

A natural feeding experiment on a declining snowshoe hare population

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Summary. A snowshoe hare (*Lepus americanus*) population on a 9-ha area was supplied with extra natural food by chopping down large white spruce (*Picea glauca*) and aspen (*Populus tremuloides*) trees throughout 3 winters from 1981 to 1984. Hares fed vigorously on the downed trees, but the phase of decline of the ten-year cycle occurred equally on control and experimental grids from 1981–1983, and we could detect no improvement in survival or reproduction on the food area. Growth rates were improved on the food grid during the first winter of the decline (1981–82). We concluded that food shortage is not necessary for the cyclic decline of snowshoe hares in the southern Yukon.

Key words: Snowshoe hare – Food – Population declines

The ten-year cycle in snowshoe hares (*Lepus americanus*) is believed to be driven by a combination of winter food shortage in the peak and early decline phases, followed by heavy predation in the decline phase (Keith and Windberg 1978; Keith 1983). If winter food could be supplemented, the Keith hypothesis would predict a delay in the decline phase and an alleviation of the symptoms of peak populations (reduced growth and reproduction). We report here an experiment of supplying extra natural food to a snowshoe hare population in the southern Yukon during the late peak and decline phases of the ten-year cycle from 1981 to 1984.

Methods

We provided extra food on one 9-ha site called grizzly grid by cutting down mature white spruce (*Picea glauca*) trees during the winter months from October 1981 to March 1984. We also cut small aspen (*Populus tremuloides*) trees from nearby sites and hauled them onto grizzly grid. Sinclair and Smith (1984) have shown that mature white spruce foliage is highly preferred by snowshoe hares in cafeteria-type winter feeding experiments. We monitored the response of hares by live-trapping, marking, and releasing individuals on a 10 × 10 checkerboard grid with 30 m spacing. Details of the trapping procedures are given in Boutin (1980). Grizzly grid was used by Boutin (1983) as an adult removal area in 1980 and as an artificial food supplement grid from March 7–May 15, 1981. The effects of the feeding

experiment had dissipated by the time we began this manipulation in October 1981 (Boutin 1984).

We trapped two control grids near the experimental area. Beaver Pond is a site about 5 km south of grizzly grid, and is located in a similar white spruce forest habitat. A second control grid, 1050, is located about 2 km north of grizzly grid. The 1050 site is a much more open willow (*Salix glauca*) and scrub birch (*Betula glandulosa*) community with only a few scattered spruce trees. All these areas were live-trapped for two nights at 2–6 week intervals throughout the year. Population parameters were estimated by the Jolly-Seber model (Seber 1982). The actual trapping grids were 9 ha but the effective grid size with the edge effect is 25 ha (Krebs et al. 1986).

Results

We began supplying freshly-cut aspen and white spruce trees to hares on grizzly grid on 4 October 1981. By late October we had cut 7 spruce trees and 6 aspen. Spruce were cut on the grid; aspen were cut off the area and hauled onto the grid area and spread evenly across the grid. Spruce trees cut averaged 25-cm diameter and aspen averaged 10-cm diameter. We cut 26 spruce trees in the autumn of 1981 and 19 more in January 1982. After this time we monitored the area and cut spruce trees as necessary to have a fresh supply available to the hares throughout the winter. We cut many fewer trees during the winters of 1982–83 and 1983–84 because there were few hares using the extra food. Hares fed vigorously on the fallen trees and also used fallen spruce trees for cover.

Figure 1 shows the changes in snowshoe hare numbers on grizzly food grid and on the two control grids. The three areas showed very similar numerical trends (Table 1). During the critical winter of population decline in 1981–82 the grizzly food grid lost 77% of its population between October 1981 and March 1982. Similar losses for beaver pond were 79% lost and for 1050 96% lost. Through the next two summers and winter from 1982 to 1983 the grizzly hare population was always intermediate in its numerical changes between the two control grids. We can thus detect no difference in the timing, duration, or magnitude of the hare decline from 1981–83 between the controls and the experimental area provided with extra natural food in winter.

Survival rates estimated from mark-recapture were similar for all 3 grids (Table 2). Survival rates were generally

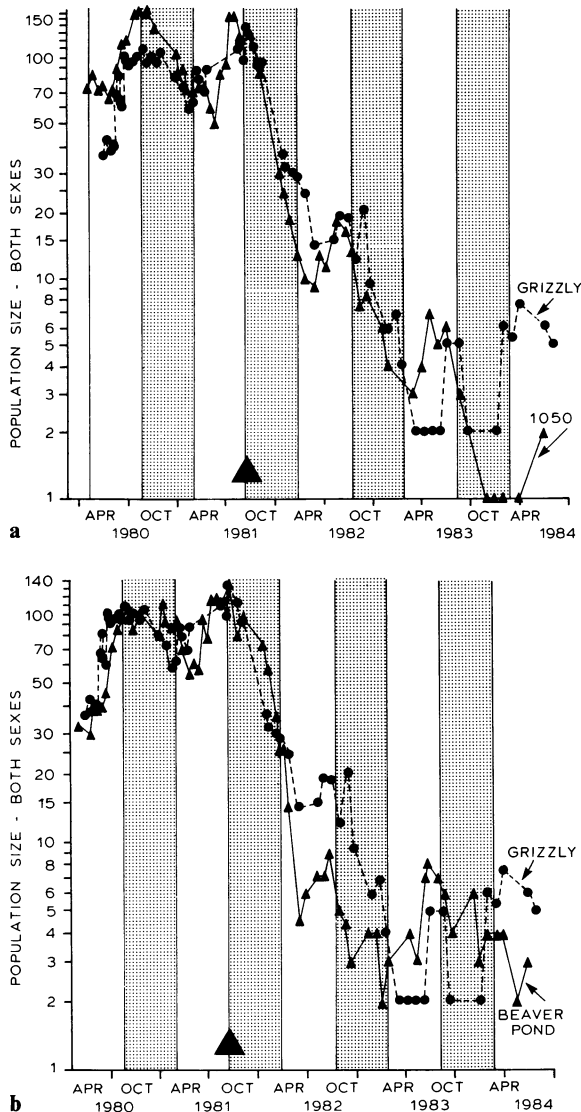


Fig. 1 a, b. Population changes in snowshoe hares on control and experimental areas, 1980–1984. **a** 1050 control compared with grizzly experimental. **b** Beaver Pond control compared with grizzly. Both sexes combined. Winter months (October to March) shaded. Population estimates from Jolly-Seber model. \blacktriangle marks start of natural feeding experiment in October 1981

Table 1. Finite rate of population change (λ) per 6 months for snowshoe hares from beaver pond and 1050 control grids and grizzly experimental grid. Summer = April to September, Winter = October to March. Both sexes combined. Values in parentheses estimated from minimum number known to be alive; other values estimated from Jolly-Seber model

	Grid		
	1050 control	Beaver pond control	Grizzly experimental
Winter 1981–82	0.04	0.21	0.23
Summer 1982	3.20	0.23	0.49
Winter 1982–83	0.12	0.79	0.29
Summer 1983	(1.50)	8.81	7.88
Winter 1983–84	(0.17)	0.25	0.53
Summer 1984	(2.00)	0.93	0.94

Table 2. Probability of survival (per 28 days, ± 1 S.E.) for snowshoe hares from the three grids. Both sexes combined. Estimates obtained from the Jolly-Seber model except those in parentheses obtained from direct enumeration

	Grid		
	1050 control	Beaver pond control	Grizzly experimental
Winter 1981–82	0.63 \pm 0.03	0.70 \pm 0.03	0.69 \pm 0.06
Summer 1982	0.89 \pm 0.08	0.55 \pm 0.07	0.77 \pm 0.07
Winter 1982–83	0.74 \pm 0.09	0.65 \pm 0.16	0.76 \pm 0.09
Summer 1983	(0.57)	0.93 \pm 0.09	0.86 \pm 0.15
Winter 1983–84	(0.55)	0.65 \pm 0.11	0.86 \pm 0.11
Summer 1984	–	0.77 \pm 0.12	0.77 \pm 0.11

Table 3. Percentage of adult female hares caught in live traps between May 15 and September 15 judged to be lactating. Sample size in parentheses

	Grid		
	1050 control	Beaver pond control	Grizzly experimental
Summer 1981	66.7 (99)	58.9 (95)	25.0 (8)
Summer 1982	60.0 (25)	46.2 (13)	52.6 (19)
Summer 1983	66.7 (6)	100.0 (4)	80.0 (4)
Summer 1984	–	100.0 (4)	–

low during the winters of both 1981–82 and 1982–83, and there is no suggestion that the extra food and cover provided on grizzly grid were beneficial in preventing heavy losses.

The percentage of adult female hares with enlarged teats and signs of lactation was used as the best index of reproduction. Table 3 gives these data for the three grids. There is no indication of improved reproduction among females on the experimental grid in either 1982 or 1983. The same analysis was done for the percentage of adult males with scrotal testes with the same results.

The start of the breeding season can be judged from the time the first males show scrotal testes, the time the first females are noted as lactating, and the time of appearance in the live-traps of the first juvenile hares. For each of these three criteria, there was no difference between the beaver pond control and the grizzly experimental grid in either 1982 or 1983.

If natural feeding was effective on grizzly grid, we might expect less weight loss during the winter months (cf. Keith and Windberg 1978). Table 4 gives growth rates (as % per day) for female hares from the three study areas. There is a suggestion of reduced weight loss on grizzly grid in 1981–82. An analysis of covariance (UBC GENLIN) was run on fall 1981, winter 1981–82, and spring 1982 data with both sexes included and body weight used as a covariate. All three grids differed significantly in growth rates

Table 4. Growth rates (% per day \pm S.E.) for female snowshoe hares Autumn = Sept.–Nov., Winter = Dec.–March, Spring = April–May, Summer = June–August. Sample size in parentheses

	Grid		
	1050 control	Beaver Pond control	Grizzly experimental
Autumn 1980	0.25 \pm 0.05 (130)	0.31 \pm 0.05 (81)	0.53 \pm 0.06 (98)
Winter 1980–81	–0.07 \pm 0.03 (78)	–0.15 \pm 0.03 (80)	0.07 \pm 0.04 (32)
Spring 1981	0.15 \pm 0.08 (33)	0.17 \pm 0.10 (54)	0.24 \pm 0.16 (44)
Summer 1981	0.67 \pm 0.17 (80)	0.79 \pm 0.22 (63)	–
Autumn 1981	0.18 \pm 0.12 (57)	0.34 \pm 0.09 (77)	0.11 \pm 0.08 (50)
Winter 1981–82	0.11 \pm 0.30 (7)	–0.28 \pm 0.07 (49)	–0.04 \pm 0.13 (25)
Spring 1982	–	–0.45 \pm 0.11 (13)	–0.06 \pm 0.04 (12)
Summer 1982	0.37 \pm 0.24 (15)	0.23 \pm 0.09 (7)	0.33 \pm 0.21 (10)
Autumn 1982	0.68 \pm 0.30 (10)	0.13 \pm 0.11 (4)	0.36 \pm 0.22 (19)
Winter 1982–83	0.17 \pm 0.11 (2)	0.07 \pm 0.06 (5)	–0.03 \pm 0.09 (3)
Spring 1983	–	–	0.13 \pm 0.25 (2)
Summer 1983	0.10 \pm 0.25 (3)	0.48 \pm 0.59 (5)	0.76 \pm 0.71 (3)

in the autumn of 1981, with beaver pond having the highest and grizzly the lowest growth rates. But in winter and spring 1982 growth rates on grizzly were significantly higher than on beaver pond. Figure 2 shows that in spring 1982 better growth was confined to female hares on grizzly. In winter 1981–2 both sexes lost less weight on grizzly grid. There was no difference over this period in the distribution of body weights on the three areas.

Discussion

Few feeding experiments have used natural food supplies and none has been done on snowshoe hares. The obvious advantages to using natural food additions have typically been offset by the difficulty of supplying added natural food in sufficient volume to have a potential population impact.

A second unique aspect of this experiment is that no one has ever started a feeding experiment of a cyclic population at the end of the peak phase. The inference that cyclic declines cannot be prevented by adding food has come from experiments begun in the early phase of increase (Cole and Batzli 1978; Krebs et al. 1986). One additional benefit that we saw in the present experiment was that cutting spruce trees would provide not only additional food for snowshoe hares but also more cover from predation. In our artificial feeding experiments with rabbit chow we were concerned

SNOWSHOE HARE SPRING GROWTH RATES - 1982

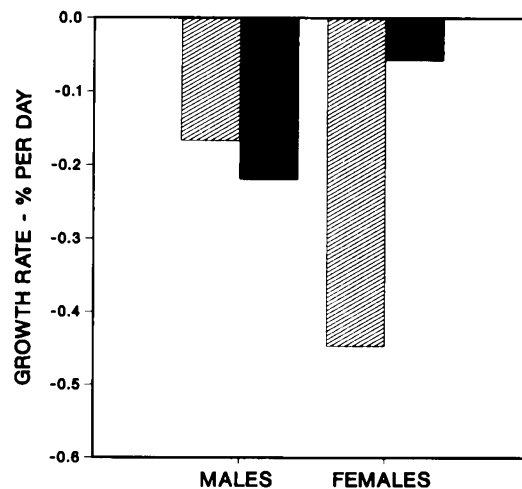


Fig. 2. Growth rates in body weight of male and female snowshoe hares on beaver pond control and grizzly experimental grid during the spring of 1982 (April–May). Males lost weight equally on both areas, but grizzly females did not lose weight as rapidly as beaver pond females; □ beaver, ■ grizzly

that we were increasing the exposure of hares to predators at relatively few feeding stations (Krebs et al. 1986).

The demographic consequences of this simple experiment were very clear. Density of hares on the grizzly food grid did *not* increase. This contrasts sharply with the 2- to 3-fold increases in density we have obtained in both short-term (Boutin 1984) and long-term (Krebs et al. 1986) artificial feeding experiments on snowshoe hares. The rapid population decline during the winter of 1981–82 occurred equally on control and experimental areas. Extra natural food did not increase survival or reproduction, but it did prevent the loss in body weight that seems to accompany declining hare populations (Keith and Windberg 1978).

There are three alternative explanations for these results. (1) *Food shortage is not necessary for the cyclic decline of snowshoe hare populations in the southern Yukon.* This interpretation assumes that all hares on grizzly grid had access to sufficient food from the cut trees and that the quality of food in the cut trees was high. (2) *The experiment failed because large spruce and aspen trees are not an adequate food source for hares, and a shortage of high quality natural food acted to cause the decline in the same way it did on the control areas.* Plant secondary chemicals are one possible reason why this type of experiment might fail (cf. Bryant 1981). This second explanation is consistent with the fact that immigrants did not flood into grizzly grid as Boutin (1984) found on a nearby area fed with rabbit chow. It is inconsistent with the fact that growth rates were improved on grizzly grid during the critical winter of the decline in 1981–82.

A third interpretation is that *food supplies interact with predation during the hare decline*, so that variations between areas in the amount and quality of hare food are swamped by highly mobile predators. On any given small area, food shortage would not be necessary for the cyclic hare decline because predation losses would be sufficient. This interpretation is similar to explanation (1) above and fits the results reported here. This conclusion complements the results ob-

tained from artificial feeding of hares by Krebs et al. (ms) and from natural observations by Keith et al. (1984). To obtain more supportive evidence we would need measurements (Sinclair et al. 1982) of the nutritive value of the forage we supplied and direct autopsy evidence of body condition in hares from grizzly grid during the decline.

Further work on predator foraging rates during the hare decline is required to test the view that predation losses are sufficient to explain the numerical dynamics on both control and food-supplemented populations. Peak densities of hares in the autumn of 1980 and 1981 were 5–6 hares/ha on both control and experimental areas, and these densities were typical for this peak in the Kluane region. We do not know the densities of predators operating on this prey base and this is a major objective for future research on the causes of the cyclic decline.

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