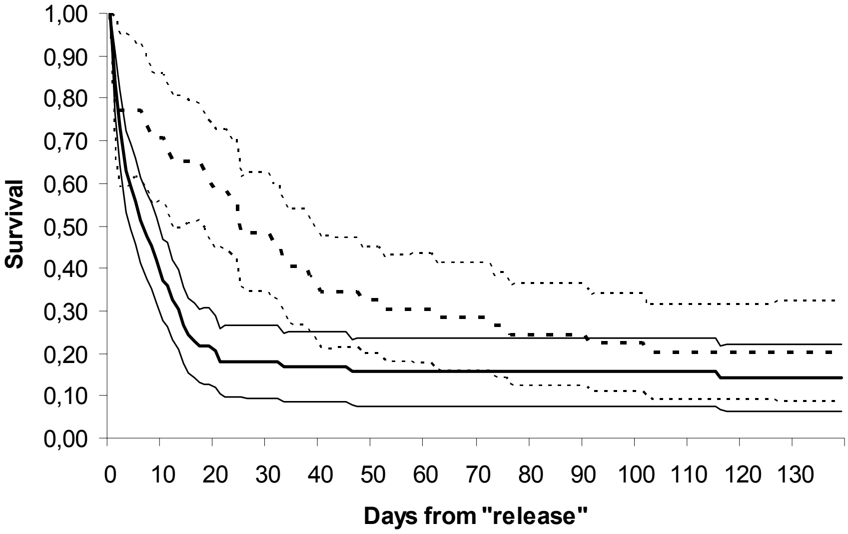

Figure 5. Survival and 95% CI of wild mountain hare leverets (dotted lines) and captive reared and released leverets (unbroken lines). Wild leverets were monitored from 14 days of age, while the captive reared hares were at least five weeks when released. Both groups start at 0 days from “release” on the X-axis.

I believe that the high survival rate shown by adult hares is, apart from their physical advantages compared to leverets, connected to their accumulated knowledge of and experience from their home range, *e.g.* ability to find escape routes and hiding places. Since mountain hares are non-territorial, usually overlapping other individuals’ home ranges (Flux, 1970; Hewson, 1976; Hewson, 1990), they are free to move wherever they please. They also have the physical capacity to do so, as shown by the males’ excursions in spring (Paper IV). Still, none of 46 individuals, followed for up to 4 years each, ever moved permanently from their established home range. Adult hares thus showed high site fidelity, and in Paper (IV) we speculated that this may somehow be connected to the habitat within their home ranges. In Paper (V) I found that the hares were highly selective in their choice of seasonal habitats, and that these selections seemed to be connected to the prevailing food availability. Although highly selective during all seasons, the resource selection was weaker and unclear on an annual basis, and I considered it unlikely that they should never have encountered better habitats, in terms of physical resources, during their years of excursions. If physical resources alone determine where they should stay, at least some of them should have moved. In paper (V) I conclude that on an annual basis almost any random area of adequate size will probably be good enough in quality for the generalist hare to survive in within this homogenous landscape. I also suggest that the local knowledge gained from an area might be one likely explanation to their annually sedentary behaviour. To test this hypothesis, I challenged a hare with two trained hunting dogs to see if the knowledge gained from an area over the years could explain the hare's reluctance to leave it (Unpublished data). During the two trials, the hare remained almost exclusively within its "area of experience" (*i.e.* a home range built on all triangulation positions from the three years the hare was followed) when being chased, using the same escape routs for both dogs even though they chased the hare separately and two weeks apart in time (Unpublished data). Apart from finding escape routs, experience may also be valuable for finding good shelter. Captive-reared hares were, for example, found to select worse day-rest cover than wild adults, who almost always had the best possible cover (Paper II, III). The cover quality at the rest sites chosen by wild adults was independent of which stand type the hare was laying in, in other words all rest sites in all habitat types had equally dense cover (Paper III). On random locations inside the study area young and mature stand types otherwise had a significantly higher cover index than non-forested land (Paper III). These results indicate that knowledge about the area and/or experience about what constitutes a good cover is very important.

Both males and females had the highest survival rates between December and February (Paper I). This is probably due to the species' high adaptation to winter conditions. Males, however, had a distinctly lower survival than the females during late winter and spring, which once again may be connected to their experience, or more specifically, how well they utilize this experience during different circumstances. The males expanded their home ranges into otherwise unvisited areas during the mating season (paper IV). This probably exposed them to greater danger as a higher proportion of the males were predated during spring than during any other period (Paper I). The lowered vigilance of males during spring is also a likely explanation for the skewed sex ratio among the captured adults (Paper I), and for the males long flushing distances in spring compared to other seasons (Paper III).

Conclusions

1. The survival rate of mountain hare leverets is in general very low in the boreal forest. From about two weeks of age they start exposing themselves when feeding, playing and exploring their neighbourhood, and are thereby an easy target for a wide range of predators due to their lack of experience and limited physical capacity. Once they have found and established a home range of their own, at approximately 80-100 days of age, their survival is no longer lower than for adult hares.

2. Adult hares have very high survival rates during most years, and survival was especially high during the winter period to which they are well adapted. The lowest seasonal survival was found in males during the mating season in spring, when they explore otherwise unvisited areas in their search for females.

Knowledge about and experience from their life-time home ranges seem important (*i.e.* ability to find escape routes and hiding places and how to act when encountering a predator), and may explain their high annual site fidelity and, in effect, their generally high survival.

3. Predation is the main cause of death for both leverets and adult mountain hares and the red fox is the main predator in both age classes. Domestic cats and goshawks also have a large impact on leveret survival.

4. Population dynamics of mountain hares in northern Sweden is, as for snowshoe hares in North America, driven by predation. Yet, unlike the snowshoe hare, where a high predation rate on newborn leverets in peek years initiates the decline phase (Krebs *et al.*, 1995, Boutin *et al.*, 2002), predation on mountain hare leverets did not start before two weeks of age. At this age the leverets start feeding on vegetative food and exploring their neighbourhood, thereby exposing themselves to great danger as many predators are capable of killing such a small and clumsy prey. Survival rates of both leverets and adult mountain hares were synchronized with the 3-4 year cyclic density pattern of voles; as vole density decreased, hares mortality increased. Survival of adults was, however, always much higher than for leverets, probably because fewer predator species were capable of killing this larger prey in combination with their superior experience. A larger proportion of the marked hare population was predated during vole lows than during peek years. It is therefore likely that generalist predators such as the red fox increased their search activity for other prey during vole lows, *i.e.* a predator functional response (Holling, 1959; Hanski, Hansson & Henttonen, 1991), but, I do not have data on predator density over the investigated years to support this in full. My results do, however, still strongly support previous studies (Hornfeldt, 1978; Marcstrom *et al.*, 1989; Lindstrom *et al.*, 1994) suggesting that mountain hare population dynamics in Sweden is driven by predation in accordance with the alternative prey hypothesis (Hagen, 1952; Lack, 1954).

5. Home range sizes of the mountain hare in the boreal forest of northern Sweden are large compared to those in mid-Sweden and Scotland. Although highly selective during all seasons, the resource selection is weaker and unclear on an annual basis. The result on resource selection based on annual home ranges is thus probably just an artefact of the hares' distinct seasonal selection. I suspect that local knowledge, *i.e.* the hare's accumulated experience, of an area rather than physical resources may explain the hares' annually sedentary behaviour. On such a large spatial scale, the landscape is homogenous and the habitat quality high. Little will therefore be gained by moving to a new area. Instead there should be a greater benefit in staying in the same area, where the hare has a local knowledge that can be of value *e.g.* in avoiding being detected by predators. On a smaller scale, within this "area of experience", the hares are, however, tracking changing physical resource availability between seasons.

6. The mountain hare in the boreal forest of Sweden may potentially show very local population dynamic patterns. Only a small proportion of the leverets clearly dispersed from their birth place and none of the adults ever moved from the home

range where they were initially captured. An individual's contribution to coming generations will thus, in effect, mainly be made in the same area as where they were born.

Management implications

The scale at which we manage populations may be of critical importance, especially for open populations where immigration and emigration can have a significant impact on the spatial dynamics (Weins, 1989; Levin, 1992; Otis, 1998; Turchin, 2003). Knowledge of home range sizes and placements at different times of the year, together with dispersal rates and distances, are thus important for our understanding of the population dynamics of a species (paper IV). Only by incorporating areas large enough to include both home ranges and dispersal of individuals within a population we can truly say we base our management decisions on the population dynamics of the species.

Small-game species' such as mountain hares and tetraonids are, mainly by tradition, managed as one coherent group in Scandinavia. I have shown that leveret survival is central to the population dynamics of the mountain hare, and that predation, especially by red fox, is their major limiting factor. Tetraonids in the boreal forest have similar high chick mortality due to predation (Willebrand, 1988; Smith, 1997). Over larger areas, management efforts can, if they are efficient enough, be of gain to both mountain hares and tetraonids, since dispersal is then incorporated for both groups of animals. This has for example been shown by Lindstrom *et al.* (1994) in a natural experiment. The same study also reported that small game densities multiplied when the red fox decreased heavily due to sarcoptic mange, indicating that the small game community in the boreal forest is generally limited by predation. In addition, it also suggests that small game densities lay considerably below the carrying capacity set by the physical resources. On small confined islands, without immigration or emigration, Marcstrom, Kenward & Engren (1988) and Marcstrom *et al.* (1989) managed to increase both mountain hare and tetranoid densities by culling predators. The potential for local population dynamics shown by the hares in my study suggests that it should also be possible to manage the mountain hare successfully on relatively small areas on the mainland, at least compared to tetranoids in the same region. While young female grouse invariably disperse long distances (>30km) after brood break-up in autumn and/or during breeding in spring (Willebrand, 1988; Smith, 1997; Warren & Baines, 2002), most leverets will stay within 2 km from where they were born. A successful local predator reduction should, at least theoretically, result in a local population increase of hares, while the increase in grouse would be spread out over a larger area as chicks disperse and thus not gain the local management unit area much. The low dispersal rate and distances of the mountain hare, however, also suggest that re-colonization in areas where populations have gone locally extinct (*e.g.* due to disease or over-harvesting) will be slow.

In Finland, Kauhala, Helle & Helle (1999) investigated the effect of predator control, reducing foxes and marten (*Martes martes*), on hares on the mainland. The response of hares was, however, rather contradictory as hare numbers increased on both areas with and without predator reduction. They suggest that the effectiveness of the study was compromised partly by the size of the study areas, which allowed for high immigration of foxes from the surrounding areas, and the fact that predators were only controlled during the hunting season. This limited control meant that predators were free to breed in the study areas, and may have reproduced at higher levels due to reduced competition. Nevertheless, based on my results, I am convinced that it is possible to increase the mountain hare population by controlling predators also in relatively small areas, provided the appropriate scale is taken into account. On such a scale, including the home ranges of all foxes which can reach the local management unit area, and given that enough foxes are culled, an effect on hare density should be apparent already after one year as hares have relatively high fecundity. After a certain number of years, when the hare density approaches carrying capacity, individuals will probably start dispersing at a higher rate and distance (Boutin *et al.*, 1985). The density should then eventually reach an azymptote, although at a significantly higher level than before. It is important to continue the predator control even after an effect is apparent, as new foxes will immigrate each year in search of unoccupied territories (Reynolds & Tapper, 1996). If the local hare density is much higher than in surrounding unmanaged areas when predator control ceases, predators may be drawn to this local food source area, which at least initially may sustain more predators than any other area (Pulliam & Danielson, 1991). As a result, the population density may eventually become even lower than before the management action started.

It should be noted, however, that the management actions suggested for the potentially local population dynamics of this low density mountain hare population in the boreal forest, need not be general for all hare species, or even for the mountain hare in other areas. Landscape fragmentation, population density, social interactions or territoriality might affect both the distance and the rate of dispersal, as well as home range size. Boutin *et al.* (1985), for example, showed that the rate of natal dispersal increased for snowshoe hare in North America during increasing densities, and Hulbert *et al.* (1996) found mountain hare home range sizes to differ between habitats. Consequently, even populations as close as in the fragmented forest/agricultural landscape of southern Sweden may behave differently than the population in this study.

Future research

Apart from theoretical modelling to suggest scales at which the mountain hare can be successfully managed, there is a need for applied experimental studies to test the theoretical predictions made in this thesis. I suggest two different experiments; 1) reducing the impact of red foxes at appropriate scales and monitoring the response of the hare population, as well as of other small game species such as capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*), in comparison to control areas, and 2) reducing the hare population in an area through hunting to find out if hunting can push the population to local extinction, and if so, what time span is needed for re-colonization.

Since the mountain hare may potentially show very local population dynamics, it is appropriate to use as a model species for habitat studies. Even though not considered limiting in my studies on the mountain hare conducted in a single region, physical resources such as food and shelter probably explain a lot of the assumed variation in density between different regions. The mixed agricultural/forest landscape in southern Sweden differs from the boreal forest landscape in northern Sweden, as do the mountain region, the boreal forest region and coastal regions in the northern part of the country. Using GIS-based habitat modelling, such as applying resource selection functions to construct habitat suitability maps, would further increase our knowledge of the species and probably improve our management methods considerably (Manly *et al.*, 2002).

Although considered highly important for the population dynamics in other countries (Newey, 2005 and references therein), the occurrence and effect of parasites and pathogens are largely unknown for the mountain hare in Scandinavia. A thorough investigation on this matter is timely.

Studying aspects of dispersal and estimating population densities of a species as the mountain hare in the boreal forest is difficult with conventional methods such as radio telemetry and capture/recapture methods. Recent developments in genetic techniques, using scats to recover DNA, has, however, enabled us to study these subjects at a level of detail and scale not realistically possible before (*e.g.* Kovach, Litvaitis & Litvaitis, 2003; Burton & Krebs, 2003). Emphasis should be put on adjusting these methods and creating protocols for the mountain hare.

Mountain hare hunters in Scandinavia spend a considerable amount of time on their hobby and show a much lower catch per unit effort compared to those concentrating their hunting on other small-game species (Unpublished data). Hares are mainly hunted with dogs trained to follow the fresh ground scent of the hare and to bark while doing so. The hunters take stand on the assumed passageway of the hare, and thereby have time to decide whether to bag the animal or not. This differs from *e.g.* the willow grouse (Lagopus lagopus) hunters, using pointing dogs, which invariably try to bag the grouse when given the chance. The hare hunting bag is probably in most cases related to hare density but other factors, such as weather conditions, may also trigger the hunters' response, as suggested in Paper I. Little is known about the behaviour of the hunters and what influences their decisions. To further improve the management of the mountain hare we need to include the human dimension.

References

Ahti, T., Hamet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5, 169-211.

Angelstam, P., Lindstrom, E. & Widen, P. 1984. Role of predation in short term population fluctuations of birds and mammals in Fennoscandia. *Oecologia* 62, 199-208.

Angelstam, P., Lindstrom, E. & Widen, P. 1985. Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia - occurrence and distribution. *Holartic Ecology* 8, 285-298.

Angerbjorn, A. 1981. *Winter food as a limiting factor of dense mountain hare populations on islands, a comparative study*. In: Myers, K. & Macinnes, C. D. (eds). World Lagomorph Conf., Guelph, Ontario, 1979, pp. 395-440.

Angerbjorn, A. 1986. *Population dynamics of mountain hares Lepus Timidus L. on Islands*. Ph.D Thesis, University of Stockholm, Department of Zoology, Stockholm, Sweden. ISBN 91-7900-069-X.

Angerbjorn, A. 1989. Mountain hare populations on islands: effects of predation by red fox. *Oecologia* 81, 335-340.

Angerbjorn, A. & Flux, J.E.C. 1995. Lepus timidus. *Mammalian Species* 495, 1-11.

Barikmo, J. & Pedersen, H.C. 1997. *Harer og harejakt*. Gyldendal Norsk Forlag, Oslo. 256 pp.. (in Norwegian).

Begon, M., Harper, J.L. & Townsend, C.R. 1996. *Ecology, individuals, populations and communities*. Blackwell Science, Great Britain, 1068 pp.

Bergengren, A. 1969. On genetics, evolution and history of distribution of the heath-hare, a distinct population of the Arctic hare, Lepus timidus Lin. *Swedish Wildlife* 6, 381-460.

Berryman, A.A. 2002. *Population cycles: Causes and analysis*. In: Berryman, A.A. (ed.), Population cycles: the case for trophic interactions. Oxford University Press. New York, New York. pp. 3-28.

Best, T.L. & Henry, T.H. 1994a. *Lepus othus*. Mammalian Species 458, 1-5.

Best, T.L. & Henry, T.H. 1994b. *Lepus arcticus*. Mammalian Species 457, 1-9.

Boutin, S., Gilbert, B.S., Krebs, C.J., Sinclair A.R.E. & Smith J.N.M. 1985. The role of dispersal in the population dynamics of snowshoe hares. *Canadian Journal of Zoology* 63, 106-115.

Boutin, S., Krebs, C.J., Boonstra, R., Sinclair, A.R.E. & Hodges, K. 2002. *Understanding the snowshoe hare cycle through large scale field experiments*. In: Berryman, A. A. (ed.), Population cycles: the case for trophic interactions. Oxford University Press. New York, New York. pp. 70-91.

Broseth, H. & Pedersen, H.C. 2000. Hunting effort and game vulnerability studies on a small scale: a new technique combining radio-telemetry, GPS, and GIS. *Journal of Applied Ecology* 37, 182-190.

Burton, C. & Krebs, C.J. 2003. Influence of relatedness on snowshoe hare spacing behavior. *Journal of Mammalogy* 84, 1100-1111.

Cary, J.R. & Keith, L.B. 1979. Reproductive change in the 10-year cycle of snowshoe hares. *Canadian Journal of Zoology* 57.

Corbet, G.B. 1983. A review of classification in the family Leporidae. *Acta Zoologica Fennica* 174:11-15.

Elton, C. 1927. *Animal Ecology*. Sidgewick & Jackson. London.

Ericsson, G. 1999. *Demographic and life history consequences of harvest in a Swedish moose population*. Ph.D Thesis, Swedish University of Agricultural Sciences, Umeå, Sweden. ISSN 1401-6230, ISBN 91-576-5631-2.

Flux, J.E.C. 1970. Life history of the mountain hare (Lepus timidus scoticus) in north-east Scotland. *Journal of Zoology, London*. 161, 75-123.

Flux, J.E.C. & Angermann, R. 1990. *The Hares and Jackrabbits*. In: Chapman, J.A. & Flux, J.E.C. (eds), Rabbits, Hares and Pikas: Status, Survey and Conservation Action

Plan. IUCN/SSC Lagomorph Specialist Group, Information Press, Oxford, U.K. ISBN 2-8317-0019-1.

Gillis, E.A. & Krebs, C.J. 1999: Natal dispersal of snowshoe hares during a cyclic population increase. *Journal of Mammalogy* 80, 933-939.

Hagen, Y. 1952. *Rovfuglene og viltpleien*. Gyldendal Norsk Forlag, Oslo. (In norwegian).

Hanski, I., Hansson, L. & Henttonen, H. 1991. Specialist predators, generalist predators, and microtine rodent cycle. *Journal of Animal Ecology* 60, 353-367.

Hewson, R. 1965. Population changes in the mountain hare, Lepus timidus L. *Journal of Animal Ecology* 34, 587-600.

Hewson, R. 1968. Weights and growth rates in mountain hares Lepus timidus scoticus. *Journal of Zoology, London*. 154, 249-262.

Hewson, R. 1970. Variation in reproduction and shooting bags of mountain hares on two moors in north-east Scotland. *Journal of Applied Ecology* 7, 243-252.

Hewson, R. 1976. A population study of mountain hares (Lepus timidus) in north-east Scotland from 1956-1969. *Journal of Applied Ecology* 45, 395-414.

Hewson, R. 1990. Behavior, Population changes and Dispersal of Mountain Hares (Lepus timidus) in Scotland. *Journal of Zoology, London*. 220, 287-309.

Hewson, R. & Hinge, M.D.C. 1990. Characteristics of the home range of mountain hares Lepus timidus. *Journal of Applied Ecology* 27, 651-666.

Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91, 385-398.

Hudson, P.J., Dobson, A.P. & Newborn, D. 1998. Prevention of population cycles by parasite removal. *Science* 282, 2256-2258.

Hudson, P.J., Dobson, A.P. & Newborn, D. 2002. *Parasitic worms and population cycles of red grouse*. In: Berryman, A. A. (ed.), Population Cycles: the case for trophic interactions. Oxford University Press. New York, New York. pp. 109-129.

Hulbert, I.A.R., Iason, G.R. & Mayes, W. 2001. The flexibility of an intermediate feeder: dietary selection by mountain hares measured using faecal n-alkanes. *Oecologia* 129,l 197-205.

Hulbert, I.A.R., Iason, G.R., Elston, D.A. & Racey, P.A. 1996. Home-range sizes in a stratified upland of two lagomorphs with different feeding strategies. *Journal of Applied Ecology* 33, 1479-1488.

Hoglund, N.H. 1957. Fortplantningen hos skogsharen (Lepsu t. timidus Lin.). *Viltrevy* 1, 267-282. (In Swedish with English summary).

Hornfeldt, B. 1978. Synchronous population fluctuations in voles, small game, owls, and tularaemia in Northern Sweden. *Oecologia* 32, 141-152.

Hornfeldt, B. 2004. Long-term decline in numbers of cyclic voles in boreal Sweden: analysis and presentation of hypotheses. *Oikos* 107, 376-392.

Hornfeldt, B. 2005. Miljöövervakning av smådäggdjur. http://www.emg.umu.se/personal/lankar/hornfeldt/index3.html.

Kauhala, K., Helle, E. & Helle, P. 1999. Impact of predator removal on predator and mountain hare populations in Finland. *Annales Zoologici Fennici* 36, 139-148.

Keith, L.B. 1974. *Some features of population dynamics in mammals*. In: Kjerner, I. & Bjurholm, P. (Eds). Proceedings of the XI International congress of game biologists, Liber, Stockholm, pp. 17-58.

Keith, L.B. 1981. *Population dynamics of hares*. In: Myers, K. & MacInnes, C.D. (Eds). World Lagomorph Conf., Guelph, Ontario, 1979, pp 395-440.

Keith, L.B. 1983. Role of Food in Hare Population-Cycles. *Oikos* 40. 385-395.

Keith, L.B., Cary, J.R., Rongstad, O.J. & Brittingham, M.C. 1984. Demography and ecology of a declining snowshoe hare population. *Wildlife Monographs* 90, 1-43.

Keith, L.B. & Windberg, L. A. 1978. A demographic analysis of the snowshoe hare cycle. *Wildlife Monographs* 58, 1-70.

Kenward, R. 1987. *Wildlife radio tagging: equipment, field techniques and data analysis*. Academic Press, London, 222pp.

Kjellander, P. 2000. *Density Dependence in Roe Deer Population Dynamics*. Ph.D Thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden. ISSN 1401-6230, ISBN 91-576-5888-9.

Kovach, A.L., Litvaitis, M.K. & Litvaitis, W.I.N. 2003. Evaluation of fecal mtDNA for analysis as a method to determine the geographic distribution of a rare lagomorph. *Wildlife Society Bulletin* 31, 1061-1065.

Krebs, C.J., Boutin, S., Boonstra, R., Sinclair, A.R.E., Smith, J.N.M., Dale, M.R.T., Martin, K. & Turkington, R. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* 269, 1112-1115.

Krebs, C.J., Boonstra, R., Boutin, S. & Sinclair, A.R.E. 2001. What Drives the 10-year Cycle of Snowshoe Hares? *BioScience* 51, 25-35.

Krebs, C.J., Boutin, S. & Boonstra, R. 2001. *Ecosystem Dynamics Of The Boreal Forest: The Kluane Project*. Oxford University Press, New York, New York, 511pp.

Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Oxford University Press, London.

Lemnell, P.A. & Lindlof, B. 1982. Experimental release of captive-reared mountain hares. *Viltrevy* 12, 115-128.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73, 1943-1967.

Liljegren, R. & Lageras, P. 1993. *Fran mammutstapp till kohage: Djurens historia i Sverige*. Wallin & Dalholm Boktryckeri AB, Lund. (In Swedish).

Lindlof, B. & Lemnell, P.A. 1981. *Differences between island and mainland mainland populations of mountain hare*. In: Myers, K. & MacInnes, C.D. (Eds); World Lagomorph Conf., Guelph, Ontario, 1979, pp 478-485.

Lindlof, B. 1987. *Lar kanna skogsharen*. Svenska Jagareforbundet, Stockholm, Sweden. 49pp. (In Swedish).

Lindstrom, E.R., Andren, H., Angelstam, P., Cederlund, G., Hoernfeldt, B., Jaederberg, L., Lemnell, P.A., Martinsson, B., Skoeld, K. & Swenson, J.E. 1994. Disease reveals the predator : sarcoptic mange, red fox predation, and prey populations. *Ecology* 75, 1042-1049.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. 2002. *Resource selection by animals, statistical design and analysis for field studies*. Kluwer Academic publishers, Dordrecht, 220pp.

Marboutin, E. & Hansen, K. 1998: Survival rates in a nonharvested brown hare population. *Journal of Wildlife Management* 62, 772-779.

Marcstrom, V., Keith, L.B., Engren, E. & Cary, J.R. 1989. Demographic responses of arctic hares (Lepus timidus) to experimental reductions of red foxes (Vulpes vulpes) and martens (Martes martes). *Canadian Journal of Zoology* 67, 658-668.

Marcstrom, V., Kenward, R.E. & Engren, E. 1988. The Impact of Predation on Boreal Tetraonids During Vole Cycles: An Experimental Study. *Journal of Animal Ecology* 57, 859-872.

Myrberget, S. 1990. *Haredyrene*. In: Semb-Johansson, A. & Frislid, R. (Eds). Norges Dyr. Pattedyrene 3. J.W Cappelen, Oslo. (In Norwegian).

Naumov, S.P. 1947. *Ecology of the alpine hare Lepus timidus L*. Moscow Natural History Society. Moscow, 206pp.

Naumov, S.P. 1960. *Investigations into the causes and Regularities of the Population Dynamics of the Snow Hare in Yukatia*. USSR Academy of Sciences.

Newey, S. & Thirgood, S.J. 2004. Parasite-mediated reduction in fecundity of mountain hares. *Proceedings of the Royal Society of London. Series B. Biological sciences* 271, 413-415.

Newey, S., Thirgood, S.J. & Hudson, P.J. 2004. Do parasites burdens in spring influence condition and fecundity of female mountain hares Lepus timidus? *Wildlife Biology* 10, 171-176.

Newey, S. 2005. *Population fluctuations in mountain hares: A role for parasites?* Ph.D. Thesis, University of Agricultural Sciences, Umeå, Sweden. ISSN 1652-6880, ISBN 91-576-7025-0.

Newey, S., Shaw, D.J., Kirby, A., Montieth, P., Hudson, P.J. & Thirgood, S.J. 2005. Prevalence, intensity and aggregation of intestinal parasites in mountain hares and their potential impact on population dynamics. *International Journal for Parasitology* (In Press).

Odonoghue, M. 1994. Early survival of juvenile snowshoe hares. *Ecology* 75, 1582-1592.

Otis, D.L. 1998. Analysis of the influence of spatial pattern in habitat selection studies. *Journal of agricultural, biological, and environmental statistics* 3, 254-267.

Pehrson, A. 1981. *Winter food consumption and digestibility in caged mountain hares*. In: Myers K, MacInnes CD (Eds.); World Lagomorph Conf. Guelph, Ontario, 1979, pp. 478-485.

Pehrson, A. 1983. Digestibility and retension of food components in caged mountain hares Lepus timidus during the winter. *Holarctic Ecology* 6, 395-403.

Pehrson, A. & Lindlof, B. 1984. Impact of Winter Nutrition on Reproduction in Captive Mountain Hares (Lepus timidus) (Mammalia, Lagomorpha). *Journal of Zoology, London*. 204, 201-209.

Pehrson, A. 1990. Harens effektiva matsmaltning. *Jaktjournalen* 11, 120-123. (In Swedish).

Pehrson, A., Jansson, G. & Helldin, J-O. 2002. *Situationen for skogsharen i Sverige: Rapport fran en orienterande studie*. University of Agricultural Sciences, Grimsö forskningsstation, Report. (In Swedish).

Pollock, K.H., Winterstein, S.R., Bunck, C.M. & Curtis, P.D. 1989: Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53, 7-15.

Pulliam, H.R. & Danielson, B.J. 1991. Sources, sinks, and habitat selection - a landscape perspective on population dynamics. *American Naturalist* 137, 50-66.

Rao, S.J., Iason, G.R., Hulbert, I.A.R. & Racey, P.A. 2003. The effect of establishing native woodland on habitat selection and ranging of moorland mountain hares (Lepus timidus), a flexible forager. *Journal of Zoology, London* 260, 1-9.

Reynolds, J.C. & Tapper, S.C. 1996. Control of mammalian predators in game management and conservation. *Mammal Review* 26, 127-155.

Royama, T. 1992. *Analytical population Dynamics*. Chapman & Hall, London, 392pp.

Seiskari, P. 1957. Winter home range of the snow hare. *Suomen Riista* 16, 46-55. (In Finnish with English summary).

Sievert, P.R. & Keith, L.B. 1985. Survival of snowshoe hares at a geographic range boundary. *Journal of Wildlife Management* 49, 854-866.

Siivonen, L. 1948. Structure of short cyclic fluctuation in numbers of mammals and birds in the northern parts of the northern hemisphere. *Papers in Game Research* 1, 1-166.

Sinclair, A.R.E. 1989. *Population regulation in animals*. In: Cherrett, J.M. (Ed.), Ecological Concepts. British Ecological Society Symposium 29, Blackwell Science, pp. 197-241.

Smedshaug, C.A., Selas, V., Lund, S.E. & Sonerud, G.A. 1999. The effect of a natural reduction of red fox Vulpes vulpes on small game hunting bags in Norway. *Wildlife Biology* 5, 157-166.

Smith, A.A. 1997. *Movement, dispersal and survival patterns of Swedish willow grouse (Lagopus lagopus L.)*. PhD Thesis, Edward Grey Institute, Department of Zoology, Oxford, UK, 168 pp.

Sutherland, G.D., Harestad, A.S., Price, K. & Lertzman, K.P. 2000: Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology* 4 (1), 16. [online] URL: http://www.consecol.org/vol4/iss1/art16.

Sutherland, W.J. 1996. *From Individual Behaviour to Population Ecology*. Oxford University Press, New York. 213pp.

Thulin, C-G. 2000. *Hybridisation Between Introduced Brown Hares and Native Mountain Hares in Sweden.* Ph.D. Thesis, Uppsala University, Uppsala, Sweden. ISSN 1104-232X, ISBN 91-554-4704-4.

Turchin, P. 2003. *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press, New Jersey, 456pp.

Warren, P.K & Baines D. 2002: Dispersal, survival and causes of mortality in black grouse Tetrao tetrix in northern England. *Wildlife biology* 8, 91-97.

Watson, A. & Hewson, R. 1973. Population densities of mountain hares (Lepus timidus) on western Scottish and Irish moors and Scottish hills. *Journal of Zoology, London*. 170, 159.

Watson, A., Hewson, R., Jenkins, D. & Parr, R. 1973. Population densities of mountain hares compared with red grouse on Scottish moors. *Oikos* 24, 225-230.

Vaughan, M. & Keith, L.B. 1981. Demographic response of experimental snowshoe hare populations to overwinter food shortage. *Journal of Wildlife Management* 45, 354-380.

Weins, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3, 385-397.

Willebrand, T. 1988: *Demography and ecology of a black grouse (Tetrao tetrix L.) population*. PhD thesis, Uppsala University, Sweden.

Wolfe, A. & Hayden, T.J. 1996. Home range sizes of Irish mountain hares on coastal grassland. *Biology and Environment-Proceedings of the Royal Irish Academy 96B*, pp. 141-146.

Liv och Död hos Skogsharen i Norra Sverige

Skogsharen är historiskt sett en av Sveriges mest uppskattade viltarter, mellan 40,000 och 200,000 harar har skjutits per år i landet från 1939 fram till idag. Trots detta stora intresse vet vi förvånansvärt lite om hur skogsharen lever sitt liv, framför allt i den boreala skogen vilken är dess huvudsakliga hemvist. Antalet födslar, dödsfall, invandrade och utvandrade individer utgör grunden för hur många individer som finns i en population. En förutsättning för att kunna bedriva en bra förvaltning är att man har kännedom om vad som påverkar dessa faktorer.

Min avhandling syftar till att öka vår kunskap om skogsharen i det boreala skogslandskapet. Jag har särskilt behandlat följande frågor; 1) överlevnad och dödsorsaker hos vilda vuxna och unga skogsharar, 2) överlevnad och dödsorsaker hos uppfödda skogsharar utsatta i olika delar av landet, 3) vilka val haren gör när den väljer daglega, 4) hemområdesstorlekar, spridningsmönster och ortstrohet hos skogsharen och 5) habitatval inom hemområden. Resultaten i avhandlingen bygger i huvudsak på information från vilda radiomärkta harar (74 vuxna harar och 48 ungar) i Kroksjö, Västerbotten (30 km NV Umeå), men även från buruppfödda och radiomärkta harar (65 ungar).

Resultat och diskussion

Harungarna i studien hade en mycket låg överlevnad, bara ca två av tio harungar som föddes var fortfarande i livet nästkommande vår, när parningssäsongen startade. Den största dödligheten inträffade från att de började utforska sin omgivning, vid ca två veckors ålder, fram till de var ca 100 dagar gamla. Innan dess låg de till stor del stilla i väntan på att honan skulle komma och dia dem. I och med att de började exponera sig, t. ex. genom att söka föda, utsattes de för större risk att bli upptäckta av predatorer, och de flesta predatorer klarar av att ta ett så litet och klumpigt bytesdjur. Efter ca. 100 dagar från födsel hade de flesta överlevande harungar hittat och slagit sig ner i ett eget hemområde. Från denna tidpunkt hade ungarna i stort sett lika bra överlevnad som de vuxna hararna, eftersom de förutom att ha vuxit sig större och snabbare även skaffat sig kännedom om sitt område, t. ex. var det finns bra skyddsmöjligheter. Överlevnaden hos uppfödda och utsatta skogsharar var fem månader efter frisläppandet jämförbar med de vilda harungarnas överlevnad. De uppfödda hararna dog dock mycket snabbt den första månaden efter utsläpp eftersom de då redan var 5-8 veckor gamla och genast påbörjade sin riskfyllda utforskning av omgivningarna. Anledningen till att både uppfödda harar och vilda harungar hade en liknande låg överlevnad beror förmodligen på att de båda saknar erfarenhet och har en mycket begränsad fysisk förmåga jämfört med t. ex. en rödräv. Hos vuxna harar varierade årsöverlevnaden mellan 42% och 88% under de fem år studien pågick. Hanar hade lägre överlevnad än honor, särskilt under parningstiden på våren då hanarna rörde sig över stora och okända områden i sitt sökande efter parningsvilliga honor. Därigenom utsatte de sig troligtvis för en ökad risk att bli upptäckta av predatorer. Under vintern, till vilken skogsharen är väl anpassad, hade både honor och hanar mycket hög överlevnad. Både de vuxna hararnas och harungarnas överlevnad mellan år var synkroniserad med den rådande smågnagartillgången. När smågnagarna minskade i antal ökade hararnas mortalitet eftersom rovdjuren då koncentrerade sig mer på harar som födoresurs, i enlighet med den alternativa byteshypotesen.

Den vanligaste dödsorsaken hos både vuxna och unga skogsharar var predation. Av de skogsharar som dog i studien utgjorde rovvilt ca 63% av dödsorsakerna hos de vuxna hararna och 80% hos ungarna. Rödräven var den dominerande predatorn hos båda åldersklasserna, men ett bredare spann av rovvilt dödade harungarna, bl.a. duvhök och huskatt. Jakt utgjorde ca 24% av de vuxna hararnas dödsorsaker i studieområdet.

Storleken på hararnas hemområden skiljde sig mellan könen, hanarna hade i medeltal en hemområdesstorlek på 280 hektar sett över ett helt år, medan honornas hemområden var betydligt mindre, 116 hektar. Framför allt finner man orsaken till denna skillnad på våren, under parningstiden, då hanarna rörde sig över mycket större områden än honorna. Ingen av de radiomärkta hararna valde dock att helt lämna sitt hemområde och uppvisade därför en hög trohet till det område där de var fångade. Individuella harar behöll alltid stora delar av sitt hemområde från ett år till ett annat, medan en mindre andel behölls mellan de olika säsongerna. Från en säsong till en annan bytte således hararna område inom sitt stora årshemområde. Under vintern föredrog de t.ex. skog med hög lövandel och områden runt gamla inägor i skogslandet, d.v.s. områden där de kan finna kvistbete vilket är deras huvudsakliga vinterföda. Under våren flyttades hemområdet till granskogar och blandskogar där det bl.a. finns gott om blåbärsris vilket är en viktig föda när snön försvunnit. Harungarna uppvisade endast en begränsad spridning från sin födelseplats, de flesta etablerade ett eget hemområde inom två km från där de var födda. Detta innebär att de flesta harungars hemområden ligger överlappande med, eller nära intill, sin mors hemområde. Ett fåtal harar flyttade dock längre, som mest 5.5 km. Både vuxna och unga harar har således kapacitet att flytta långa sträckor, men ingen av de vuxna hararna och endast ett fåtal av harungarna valde att flytta. Troligtvis finns det tillräckligt med resurser för att överleva, t.ex. föda, inom stora delar av det boreala skogslandskapet. Att flytta skulle kunna innebära en större risk genom förlorad lokalkännedom (t.ex. var det finns bra gömslen), än vad som skulle vinnas på en marginellt bättre födoresurs. Att vuxna skogsharar har en god lokalkännedom och/eller erfarenhet visades av deras val av daglegoplatser. Vilda vuxna harar valde alltid tätare skydd för sina daglegor än utsatta harar. De valde även lika bra skydd oavsett vilken beståndstyp (d.v.s. mogen skog, ungskog eller obeskogat land) deras daglega låg inom, även om den obeskogade beståndstypen generellt sett hade mindre skyddsmöjligheter.

I och med skogsharens lokala levnadssätt och begränsade spridning tror jag att lokala viltvårdsinsatser kan visa sig mer värdefulla för skogsharen än för många andra småviltsarter. Det bör dock även innebära att vid en lokal utrotning, t.ex. genom sjukdom eller hård jakt, tar det längre tid för den lokala skogsharepopulationen att återhämta sig än för arter där en större andel sprider sig längre sträckor. Antalet skogsharar i det boreala skogslandskapet begränsas i första hand av predation och rödräven är den huvudsakliga predatorn. Om antalet rödrävar begränsas inom ett område kommer både fler harungar och t. ex. skogshönskycklingar att överleva sommaren. Hos skogshönsen (tjäder, orre och dalripa) sprider sig, till skillnad från hos skogsharen, i stort sett alla unghöns långa sträckor (ca 30 km) efter att kullarna har splittrats på hösten och under våren. Under hösten och vårvintern kommer därför hönskycklingarna att sprida sig över stora områden och effekten av viltvården riskerar i stort sett utebli från där den företogs. Harungarna däremot kommer till stor del att stanna kvar inom samma område vilket bör resultera i fler harar. Efter ett antal år av predatorkontroll, när hararna blivit så många att resurserna inte kan försörja alla, kommer förmodligen harungarna börja sprida sig längre bort och tillväxten på den lokala populationen därmed stagnera, men på en mycket högre täthetsnivå än tidigare. Man kan dock vara tämligen säker på att om viltvården upphör kommer hartätheten sjunka mycket snabbt i och med att nya rävar hela tiden vandrar in i de rävtomma områdena där det dessutom finns gott om föda.

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