Proximate causes of losses in a snowshoe hare population

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We used radiotelemetry to monitor proximate causes of mortality of snowshoe hares during a population increase, peak, and decline at Kluane Lake, Yukon. Predation and starvation rates increased 1.6- and 9-fold, respectively, in the winter of peak population density. Predation accounted for 58% of the losses during the winter of peak densities while losses were equally divided between predation and starvation in the winter following the peak. Starvation and predation rates were lower on a food-supplemented grid than on control grids in the peak winter. In the following spring and winter, starvation rates remained low on the food grid while predation rates increased to equal those on control areas. We conclude that both starvation and predation were the proximate causes of mortality during the hare decline at Kluane Lake.

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Nous avons utilisé une technique de radiotélémétrie pour enregistrer les causes immédiates de la mortalité des lièvres durant l'augmentation, le sommet et le déclin de la densité de la population de Kluane Lake, Yukon. Les taux de prédation et de famine ont augmenté respectivement d'un facteur de 1,6 et de 9 au cours de l'hiver où la densité de la population était à son zénith. La prédation a été responsable de 58% des pertes durant l'hiver où la densité de la population était à son sommet, alors que la prédation et la famine étaient responsables des pertes à parts égales au cours de l'hiver qui a suivi le sommet de densité de la population. Les taux de famine et de prédation se sont avérés plus faibles dans un territoire où les lièvres ont reçu de la nourriture additionnelle que dans les territoires témoins au cours de l'hiver où la densité était maximale. Au cours du printemps et de l'hiver suivants, les taux de famine sont demeurés faibles dans le territoire à nourriture additionnelle, alors que les taux de prédation ont augmenté jusqu'à atteindre les valeurs enregistrées dans les territoires témoins. La famine et la prédation ont donc été les causes premières de la mortalité durant le déclin de la population de lièvres de Kluane Lake.

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Introduction

Snowshoe hares undergo regular population fluctuations on a wide geographic scale (Keith 1963). Numbers decline from peak densities primarily because of decreased juvenile survival rates (Keith and Windberg 1978; Krebs et al. 1986). Keith (1974) hypothesized that this decline is due to overwinter food shortage. Food shortage continues for 1–2 years after the peak but predation is thought to account for more of the mortality as the decline proceeds. Keith et al. (1984) have recently monitored a hare population during the winter following peak densities. They concluded that predation accounted for most of the losses at this time and that predation may be more important during the initial decline than was originally thought.

As part of our studies of snowshoe hare populations in the southwestern Yukon (Krebs et al. 1986; Boutin et al. 1985) we monitored proximate causes of mortality of hares during a population increase, peak, and early decline. If the hypothesis that hare declines are initiated by food shortage is correct, the majority of losses during the initial decline should be due to starvation. Further, food-supplemented areas should suffer fewer losses to starvation than control areas. Alternatively, if predation is the major cause of the decline, starvation should be rare and kills by predators frequent.

Methods

Hares were livetrapped on square grids of 100 stations in a 10 × 10 checkerboard with 30.5 m between stations. The grids were located near Kluane Lake, Yukon, and were trapped from May 1977 to July 1985. For a complete description of trapping methods and the study areas see Boutin (1984). The most common predators in the area included goshawks (*Accipiter gentilis*), great horned owls (*Bubo virginianus*), coyotes (*Canis latrans*), and lynx (*Lynx canadensis*). Other predators included Harlan's hawk (*Buteo harlani*), golden eagle (*Aquila chrysaetos*), foxes (*Vulpes vulpes*), and wolves (*Canis lupus*).

We used radiotelemetry to monitor losses of hares. Hares weighing more than 700 g were fitted with 30- to 40-g transmitters. The number of animals collared varied with the availability of manpower and transmitters. We radio-collared most of the animals on one site (Silver Creek) from May 1978 to April 1982. Animals on another site (Telemetry) were monitored from May 1978 to August 1981. We also collared animals on a third site (Beaver Pond) from January 1982 to April 1982 to increase sample size. The Telemetry site was experimentally manipulated (food added) in March 1980 and March to May 1981 (Boutin 1984). Data from these periods are not included in the analysis. Animals were monitored on a fourth site (Microwave) from August 1980 to May 1982. This area received supplemental food in the form of laboratory rabbit chow (16% crude protein) from September to May in each year from 1977 to 1982 (Krebs et al. 1986).

Radio-collared animals were checked for location and activity from permanent towers. Activity was monitored by holding the receiving antenna stationary and if signal strength changed the animal was considered to be alive. Animals found to be inactive were located with a hand-held antenna. Dead animals were classed as predator kills if there were signs of predation at the kill site or if autopsy revealed teeth marks or hemorrhaging underneath the skin. Deaths judged to be from starvation were animals found intact with no signs of predation; they were often found in cavities under snow or logs and autopsy revealed no heavy parasite loads or overt abnormalities in the heart, lungs, and liver. Animals that appeared to be scavenged or for which there was not enough information to classify cause of death were scored as cause of death unknown.

The frequency of animal monitoring varied but generally activity was determined every 1–2 days from May to September and February to March. At other times of the year the rate was usually at least once per week. We tried to monitor animals every 3–4 days from September 1981 to April 1982.

Losses due to predation could be overestimated if predators scavenged animals that had died from other causes. The rate of scavenging

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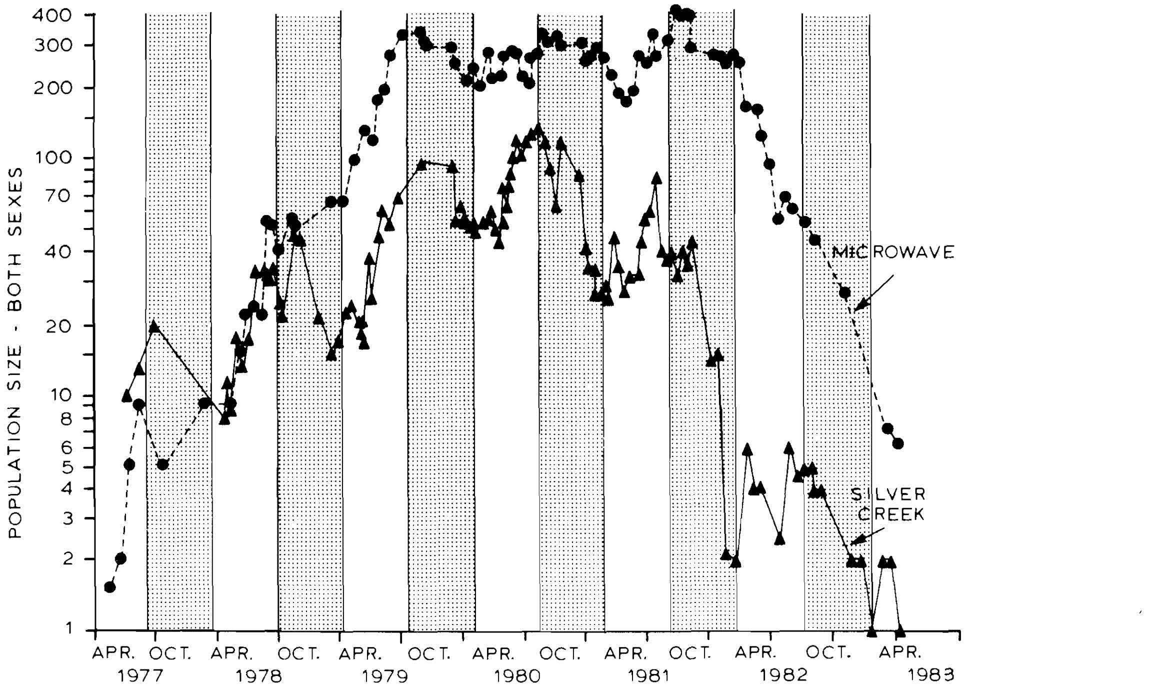

FIG. 1. Changes in population size on a control (Silver Creek) and food-supplemented (Microwave) grid as estimated by the Jolly–Seber method (Seber 1982). Shaded areas represent winter months (October–March).

appeared to be low in the study area. Periodically we left carcasses of hares on the sites and monitored how long they remained undisturbed. In all cases the carcass remained intact for at least 10 days, a period greater than the amount of time that most radio-collared dead hares remained undetected in the field.

Data were lumped into four 3-month seasons with spring being March to May. We combined data from the unmanipulated sites rather than treating them as replicates because sample sizes were too small on Telemetry for a number of periods. We calculated survival and cause-specific mortality rates using the program MICROMORT as described by Heisey and Fuller (1985). All rates are presented as seasonal (91 days) values. We also used MICROMORT to test for significant differences between rates by means of a likelihood ratio statistic, which has a χ^2 distribution for large sample sizes (Heisey and Fuller 1985).

Results

The effect of radio-collaring

Keith et al. (1984) argued that radio collaring increased mortality of hares for up to 1 week after collaring. We tried to assess this problem by comparing the proportion of hares lost within 1 week of collaring versus within any one of the following 3 weeks. Losses were higher in the week after collaring than in subsequent weeks in only three periods. In winter 1980–1981, spring 1981, and spring 1982, the proportion of collared hares lost in the 1st week after collaring was 1.24 to 2.8 times higher than the average over the next 3 weeks (Table 1). These elevated losses were never significantly higher than the rate of loss in subsequent weeks (χ^2, $P > 0.05$). We therefore conclude that radio collaring may have had a slight effect on the loss rate of hares in the peak winter and in the following spring but at no other time.

Changes in population size and causes of mortality

Figure 1 shows changes in population size of hares on Silver Creek and Microwave as estimated by the Jolly–Seber model (Seber 1982). Numbers on the other control grids followed a pattern similar to those on Silver Creek. The population increased to a peak in 1980–1981 and began to decline in winter 1980–1981 so that by spring 1981 numbers were lower than 1 year earlier. There was some recovery in summer 1981 but numbers began to decline again in August 1981. The decline became particularly pronounced in winter and spring 1981–1982.

TABLE 1. Proportion of collared hares lost in subsequent weeks following radio-collaring

	Time after collaring (weeks)			
	0–1	1–2	2–3	3–4
Winter 1980–1981	0.17 (47)	0.05 (39)	0.03 (37)	0.11 (36)
Spring 1981	0.13 (46)	0.05 (40)	0.05 (38)	0.03 (36)
Spring 1982	0.31 (16)	0.18 (11)	0.33 (9)	0.17 (6)

NOTE: Animals were collared on control grids (Silver Creek, Telemetry, Beaver Pond). Samples sizes are in parentheses.

Numbers on the Microwave food grid were double those on Silver Creek. They reached peak levels in autumn 1979 and did not begin to decline until May 1982.

Survival rates of hares showed a major decline in winter 1980–1981 (Table 2). They were low for the remainder of the study with the exception of summer 1981. This decline in survival was accompanied by a 9- and 1.6-fold increase in starvation and predation rates, respectively (winter 1979–1980 versus winter 1980–1981). Despite the higher increase in starvation rates, predation still accounted for 58% of all losses of collared hares at this time. Starvation rates were highest (0.3352) in the winter following the population peak (1981–1982) and were equal to predation rates at this time. Predation rates were highest (0.5768) in spring 1982.

In general, predation rates (0.2278) were 2.9 times higher than starvation rates (0.0792) (averaged over all seasons and all years). Starvation rates (averaged over all years) were low in

TABLE 2. Seasonal rates of losses due to predation and starvation of radio-collared hares on Silver Creek, Telemetry, and Beaver Pond trapping grids from 1978 through 1982

Season	No. collared	Hare-days	Seasonal rates: Survival	Starvation	Predation	% losses due to predation
Summer 1978	36	1484	0.8318 (3) 0.6752–1.0000	0 (0) 0	0.0561 (1) 0–0.1628	33
Autumn 1978	48	3297	0.7798 (9) 0.6627–0.9173	0 (0) 0	0.2202 (9) 0.0935–0.3469	100
Winter 1978–1979	38	2485	0.8025 (6) 0.6729–0.9568	0.0658 (2) 0–0.1539	0.1316 (4) 0.0116–0.2517	66
Spring 1979	59	2184	0.6586 (10) 0.5082–0.8529	0.1365 (4) 0.0125–0.2606	0.1707 (5) 0.0348–0.3066	50
Summer 1979	67	3514	0.8352 (7) 0.7308–0.9543	0.0471 (2) 0–0.1106	0.0471 (2) 0–0.1106	29
Autumn 1979	74	3647	0.9050 (4) 0.8205–0.9979	0 (0) 0	0.0950 (4) 0.0065–0.1836	100
Winter 1979–1980	79	3864	0.7715 (11) 0.6617–0.8992	0.0208 (1) 0–0.0611	0.2077 (10) 0.0934–0.3220	91
Spring 1980	68	3710	0.6267 (19) 0.5078–0.7730	0.1179 (6) 0.0295–0.2063	0.2357 (12) 0.1197–0.3518	63
Summer 1980	74	3451	0.7479 (11) 0.6298–0.8878	0.0458 (2) 0–0.1079	0.1604 (7) 0.0517–0.2691	64
Autumn 1980	80	4900	0.7289 (17) 0.6270–0.8470	0.0319 (2) 0–0.0754	0.1914 (12) 0.0943–0.2885	71
Winter 1980–1981	92	3276	0.4210 (31) 0.3103–0.5706	0.1868 (10) 0.0829–0.2907	0.3362 (18) 0.2111–0.4614	58
Spring 1981	41	2100	0.5441 (14) 0.3953–0.7480	0.1303 (4) 0.0115–0.2490	0.2931 (9) 0.1333–0.4529	64
Summer 1981	83	4011	0.7275 (14) 0.6157–0.8593	0 (0) 0	0.2725 (14) 0.1513–0.3938	100
Autumn 1981	51	2443	0.4733 (20) 0.3408–0.6565	0.0263 (1) 0–0.0772	0.3160 (12) 0.1695–0.4625	60
Winter 1981–1982	31	1085	0.2817 (15) 0.1480–0.5337	0.3352 (7) 0.1352–0.5352	0.3352 (7) 0.1352–0.5352	47
Spring 1982	28	721	0.0523 (23) 0.0156–0.1734	0.1236 (3) 0–0.2543	0.5768 (14) 0.3840–0.7697	61

NOTE: Each season is 13 weeks long: summer, June–August; autumn, September–November; winter, December–February; spring, March–May. Rates and 95% confidence limits are calculated following Heisey and Fuller (1985). Confidence limits are shown below each rate and number of animals dying is shown in parentheses. Percent losses due to predation were calculated with total losses, including animals dying of unknown causes.

TABLE 3. Mean weight (grams) of animals that either died from predation or starvation or survived in each of the seasons (all years combined)

	Survivors		Predation		Starvation	
	Mean	SE	Mean	SE	Mean	SE
Winter	1444	17.8 (77)	1537	63.4 (17)	1369	46.8 (18)
Spring	1403	15.5 (100)	1404	28.8 (29)	1341	28.2 (18)
Summer						
Adults	1533	19.9 (87)	1522	123.6 (6)	2140	— (1)
Juveniles	1124	42.8 (54)	1140	385.9 (3)	942	162.5 (2)
Autumn						
Adults	1579	23.0 (53)	1635	48.1 (8)	—	
Juveniles	1375	20.9 (84)	1220	69.3 (11)	1269	197.2 (3)

NOTE: Values for each animal were obtained from livetrapping information in that season or from intact carcasses obtained in the field. Sample sizes are in parentheses.

summer (0.0232) and autumn (0.0145) and relatively high in winter (0.1521) and spring (0.1270). Predation rates showed a similar pattern, with spring having the highest rates (0.3190) and summer the lowest (0.1340).

To summarize, predation accounted for most of the losses of radio-collared animals throughout the study. Both predation and starvation rates increased in the winter of peak hare densities. Predation rates were never lower than starvation rates even during the population peak.

Characteristics of hares that died

Neither starvation nor predation rates differed between males

TABLE 4. Seasonal rates of survival and losses to predation and starvation of radio-collared hares on control (Silver Creek, Telemetry, and Beaver Pond) and Microwave food grids

	No. collared	Hare-days	Seasonal rates Survival	 Starvation	 Predation
Autumn 1980					
Control	80	4900	0.7289 (17) 0.6270–0.8470	0.0319 (2) 0–0.0754	0.1914 (12) 0.0943–0.2885
Food	29	2170	0.8454 (4) 0.7171–0.9965	0 (0) 0	0.1159 (3) 0–0.2392
Winter 1980–1981					
Control	92	3276	0.4210 (31) 0.3103–0.5706	0.1868 (10) 0.0829–0.2907	0.3362 (18) 0.2111–0.4614
Food	27	2275	0.8520 (4) 0.7282–0.9967	0.0370 (1) 0–0.1081	0.0740 (2) 0–0.1726
Spring 1981					
Control	41	2100	0.5441 (14) 0.3953–0.7480	0.1303 (4) 0.0115–0.2490	0.2931 (9) 0.1333–0.4529
Food	33	2072	0.6161 (11) 0.4625–0.8199	0.0349 (1) 0–0.1021	0.3490 (10) 0.1759–0.5221
Autumn 1981					
Control	51	2443	0.4733 (20) 0.3408–0.6565	0.0263 (1) 0–0.0772	0.3160 (12) 0.1695–0.4625
Food	20	777	1.00 (0)	0	0
Winter 1981–1982					
Control	31	1085	0.2817 (15) 0.1480–0.5337	0.3352 (7) 0.1352–0.5352	0.3352 (7) 0.1352–0.5352
Food	30	2107	0.5220 (15) 0.3754–0.7249	0.0956 (3) 0–0.1983	0.2549 (8) 0.1034–0.4065
Spring 1982					
Control	28	721	0.0523 (23) 0.0156–0.1734	0.1236 (3) 0–0.2543	0.5768 (14) 0.3840–0.7697
Food	27	1295	0.2798 (18) 0.1550–0.5030	0.0400 (1) 0–0.1168	0.6002 (15) 0.4153–0.7851

NOTE: Rates and 95% confidence limits are calculated following Heisey and Fuller (1985). Confidence limits are shown below each rate and number of animals dying is shown in parentheses. Each season is 13 weeks long.

and females in any season of the study (likelihood ratio, $P > 0.05$). Juveniles suffered higher predation rates than adults did in autumn 1981 ($P < 0.01$, likelihood ratio). Predation and starvation rates were not significantly different between age-classes for any other season.

We next asked whether animals that died from predation or starvation differed in body size or condition from those that survived. We measured body weight and length of the right hind foot as a measure of skeletal size. Measurements were taken from intact carcasses when they could be obtained. To increase sample size we used values obtained from collared animals that had been livetrapped within a given season. If they were trapped more than once the mean value was used. Animals caught at least once in a season were divided into those that died within that season and those that lived to the next season. Juveniles were analyzed separately from adults in summer and autumn seasons. We could not distinguish between some adults and juveniles at other times and so we lumped the data.

There was no significant difference in foot length between animals that died from predation or starvation and animals that survived (one-way ANOVA, $P > 0.05$). Overall, animals dying of starvation were significantly lighter in weight than those killed by predators or those that survived ($P = 0.006$, Table 3). This is similar to the findings of Keith et al. (1984).

Losses on the food-supplemented area

Hares on control grids suffered starvation rates four times higher than those on the food-supplemented grid (averaged over all seasons; Table 4). Starvation rates were significantly lower on the food grid than on the control grids in the winters of 1980–1981 and 1981–1982 ($P < 0.01$, one-tailed likelihood ratio test).

Predation rates were significantly higher for control hares than for those on the food grid in winter 1980–1981 and autumn 1981 ($P < 0.01$, likelihood ratio test). However, hares on the food grid suffered higher rates of predation than those on control areas in spring 1981 and 1982.

Discussion

A proximate cause of the snowshoe hare decline at Kluane Lake was increased mortality due to both predation and starvation beginning in winter 1980–1981. Although the increase was more pronounced for starvation than for predation (9-fold versus 1.6-fold), predation still accounted for the majority of losses (58%) in the peak winter. Starvation and predation contributed equally to the losses in the first winter after the peak (Table 2). Keith et al. (1977) used predator densities and kill rates to estimate that 22% of total deaths were caused by predation during a hare peak in 1970–1971. After monitoring a second hare decline in 1981–1982, Keith et al. (1984) concluded that predation could not replace starvation as the primary cause of death at peak population densities. Our findings indicate that predation can be the primary cause of death during the population peak.

Keith et al. (1984) found that predation accounted for 92% of the losses of hares in the winter (December to April) following peak densities in a population near Rochester, Alberta. We found that predation accounted for 54% (Table 2) of the losses over the same time period in Kluane Lake populations. Starvation accounted for a much higher percentage of losses (30% vs. 8%) at Kluane than at Rochester.

Keith et al. (1984) found that coyotes cached 21% of hare kills in winter 1981–1982. We found 25% (6 of 24) of the predator kills were cached over the same time period. Although Keith et al. (1984) classified this caching behaviour as "surplus killing," the carcasses would not have been surplus if utilized at a later date. However, we were unable to test whether or not cached carcasses were utilized as we removed all carcasses for autopsy. We did observe at least two instances where collared hares were found in completely exposed locations. Autopsy indicated that they had been killed by predators. It seems unlikely that these carcasses would have been revisited.

We found predation rates to be much higher in winter and spring versus summer (Table 2). Our data include only hares weighing more than 700 g, which would be the majority of animals after mid-September. We do not have a measure of predation on small juveniles during summer. Estimated losses at this time (Krebs et al. 1986) suggest that predation rates on these animals could be considerable.

The interaction of food shortage and predation

Proximate causes of mortality are often difficult to determine. We cannot be certain that animals classified as dying of starvation did not die from disease or stress. Evidence to support starvation as a proximate cause of death comes from three sources. Firstly, apparent starvation occurred primarily in winter and spring, the season when food shortage was most likely to occur. Secondly, animals classified as dying of starvation were lighter in weight than those that survived. Finally, starvation losses were virtually absent on the Microwave food grid. We will present more data to address this problem in later publications (A. R. E. Sinclair, C. J. Krebs, and J. N. M. Smith, in preparation).

Predation rates may have been inflated by inclusion of animals scavenged after they had died from other causes. However, we believe such inflation to be small. We tried to reduce scavenging by recovering radios promptly, and any carcasses for which there was some doubt as to whether they had been scavenged were classed as unknown mortality. Furthermore, animals classified as dying of starvation were characteristically found in forms well protected from scavengers.

Another problem in determining proximate causes of mortality is that a variety of factors could act in a compensatory fashion. For example, malnutrition, disease, or aggressive interactions might make animals more susceptible to predation. We attempted to address the relationship between malnutrition and predation. If hares in poor condition were more susceptible to predation we would predict that hares on the food-supplemented grid would suffer lower rates of predation. This assumes that the food added to the food grid reduced food shortage despite the increased density there and that the predator to hare ratio was similar to that on control areas. Starvation rates were considerably lower on the food grid than on the control, although some starvation loss still occurred. We will provide data to address whether food-supplemented hares were receiving adequate food in a later paper (Sinclair et al., in preparation). We do not have a measure of predator densities on our study areas and so cannot determine predator to hare ratios. Predation rates were definitely lower on the Microwave food grid in winter 1980–1981 and to a lesser extent in winter 1981–1982 (Table 4). However, the high rates of predation on the food grid in spring 1981 and 1982 (Table 4) indicates that predation can cause heavy mortality in populations with adequate food supplies as concluded by Keith et al. (1984).

It appears then, that both predation and food shortage acted to initiate the decline from peak numbers in winter 1980–1981. Although predation accounted for the majority of losses of hares on control grids at this time, it was not sufficient to cause the food-supplemented grid to decline. Predation rates did lower survival on this area in winter and spring 1981–1982, however. We wished to test the hypothesis that hare declines are initiated by overwinter food shortage. Our findings are consistent with this hypothesis but they also suggest that predation can be an important proximate cause of losses even during the peak. Our experimental design did not allow us to separate the interactive effect of predation and food shortage. Future studies should experimentally exclude predators from food-supplemented and unmanipulated sites.

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