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Population dynamics of mountain hare *Lepus timidus* populations in Finland

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During 1998-2001 we studied population dynamics of the mountain hare *Lepus timidus* in three areas of Finland which were in different phases of the hare population cycle and in different geographical locations. The aim of our study was to examine the survival and reproductive rates of hare populations under different circumstances. Hare numbers were monitored using the wildlife monitoring data. Hare samples were collected by hunters in southern Finland (prolonged hare population low), central Finland (increasing hare population) and northern Finland (declining hare population). The survival rates of both adult and young hares were lowest in northern Finland. Litter size did not differ between the populations, but the proportion of breeding females and consequently, productivity of the hare population was highest in central Finland and lowest in southern Finland. The possible effects of especially the phase of the hare population cycle, condition and size of female hares, predator abundance and weather/climatic factors on the population dynamics of hares are discussed.

Key words: Lepus timidus, mountain hare, hare population cycle, productivity, survival rate

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Mountain hare *Lepus timidus* numbers are known to fluctuate in many areas of Eurasia (e.g. Keith 1963, Watson et al. 1973, Hewson 1976, 1985). In Fennoscandia, including northern and central Finland, mountain hare numbers tend to vary cyclically, usually with a cycle length of 4-11 years (Pulliainen & Tunkkari 1987, Hörnfeldt 1978, Lindén 1988). The cycles are not so obvious in southern Finland (Kauhala & Helle 2000). Monitoring data from Russian Karelia, the eastern neighbour of Finland, also suggest 10-year population cyclicity of mountain hare (Danilov et al. 1996).

It is important to study the population dynamics of hares in order to understand the driving forces behind population cycles; the species is eagerly hunted and hunting managers would also appreciate deeper understanding of hare population dynamics. Productivity and sur-

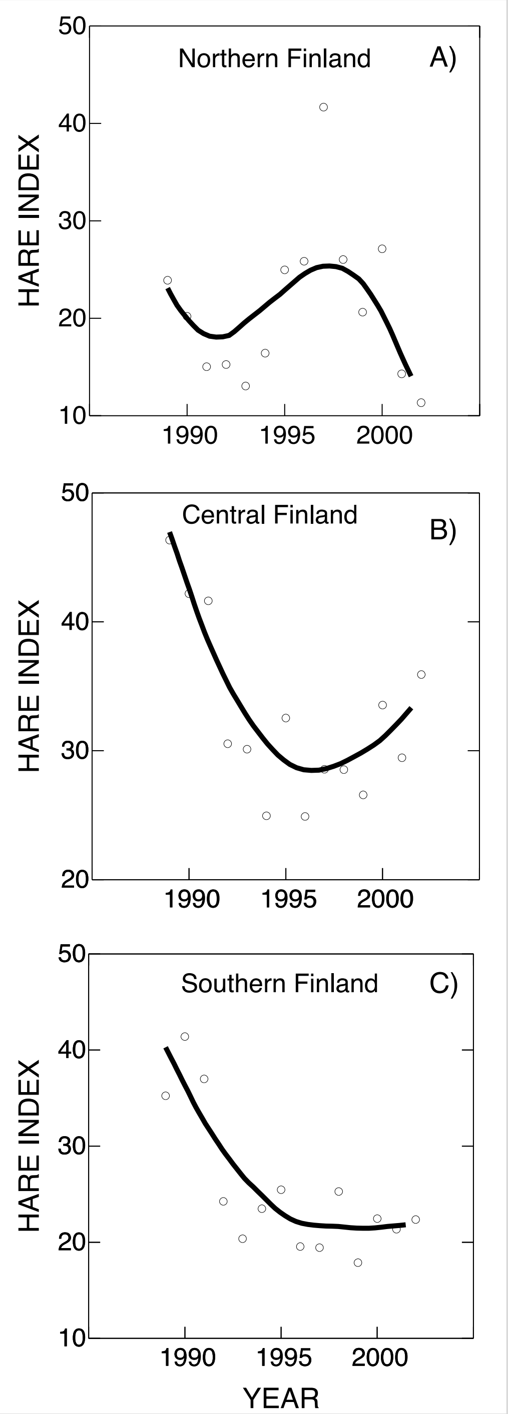

Figure 1. Trends of hare populations based on wildlife monitoring counts (snow-track counts) in three areas of Finland: A) northern Finland (the game management district of Oulu), B) central Finland (Etelä-Savo, Keski-Suomi, Pohjois-Karjala and Pohjois-Savo) and C) southern Finland (Etelä-Häme, Kymi and Satakunta). The hare index gives the number of tracks crossing the transect lines per 10 km/24 hours (Lindén et al. 1996).

vival rates of hare populations presumably vary during different phases of the cycle. However, other factors, such as predator abundance, size and condition of female hares, food abundance and weather/climate may also be responsible for the variation in hare population dynamics, irrespective of the phase of the hare cycle (Flux 1970, Angerbjörn & Hjernquist 1984, Hewson 1985, Angerbjörn 1986, Danell & Hörnfeldt 1987, Marcström et al. 1989). For instance, Hewson (1985) and Angerbjörn & Hjernquist (1984) found that population declines were due to low survival rate of adult hares caused by harsh weather and, consequently, a shortage of food. Low food availability caused by thick snow cover also resulted in big loss of embryos and, thus, low productivity among mountain hares (Flux 1970). An epizootic of sarcoptic mange that killed many foxes *Vulpes vulpes* (Danell & Hörnfeldt 1987) or predator removal from islands (Marcström et al. 1989) resulted in better survival rates of hares.

The aim of our study was to compare the productivity and survival rate of mountain hare populations in three areas of Finland and to discuss the possible causes behind the differences. The areas differed e.g. in their phases of the hare cycle, predator abundance and the climate affecting growing season for plants, including food plants for hares (see Helle & Kauhala 1991). In southern Finland there was a prolonged low phase in the hare cycle, in central Finland the hare population was increasing, and in northern Finland it was declining (Fig. 1; see also Kauhala & Helle 2000: Fig. 4). We expected the productivity and survival rate of the hare populations to differ between the areas, partly reflecting the different phases of the hare cycles. We also discuss the possible effects of other factors that may have resulted in spatial variation in the productivity and survival rates of the hare populations. These factors include e.g. predator abundance, size and condition of female hares and geographical location.

Material and methods

Wildlife monitoring data

Wildlife triangle counts have been performed all over Finland every winter since 1989 (Lindén et al. 1996). About 1,200 permanent routes are situated randomly in forested areas. Each side of a triangle-shaped transect is 4 km, and the total inventory route is thus 12 km long. Voluntary assistants perform snow-track counts each year, counting the tracks of all game animals including the mountain hare and red fox, after a snow fall or precheck of the line. The snow-track index gives the num-

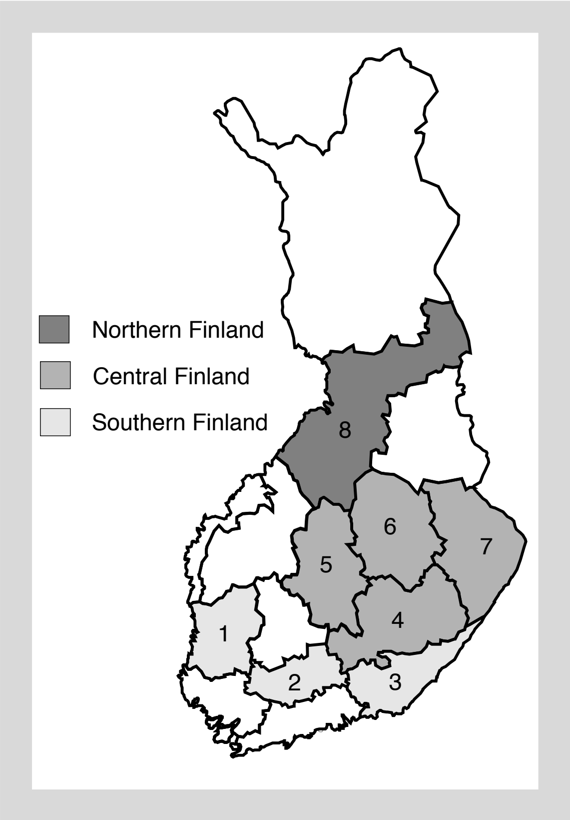

Figure 2. The study area which included northern, central and southern Finland. Hare samples were collected from eight game management districts: 1) Satakunta, 2) Etelä-Häme, 3) Kymi, 4) Etelä-Savo, 5) Keski-Suomi, 6) Pohjois-Savo 7) Pohjois-Karjala and 8) Oulu.

ber of tracks crossing the inventory route per 10 km/24 hours. We assumed a linear relationship between the track index and population density (see also Högmander & Penttinen 1996). Also Kurki et al. (1998) found significant positive correlations between the track indices and annual hunting bags of foxes and pine martens *Martes martes*. The track indices were calculated for three areas: southern Finland (the game management districts of Etelä-Häme, Satakunta and Kymi), central Finland (Etelä-Savo, Pohjois-Savo, Pohjois-Karjala and Keski-Suomi) and northern Finland (Oulu; Fig. 2).

Non-parametric smoothing was applied to the track-index data to get a better picture of the phase of the hare cycle in each area. The smoothing method used was kernel weighted polynomial regression (degree of polynomial = 1). Function for data weighting was epanechnicov kernel. Fixed bandwidth was 4.935. We used the software Systat 10.

Carcass material

Hare samples (N = 563) were collected by hunters in southern (N = 156), central (170) and northern (237) Finland during 1998-2001 (see Fig. 2). Carcasses were collected during the hunting season (1 September - 28 February). The data were divided into two seasons: autumn (September-November; N = 310) and winter (December-February; N = 253).

Age of hares was mainly determined from the ossification stage of radius and ulna, but the dry weight of the eye lens was also used (Kauhala & Soveri 2001). The hares were classified into two groups: animals < 1 year old (called 'young' if killed in September-November and 'subadult' if killed in December-February) and 'adult'. An eye lens weight of 0.25 g was used as a discriminating value between young/subadult and adult hares, when age determination from the bones was not clear.

The hares were weighed and uteri were examined for placental scars. Hind-foot length was used as a measure of size. We also calculated a condition index: body weight/hind-foot length (see Iason 1990). Because the mean number of scars between females killed in autumn vs winter did not differ (t = 1.68, df = 68, P = 0.098), we used the data from both seasons to determine the number of young produced. We assumed that the number of scars in each uterus indicated the total number of young born during the previous breeding season as Frylestam (1980) suggested. The proportion of adult females with placental scars was also calculated. In this calculation we included all uteri with signs of scars, even if the number of scars could not be counted (for instance, if only one horn of uterus was sent to us). We then calculated the productivity of the population: the proportion of females with scars multiplied by the mean number of scars per uterus. We also divided the scars into three classes: light, dark and black scars, supposing that they represented spring, summer and autumn litters, respectively (see also Frylestam 1980, 1990). We then calculated the proportion of females with one, two or three sets of scars (litters) during one breeding season.

Some hunters did not include the uteri of some of the female hares they sent to us, and these 'females' were excluded from the data, because some of them may actually have been males. Thus, the sample was biased towards males and the true sex ratio could not be calculated. The sex ratio differed, however, between areas ($\chi^2 = 12.53$, df = 2, P = 0.002), being almost 1:1 in the north where most hares were hunted by our own field assistants who could certainly distinguish between males and females. Therefore, we assumed that the true sex ratio in the populations was 1:1, as also Bergengren (1969) noticed. Because the age structure of males and females did not differ (see the section Results), the bias of the sex ratio in the samples did not affect the results of this study. There may also be bias in the age ratios of

Table 1. Proportion (in %) of young/subadults in the mountain hare samples collected in autumn and winter from southern (low hare numbers), central (increasing hare numbers) and northern (decreasing hare numbers) Finland. Also the change in the age ratio from autumn to winter is given. Sample size is given in parentheses. χ^2-test was used to test the differences in age ratios between areas and seasons.

Area/phase	% young in autumn		% subadults in winter		Change (in %)	χ^2	df	P
Southern/low phase	52	(64)	46	(92)	- 6%	0.78	1	0.371
Central/early increase phase	54	(124)	52	(46)	- 2%	0.04	1	0.829
Northern/decrease phase	50	(122)	34	(115)	- 16%	6.28	1	0.012
	$\chi^2 = 0.41$		$\chi^2 = 5.54$					
	df = 2		df = 2					
	P = 0.817		P = 0.063					

the samples, because young hares are probably easier to catch than older, more experienced animals. Since the bias probably is similar in all areas, it is unlikely that it affected the results when we compared different areas.

Mean number of scars, female body weight, condition index and hind-foot length did not differ between years (ANOVA; scars: F = 1.33, df = 3,71, P = 0.271; body weight: F = 0.15, df = 2,88, P = 0.859; condition index: F = 1.83, df = 2,68, P = 0.168; hind foot: F = 1.01, df = 2,77, P = 0.368). Although the proportion of females with scars differed between years ($P < 0.05$), we pooled the data for different years, because the data for each year were small. We are fully aware that there may be year-to-year variation in the population parameters we are employing, but averages over few years are justified, since the time periods sampled cover population trends prevailing for several years.

When examining population dynamics, we started from a population of 1,000 hares in winter t (based on the age structure of the winter samples). We then calculated population growth rate (λ = population size in winter$_{t+1}$/population size in winter$_t$) from the wildlife triangle data and used it to estimate the size of the populations in winter t+1. We calculated the number of subadults and adults in winter t+1 by using the average age structures in each area (see above). We then calculated the annual survival rate of adults (adults in winter$_{t+1}$)/(adults + subadults in winter$_t$). Then we estimated the number of adults alive during the breeding season by assuming a constant mortality rate and three months between winter and the breeding season. We used the figures for productivity in each area to calculate the number of young produced, supposing an equal sex ratio (Bergengren 1969).

Results

Age structure of the hares sampled

The total sample (N = 563) consisted of 115 adult females, 182 adult males, 93 young/subadult females and 173 young/subadult males. The proportion of young/subadults was 47% in the total sample; 45% for females and 49% for males ($\chi^2 = 0.75$, df = 1, P = 0.388). In the autumn sample, 52% of hares were young, in the winter sample the corresponding figure was 41.5% ($\chi^2 = 6.08$, df = 1, P = 0.014). The proportion of young did not differ significantly between the areas, although in winter the proportion of subadults was numerically highest in central Finland and lowest in northern Finland (P = 0.063; Table 1). The age ratios differed between seasons in northern Finland.

Productivity of the hare populations

Body weight and hind-foot length of adult females were lowest in southern Finland and highest in central Finland (Table 2). The condition index correlated positively with body weight in adult females (r = 0.91, df = 51, P <

Table 2. Mean weight (in g) and hind-foot length (in cm) of adult females, litter size in summer (i.e. the number of dark scars, mean ± SD, N), the total number of placental scars in each uterus with scars, percentage of adult females with placental scars and productivity of the population (productivity = total number of scars x proportion of females with scars) in southern (low hare numbers), central (increasing hare numbers) and northern (decreasing hare numbers) Finland.

Area/phase	Weight (g) of females	Hind-foot length (cm)	Litter size (summer)	Total number of scars	% females with scars	Young/ female
Southern/low phase	3308 ± 349.8 (18)	15.0 ± 0.77 (20)	4.3 ± 1.4 (14)	7.9 ± 1.64 (15)	63 (24)	4.9
Central/early increase phase	3616 ± 406.3 (27)	15.8 ± 0.65 (24)	3.6 ± 2.0 (19)	8.0 ± 2.13 (19)	92 (26)	7.4
Northern/decrease phase	3563 ± 446.5 (46)	15.7 ± 0.70 (37)	3.9 ± 1.6 (33)	7.4 ± 2.06 (40)	80 (60)	5.9
ANOVA/χ^2-test	F = 3.30	F = 7.63	F = 0.60	F = 0.63	$\chi^2 = 6.50$	
	df = 2, 88	df = 2, 77	df = 2, 63	df = 2, 71	df = 1	
	P = 0.043	P = 0.001	P = 0.554	P = 0.537	P = 0.039	

0.001). Body weight and hind-foot length did not correlate (r = -0.02, df = 51, P = 0.873). The mean numbers of black, dark or light scars (i.e. the number of leverets in autumn, summer and spring litters, respectively) did not differ between populations (ANOVA; black scars: F = 1.80, df = 2,71, P = 0.173; dark scars: F = 0.81, df = 2,71, P = 0.451; light scars: F = 0.89, df = 2,71, P = 0.414), nor did the total number of scars (see Table 2). In central Finland, all females with scars had at least two sets of them, while 12.5% of females in northern Finland and 7% of females in southern Finland had only one set of scars. The difference was not, however, significant (χ^2= 2.77, df = 4, P = 0.597). The proportion of females with scars and the productivity of the hare population were highest in central Finland and lowest in southern Finland (see Table 2).

In the total data, 79% of adult females had placental scars. Of these, 73% had two sets of scars, 19% had three sets and 8% had only one set. Mean litter size (i.e. the number of scars in a set of scars) was 3.6 (range: 1-9; SD = 1.81, N = 156). The mean number of black scars (when present) was 3.9 (SD = 1.47, N = 47), that of dark scars 3.9 (SD = 1.69, N = 66) and that of light scars 3.0 (SD = 2.14, N = 43). The mean number of placental scars in uteri with scars was 7.7 (range: 3-13; SD = 2.00, N = 74). Mean productivity of the hare population in Finland was 6.1 (0.79 x 7.7).

Population dynamics

The survival rates of both adults and young were lowest in northern Finland (Table 3). Although the absolute number of young produced by a population of 1,000 hares was higher in northern than in southern Finland, the number of subadults the next winter was lowest in northern Finland. The numbers of young produced and subadults alive in winter (i.e. recruitment) were highest in central Finland.

Discussion

Productivity

The productivity of hares was highest in central Finland, where the population was at the early increase phase and females were large and in good condition, and lowest in southern Finland where females were smaller and in poorer condition. Also Cary & Keith (1979) found that among snowshoe hares *Lepus americanus*, the productivity was highest during population increase. The females which were all killed after the breeding season in central Finland were heavier and in better condition, on average, than females in southern Finland, although the theory of reproduction costs would predict poorer condition after the breeding season among females that have invested heavily in reproduction (e.g. Clutton-Brock et al. 1982). Probably females in central Finland were in better condition (and certainly larger) the year round and could invest heavily in reproduction.

Flux (1970) and Iason (1990) found that large, heavy mountain hare females produced more offspring than did small females. In our study, however, there was no difference in litter size between areas, but a higher proportion of females reproduced annually in central Finland than in the other populations. There are two possible explanations for this. First, it is possible that the abortion rate at the early stages of pregnancy was high espe-

Table 3. Estimation of the population dynamics of mountain hare populations in different areas of Finland, starting from 1,000 individuals in winter t, and based of the average age structure of hare samples in winter and the productivity of the populations (on the basis of placental scars). Population growth rate, λ (N_{t+1}/N_t), was calculated from the wildlife monitoring data, and a sex ratio of 1:1 was assumed. Survival rate of adults was calculated from winter t to winter t+1, and that of young from summer t to winter t+1.

	Southern Finland	Central Finland	Northern Finland	
λ	1.05	1.20	0.60	
Winter t:				
Subadult	460	520	340	
Adult	540	480	660	
Total	1000	1000	1000	
Summer t:				
Young	2185	3308	2504	
Adult	892	894	849	
Total	3077	4202	3354	
Winter t+1:				
Subadult	483	624	204	
Adult	567	576	396	
Total	1050	1200	600	
Survival rate of adults	0.57	0.58	0.40	χ^2 = 81.96, df = 2, P < 0.001
Survival rate of young	0.22	0.19	0.08	χ^2 = 190.97, df = 2, P < 0.001

cially in southern Finland due to poor condition of females. If all embryos die at the early stages of pregnancy, no scars can be seen in the uterus. Calculations by Flux (1970) showed that 25.9% of females lost their entire litters between implantation and half-term of the pregnancy in Scotland. Second, large and heavy females may produce heavy leverets, which may reach sexual maturity early (because they are heavy, see Reiss 1989) and consequently, a high proportion of them reproduce the next spring. Thus, the large size and good condition of females probably resulted in a high percentage of breeding females in central Finland. This is supported by the study of Pehrson & Lindlöf (1984) who did not find any connection between condition of females and litter size. Instead they found that heavy females produced heavy leverets.

Furthermore, Angerbjörn (1986) found that population density and body condition of mountain hare females were negatively correlated. Population density also correlated negatively with the percentage of leverets caught in autumn (i.e. reproductive output), but there was no relationship between population density/body condition and litter size or the number of litters. He concluded that density/body condition of females affected the birth weight of leverets and their growth during lactation.

Body weight and productivity of hares were lowest in southern Finland, although the growing season for food plants and the breeding season for hares are longest in the south (Helle & Kauhala 1991). Furthermore, because hare numbers were low, it is unlikely that density-dependent factors limited reproduction. Thus, body condition and reproduction rate should actually have been highest, not lowest, in the south. The reasons behind the spatial variation in the body condition of females are not clear. One possibility is the difference in fox density between the areas. The red fox is known to commonly prey on hares in Finland (Vainio et al. 1997, Kauhala et al. 1998), and there is evidence that reductions in fox numbers have resulted in an increase in hare numbers/hunting bags or *vice versa* (Danell & Hörnfeldt 1987, Angerbjörn 1989, Marcström et al. 1989, Lindström et al. 1994, Smedshaug et al. 1999). Thus, the fox probably is the main predator of hares in Fennoscandia and it can also limit hare numbers.

The fox index, calculated using the wildlife triangle data, was highest for southern Finland (mean for 1998-2001 was 10.0), lowest for northern Finland (3.8) and rather low also for central Finland (5.4). The ratio between fox vs hare track index in southern Finland was about seven times higher than in central and about four times higher than in northern Finland. The dense fox population may have resulted in poor condition and low productivity of hares in southern Finland; hares may have avoided the best feeding habitats, lost weight and produced small leverets, which in turn are poor reproducers the next spring. This would fit to the 'predator-avoidance constraint hypothesis' presented by e.g. Gilbert & Boutin (1991), Hik (1995) and Krebs (1996). Hares may also have suffered from chronic stress because of the dense fox population; Boonstra et al. (1998) found that a high predation risk causes chronic stress and poor reproduction in snowshoe hares. Young et al. (2004) also showed that chronic stress in meerkats *Suricata suricata* resulted in loss of body condition, reduced rates of conception and increased rates of abortion. It is also known that the presence of predators (or their odours) can suppress reproduction in voles *Clethrionomys* spp. (Ylönen 1989, 1994, Korpimäki et al. 1994, Fuelling & Halle 2004). When the predation pressure is heavy, females can also delay their sexual maturation (Ylönen 1989, Heikkilä et al. 1995).

Hare cycles are not so evident in southern Finland as in more northerly areas. Possibly the low rate of reproduction, because of a dense population of generalist predators, such as the fox, is among the factors preventing the population increase in southern Finland. Generalist predators have also been found to stabilise vole cycles (Hanski et al. 1991). In the earlier study of hare and fox interactions (Kauhala & Helle 2000), a strong connection between fox and hare was found in southern Finland, fox numbers both following hare numbers and affecting the growth rate of the hare population. This also points to the conclusion that predators (i.e. foxes) may have a strong impact on the hare population in southern Finland.

Furthermore, better condition and higher reproductive rate of females in northern than in southern Finland, despite of the shorter growing and breeding seasons in the north, also suggests that productivity of hares may be more dependent on other factors, such as predator abundance, than on geographical location. The hares were, however, larger in the north, as Bergmann's rule suggests (James 1970), which may also have affected reproduction (Iason 1990).

Productivity in Finland and other areas

The mean litter size in our study was 3.6 and, if light, dark and black scars correctly represent spring, summer and autumn litters, respectively, spring litters were smaller than summer or autumn litters. It is also possible that some scars (from spring litters) had disappeared by autumn, and therefore the number of light scars was lower than that of dark or black scars. Iason (1990) found, however, that prenatal mortality rate was highest among early litters and, thus, spring litters may indeed be smaller than later litters. Also Höglund (1957) found that in captivity the first litter was smaller (mean: 2.15) than the second (3.24), the mean litter size being 2.7. Pehrson & Lindlöf (1984) reported that the litter size of mountain hares varied between 3.5 and 4.3 in captivity, a figure similar to the one found in our study. According to Flux (1970), the mean litter size was only 2.3 in Scotland where hares are smaller than in Finland (Angerbjörn & Flux 1995). Thus, the larger size of hares in the north may be responsible for larger litters (Iason 1990).

The majority of females had two litters per breeding season in Finland. Angerbjörn (1986) found that in southern Sweden the mean air temperature in February and March affected the number of litters produced during the breeding season; when spring came early, hares produced three litters, but in years with late springs, only two litters were produced. The spring comes late to Finland compared to southern Sweden, and usually only two litters are produced. Also in Norrland (Sweden) and in Norway mountain hares usually have two litters per breeding season (Höglund 1957, Myrberget & Krigsvoll 1983). In northern Russia where winters are long, there is only one litter per year, whereas in Belorussia 3-4 litters are usual (Naumov & Shatalova 1974, Gaiduc 1973, according to Angerbjörn & Flux 1995). Weather/climate conditions may thus be the most important factor affecting the number of litters produced in one breeding season.

The mean productivity (young/female) during one breeding season was 6.1 in our study. In Scotland, productivity varied between 5.4 and 6.3 (Flux 1970, Hewson 1976). In southern Sweden the mean productivity was 2-5, depending on population density (Angerbjörn 1986). This estimation was based on the number of leverets in the population after weaning, giving a lower estimation than our study, because some leverets have certainly died before the counts. Productivity may be rather similar in different areas, because in areas where litter sizes are smaller, the number of litters per breeding season is higher and *vice versa*.

Survival rate

In central Finland, the survival rate of hares was rather high, indicating that density-dependent factors (e.g. lack of food and disease) did not limit population growth, and predation pressure was probably low. Also according to the wildlife monitoring data, the connection between hare and fox numbers was weak in central Finland (Kauhala & Helle 2000). Thus, when hare numbers are increasing and/or high and fox numbers are low, the effect of foxes on hare survival is probably negligible. If predation is the main process affecting hare cycles and causing the decline as Hik (1995), Krebs et al. (1995) and Krebs (1996) suggested, the lack of predation most probably leads to increased hare survival. However, lynx *Lynx lynx* numbers are rather high in east-central Finland, and lynx also commonly prey on hares (Pulliainen et al. 1995, Kauhala & Helle 2000). But although lynxes consume many hares, there is no evidence that they limit the growth of the hare population. Lynx is a large predator, and it is unlikely that its numbers are high enough in Finland to prevent the rapid population growth of a smallish herbivore.

Rather high survival rates balanced the low productivity of the hare population in southern Finland with low but stable hare numbers during the last decade. Hik (1995) found that under very high risk of predation, hares favoured survival over condition by avoiding risky habitats. It is also possible that foxes, which are generalist predators, have turned to alternative prey in southern Finland because hare numbers have been low for many years (Lack 1954).

The survival rate of both adult and juvenile hares was lowest in northern Finland. Density-dependent factors (e.g. disease, parasites and lack of food) and a high predation pressure may have been responsible for the low survival rate during the decline phase. Keith et al. (1993) suggested that predation mainly determines the survival rate of hares. Krebs et al. (1986) found that the survival rate of hares was low during the population decline although extra food was offered to them, suggesting that high predation pressure was connected to the low survival rate. Boonstra et al. (1998) also found that during the decline phase of the snowshoe hare cycle, virtually every hare that died was killed by a predator.

Also according to Keith et al. (1984) predation is most important during the decline and low phases of the snowshoe hare cycle, and Hik (1995) suggested that mortality from predation causes the decline phase of the cycle. Keith & Windberg (1978) found that especially juvenile survival rate correlated with changes in hare density. Our previous study based on wildlife monitoring data (Kauhala & Helle 2000) also suggested a strong connection between hare and fox numbers in northern Finland (during 1989-1999). Also avian predators, like the goshawk *Accipiter gentilis*, may have been involved (Tornberg et al. 1999, Tornberg & Colpaert 2001).

Conclusions

Productivity and survival rate of the hare population were highest in central Finland where hare numbers increased, suggesting that during the increase phase density-dependent factors did not limit the growth of the hare population, and the effect of predators was negligible. During the low phase, productivity of the hare population was low, probably because of the poor condition of females. The high risk of predation may have affected the condition and reproduction of hares, either by affecting their feeding behaviour or by causing chronic stress to hares. The survival rate of hares and the recruitment of subadults into the population were lowest in northern Finland, probably because of density-dependent factors and a strong predation pressure during the decline phase of the hare population cycle.

Ideally, population dynamics of hare populations should be studied with data covering the whole hare population cycle in each area. Only then would it be possible to critically evaluate the roles of geographical location, phase of the hare population cycle and predation pressure on hare characteristics (body weight/condition index, body size) and population parameters (reproduction, survival), which were here mainly interpreted as effects of the phase of the population cycle and predator density. However, the data presented in this study strongly suggest that there is great potential for multiple use of the extensive wildlife monitoring data when combined with other special data such as for instance the carcass material on reproduction used in this study.

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