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A Rapid Summer Decline in a Mountain Hare Population on an Island

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A mountain hare, *Lepus timidus* Linnaeus, 1758, population was followed from 1973 to 1978 on Lilla Karlsö island in the Baltic Sweden. Density estimates were first based on direct counts, and later on marking and re-observation of hares. The density was fairly stable at a very high level, about 400 hares on 160 ha, for several years. During the severe winter 1976/77 the number decreased to 162 hares in January, 107 in May and in August less than 10 hares remained. The monthly adult survival rate during the summer was therefore less than 0.75. In early spring, male hares especially, were in bad condition and probably suffered a higher mortality, while females probably died during early summer. The possible role of food shortage and parasitic infestation is discussed.

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1. INTRODUCTION

The mountain hare, Lepus timidus Linnaeus, 1758, normally has low population density on the Swedish mainland, with only a few hares per sq km (Lindlöf, 1979). The highest density that has been reported on a mainland is 51 hares per sq km in Scotland (Watson et al., 1973). Conversely, on islands one can find very high densities with more than 300 hares per sq km (Angerbjörn, 1977, 1981; Häkkinen & Jokinen, 1981). Dramatic decreases on island have been reported earlier (Angerbjörn, 1981; Häkkinen & Jokinen, 1981), and in these cases mortality has been highest during winter to spring. Studies on other Lepus species also show the highest mortality in winter to spring, both during normal years and years of a rapid decline (Hewson 1965, 1976; Flux, 1970; Abildgard et al., 1972; Keith & Windberg, 1978). Here, we raport of a mountain hare population that have a normal decline during winter and early spring after a severe winter. However, instead of a recovery during the summer, the population crashed, with the highest mortality measured in June to July. We discuss different factors and their possible role in the dynamics of this island population of the mountain hare.

2. STUDY AREA

Lilla Karlsö island (Fig. 1) with an area of 1.6 sq km, is situated 4.5 km west of Gotland in the Baltic Sea. Lilla Karlsö island has been influenced by sheep grazing for hundreds of years. This has resulted in a shrub-less grassland pasture with solitary giant trees on the steep stony slopes. The grass (*Festuca ovina*) dominated vegetation has an annual maximum productivity in early summer (May-June), with the crop varying 0.7-1.6 ton (dry matter) per ha productive area ($80^{0}/_{0}$) (Fig. 2) depending on the weather (Hjernquist & Hjernquist, 1974).

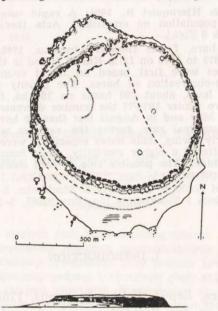
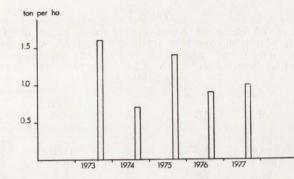
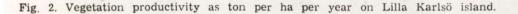


Fig. 1. Map over the Lilla Karlsö island. Dotted line shows the fixed observation route.

The crop value for 1977, the year of the decline, was not exceptionally low, 1.0 compared to previous years, 0.9 and 1.4 (Fig. 2). The vegetation can probably withstand a grazing pressure of 1.4 sheep per productive ha during the summer (Hjernquist & Hjernquist, 1974) but in 1977 grazing pressure was 0.9 ewes per productive ha lasting for about ten months. The joint grazing by sheep and hares leads to overgrazing. According to Hjernquist & Hjernquist (1974) there is a clear competition for food between hares and sheep.

Since at least 1725 hares have been released on the two Karlsö islands for hunting. In 1882 19 mountain hares caught on a nearby island were let out on Stora Karlsö island. Ten years later, in 1891, 237 animals were shot. In 1942, the hare population, which earlier was estimated at some 250—350 animals (Wahlin, 1945), was reduced to a very low density when foxes appeared on the island. Many hares then emigrated across the ice (4.5 km), and 50 hares arrived, according to Wahlin (1942), to the Lilla Karlsö island in January 1942. At that time the island had been without hares for over one hundred years. Since 1942 hunting has been irregular and not occurred after 1972. The winters 1972/73 to 1974/75 were all mild with 0-8 days of snow cover, but winters 1975/76 to 1977/78 were cold with 36-50 days snow (Fig. 3). Since the island is very exposed to wind, the snow surface becomes very hard, making access to the vegetation difficult for the hares.





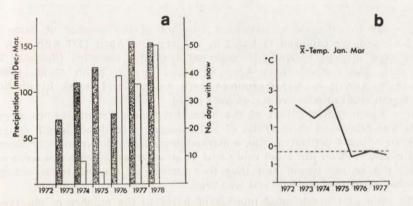


Fig. 3a. Precipitation (mm) during December to March (dark bars), and no. of days with snow cover (light bars) on Stora Karlsö island (SMHI).
Fig. 3b. Mean temperature during January to March on Stora Karlsö island, and 30-years mean temperature (dotted line) (SMHI).

3. METHODS

To get an index of hare density on the island, systematic observations were made during the spring from 1973 to 1978. The observer walked a fixed route around the island (about 3 km, Fig. 1) and recorded all adult hares encountered, juveniles excluded. The observations during one season were made by 2—3 persons, and in total 5 persons. The observation periods are comparable in length and date (Table 1), and no significant differences were found between the observations made by the five observers, time of the day or weather conditions, during 1974, 1976 and 1977 (analysis of variance). Dead hares were also counted and each carcass was removed over the whole island. Hares that died during autumn, winter or early spring were found during the spring routes (to April), while hares that died during late spring or summer were found during the summer routes. Since carcasses were counted not only on the systematic routes, but also by the reserve keepers the whole summer through, it is assumed that dead hares were found with an equally high probability.

Table 1

Number of observed hares on a fixed route on Lilla Karlsö island, during 1973—1978. \bar{x} =mean no. of observed hares, n=no. of routes, \bar{N} =estimated population no. (including correction ratio 5.39, see text for further explanation).							
Year	Ŧ	SE	n	Aver. date	Ñ		
1973	83		13	_	447		
1974	70.2	9.6	9	11/3	378		
1975	107		1	18/4	577		
1976	73.0	7.9	4	1/5	393		
1977a	25.0	1.6	17	2/5	(123)		
1977b	1.00	0.53	7	25/9	5.4		
1978	0.86	0.26	7	29/4	4.6		

In order to calculate an unbiased estimate of the number of hares present on the island, we captured 18 hares in January and April 1977 with nets. All the hares were marked individually with ear tags and toe clips (National Band & Tag Co.). The methods have been described by e.g. Keith *et al.*, (1968) and Angerbjörn (1977). All hares captured were weighed and sexed. In addition hind foot length and reproductive status were noted.

To compare the condition of the hares between different seasons a condition index was calculated as the ratio of body weight to hind-foot length (Angerbjörn, 1979). To estimate population size, a marked-unmarked ratio from daily observations were made, both on the fixed route and in other areas. Since hares were captured during the census period and thus the number of marked hares changed, the Schnabel estimation (Seber, 1973) was used.

The ratio of the estimated number of hares to the number of observed hares was calculated for January (ratio: 5.35) and April 1977 (ratio: 5.42). The average, 5.39, was used to correct earlier observations (Table 1) for estimating the number of hares. There is a high correlation between number of observed hares and unbiased estimates of different densities on other islands (Angerbjörn unpubl.). In most statistical analyses, methods and abbreviations from Sokal and Rohlf

(1969) have been used.

4. RESULTS

A regression analysis between number of observed hares over the whole observation period and time was made for each year to estimate the mortality rate (in the test — the slope, Caughley 1977 p. 151) during the observation period. Since no mortality was found in any year (Table 2), we conclude that the average number of observed hares may be used as an estimate of the density for the period. However, there was a tendency for a decline in spring 1976 and for the marked hares in spring 1977. The number of observed hares (Table 1) was significantly

Table 2

the differen	t periods of o b , $b \neq 0$, that	bservation, t is statisti	1974—19 ically si	77. t-test fo ignificant r	ion to time in days, during or different slope (regression nortality during the period of determination.
Year	r ²	ь	n	t	Р
1974	0.06	0.008	9	0.69	P>0.05
1976	0.86	-0.03	4	-3.76	0.10>P>0.05
1977a	0.07	-0.002	18	-1.08	P > 0.2 total obs.
10001	0.00	0.00	10	1.01	0.10 D 0.05

1977b	0.20	-0.02	16	-1.91	0.10 > P > 0.05 marked obs.
	No	hares ±SE			
	500		1		
	400		/	1	
	300	1.	T	1	
	200				
				/	٨.
	100			6	
	50				
		10.3.45			
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	5				
		1973	1974 19	975 1976	1977 1978

Fig. 4. Number of mountain hares, and no. of carcasses found, dark bars during winter and spring, light bars during the summer.

lower (analysis of variance, Neuman-Keul test, $\alpha = 0.05$) in 1977 than in 1974 and 1976.

According to Figure 4 the population has remained fairly stable at a very high level for a couple of years. After the winter 1975/76, which was the first with snow since 1970/71 (Fig. 3), there was a nonsignificant tendency for a decline in density. The following winter, 1976/77, was also severe with snow and cold weather. In January 1977, the density

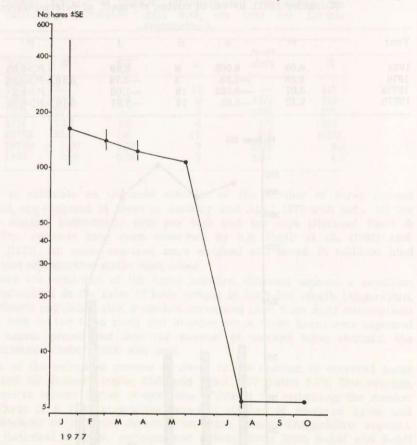


Fig. 5. Number of mountain hares during 1977, Jan. to Sept. (on Lilla Karlsö island).

had decreased to 160 hares (Fig. 4). From April to September normally no or only single carcasses were found, but in the summer 1977, we found 29.

In August nearly all hares were dead, and only five were estimated to remain in the population. A more detailed look at the density during spring 1977 (Fig. 5) also shows a very sharp decline in June and July. In January, week 3, the population size was 162 and in May, week 22,

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Summer decline in a hare population

107. From this level the population decreased to 5 hares in August, week 31. This indicates that the mortality rate from Table 3 is underestimated. If the mortality rate is constant during June and July the monthly mortality rate based on population densities should instead be 0.66.

During the years of 1979, 1980 and 1981, hares remained on the island in very low numbers. In 1982, however, there were more observations of hares, which could be a sign of a small increase in hare density.

Mortality rate q_n	(Caughley, 1977) and survival values during spring 1977, h on number of dead hares found.	baseď
	Marked hares	

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-	Marked hares		Survival	Mortality q_m	
Time	Total	Dead	value	rate per months	
FebMar.	9	2	0.78	0.11	
AprMay	16	2	0.87	0.07	
JunJul.	14	7	0.50	0.25	
Total	18	11 1	0.34	0.15	

¹ Later, in 1980, two more marked hares were found.

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Analysis of variance of condition index, body weight over hind-foot length, in January and April 1977.

	Average con	Average condition index		
	Males	Females		
Jan.	0.168	0.198	E (1 19) -0 C0 MC	
Apr.	0.171	0.211 ²	F (1.13)=0.62 NS	
2 Ind -	F(1.13) = 12.4 $P \le 0.01$	= bystowner	Interaction F (1.13)=0.25 NS	

¹ NS=non significant results at P>0.05 level.

² The females were pregnant in April.

The mortality rate in Table 3 is based on the number of marked hares found dead, compared to the total number of marked hares. The monthly mortality rate during spring 1977 was fairly constant from February to May. However, in the next two month period, June-July, the mortality rate increased to 0.25 per month. Since these figures assume that all marked dead hares should be found within a month, this is probably an underestimation.

There were no significant differences in the condition index between hares captured in January and April 1977 (Table 4). But the only two recaptures in April of hares marked in January, a male and a female, both showed a body weight decrease. The male decreased from 2.4 to 2.0 kg and the female from 3.4 to 3.3 despite that she was pregnant in April. All females were pregnant in April (n=5), and all males (n=5)were in reproductive phase as is normal for this time of the year, although the males had small testes. Moreover, juvenile hares were observed in June, but only very few, and not in the high numbers as in previous years.

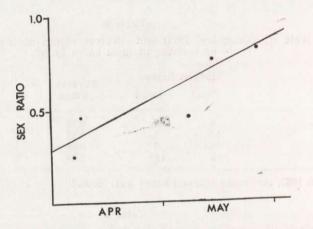


Fig. 6. The linear trend in sex ratio (males of total), based on observations of hares during spring 1977. The slope is significantly different from 0 (P=0.03, Snedecorand Cochran, p. 206, 1980), y=0.01x+0.32.

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Endoparasites on mountain hares (n=no. of hares) on Lilla Karlsö island and on mainland (Burgaz, 1970).

Species	Mainland ¹ 1970		Lilla Karlsö ¹ 1970		Lilla Karlsö ² 1973—1977	
	0/0	n	0/0	n	0/0	n
Eimeria spp.	63	(12)	63	(16)	100	(6)
Dicocoelum dendriticum	0	(12)	25	(16)	0	(6)
Andrya spp.	0	(12)	33	(30)	33	(6)
Cittotaenia spp.	11	(12)	33	(30)	0	(6)
Graphidium strigosum	0	(12)	10	(30)	0	(6)
Trichostrongylus retortaeformis	99	(12)	90	(30)	83	(6)
Trichurus leporis	0	(12)	20	(30)	33	(6)
Protostrongylus pulmonalis	50	(12)	100	(30)	89	(9)
Fasciola hepatica	0	(12)	6	(16)	0	(6)

¹ From Burgaz, 1970.
 ² In this study all the examinations of hares from 1973—1977 have been made by National Veterinary Institute, Uppsala.

Fig. 6 shows a significant linear trend (Snedecor & Cochran 1980, p. 206, p=0.03) in sex ratio (M:total) of observed marked hares during the spring. This trend is underlined by the sex ratio in captures, i.e. 0.33 in January and 0.55 in mid April.

Only a few hares were examined for parasites. They had all severe endo-parasitic infestations (Table 5), especially lungworms. Compared with a previous study on endo-parasites by Burgaz (1970) on Lilla Karlsö island, there are no differences (Table 5).

Both Ixodes ricinus and Haemaphysalis punctata have earlier been found on Stora Karlsö island (Schulze, 1939). All hares captured were heavily infected by ticks, both in January and April, probably primarily by *I. ricinus*. On one occasion we found a leveret with 50 ticks around one eye.

5. DISCUSSION

The basic pattern in adult mortality for the *Lepus* genus seems to be a rather high mortality in winter, and in decline years even in spring. Flux (1970) describes adult mortality for mountain hares as highest in February to May. In the snowshoe hare, *L. americanus*, Keith & Windberg (1978) concluded that the greatest adult mortality occurs in winter, even during years of a rapid decline.

The hare mortality on Lilla Karlsö island before January 1977, and through the spring, seems to be normal in decrease years for mountain hares. Contrasting to other studies, however, the survival rate for adults is lowest in the summer, in July 0.75 or even as low as 0.34. Usually, there is no adult mortality for mountain hares during June to October at all (Angerbjörn, unpubl.).

In a study with manipulated high densities on islands, Windberg and Keith (1976) calculated monthly adult survival rates for snowshoe hares during the summers of three different years. In unmanipulated areas these were 0.94, 0.84 and 0.78, with the third survival rate after a winter with a crash. On manipulated high density islands the survival rates were 0.88, 0.80 and 0.85 (the 3rd value adjusted for abnormal predation). In another island study of European hare (*L. europeus*) Abildgård *et al.* (1972) found that adult hares have an average monthly mortality of 4 to 5 0/6 with no clear differences between seasons.

Studies on the mountain hare and the snowshoe hare show a pronounced decrease in average body weight during winter and spring declines (Keith & Windberg, 1978; Angerbjörn, 1981). During our study we could not show a similar trend. In an experimental snowshoe hare study (Windberg & Keith, 1976), surviving adults in high density populations with limited food, did not respond by loss of body weight, but juvenile survival was markedly lower. On Lilla Karlsö island, especially the males had very low body weights and condition indices. Some of them showed clear signs of starvation. Comparing the average index value in January 1977 from Lilla Karlsö with an island without a crash (Angerbjörn, 1979) at the same time, one obtains 0.168 and 0.198 for males and 0.198 and 0.193 for females.

The linear trend in sex ratio, i.e. relatively fewer males observed during the spring, suggests a higher male mortality in early spring. Thus, the male loss in condition during the winter is followed by a higher male mortality during the spring. Following the shift in the sex ratio, the females should in contrary suffer a higher mortality in the early summer.

All female hares in this study were pregnant in the spring, but only a few leverets were observed in May to June. Hewson (1976) discusses the possibility that females could die after the birth on early litters in a year of sharp decline. The energy necessary for reproduction and lactation could decrease the condition of the female hares (see e.g. *Microtus arvalis* by Stenseth *et al.*, 1980).

There are many thoughts of what regulates hare populations, through intrinsic (e.g. Christian *et al.*, 1965; Chitty, 1967) or extrinsic factors such as food, predation and diseases (e.g. Lack, 1954; Wagner & Stoddart, 1972; Keith, 1974). In this paper we will only discuss the extrinsic effects of food in winter and summer, predation i.e. goshawk (Accipiter gentilis) and golden eagle (Aguila chrysaetos), and parasites and disease.

The hypothesis that predators caused the summer decline is not likely, since not a single bird of prey were observed although observers and reserve keepers were present on the island the whole summer. Predators could, however, have been involved in the winter decline.

Facts that favour the hypothesis of winter food shortage are: the severe winter with vegetation covered by snow, and the obvious density decline in hares before January. Furthermore the hares seem to have been in poor condition in January, although the highest mortality is measured in the summer. But the mortality pattern does not differ compared to other islands where no crash did take place (Angerbjörn 1981, and unpubl.).

It is also possible that the food in spring is a limiting factor: 1977 had the lowest mean temperature for April this century. There could be severe competition for available food between hares and sheep (Hjernquist & Hjernquist, 1974; Hewson, 1976). One hundred sheep were let out in early April, before the vegetation season started, and seven ewes died that spring compared to not more than one in previous years. The role played by parasities and diseases in this population is unclear. All hares captured were infested by ticks, *Ixodes ricinus* or *Haemaphysalis punctata*. Ticks of these species are known to infest hares of the *Lepus* genus in high numbers (Mohr & Lord, 1960; Wasylik, 1965; Nosek, 1971a, 1971b; Kadulski & Dobryńczuk, 1976). The ticks show a clear seasonality, with peaks in infestation in spring and early summer. Ticks are also vectors of encephalitis virus of different types that can infect hares (Yuill & Hanson, 1964; Nosek, 1971a, 1971b), and may cause a higher mortality (Hoff *et al.*, 1969; Yuill *et al.*, 1969). There are yearly infections of Russian spring and summer encephalitis (RSSE) from the tick *I. ricinus* on man on the two Karlsö islands. Therefore, it seems likely that tick borne virus could have caused some of the observed increased summer mortality of the hares on the Lilla Karlsö island.

It is not possible to sort out a single factor that causes the decline, but one explanation of the above results could be: After a severe winter with food shortage, the hares had to compete for food with the sheep during spring. Their poor body condition made them susceptible to ticks and diseases that thereby lowered their possibilities for recovering during the summer.

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GWAŁTOWNY LETNI SPADEK POPULACJI WYSPOWEJ LEPUS TIMIDUS

Streszczenie

Populację zajęcy żyjącą na wyspie Lilla Karlsö, na Bałtyku, obserwowano w latach 1973—1978 (Tabela 1, 2; Ryc. 1). Wykonywano również w tym czasie obserwacje meteorologiczne (temperatura, opady) oraz szacowano ilość dostępnego dla zajęcy pokarmu (Ryc. 2, 3a, b). Ocenę zagęszczenia *Lepus timidus* oparto na bezpośrednim liczeniu oraz na znakowaniu i obserwacji znakowanych sztuk. Zagęszczenie było właściwie stałe, na bardzo wysokim poziomie, około 400 zajęcy na 160 ha w kolejnych latach. W ciągu surowej zimy 1976/1977 liczba ich spadła do 152 zajęcy w styczniu, 107 w maju a w sierpniu pozostało już mniej niż 10 sztuk (Ryc. 4, 5). Średni miesięczny poziom przeżywania był zatem w lecie niższy niż 0.75 (Tabela 3; Ryc. 6). Wczesną wiosną, szczególnie samce zajęcy, były w złej kondycji i prawdopodobnie masowo padały, podczas gdy samice prawdopodobnie padały w ciągu wczesnego lata (Tabela 4). Przedyskutowano możliwość wpływu niedostatku pokarmu i inwazji pasożytów, na zaistniałą sytuację.