POPULATION BIOLOGY OF SNOWSHOE HARES. I. DEMOGRAPHY OF FOOD-SUPPLEMENTED POPULATIONS IN THE SOUTHERN YUKON, 1976–84

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SUMMARY

(1) We studied the population dynamics of snowshoe hares (*Lepus americanus*) in the Kluane Lake region of the Yukon by live-trapping nine areas year-round. We provided rabbit chow as winter food to three of these populations from September to May, 1977 to 1984.

(2) Peak densities were reached in 1980 and 1981 on all areas except Jacquot Island. Two areas with extra winter food maintained densities three times that of their controls, while one food-supplemented area on Jacquot Island showed little effect of improved feeding on hare density.

(3) Supplementary food did not prevent the cyclic decline and all areas reached low densities by 1984. The beginning of the decline was delayed 6 months on one food area but not delayed on the other.

(4) The amplitude of the cycle was 141-fold based on spring numbers and 268-fold based on August numbers. This is considerably higher than the amplitudes measured in Minnesota and Alberta.

(5) The hare cycle was caused by changes in recruitment (probably determined by losses during the first 8 weeks of life), juvenile survival in autumn, and adult survival in autumn. Survival rates gradually decreased during the cycle, and were lowest in its decline phase.

(6) Extra winter food did not prevent the drop in survival that occurs during the decline phase of the hare cycle, nor did it prevent the low recruitment rate that occurs during the decline.

INTRODUCTION

Snowshoe hare populations fluctuate in a 9–10 year cycle across much of the boreal forests of Canada (Elton & Nicholson 1942; Keith 1963). Two intensive studies have been undertaken to describe the demography of fluctuating snowshoe hare populations. Green & Evans (1940a,b,c) studied a population in Minnesota from 1932 to 1939. Keith & Windberg (1978) provided detailed demographic data for snowshoe hares in central Alberta from 1961 to 1976. In this paper we provide a third time-series for snowshoe hare populations, this one in the Kluane Region of the Yukon Territory.

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The purpose of this paper is to describe changes in population density, reproduction, mortality, and movements, for several live-trapped populations of snowshoe hares (*Lepus americanus* (Erxleben)) in the southern Yukon. In addition to monitoring control populations, we experimentally manipulated three populations by providing food during the winter. In subsequent papers we shall analyse food and habitat selection by hares and evaluate the Keith Hypothesis (Keith 1981) which suggests that hare cycles are caused by a limited supply of food in peak populations and by predation in declining populations.

METHODS

Snowshoe hares were live-trapped on square grids of 100 stations in a 10 × 10 checkerboard with 30·5 m between stations. Nine areas (Table 1) were live-trapped with at least fifty double-door Tomahawk live traps (No. 205, 66 × 23 × 23 cm) set at alternate stations on the grid. We placed these in hare runways or other preferred locations near the grid station and baited them with alfalfa cubes in winter and apples in summer (May–August). As population density rose, we added traps as required until some areas had up to 100 live-traps.

TABLE 1. Description of live-trapping areas near Kluane Lake, Yukon. Paired areas (adjacent, similar habitat) are indicated by brackets. MP = milepost. All areas are mainland sites unless indicated otherwise

Grid	Treatment	Location	Comments
1050	Control	MP 1050 Alaska Highway	
Microwave	Food-supplement	MP 1048, old Alaska Highway	
Gribble's	Control	MP 122, Haines Road	
Dezadeash	Food-supplement*	MP 132, Haines Road	30 ha island in Dezadeash Lake
Jacquot Control	Control	Jacquot Island: north end	800 ha island in Kluane Lake
Jacquot Food	Food-supplement	Jacquot Island: south end	
Silver Creek	Control	MP 1054 Alaska Highway	
Beaver Pond	Control	MP 1047 Alaska Highway	
Kloo Lake	Control*	MP 1042 Alaska Highway	

* Originally designated also for a predator-control manipulation, but we were unable to achieve any predator-removal so used as indicated (see text).

We tried to trap once a month throughout the year, but this was not always possible. In severe winter weather (−30 °C or below) we did not trap. In summer we trapped every 3 weeks when possible in order to increase data on juveniles. Traps were set for two nights and checked each morning. They were locked open when not in use and left in position with the unused bait.

Each hare captured was tagged with No. 3-size monel ear tag (National Band and Tag Co., Newport, Kentucky) in its right ear. We experimented with tattoo marking and plastic ear tags from 1976 to 1978 but found little tag loss with monel tags. For each hare we recorded grid location, sex, reproductive condition, weight, and length of right hind foot. We separated juvenile from adult hares by their body weight during the summer months, and by the criteria used by Keith, Meslow & Rongstad (1968) during the autumn and winter months. Because we live-trapped frequently we think few individuals were misclassified. Juveniles first entered the live traps at 3–5 weeks of age (400–600 g).

Vegetative cover was estimated for each trapping area by placing a 3 m radius circle at each trapping point and visually estimating cover for the dominant plants. Spruce trees

(*Picea glauca* Blake) were also counted if the trunk exceeded 5 cm diameter, and the diameter of the nearest spruce tree was measured.

Winter food was supplemented on three areas: Microwave, Dezadeash Island, and Jacquot Island. We used large range feeders (Model DR-11, Peacock Equipment Ltd, Surrey, B.C.), which hold 70 kg of chow, and put 10–20 feeders on each feeding grid. We fed alfalfa pellets to hares from October 1977 until May 1978. Beginning in 1978, we fed rabbit chow from September to May each year. Rabbit pellets from several manufacturers were used; the pellets were always minimum 16% protein, 3% fat, 12–24% crude fibre, 0·8–1·2% calcium, 0·5–0·6% phosphorus, and included vitamins A, D, and E. Feeding stations at Microwave and Dezadeash Island were disturbed by moose and grizzly bear. Moose disturbance was particularly severe in 1982–83 at Microwave until we were finally able to perfect a moose-proof exclosure. We avoided depredations by grizzly bears at Microwave by broadcasting feeding of rabbit pellets every second day in September and October from 1980 to 1984.

Population parameters were estimated by the Jolly–Seber model (Seber 1982) for reasons indicated by Jolly & Dickson (1983). All survival rates were expressed per 28 days, which is the typical interval between sampling. Survival estimates confound losses due to dispersal with those due to death. Boutin *et al.* (1985) have shown that dispersal losses were relatively low in these populations and consequently the majority of losses are presumed to be deaths.

RESULTS

Weather

Winter weather was mild in 1976–77, 1979–80, and 1980–81. More severe winter weather occurred in 1977–78 and in 1981–82. Mild winters typically had more snowfall, but snow depth was highly variable among our trapping areas (Table 2) because of slight differences in elevation and the buffering effect of Kluane Lake on the Jacquot Island grids. The winter of 1979–80 stands out as the year of maximum snowfall. In all other years snowfall was very similar.

Vegetation

Table 3 gives the percentage cover for the dominant plant species on the nine live-trapping areas. There is a gradient from dense, closed spruce forest on Silver Creek

TABLE 2. Maximum snow depth (cm) measured at 20 or more trapping stations on each live-trapping area, 1977–1984. Maximum depth was usually recorded in March, occasionally in February

Area	Feb. 1978	March 1979	March 1980	March 1981	March 1982	March 1983	March 1984
Silver Creek	29	21	51	31	34	28	29
Beaver Pond	67	49	58	58	58	68	—
Kloo Lake	48	40	62	46	47	56	36
1050 control	65	51	74	45	53	67	61
Microwave food	79	56	90	70	58	76	60
Jacquot control	14	20	41	40	37	29	13
Jacquot food	17	25	47	40	38	29	15
Gribble's control	39	69	89	59	72	—	65
Dezadeash food	27	46	63	30	48	—	44
Mean	43	42	64	47	49	50	40

Population dynamics of snowshoe hares

TABLE 3. Percentage cover of the major plant species on the live-trapping areas in the Kluane region. Cover estimated visually on 100 circular plots of 30 m² for each area in July 1982

Species	Silver creek	Beaver Pond	Kloo Lake	1050 control	Microwave food	Jacquot control	Jacquot food	Gribble's control	Dezadeash Is. food
Picea glauca Blake	18	8	17	5	0·2	29	12	15	4
Salix glauca L.	8	15	18	33	9	9	14	7	7*
Betula glandulosa Raup.	0	12	0·4	11	22	0	0	8	0
Shepherdia canadensis (L.) Nutt	8	0·5	1	0·6	0·2	8	7	0·8	2
Populus tremuloides Michx.	0	0·8	0·6	0	0	0	0	5	0·6
Populus balsamifera L.	0·2	0	0	0	0	1	0	0·8	0
Lupinus arcticus Wats.	5	2	4	3	2	6	15	4	1
Arctostaphylus uva-ursi (L.) Spreng.	5	8	12	8	3	1	4	5	10
Arctostaphylus rubra (Rehd. & Wils) Fern.	10	0·1	0·8	3	0	0	9	0	3
Potentilla spp.	0·1	0·1	1	4	0·3	0	0	0	0
Empetrum nigrum L.	0	0	3	0	0	0	1	23	0
Grasses	0·4	16	34	27	47	4	4	4	1
Mosses	25	4	4	10	3	25	26	8	14
Picea glauca (>5 cm diameter)									
Density per hectare	788	264	154	57	3	58	69	1045	38
Average diameter (cm)	20·6	18·5	10·0	18·2	7·0	8·4	13·6	10·4	19·7

* A tree willow (*Salix scouleriana* Barratt) also had 7·3% cover on this grid.

and Gribble's to a patchwork of dense forest and shrubland on Beaver Pond, and to very open spruce forest at Kloo Lake, 1050, and Microwave. The grids on Jacquot Island are unusual in having dense spruce cover but of smaller trees (< 5 cm diameter) than are found on the other areas. Herbaceous cover in summer is more luxurious at Dezadeash Island and Gribble's because these areas are nearer the coast and have higher rainfall. The two major winter food plants of hares (*Salix glauca* L. and *Betula glandulosa* Raup) vary in abundance on the live-trapping areas. *Salix glauca* is common to abundant on all areas, but shrub birch (*Betula glandulosa*) is absent from Silver Creek, Jacquot Island, and Dezadeash Island, and nearly absent from Kloo Lake.

Population density

Population parameters were estimated for all hare populations by the Jolly–Seber model. These estimates have an unknown bias because snowshoe hares violate the equal catchability assumption of this model (C. J. Krebs &, S. A. Boutin, unpublished). However, the Jolly–Seber estimates are still the best available (Jolly & Dickson 1983). Figure 1 shows the Jolly–Seber estimate of total population size and the minimum-number-known-to-be-alive estimate (MNA, Krebs 1966) for the Silver Creek trapping area. Trappability for hares is usually 40–50% (C. Krebs, unpublished data) and consequently minimum-number-alive estimates are expected to be low (Hilborn, Redfield & Krebs 1976). Two points should be noted: (i) the MNA and Jolly estimates are highly correlated; and (ii) the Jolly estimate becomes unreliable and impossible to calculate when population size falls very low and no tagged hares are recaptured. It is necessary to use the minimum-number-alive estimate under these conditions. We believe that the MNA estimates at low densities are close to true densities because we can track individual hares in winter on our study areas.

Changes in population density occurred simultaneously in males and females, and we have been unable to detect any differences in the dynamics of the two sexes. Figure 2 shows population changes in males and females on the Beaver Pond control area and
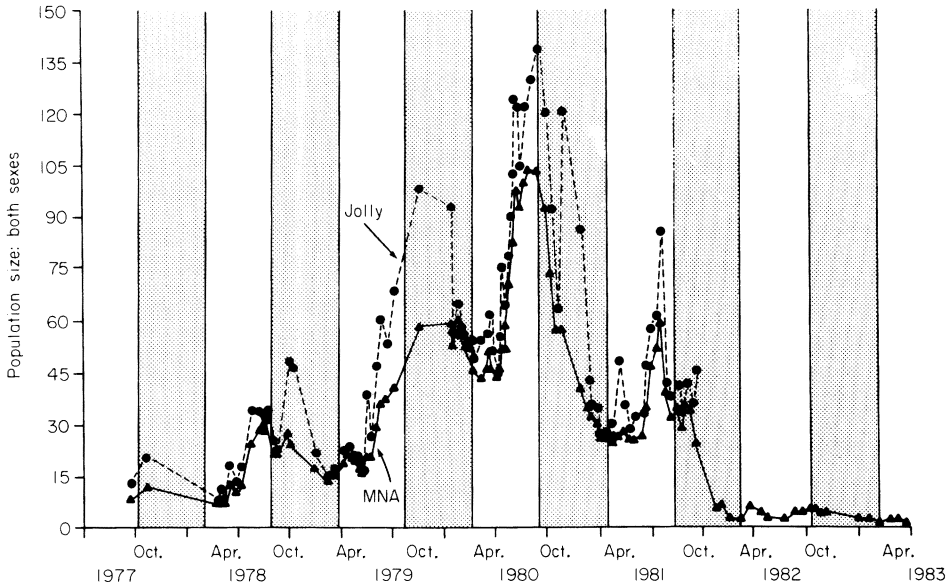
FIG. 1. Estimation of total population size for both sexes of snowshoe hares on the Silver Creek Control grid. Jolly–Seber estimates exceed MNA (minimum-number-alive) estimates by 22% on average. Winter months (October–March) are shaded. Abcissa marked at 20-week intervals.
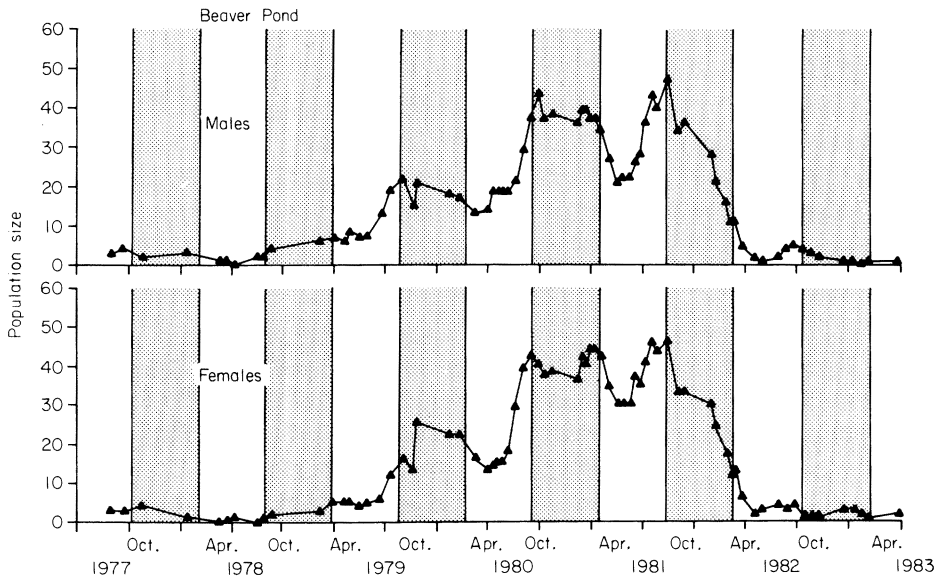

FIG. 2. Population trends in male and female snowshoe hares on Beaver Pond control grid. MNA (minimum-number-alive) estimates are used. Trends are identical in the two sexes.

illustrates a pattern of similarity that is repeated on all control areas. We could detect no systematic changes in the sex ratio over this population cycle.

Table 4 lists the population estimates for the start of the biological year (April 1) for each trapping area. Peak densities were reached in 1980 and 1981 on all areas. Some areas,

TABLE 4. Population size estimated by Jolly–Seber model for the start of the biological year on 1 April. Numbers in parentheses are minimum number known alive. 1 April is approximately the start of the breeding season for snowshoe hares. M = males, F = females

Year	Silver Creek		Beaver Pond		Kloo Lake		1050 control		Microwave food		Jacquot control		Jacquot food		Gribble's control		Dezadeash food	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
1977	(0)	(0)	(1)	(1)	(0)	(0)	(0)	(1)	(0)	(0)	?	?	?	?	(0)	(0)	(1)	(0)
1978	4	5	(2)	(1)	5	6	8	13	5	3	27	46	17	37	15	11	8	7
1979	9	9	5	4	9	12	21	16	26	32	16	12	10	10	20	16	32	36
1980	24	30	18	30	41	25	32	41	98	136	17	24	21	22	25	39	71	70
1981	13	18	39	52	36	31	37	32	111	152	32	40	41	47	30	32	109	143
1982	(1)	(1)	14	13	5	5	(4)	14	58	126	17	14	31	58	10	20	67	81
1983	(0)	(1)	(1)	(1)	3	(1)	(2)	(1)	(1)	(8)	5	7	6	18	3	8	6	12
1984	(3)	(1)	(2)	(2)	4	(1)	(0)	(1)	(0)	(2)	8	9	11	13	3	3	5	7

TABLE 5. Average population density for each 6-month period for control and food supplemented grids. Densities estimated from Jolly–Seber model. Both sexes combined

	Summer 1978	Winter 1978–79	Summer 1979	Winter 1979–80	Summer 1980	Winter 1980–81	Summer 1981	Winter 1981–82	Summer 1982	Winter 1982–83
1050 control	45·4	56·2	101·8	108·3	101·1	114·9	93·9	140·2	17·2	4·3
Microwave food	27·9	109·8	172·8	316·3	257·5	293·9	243·2	324·8	146·8	45·8
Gribble's control	41·1	62·9	43·4	114·0	63·2	79·9	64·7	56·2	28·0	22·3
Dezadeash food	40·6	68·6	198·0	137·3	191·6	266·6	206·1	187·3	82·7	31·7

like 1050, had nearly equal densities in 1980 and 1981 while other areas peaked in 1980 (Silver Creek) or 1981 (Beaver Pond). There are two striking exceptions shown in Table 4 that require further discussion: (i) densities were higher on the Microwave and Dezadeash food grids than elsewhere; and (ii) densities did not fluctuate cyclically on Jacquot Island.

Table 5 gives the average Jolly estimates for population density on the Microwave and Dezadeash food grids and their paired controls for 6-months periods from the start of the feeding experiment. The effects of feeding were not evident for one year after we began (in October 1977), but then densities rose to an average of 2·4 times the control for Microwave and 2·8 times the control for Dezadeash. These increments were stable for 2·5 years during the peak of the cycle. Highest densities reached were 338 for Dezadeash food grid in October 1980, compared with 98 hares on the Gribble's control grid at the same time. For Microwave food grid there were 398 hares in October 1981, compared with 154 hares on the 1050 control grid at the same time.

The cyclic decline in 1982 and 1983 occurred on all areas except Jacquot Island. Figure 3 shows the details of the population changes on Microwave food and 1050 control grids. The rapid decline that occurred in midwinter 1981–82 on the 1050 control area did not occur on the Microwave food grid until the summer of 1982. Both populations declined over the winter of 1982–83, and by 1983 and 1984 numbers were very low on both areas regardless of treatment.

By contrast, Fig. 4 shows that the population decline of 1981–83 began at the same time on the Gribble's control grid and the Dezadeash Island food grid. In particular, during the first winter of the decline (1981–82), the population on the control grid declined 62% over 6 months and on the food grid 66% over the same time period. From 1981 to 1983 the Dezadeash population declined as much as, or more than the control (Dezadeash: 52%
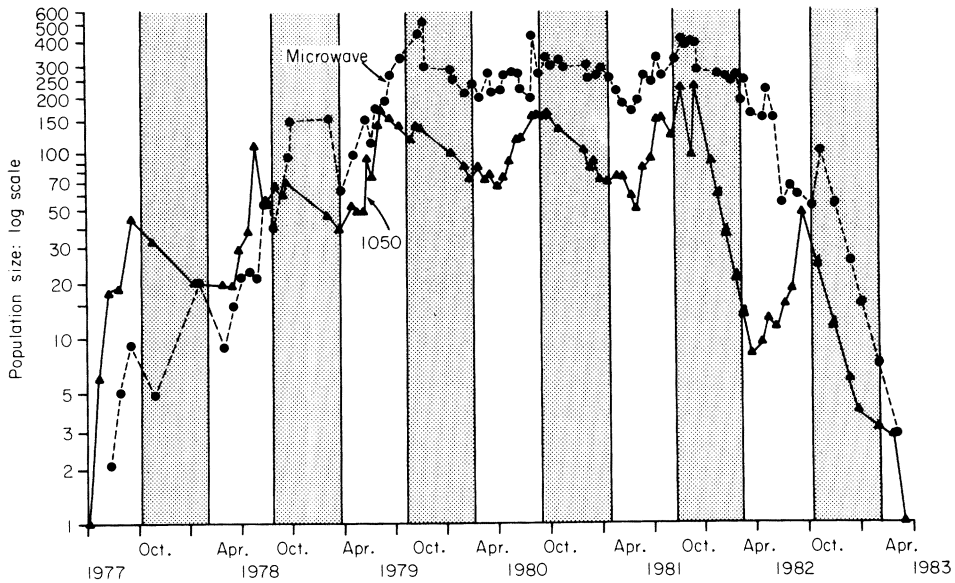
FIG. 3. Population size on 1050 (control) and Microwave (food) grids, 1977–83. Both sexes combined, winter months shaded. Jolly–Seber estimates plotted on log scale.
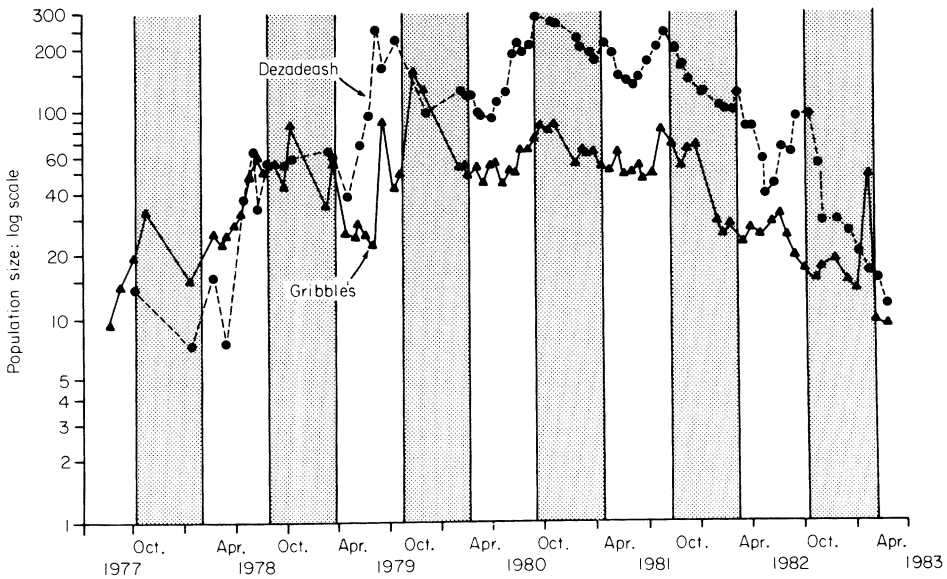

FIG. 4. Population size on Gribble's (control) and Dezadeash Island (food) grids, 1977–83. Both sexes combined, winter months shaded. Jolly–Seber estimates plotted on log scale.

decline in 1981–82, 86% in 1982–83; Gribble's control: 50% in 1981–82, 59% in 1982–83). Thus, on the Microwave and Dezadeash food-supplemented grids, population density was increased 2–3 fold by the addition of food and the cyclic decline started on these two food grids either simultaneously or with a half-year delay when compared with the controls. By 1983 all populations were back to low numbers.

Jacquot Island is unique in two respects. The food grid on Jacquot maintained a density that was on average 1·45 times that of the control grid. Figure 5 shows that the food and control populations were nearly identical for every year except 1982, when there was a temporary divergence. Moreover, there is no trace of the population cycle on Jacquot Island on either grid. Population density was moderately high throughout the study from 1977 to 1984, compared with the mainland controls (Table 4).

The amplitude of the hare cycle at Kluane Lake is difficult to estimate because we do not have an accurate fix on the low densities of 1976–77. If we assume for each of our control areas a low density of 0·5 hares per grid (probably a generous estimate based on our snow tracking during 1976–77), we obtain the following crude estimates of amplitude (maximum density/minimum density) for four control areas (Silver Creek, Beaver Pond, 1050, Gribble's): 141 in spring (range 108–182) and 268 in August (range 200–324). We emphasize that these estimates are crude, and we feel they could be anything between one-half to twice these values but are unlikely to be outside this range. The amplitude of spring density change on Jacquot Island was only 4 to 6 fold from 1977 to 1984.

We have expressed all population densities in terms of hares per trapping grid. Boutin (1984a) has discussed the problems of absolute density estimation in snowshoe hares, and has shown that densities based on observed hare numbers from live-trapping divided by the actual grid size are 3 to 9 times higher than densities based on radiotelemetry. Hares have large home ranges and many individuals live mostly off the live trap areas. Bondrup–Nielson (1983) simulated this edge-effect of live-trapping, and his results suggest for our 8·1 ha trapping areas, with a home range size averaging 4·9 ha, the actual trapping area should be 25·6 ha. If absolute density data are required from our areas, we would recommend as an average correction that effective grid size be estimated as 25·6 ha for all areas except the three island grids. Absolute density estimates based on this correction factor may still be slightly too large (Boutin 1984a).

In summary, population density of snowshoe hares increased from 1976 to 1980 and was at a peak during 1980 and 1981. The decline began during the 1981–82 winter and continued until 1983. The cycle occurred synchronously on all our study areas with the exception of Jacquot Island, which has maintained a less strongly fluctuating density from 1977 to 1984.
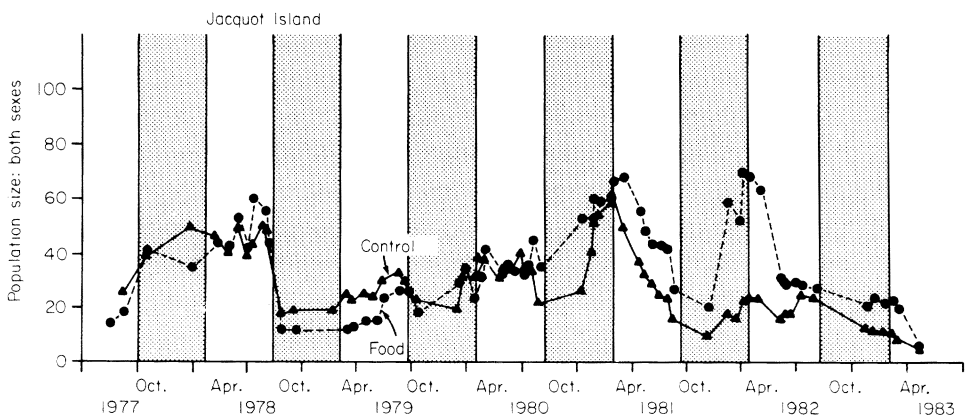

FIG. 5. Population size on Jacquot Island Control and Food grids, 1977–83. Both sexes combined, winter months shaded. Jolly–Seber estimates.
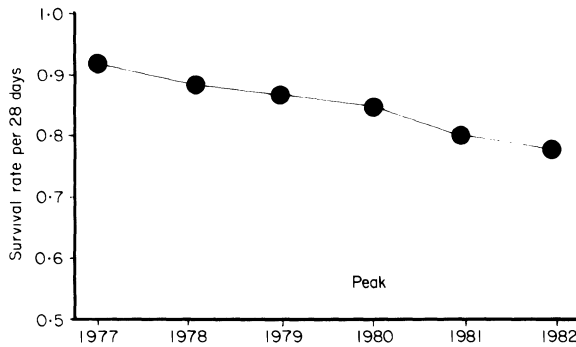
FIG. 6. Survival rate averaged for the biological year (1 April to 31 March) for both sexes combined, all controls grids combined. Survival estimated from Jolly–Seber model. The standard error of the estimates ranges from 0·01 to 0·02.

TABLE 6. Probability of survival per 28 days estimated from the Jolly–Seber model (± 1 S.E.) for spring and summer (1 April–30 September) and autumn and winter (1 October–31 March). Both sexes combined. Estimates in brackets are minimum survival rates calculated as in Krebs (1966)

Season	Silver Creek	Beaver Pond	Kloo Lake	1050 control	Microwave food	Jacquot control	Jacquot food	Gribble's control	Dezadeash food
Summer 1977	1·00	—	0·91	0·93	0·89	0·71	0·67	0·92	—
	±·11		±·09	±·07	±·05	±·09	±·09	±·08	
Winter 1977–78	0·94	—	0·96	0·90	0·97	0·98	0·87	0·87	0·87
	±·05		±·03	±·04	±·03	±·03	±·03	±·04	±·05
Summer 1978	0·73	—	1·00	0·89	0·88	0·61	1·00	0·88	0·91
	±·06		±·04	±·04	±·05	±·04	±·23	±·04	±·04
Winter 1978–79	0·82	1·00	0·87	0·93	0·94	0·94	0·65	0·86	0·88
	±·04	±·04	±·04	±·02	±·04	±·04	±·09	±·03	±·03
Summer 1979	0·85	0·91	0·97	0·86	0·89	1·00	0·87	1·00	1·00
	±·03	±·05	±·02	±·03	±·02	±·14	±·08	±·16	±·05
Winter 1979–80	0·79	0·81	0·80	0·89	0·89	0·70	0·84	0·80	0·80
	±·03	±·03	±·02	±·02	±·02	±·11	±·07	±·10	±·02
Summer 1980	0·79	0·87	0·91	0·82	0·83	0·74	0·89	0·80	0·92
	±·02	±·03	±·02	±·02	±·02	±·03	±·11	±·03	±·01
Winter 1980–81	0·71	0·88	0·85	0·84	0·87	0·96	0·88	0·85	0·91
	±·03	±·02	±·02	±·02	±·01	±·02	±·08	±·02	±·01
Summer 1981	0·75	0·86	0·85	0·82	0·86	0·86	1·00	0·82	0·90
	±·03	±·02	±·03	±·03	±·02	±·17	±·22	±·02	±·02
Winter 1981–82	0·56	0·70	0·67	0·63	0·85	0·71	0·71	0·82	0·81
	±·06	±·03	±·04	±·03	±·02	±·08	±·08	±·03	±·02
Summer 1982	0·70	0·55	0·96	1·00	0·83	0·84	0·81	0·83	0·79
	±·10	±·07	±·07	±·19	±·10	±·06	±·04	±·03	±·03
Winter 1982–83	0·82	0·65	0·83	0·74	0·61	0·81	0·90	0·83	0·80
	±·11	±·16	±·09	±·09	±·10	±·04	±·03	±·04	±·04
Summer 1983	0·80	0·93	0·87	(0·57)	(0·82)	0·93	0·97	0·82	0·90
	±·12	±·09	±·09			±·03	±·04	±·09	±·03
Winter 1983–84	0·76	0·65	0·93	(0·55)	(0·75)	0·91	0·86	0·98	0·85
	±·08	±·11	±·04			±·04	±·05	±·12	±·07
Summer 1984	0·70	0·77	0·78			0·73	0·84	0·69	0·73
	±·13	±·12	±·11			±·06	±·05	±·13	±·10

Survival

Survival rates declined gradually from the phase of increase in 1977 to the peak in 1980–81 and fell lower in the decline (Fig. 6). This drop in survival, which could be due to mortality or to emigration, is an important parameter causing the changes in numbers, and we need to analyse the drop in survival in more detail.

Table 6 gives the survival estimates for spring and summer (April–September) and autumn and winter (October–March) for each of the live-trapping areas. Both sexes are combined in this analysis because in an analysis of variance we could detect no systematic effect of sex on survival rates. Survival rates varied on different grids, changed seasonally,

TABLE 7. Annual finite rate of population change for both sexes combined. Year begins 1 April. Rates estimated from Jolly–Seber model except those in parentheses estimated from changes in population size directly

	Silver Creek	Beaver Pond	Kloo Lake	1050 control	Microwave food	Jacquot control	Jacquot food	Gribble's control	Dezadeash food	All four control grids*
1977–78	(8·21)	(0·15)	(7·39)	8·92	4·62	3·07	2·13	6·05	8·57	7·62
1978–79	3·12	3·85	3·53	2·76	11·89	0·39	0·86	1·08	2·59	2·19
1979–80	2·92	1·21	1·76	1·75	2·23	1·44	1·16	2·19	2·71	2·32
1980–81	0·67	3·16	1·64	0·93	1·15	1·97	1·71	1·13	2·21	1·14
1981–82	0·15	0·31	0·20	0·12	1·19	0·46	1·08	0·50	0·48	0·38
1982–83	0·67	0·17	0·47	0·16	0·02	0·40	0·32	0·41	0·14	0·21
1983–84	4·04	2·52	2·42	0·25	0·83	0·90	0·91	1·59	1·28	2·16

* Silver Creek, Beaver Pond, 1050, Gribble's.

TABLE 8. Survival rate per 28 days for juvenile hares born each summer. All litters combined, males and females combined. Survival estimated by Jolly–Seber model from live-trapping data. Summer = May to September; Autumn = October to December; Winter = January to March

Year-class and seasons	Silver Creek	Beaver Pond	Kloo Lake	1050 control	Microwave food	Jacquot control	Jacquot food	Gribble's control	Dezadeash food
1977									
Summer	1·00	0·73	0·84	0·91	0·71	0·61	0·73	0·88	0·51
Autumn		0·89	0·93	0·88	0·87	1·00	0·79	0·87	0·87
Winter	0·91	—	0·94			1·00	0·86	0·88	0·75
1978									
Summer	0·60	0·58	0·97	0·88	0·63	0·48	0·97	0·78	0·84
Autumn	0·81	0·98	0·72	0·91	1·00	0·51	0·48	1·00	0·88
Winter	0·76	1·00	0·87	0·94	0·74	0·78	1·00	0·74	1·00
1979									
Summer	0·58	0·69	0·72	0·70	0·76	0·91	0·76	0·74	0·91
Autumn	0·73	0·76	0·71	0·83	0·85	0·87	1·00	0·86	0·79
Winter	0·72	0·78	0·62	0·91	0·81	0·72	0·55	0·74	0·90
1980									
Summer	0·69	0·66	0·54	0·70	0·67	0·77	0·80	0·39	0·81
Autumn	0·73	0·69	0·74	0·73	0·84	1·00	0·98	0·79	0·87
Winter	0·64	0·81	0·77	0·75	0·86	0·83	0·99	0·83	0·87
1981									
Summer	0·61	0·71	0·67	0·79	0·70	0·60	0·84	0·63	0·73
Autumn	0·38	0·62	0·54	0·52	0·83	0·77	0·78	0·57	0·66
Winter	0·49	0·52	0·54	—	0·87	0·87	0·75	0·49	1·00
1982									
Summer	1·00	0·40	0·49	0·89	0·72	0·93	0·58	0·78	0·35
Autumn	0·86	0·69	0·63	0·41	0·62	0·75	0·75	0·90	0·70
Winter	0·92	0·85	1·00	—	—	0·76	1·00	0·74	0·89
1983									
Summer	0·96	0·67	0·64	0·40	—	0·74	0·96	0·78	0·96
Autumn	0·76	0·79	1·00	0·66	—	0·84	0·93	1·00	0·77
Winter	0·67	0·63	0·73	—	—	0·93	0·71	0·83	0·86

and changed greatly over the cycle. We can use these survival estimates to determine whether the annual rate of population change is more closely related to *summer* or to *winter* survival. Table 7 gives the annual finite rates of population growth for all the live-trapping areas. The rate of population growth is more closely related to winter survival rates ($r = 0.64$, $n = 63$) than to summer survival rates ($r = 0.36$).

We can break this analysis down further by looking at the survival of juvenile and adult age classes. Table 8 gives the survival rates for juveniles during their first year of life for all nine study areas. The annual rate of population growth is most highly correlated with the juvenile survival rate in the autumn (October–December) ($r = 0.60$) and shows a poor correlation with juvenile survival in the summer months (May–September) ($r = 0.24$) and winter months (January–March) ($r = 0.18$). A similar analysis for adult hares for all nine study areas showed almost the same thing. The annual rate of population growth is most highly correlated with adult survival rate in the autumn ($r = 0.49$) and less well correlated with adult survival in summer ($r = 0.20$) and winter months ($r = 0.42$). With a multiple regression we can predict the annual rate of population growth either with juvenile autumn survival ($R^2 = 0.35$) or with adult autumn and winter survival ($R^2 = 0.34$). This prediction is considerably improved if we use average survival rates for all age classes combined (Table 6) ($R^2 = 0.48$). We conclude that juvenile and adult survival act in concert to drive the population cycle, and that autumn (October–December) survival is most critical.

Does the provision of extra winter food increase the survival rate? We did an analysis of variance on the survival data of all age classes in Table 6. We omitted Jacquot Island from this analysis because a separate analysis showed no significant effect of winter feeding on Jacquot survival estimates. For the other grids there is a significant food effect which shows up as a first order interaction of food treatment × year ($P < 0.03$). For the two feeding experiments at Microwave and Dezadeash during the increase and peak phases of the hare cycle, extra food improved survival rates by about 0.05 per 28 days. In the decline year of 1982 this effect was reversed and the food-supplemented grids had a survival approximately 0.08 per 28 days less than the controls.

We could detect no clear seasonal pattern in this effect of food on survival. On Microwave grid the improved survival seemed to come mostly in autumn and winter, but on Dezadeash the improved survival occurred in all seasons of the year (Table 6).

During the late increase and peak phases we caught enough juveniles of each of the three summer litters to measure their survival independently. We calculated the proportion of each litter that survived from first capture in a live-trap to the following April 1. The first litter was most productive, and 15% of these young survived to become breeding adults. Of the second litter juveniles only 10% survived, and of the third litter juveniles only 7%. We could detect no differences among grids in this pattern which was similar from 1978 to 1981.

In summary, winter survival rates are correlated with the annual rate of population change. In particular, autumn survival of juveniles, and autumn and winter survival of adults, are both associated closely with the rate of population change. Providing extra winter food improved survival in the increase and peak phases but not in the decline phase.

Reproduction

From our live-trapping data we could determine three measures of reproductive rate: (i) length of the breeding season, (ii) proportion of adults in breeding condition during the breeding season; and (iii) number of young hares recruited per adult female.

TABLE 9. Length of the breeding season (weeks). The start of breeding is defined as the time of the first lactating female or first young born (birth date estimated from weight at capture). The end of the breeding is the week in which the last lactating female was caught or last young was born

	Silver Creek	Beaver Pond	Kloo Lake	1050 control	Microwave food	Jacquot control	Jacquot food	Gribble's control	Dezadeash food
1977	15	11	—	15	—	11	11	18	—
1978	18	—	15	16	15	18	17	19	18
1979	16	16	16	19	20	16	12	17	21
1980	21	19	19	18	19	16	16	19	21
1981	14	15	15	16	15	12	15	17	17
1982	—	9	—	13	14	8	6	17	20
1983	15	13	17	12	—	7	8	12	16
1984	—	9	—	—	—	19	21	12	16

TABLE 10. Summer reproductive indices for the two sexes. The percentage of adult females that are lactating was tallied from 1 May to 30 September. The percentage of scrotal adult males was tallied from 1 April to 31 August. Sample size in parentheses. Individual hares may be counted several times in these data

	Silver Creek	Beaver Pond	Kloo Lake	1050 control	Microwave food	Jacquot control	Jacquot food	Gribble's control	Dezadeash food
Females									
1977	50	75	0	67	100	40	50	100	67
	(2)	(4)	(1)	(6)	(2)	(5)	(2)	(3)	(3)
1978	52	100	58	55	50	33	28	46	40
	(52)	(1)	(12)	(33)	(20)	(58)	(73)	(37)	(20)
1979	49	36	34	59	56	56	29	64	49
	(67)	(11)	(38)	(75)	(82)	(25)	(17)	(39)	(59)
1980	57	49	62	56	55	56	53	65	54
	(168)	(53)	(71)	(177)	(297)	(50)	(40)	(100)	(248)
1981	62	60	52	53	55	38	39	47	50
	(99)	(94)	(66)	(124)	(218)	(37)	(57)	(68)	(287)
1982	11	46	50	65	37	42	16	48	50
	(9)	(13)	(4)	(23)	(57)	(24)	(44)	(29)	(119)
1983	50	67	50	57	25	100	75	50	36
	(6)	(6)	(4)	(7)	(4)	(1)	(4)	(10)	(25)
1984	—	80	—	—	67	42	17	80	64
		(5)			(3)	(24)	(35)	(5)	(11)
Males									
1977	—	—	100	0	—	50	50	—	—
			(1)	(1)		(2)	(2)		
1978	78	100	100	100	50	79	87	58	100
	(9)	(2)	(3)	(4)	(2)	(28)	(32)	(12)	(3)
1979	77	80	60	80	81	90	91	100	90
	(26)	(5)	(15)	(39)	(21)	(19)	(11)	(4)	(10)
1980	55	56	53	72	70	49	55	67	74
	(114)	(36)	(32)	(81)	(93)	(47)	(31)	(48)	(96)
1981	59	64	56	67	74	59	68	61	80
	(41)	(83)	(45)	(54)	(116)	(58)	(71)	(28)	(101)
1982	—	53	33	0	77	35	75	85	84
		(19)	(6)	(3)	(70)	(17)	(32)	(13)	(68)
1983	50	—	78	100	—	100	75	70	65
	(4)		(9)	(1)		(4)	(8)	(10)	(17)
1984	67	100	100	100	100	78	87	60	67
	(3)	(2)	(5)	(1)	(3)	(9)	(15)	(5)	(3)

The length of the breeding season (Table 9) was estimated from female lactation and juvenile birth dates. We estimate that these dates could be 1–2 weeks in error because of monthly intervals. The breeding season is longest in the late increase and early peak phase of the cycle (1978–80) and then is shortened in the late peak (1981) and especially in the decline phase (1982–83). We could detect no effect of extra winter food on the length of the breeding season for the Microwave or Jacquot food grids, but the data suggest for Dezadeash that extra food increased the breeding season by 2·3 weeks on average (ANOVA, $P < 0·05$).

The proportion of adults breeding was estimated by recording the percentage of adult females that were lactating between 1 May and 30 September of each year, and the percentage of males with scrotal testes between 1 April and 31 August. Individual hares were tallied each time they were captured: Table 10 gives these data. We can detect no pattern in them and conclude that reproductive status within the breeding season is independent of cyclic phase. Moreover, we could not measure any effect of the extra winter food on the proportion of adults breeding for any of the food grids. We repeated this analysis for females using the more restricted time period 15 May to 1 September with essentially the same results.

The recruitment of juveniles into the live-trapped population is a third index of reproductive rate, although it combines birth rates and early juvenile mortality. Table 11 gives the total number of juveniles caught each year and the index of recruitment (recruits per adult female). About two-thirds of these juveniles are captured in the summer and one-third from October to March. The index of recruitment is strongly correlated with the annual rate of population change ($r = 0·57$) and is the most variable reproductive parameter in the cycle. The index of recruitment is reduced on the Microwave food grid in association with the high density of adult hares, but not reduced on Dezedeash food grid (compared with its control) or on Jacquot Island food grid.

TABLE 11. Number of juveniles recruiting into the live-trap population and an index of recruitment (number of recruits per adult female). Both sexes combined. Juveniles tallied between birth and the following 1 April. Adult females censused in May and June each summer

	Silver Creek	Beaver Pond	Kloo lake	1050 control	Microwave food	Jacquot control	Jacquot food	Gribble's control	Dezadeash food
1977	9	11	6	22	8	34	46	31	19
	(9·0)	(11·0)	(12·0)	(12·0)	(8·0)	(2·8)	(7·7)	(15·5)	(9·5)
1978	46	9	18	50	43	93	83	52	52
	(11·5)	(9·0)	(3·6)	(4·5)	(7·2)	(2·1)	(2·2)	(4·3)	(10·4)
1979	88	52	77	127	202	48	51	60	141
	(7·3)	(10·4)	(5·5)	(4·7)	(3·0)	(3·4)	(5·1)	(3·3)	(3·4)
1980	136	86	72	135	289	56	59	111	239
	(4·1)	(4·8)	(3·8)	(3·1)	(2·1)	(2·7)	(2·3)	(3·0)	(3·9)
1981	70	94	69	123	225	25	56	52	166
	(4·1)	(2·5)	(3·8)	(3·6)	(1·9)	(0·6)	(1·6)	(1·4)	(1·7)
1982	4	13	5	13	13	11	11	17	40
	(4·0)	(2·2)	(1·3)	(2·6)	(0·1)	(0·9)	(0·6)	(1·1)	(0·7)
1983	12	10	5	12	2	16	12	7	36
	(12·0)	(3·3)	(5·0)	(4·0)	(0·4)	(2·7)	(0·8)	(1·4)	(5·1)
1984	7	3	0	2	1	29	28	3	13
	(3·5)	(3·0)	(0·0)	(4·0)	(0·5)	(5·8)	(2·3)	(0·8)	(2·6)

In summary, the length of the breeding season changes systematically over the hare cycle with longer breeding seasons in the increase and peak phases and shorter seasons in the decline phase. Within the breeding season there is no change in the proportion of adults breeding over the cycle. Recruitment of juveniles is most strongly related to cyclic phase and is highly correlated with the annual rate of population change. It was not affected by extra food addition.

Annual population increment

If we pool the data from all the grids, we can predict the annual rate of population change in snowshoe hare numbers (Table 7) from the annual survival rate (Table 6) and the index of recruitment (Table 11) in a multiple regression with $R^2 = 0.64$ ($n = 63$):

$$\log (\text{annual rate of change}) = 5.356 \,(\text{annual survival rate})$$
$$+ 0.1710 \,(\text{index of recruitment}) - 4.400$$

where annual survival rate is expressed as the product of summer and winter survival, as given in Table 6. Both survival and recruitment are significant in determining this multiple regression with partial correlations of 0.68 for survival vs. annual change and 0.62 for recruitment vs. annual change.

Figure 7 summarizes these results in a simple life-table model of a snowshoe hare population. If we use the observed data of Table 6 and Table 11 from our nine study areas in this life-table model, we find that we consistently underestimate the true rate of population change. We think this means either recruitment or survival is negatively biased, and we suspect that most of our survival estimates are too low by 0.05–0.10 per 28 days. The slopes the contours in Fig. 7 show that estimates of population change are much more affected by small changes in survival rate than by equivalent changes in recruitment index.

We have no evidence of extensive immigration or emigration in most of our populations (Boutin 1980, 1984a; Boutin *et al.* 1985) except for the food-supplemented areas, where immigration occurs when food is first added. We therefore consider movements unimportant in affecting the annual rate of population change.
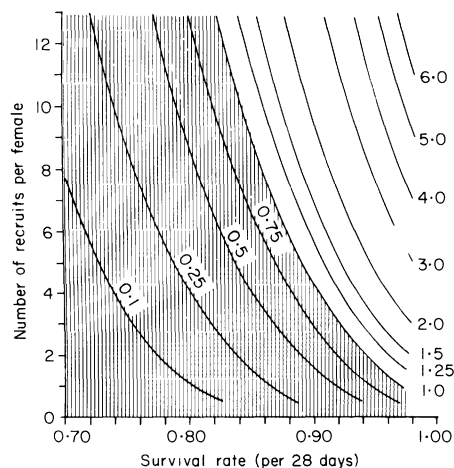

FIG. 7. Annual finite rate of population change for a snowshoe hare population as a function of average survival rate and recruitment rate. Maximum number of young per summer assumed to be 13·0, and average age at first capture assumed to be 8·0 weeks. The finite rates of population growth were established from a simple life-table model using the characteristic equation of Lotka.

Interference with our experiments

Three sources of interference with our food addition experiments must be discussed. We decided in these experiments to provide artificial food to hares rather than to supplement natural food. But when artificial food is supplied to any population, typically the carrying capacity of an area is increased. This can result in secondary limitation of food because of behavioural interactions at feeding stations. We had only eighteen feeding stations at Dezadeash Island and Microwave and nineteen at Jacquot Island. Hares show dominance behaviour at feeding stations (Graf 1985), and since there were over 300 hares on Microwave during the two peak winters of 1980–81 and 1981–82, there was potential for food to be limited through behavioural dominance. During the peak winter of 1980–81 on Microwave the average consumption of rabbit chow was 17·4 kg per day, which would feed 134 hares at an average consumption rate of 130 g per day. This was 46% of the food requirement on Microwave during this winter. Similar figures for Dezadeash Island were 21·5 kg per day consumed during the winter of 1980–81, or 62% of the food needed by the resident population. Hares clearly used natural forage as well as rabbit chow on these food grids, and the result of these high densities of hares was severe damage to the local vegetation on the food grids (J. N. M. Smith unpublished). Local competition for chow could have limited the amounts of food available to subordinate hares.

Second, to add to these problems we had disturbances to our feeding stations by grizzly bear and moose. Grizzly bear disturbances were not serious. They occurred only at the Microwave site and only in the early autumn (September–October). We overcame these disturbances by broadcast feeding of rabbit chow under spruce trees during October 1980 and every October subsequently. Moose disturbance was more disruptive and occurred on both Microwave and Dezadeash sites. On Microwave grid moose disturbance was first noted on 13 November 1980 and continued until 7 January 1981. It re-occurred from 20 October to 28 December 1981 and 24 February to 16 March 1982. In the autumn of 1982 moose disturbance occurred from 28 October to 5 December when we completed moose-proof feeding exclosures at Microwave. During these periods of disturbance rabbit chow was not always available to the hares, although we tried several designs of feeders of with partial success. At Dezedeash Island moose disturbance was more sporadic. The first serious disturbance occurred on 9 April 1982 and from 20 December 1982 to 21 January 1983, when we were able to complete moose-proof feeding stations. On Jacquot Island we had no moose or bear disturbance that was serious.

We have analysed the monthly suvival rates before, during, and after these episodes of disturbance by moose and we do not think they have had major effects on the feeding experiment results reported above. On Microwave survival remained high in 1981–82 in spite of the moose disturbance. In November 1982 some of the low survival of hares on Microwave could be explained by the disturbance of the feeding stations. On Dezadeash Island survival rates remained very high during the period of disturbances in 1982–83. The timing of the decline phase on Dezadeash Island (Fig. 4) was unrelated to the moose depredations on our feeding stations.

A third complication was that we attempted to control predators on two of our study areas, Kloo Lake and Dezadeash Island. These predator control experiments were unsuccessful, partly because the predators were too mobile and partly because we could not devote enough manpower to the removals. At Kloo Lake we removed one great horned owl and one goshawk in the spring of 1981. At Dezadeash Island we removed one goshawk and one great horned owl in the spring of 1981, and two goshawks and one great horned owl in the winter of 1981–82. We were unable to catch any mammalian predators

on these two areas. We removed no predators during the decline phase from 1982 to 1984, and we assume that these few predator removals did ṅot prevent predation losses on these grids.

DISCUSSION

There have been three long-term studies of the dynamics of the snowshoe hare cycle: one in Minnesota, one in Alberta, and the present study in the Yukon. Keith & Windberg (1978) have drawn from these and other studies a general picture of the demographic machinery behind the hare cycle. Here we compare our results with the patterns observed in previous studies (Table 12).

Maximum spring densities recorded at the peaks of the snowshoe hare cycle were 2·1 hares per ha in central Minnesota (Green & Evans 1940a), 1·5–8·9 per ha on five areas in central Alberta (Keith & Windberg 1978), and 2·1–3·5 per ha on our five control areas excluding Jacquot Island (Table 12). There seems to be relatively little difference in maximal spring densities in these different areas, and 2–4 hares per ha would be the expected peak spring density.

Minimum spring densities are much harder to estimate. Green & Evans (1940a) reported minimal densities of 0·20 hares per ha in Minnesota. Keith & Windberg (1978) estimated cyclic low densities of 0·13–0·33 hares per ha on four areas and 0·27–0·54 hares per ha on another area. The lowest densities were at the start of our study in 1976–77, when many of our control grids had no hares, and an average density for April 1977 was 0·02 hares per ha (four individuals on seven trapping grids).

Estimates of the amplitude of the hare cycle are most strongly affected by the estimates for minimum spring densities. Green & Evans (1940a) estimated the amplitude to be about 15-fold for April densities. Keith & Windberg (1978) estimated spring amplitudes from 17 to 50-fold. We estimated a much larger amplitude, ranging from 108 to 182-fold for our spring populations.

Each of the two declines studied in detail by Keith & Windberg (1978) lasted for 4 years, while Green & Evans (1940a) reported 3 years of decline. We were surprised to observe on most of our study areas only 2 years of decline from 1981 to 1983. Our results reinforce Keith's conclusion that the decline phase operates more rapidly than the increase phase of the cycle. There is no indication that the rate of population decline differs between Minnesota, Alberta, and the Yukon (Table 12).

Survival of juvenile hares was greatly reduced in the peak year and in the whole decline phase according to Green & Evans (1940c) and Keith & Windberg (1978). Keith & Windberg (1978) pointed out that early winter was the critical period for juvenile survival. Our results agree with Keith's that early winter juvenile losses are an important component of the changes in density in the hare cycle.

There is more disagreement about changes in adult survival over the hare cycle. Green & Evans (1940c) claimed that adult losses were constant over the whole cycle at 70% loss per year, although they observed higher losses in one year at the end of the decline. Keith & Windberg (1978) suggested that late winter survival of adults was reduced one year after the peak and during the remaining decline and low phases. We found that adult survival in the autumn was correlated ($r = 0·49$) with the annual rate of population change as was adult survival in winter ($r = 0·42$), and also that survival gradually deteriorated through the cycle (Fig. 6). In our data there was no significant correlation between juvenile and adult survival estimates for summer or winter; but juvenile autumn survival (October–

TABLE 12. Comparison of the demography of the snowshoe hare cycle in Minnesota (Green & Evans 1940a,b,c), Alberta (Keith & Windberg 1978) and the southern Yukon

	Minnesota	Alberta	Yukon
Maximum density (Spring)	$2 \cdot 1$ ha^{-1}	$1 \cdot 5$–$8 \cdot 9$ ha^{-1}	$2 \cdot 1$–$3 \cdot 5$ ha^{-1}
Minimal density (Spring)	$0 \cdot 2$ ha^{-1}	$0 \cdot 13$–$0 \cdot 54$ ha^{-1}	$0 \cdot 02$ ha^{-1}
Amplitude based on:			
Spring density	15	17–50	108–182
Autumn density	?40	46–70	200–324
Annual rate of population change:			
Increase phase	?	$2 \cdot 0$	$3 \cdot 9$
Decline phase	$0 \cdot 48$	$0 \cdot 29$–$0 \cdot 35$	$0 \cdot 32$
Survival rate:			
Juveniles	Low in peak and decline	Low in peak and decline	Low in peak and decline
Adult	Constant	Low one year after peak and in decline	Gradual decline through peak and decline
Reproductive rate	Reduced in decline phase*	Maximal 3 years before peak, minimal 3 years after the peak	Breeding season shortened in peak and decline

* According to Keith & Windberg (1978, p. 51). Green & Evans (1940c) stated that the reproductive rate was constant over the cycle.

December) was highly correlated with adult autumn survival ($r = 0 \cdot 68$). We suggest that at Kluane there is a critical period in the autumn for both juveniles and adults, and that the deterioration in survival is gradual through the cycle.

We did not measure reproduction directly through an autopsy study. Cary & Keith (1979) analysed reproductive changes in snowshoe hares in Alberta and found significant changes in pregnancy rate and litter size over the cycle. Our live-trapping data are consistent with the model of reproduction given by Cary & Keith (1979). The length of the breeding season is shortened in late peak and declining populations (Table 9), but the proportion of adults in breeding condition during the main breeding season is constant over the cycle. Keith & Windberg (1978) found that even though reproductive rate changed during the hare cycle, it was not the major driving force behind the demographic events.

Recruitment rate was the major force behind the hare cycle both in our study and in the Alberta study. We think that recruitment rate is strongly affected by juvenile survival during the first 8 weeks of life. Keith & Windberg (1978) believe that recruitment is set by the reproductive rate and by *autumn* survival of juveniles, not by post-partum summer survival. Changes in recruitment rate could be caused by changes in litter size and pregnancy rates over the cycle. Cary & Keith (1979) have found a $2 \cdot 4$-fold variation in reproductive output over the hare cycle in Alberta. The average index or recruitment varies $5 \cdot 3$-fold from 1977 to 1982 for our control populations (Table 11). We think that the low recruitment is partly a result of juvenile mortality in the summer months from June to August and partly a result of changes in reproductive rates. We do not have autopsy data from this study to verify Cary & Keith's (1979) findings. We catch juveniles in our live-traps when they average 4–8 weeks old, and by this time the recruitment rate is already fixed for the year (the correlation of recruitment index for summer with recruitment index for the whole year (Table 11) is $0 \cdot 90$). This is somewhat surprising because summer juvenile survival, measured on live-trapped juveniles, is not closely related to population trends ($r = 0 \cdot 24$). The important summer mortality must operate on very small juveniles before they are caught in live-traps. We do not know the causes of this juvenile mortality.

Effect of extra winter food on hare demography

The Keith Hypothesis (Keith & Windberg 1978) suggests that winter food shortage produces the peak and early decline of the hare cycle. This hypothesis predicts that if extra food is provided, the demographic decay that accompanies the peak and early decline phases will be either delayed or eliminated. Specifically, this demographic decay involves a drop in juvenile survival, a drop in recruitment rate, a fall in adult survival, and a shortening of the breeding season. In addition to these parameters, Keith & Windberg (1978) discuss changes in body weight and growth that are postulated to change because of winter food shortage; we will discuss these growth changes in a subsequent paper.

Table 13 summarizes the results of our winter feeding experiments. Each of the three areas responded differently. We do not have any explanation of why Jacquot Island showed no feeding response; clearly food supply does not limit breeding density on this island. The two other areas responded more similarly to extra winter food. In both cases extra food did not prevent the decline phase and all areas were at low densities by 1983. Nor did extra food improve juvenile survival in the autumn or prevent the drop in recruitment that is correlated with the cycle. Extra food on these two areas was clearly effective in increasing average density about 3-fold, and this could be viewed as an increase in carrying capacity such that hares continued to cycle but at a higher average density.

Boutin (1984b) described two short-term feeding experiments on snowshoe hares in our study area. He found that immigration was the main factor causing population growth when extra food was put out. His results agree with our long-term studies in that extra food did not change survival rates in declining populations, although it did improve survival in peak populations.

We suggest that the data reported here are consistent with two alternative hypotheses for explaining the cyclic decline on small areas:

(1) *Winter food shortage is not necessary for cyclic snowshoe hare declines.* This interpretation accepts the feeding experiments as successful and suggests that the severe declines on the Microwave and Dezadeash food grids were due to other factors such as predation or dispersal.

(2) *Winter food shortage is necessary for cyclic hare declines.* This interpretation accepts that the feeding experiments increased the density of hares on Microwave and Dezadeash but were unable to provide sufficient food at peak densities to stop the decline. Food

TABLE 13. Summary of the demographic responses of snowshoe hares to extra winter food on three areas, 1977–1984

	Microwave food	Dezadeash Island food	Jacquot Island food
Density increased c. 3-fold	Yes	Yes	No
Start of decline phase	Delayed <1 year	Simultaneous with control	Non-cyclic population
Extra food prevented decline to low numbers	No	No	—
Survival rates			
Increase phase	+	+	No difference from
Peak phase	+	+	control
Decline phase	−	−	
Reproduction			
Length of breeding season	0	+	0
Intensity of reproduction	0	0	0
Recruitment rate	−	0	0

shortage is therefore postulated to have occurred on all grids in 1981–83 because of moose and bear disturbances as well as behavioural dominance at feeding stations. The feeding experiments are therefore postulated as being unsuccessful in overcoming these difficulties and this is why the hares declined on the two food grids as well as on the control grids.

We cannot distinguish these two alternatives with the present demographic data, but we can distinguish between them with data from faecal pellets of hares (Sinclair, Krebs & Smith 1982). In a future paper, Sinclair will present these data to test the predictions that arise from hypothesis 1 (that hares during the decline had adequate food on the Microwave and Dezadeash sites) and from hypothesis 2 (that hares were starving on the food grids during the decline). We think our present data tend to support hypothesis 1.

Keith *et al.* (1984) studied three hare populations in Alberta during the early decline phase. They found high predation mortality on all areas and food shortage on only two of the three areas. Predation mortality was deemed sufficient to cause the decline on the area with ample winter food so that all three populations declined in synchrony. Keith *et al.*'s (1984) results are consistent with (1) that *winter food shortage is not necessary for a cyclic hare decline.*

It we were to set up these feeding experiments again, we would recommend starting with several food grids and moving the food treatment to a new grid each autumn. This should minimize the effect of increasing the carrying capacity of a site and the associated problems of localized heavy overbrowsing after several years, although it would introduce the problem of immigration at each food addition.

Two important questions about winter feeding experiments are left unanswered in all the research to date. (i) Could winter food supplements begun during the decline phase reverse the demographic trends? (ii) Can continued feeding through the decline and low phase accelerate the phase of increase so that the cycle length (or at least the period of low numbers) is shortened? We are doing this experiment now.

In subsequent papers we will describe the interaction between snowshoe hares and their winter food plants and discuss the nutritional condition of hares during the cycle. These details of the snowshoe hare–woody plant interaction must be analysed to give a comprehensive picture of this critical plant–herbivore interaction in the boreal forest.

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