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Snowshoe Hare Demography

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8.1 The Snowshoe Hare Cycle

Snowshoe hares, *Lepus americanus,* exhibit continent-wide cyclic fluctuations in abundance. Peak densities occur every 8–11 years, and densities fluctuate 5 to 25-fold during a cycle. Snowshoe hares are typically the dominant herbivore in boreal forests, and their cyclic fluctuations have widespread ramifications for the shrubs and trees that they eat, for the transient and resident predators that eat them, and for the other forest herbivores that may compete with hares for food or that may serve as alternative prey for predators (Elton 1924, Finerty 1980, Keith 1990, Krebs et al. 1992, Royama 1992).

Both mortality rates and reproductive rates of snowshoe hares also show regular cycles. Mortality rates are highest during the decline phase and lowest during the late low and early increase phases (Krebs et al. 1986b, Trostel et al. 1987, Keith 1990). The number of litters per breeding season, the proportion of females pregnant with each litter, and the number of leverets per litter all show cyclic changes, with the highest annual reproductive output occurring during the late low and early increase phases (Ernest 1974, Cary and Keith 1979, Stefan 1998).

Dispersal rates are not as well known for snowshoe hares. Dispersal appears to vary through the cycle, but the highest dispersal rates have variously been found to occur in the peak and early decline phases (Windberg and Keith 1976, Boutin et al. 1985) or in the increase phase (Keith and Windberg 1978, Wolff 1980). This discrepancy may be due to the different techniques that have been used for assessing dispersal (e.g., loss rates, removal grids, radio telemetry locations). Juvenile hares apparently disperse more than adults do (Dolbeer and Clark 1975, Windberg and Keith 1976, Keith et al. 1984, Boutin et al. 1985, Gillis and Krebs 1999).

Various explanations have been proposed to explain the demographic changes that lead to the numeric hare cycle. One set of proposals implicates the variation in food supply through the cycle, arguing that food shortage leads to reduced reproduction and increased starvation as hares spend more time searching for browse and are in poorer physical condition (Pease et al. 1979, Vaughan and Keith 1981, Keith 1983). Snowshoe hares eat woody shrubs and trees in the winter and forbs, grasses, and leaves of shrubs in the summer. Because of the heavy browsing that occurs during peak hare densities, winter forage availability is lowest during the early decline phase (Pease et al. 1979, Sinclair et al. 1988, Smith et al. 1988). Additionally, secondary compounds increase with plant regrowth and may lead to relative food limitation as plants regrow after heavy browsing (Bryant 1981, Fox and Bryant 1984). Food limitation, either absolute or relative, has therefore been suggested as a potential initiator of the cyclic declines.

An alternative hypothesis argues that patterns of predation explain the cycle. Most hares die of predation and most hares die as juveniles; survival is lowest during the decline phase (Boutin et al. 1986, Keith 1990, Krebs et al. 1995, Stefan 1998, Gillis and Krebs 1999). Hares are the predominant prey species for lynx, coyotes, goshawks, and great horned owls (Keith et al. 1977, O'Donoghue et al. 1997). These predators show both numeric and functional responses to the hare cycle, with the numeric responses typically lagging 2–4 years behind the population changes of the snowshoe hares (Keith 1990, Boutin et al. 1995, O'Donoghue et al. 1998). Leverets are often killed by red squirrels and ground squirrels (O'Donoghue 1994, Stefan 1998). Some leverets and adults die of exposure or starvation during the decline phase of the cycle, but these causes of death seldom occur at other phases (Boutin et al. 1986, Keith 1990, Stefan 1998). The predation hypothesis suggests that these regular shifts in mortality are capable of driving the cycle.

Three lines of evidence suggest that food explanations are incomplete. Food shortages are not reliably detected during cyclic peaks and declines (Sinclair et al. 1988, Smith et al. 1988), food addition experiments have failed to stop cyclic declines (Krebs et al. 1986a, 1986b), and patterns of plant chemical defenses lag behind the numeric changes of hares, which suggests that the changes in plant chemistry cannot cause the cyclic decline (Sinclair et al. 1988). Additionally, it is unclear whether food limitation can have a sufficiently large impact on hare survival rates; the predation hypothesis has a similar problem, in that changes in mortality patterns cannot explain the regular cyclic changes in reproduction.

There are several hypotheses that link the effects of food and predation on snowshoe hare population dynamics. In one scenario, cyclic declines are thought to be initiated by the scarcity of food, which increases starvation rates and also makes hares more accessible to predators; predation is then thought to lengthen the decline and sustain the low phase (Keith 1974, 1981, 1990). Alternatively, food and predation may interact throughout the cycle in their impacts on hare dynamics, rather than influencing hares sequentially (Krebs et al. 1992). A third hypothesis suggests that predators affect hare foraging behavior and physiology, with high predation pressure causing hares to have poorer diets, increased stress, and reduced fecundity (Hik 1994, 1995, Boonstra et al. 1998a). Additionally, the impacts of food and predation on hare demography may be affected by the levels of parasitic infestation of hares (Sovell and Holmes 1996, Murray et al. 1997, 1998).

The Kluane experiments were designed to evaluate the relative impacts of food and predation on hare demography. Because neither factor alone seems able to explain all of the demographic changes, they were manipulated in a factorial fashion to examine how each factor affects hare demography and how they interact in their effects on snowshoe hares.

8.2 Methods

Our primary objective was to determine the effects of food, predation, and their interaction on the demography of snowshoe hares through a population cycle. The fertilization and food addition treatments increased food availability by increasing plant growth and providing artificial food, respectively, and the two predator exclosure treatments reduced the risk of predation. We focused on twice-yearly trapping of hares for population estimates, coupled with radio telemetry for detailed study of survival and causes of death; in some years, hare reproduction was studied using maternity cages. Numerous additional questions were also addressed by individual researchers, so the precise questions asked in each year at each study site varied (table 8.1).

To obtain population estimates and to establish rates of population increase, we conducted trapping sessions on each experimental grid in March-April and October. Each session lasted 3–7 trap nights, but early in the project it became clear that animals caught night after night were losing weight from the trapping, so grids were trapped a maximum of 2 consecutive nights, then allowed to rest for at least 2 nights before additional trapping. Each grid had 86 Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) located along four traplines (CD-ROM frame 24). Traps were baited with alfalfa and

Table 8.1 Snowshoe hare demographic parameters measured during a population cycle near Kluane Lake, Yukon.

	Type of Information			
Treatment Grid	Population Censuses, Increase Rates[a] (Trapping)	Survival, Mortality Causes[b] (Radio Telemetry)	Reproduction, Leveret Survival[c] (Maternity Cages + Telemetry)	Juvenile Survival, Dispersal[d] (Radio Telemetry)
Control 1 (Sulphur)	1987–1998	1988–1996	1988–1989, 1992, 1994–1996	1995–1996
Control 2 (Silver)	1987–1998	1991–1996	1990–1992	—
Control 3 (Chitty)	1988–1990, 1993–1996	1988, 1993–1996	1989–1990, 1994–1996	1989–1990, 1995–1996
Control 4 (Lloyd)	—	1992, 1994–1995	1992, 1994, 1996	1989–1990
Control areas off-grid	—	1992–1996	1992, 1994–1995	1995–1996
Fertilizer 1 (Flint)	1988–1996	1988–1996	—	—
Fertilizer 2 (Grizzly)	1988–1996	1993–1996	—	—
Food addition 1 (Gravel Pit)	1988–1996	1988–1996	1989–1990, 1995	1989–1990, 1995–1996
Food addition 2 (Agnes)	1988–1996	1992–1996	1989–1990, 1995	1989–1990, 1995–1996
Predator exclosure (Beaver Pond)	1988–1996	1988–1996	1988	—
Predator exclosure + food (Hungry Lake)	1988–1996	1988–1996	1991–1992	—

The lettered footnotes indicate the primary literature summarizing these studies. The peak occurred in 1989–1990, and the lowest densities were in 1993. Leveret survival was monitored from birth until weaning (30 days), and juvenile survival was postweaning until March of the following year.

[a] Krebs et al. (1992, 1995, 1996), Boutin et al. (1995), Hodges et al. (1999a).

[b] Krebs et al. (1992, 1995, 1996), Hodges et al. (1999a).

[c] O'Donoghue and Krebs (1992), O'Donoghue (1994), Krebs et al. (1995), Stefan (1998).

[d] O'Donoghue and Bergman (1992), Gillis (1999), Gillis and Krebs (1999).

snow or apple for moisture. At peak hare densities, some grids had additional traps to reduce trap saturation. Traps were 30–60 m apart, and lines of traps were 150 m apart, for an effective grid size of about 60 ha. Trapping sometimes occurred at other times to replace radio collars or to obtain reproductive information. Initially, traps were left open 24 h and checked at dawn, but because this schedule was stressful to hares and because many squirrels entered traps in the day, we quickly shifted to setting traps at dusk and checking them at dawn. For each hare caught, we recorded ear tag (Monel #3, National Band and Tag Co., Newport, Kentucky), weight, right hind foot length, reproductive condition (males, scrotal or abdominal testes; females, lactating, not lactating) (CD-ROM frame 25).

To monitor adult survival, some hares >1000 g were radio collared with 40 g radio collars equipped with mortality sensors (Lotek, Newmarket, Ontario). Radio-collared hares were monitored every 1–2 days to provide survival estimates, and all animals that died were located to determine the cause of death. The predators leave distinct signs, such as scat, tracks, feathers, or pellets, and also have distinct methods of eating hares. In about 50% of cases we were able to assign cause of death to a particular species of predator (CD-ROM frame 37) and in another ~10% of cases we could distinguish avian from mammalian predation but could not identify the particular predator species.

To estimate natality and survival of leverets, we trapped pregnant females 1–14 days before parturition and held them in 60 × 60 × 120 cm chicken wire and wood cages until they gave birth (CD-ROM frame 26). Leverets were counted, ear tagged, weighed, and sexed. This method provided information on timing of reproduction and litter sizes. We calculated stillborn rates from the number of leverets born dead; necropsies were used to confirm that dead leverets died before birth (e.g., lungs not inflated, no internal trauma). At least half of the leverets in each litter were radio tagged by gluing 2–2.5 g transmitters to their backs (Biotrack, Wareham, England). The radio-tagged leverets were located daily until weaning (~4 weeks) for estimates of survival and identification of cause of death (O'Donoghue 1994, Stefan 1998). In this chapter, we present natality results following the analysis of Stefan (1998); these estimates differ from those in Krebs et al. (1995) and Boonstra et al. (1998a) because of a reappraisal of the timing of the first litter of the season. In 1995 some juveniles were fitted with 25 g radio collars (Biotrack) to obtain estimates of postweaning juvenile survival and dispersal (Gillis 1999).

8.3 Demographic Parameters

8.3.1 Density and Rates of Change

The main peak in hare densities occurred in 1989–1990, but on control 3 peak spring densities were in 1988 (figure 8.1). Peak spring densities on control sites were 1.6–2.0 hares/ha, and densities dropped to 0.01–0.1 hares/ha by spring 1993. Peak autumn densities ranged higher, with a maximum control density of 3.1 hares/ha on control 3. Averaged across all control sites, the cyclic amplitude was 18-fold. Through the rest of this chapter, we refer to the years 1989 and 1990 as peak, 1991 and 1992 as decline, 1993 and 1994 as low, and 1995 and 1996 as increase.

All experimental treatments resulted in higher hare densities, especially during the decline and low phases (figures 8.2, 8.3; CD-ROM frame 52). Averaged across the entire cycle, fertilization increased hare densities 1.3-fold, food addition 3.1-fold, removing mammalian predators 2.0-fold, and the predator exclosure + food manipulation 9.7-fold (CD-ROM frame 52). Both fertilized sites had their peak snowshoe hare densities in spring 1990, with densities of 1.8 and 2.2 hares/ha; they reached low densities of 0.3 and 0.7 hares/ha in 1993. The food addition grids had peak hare densities a year later, in 1991; the densities of 5.1 and 6.6 hares/ha were 3–5 times higher than peak control densities. The low densities on food grids were 0.2 and 0.5, again higher than the lowest densities on the control areas. The hares on the predator exclosure reached a peak density of 1.8 hares/ha in 1990, declined to 0.2 hares/ha in 1993, increased in 1994 and 1995, then decreased again in 1996. Hares on the predator exclosure + food treatment reached a high density of 6.1 hares/ha in 1990 and dropped to a low density of 1.0 hares/ha in 1993.

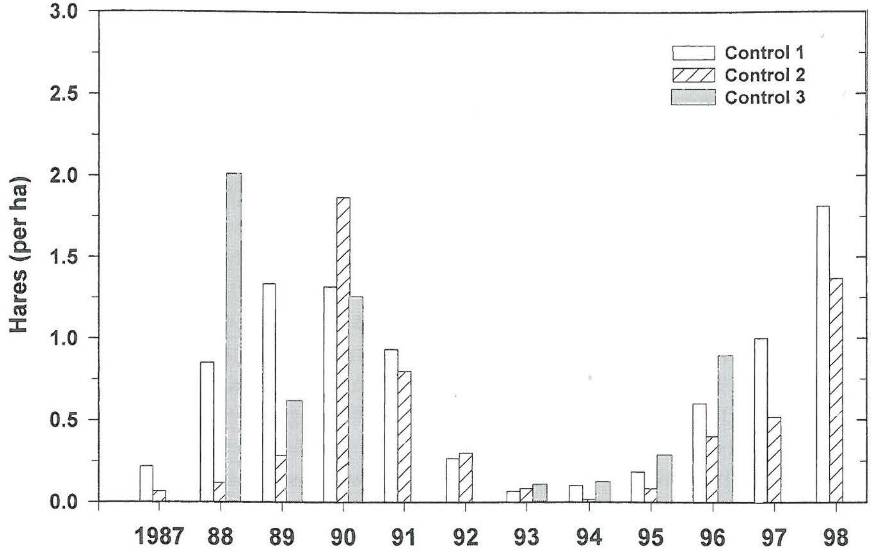

Figure 8.1. Snowshoe hare densities on control sites through a population cycle. Spring densities were calculated using the average of Jolly-Seber and jackknife estimators for trapping sessions conducted in March and April and assuming an effective grid size of 60 ha. Control 3 was not trapped in 1987, 1991, 1992, 1997, or 1998.

Population growth rates were also affected by the experimental manipulations. On control sites, hare populations declined for 4–5 years, from 1990 through 1994 (figure 8.4). The decline was most rapid from 1991 through 1993. Hares then showed some increase in 1994–1995, and a much greater rate of increase in 1995–1996. Hares on fertilizer treatments showed a population decline similar to that of control hares, but, unlike the control treatments, they showed high rates of increase during 1993–1994, then continued to increase at lower rates during 1994–1996. Hare populations on food addition treatments declined only from 1991 through 1993, but these decline rates and the subsequent rates of increase were similar to those of the control populations. The hare population on the predator exclosure had a decline similar to the control hares, then increased for 2 years before declining again in 1995–1996. The predator exclosure + food hare population declined slightly from 1990 to 1992, but the major crash in hare numbers occurred during the winter of 1992–1993.

8.3.2 Sex and Age Structure

Juvenile hares composed more of control hare populations during the low and early increase phases (~85–90%; table 8.2) than during the decline phase (~55–65%). The oldest hares (4 years old) were trapped during the decline. Neither fertilization nor food addition affected population age structures. The populations inside the predator exclosure fences had lower proportions of juveniles, and a higher proportion of hares reached ages older than 2 years; the oldest hares reached ages of 5 and 6 years. Sex ratios in the breeding population remained around 1:1 on all treatments.

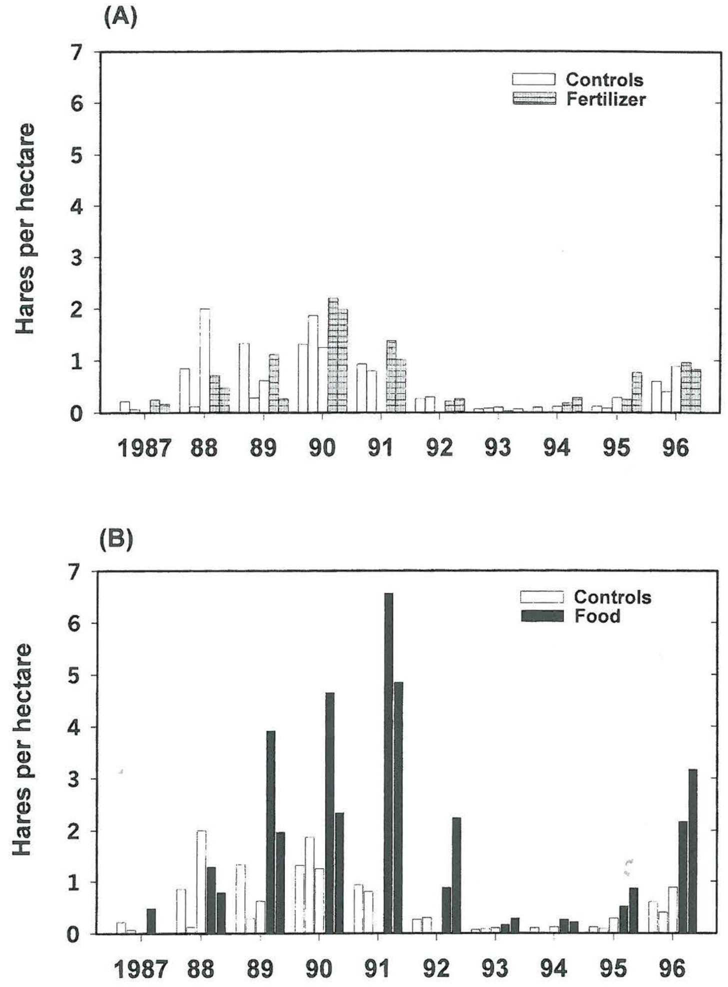

Figure 8.2 Snowshoe hare densities on fertilizer (A), food addition (B), predator exclosure (C), and predator exclosure + food (D) sites. Spring densities were calculated using the average of Jolly-Seber and jackknife estimators for trapping sessions conducted in March and April and assuming an effective grid size of 60 ha.

8.3.3 Reproduction

On control areas, the pregnancy rate varied among years and litter groups (table 8.3). Two litter groups were produced in the decline, three litter groups in late increase and peak

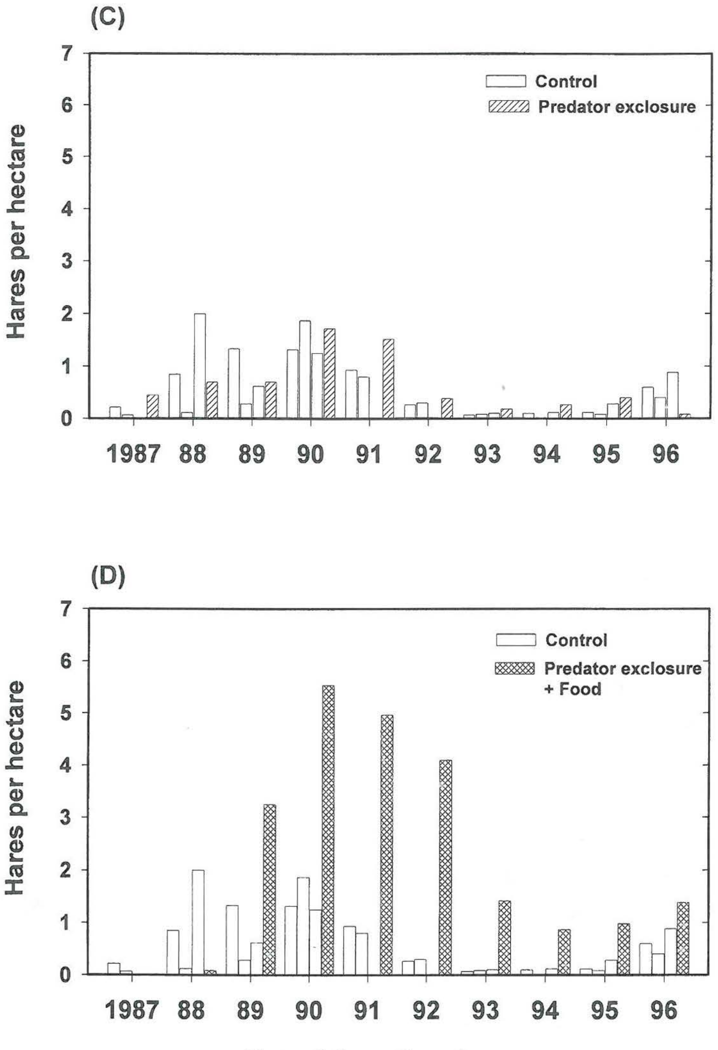

Figure 8.2 *continued*

years, and four litter groups in the late low and early increase. We did not use maternity cages for the fourth litter, but we could tell if a fourth litter was produced in a year from late summer trapping of pregnant females or autumn trapping of small juveniles. All females trapped in 1994 through 1996 were pregnant for the first three litter groups. In other years, 77–100% of females were pregnant with each litter group, and the lowest pregnancy rates usually occurred for the last litter group of the breeding season. Pregnancy rates were slightly higher on food grids relative to control areas in 1989 and 1990, but all females on both treatments were pregnant with all three litters in 1995. Unlike hares on the control areas, hares on the predator exclosure + food grid had three litters in both 1991 and 1992. On control areas, stillborn rates varied among years, with the highest rate (30.4%) occurring for litter 2 of 1991. Few leverets were stillborn in the first litter of any year (<8%), but stillborn rates increased in later litters in all years. Stillborn rates on the food grids were consistently double the rates on control areas, reaching maxima of 44.6% (1989) and 23.5% (1990) for litter 3. We do not know whether the maternity cage methodology influenced stillborn rates.

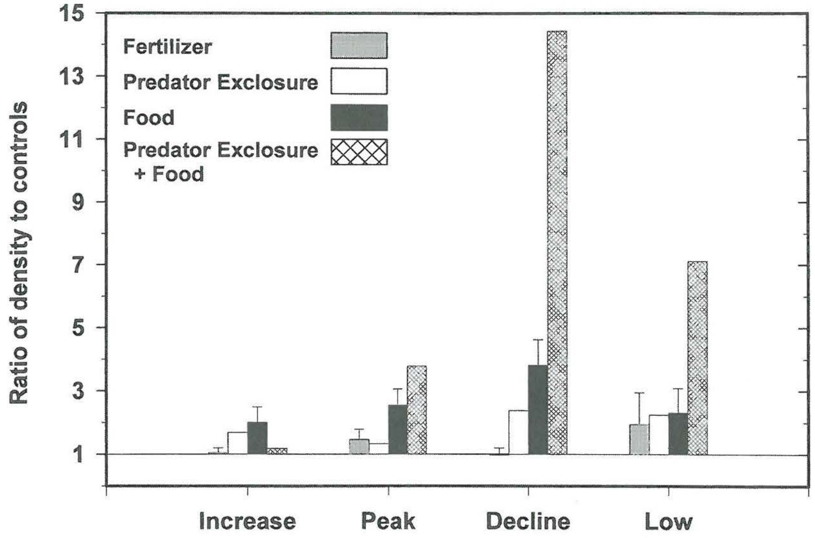

Figure 8.3 Ratio of hare population sizes on manipulated sites to mean control densities. Any value other than one indicates a treatment effect. The standard error bars are given for the replicated fertilization and food treatments.

Mean parturition dates for the first litter generally were in the fourth week of May (table 8.3). On control areas, the mean parturition date was about 7 days later in 1991 and 1992 than in 1994 through 1996; 1994 first litter parturition dates were 10–19 days earlier than in all other years. Relative to hares on control sites, hares on food addition sites had earlier mean parturition dates by 4–5 days during the peak (1989 and 1990) and by 12 days in the first year of the increase (1995). During the decline, hares on the predator exclosure + food treatment site gave birth 5–10 days earlier than did hares on control areas.

Mean litter size differed among years and litter groups on control areas (table 8.3). Except for the first litter, hares had smaller litters during the decline than during the increase phase of the cycle. The average size of the first litter (3.6) did not differ among years; litter 1 was consistently smaller than the average litter sizes for both litter 2 (5.8) and litter 3 (5.3). Litter sizes did not differ significantly between control and food grids at peak hare densities, but during the decline phase litter sizes remained high on the predator exclosure + food grid while decreasing by 25% for litter 2 on control areas. Sex ratios did not differ from 1:1 for any litter group in any treatment.

On control areas, total reproductive output was lowest during the decline (6.9 leverets/female per summer) and highest during the late low and early increase phases (18.9 leverets/female per summer) of the snowshoe hare cycle (figure 8.5a). Reproductive output

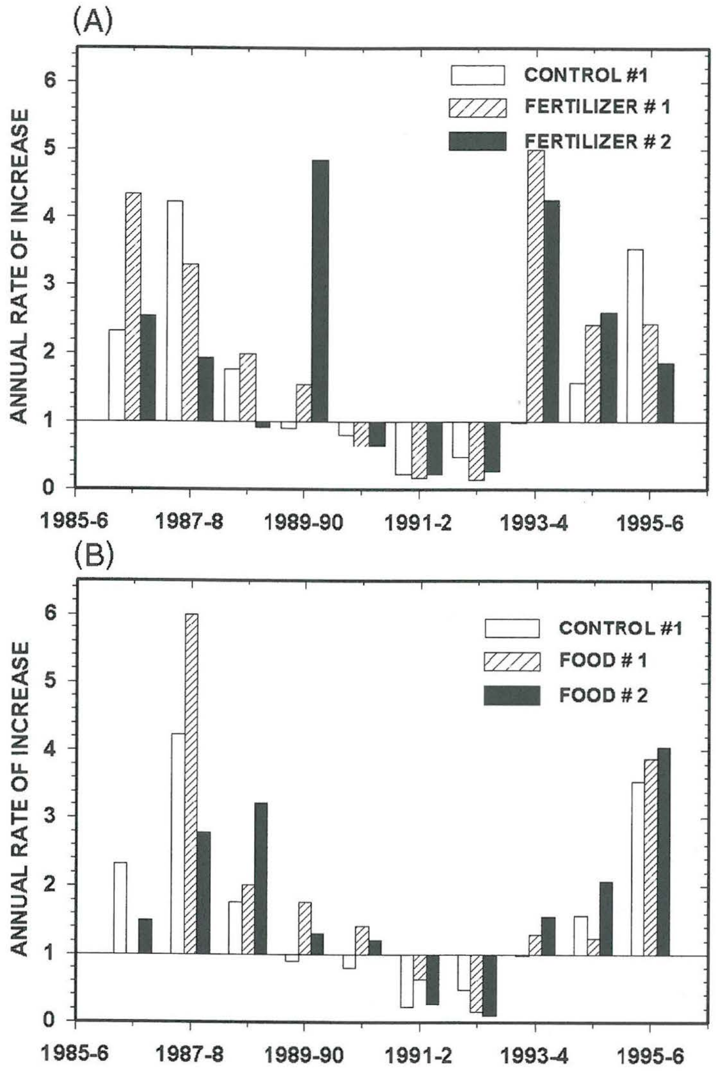

Figure 8.4 Rate of increase through the cycle. Values were calculated from spring densities as (t + 1)/*t*. A = fertilizer 1 and 2; B = food 1 and 2; C = predator exclosure; D = predator exclosure + food.

did not differ between food addition and control areas during the peak or early increase phases. However, although reproductive output decreased dramatically on the control areas during the population decline (from 12.8 in 1990 to 7.0 in 1992), it remained high on the predator exclosure + food treatment (15.5 in 1991 and 16.3 in 1992). This difference was due to hares having smaller and fewer litters on the control areas than on the predator exclosure + food grid. We do not know if reproductive output remained high on the food addition sites during the decline phase.

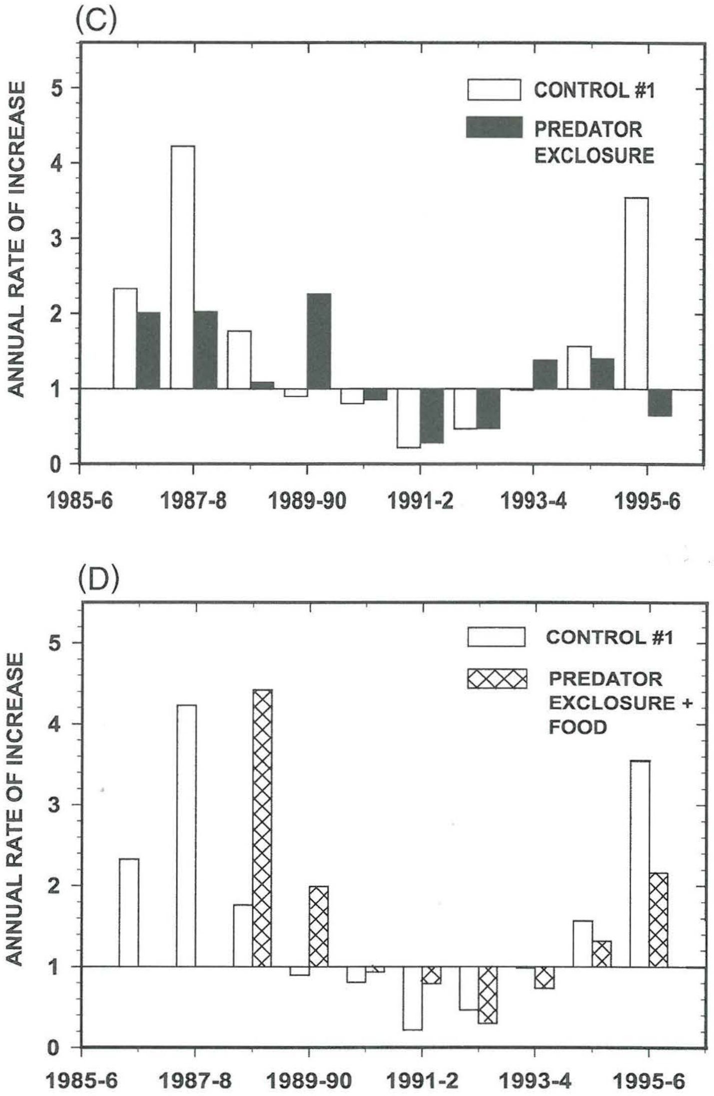

Figure 8.4 *continued*

The number of young weaned per female showed a similar pattern (figure 8.5b). On control sites, the most young were weaned during the early increase phase (9.7 weaned young/female in 1995), whereas the number of weaned young declined in each year of the population decline. Females on the food addition sites weaned more young than control females in 1990 (peak densities), but weaned fewer young in 1989 and 1995. Hares on the predator exclosure + food treatment weaned 6.2 young in 1992, while the control females we observed failed to wean any young.

Table 8.2 The age structure and sex ratio of snowshoe hare populations in spring.

Grid/Year	No. of Hares Caught	Mean Age (Years ± SE)	% Young	Age of Oldest Hare(s)	% Females
Control					
1989	72	1.24 ± 0.05	77.8	3	41.7
1990	187	1.57 ± 0.05	55.6	3	34.2
1991	87	1.47 ± 0.08	65.5	4	39.1
1992	30	1.60 ± 0.17	63.3	4	40.0
1993	12	1.17 ± 0.11	83.3	2	50.0
1994	14	1.21 ± 0.16	85.7	3	42.9
1995	28	1.11 ± 0.06	89.3	2	37.0
1996	106	1.11 ± 0.03	89.6	3	51.0
Fertilizer					
1989	60	1.08 ± 0.04	91.7	2	46.7
1990	102	1.22 ± 0.05	80.4	3	52.5
1991	61	1.39 ± 0.07	62.3	3	51.7
1992	26	1.65 ± 0.17	57.7	3	50.0
1993	5	2.40 ± 0.60	40.0	4	40.0
1994	27	1.00 ± 0.00	100.0	1	33.3
1995	53	1.08 ± 0.04	92.5	2	47.2
1996	90	1.18 ± 0.05	84.4	3	51.7
Food					
1989	116	1.08 ± 0.03	92.2	2	45.6
1990	154	1.21 ± 0.04	81.2	3	54.9
1991	355	1.45 ± 0.04	70.7	4	53.5
1992	72	1.56 ± 0.12	69.4	5	54.2
1993	20	1.55 ± 0.21	70.0	4	60.0
1994	26	1.35 ± 0.19	84.6	5	40.0
1995	53	1.08 ± 0.05	94.3	3	53.8
1996	213	1.15 ± 0.03	87.3	4	49.8
Predator Exclosure					
1989	40	1.30 ± 0.08	72.5	3	40.0
1990	181	1.34 ± 0.05	75.1	4	45.0
1991	80	1.58 ± 0.09	60.0	4	58.8
1992	23	1.48 ± 0.15	60.9	4	52.2
1993	10	1.70 ± 0.30	60.0	3	60.0
1994	15	1.53 ± 0.27	73.3	4	46.7
1995	24	1.33 ± 0.18	79.2	5	50.0
1996	5	1.60 ± 0.25	40.0	2	40.0
Predator Exclosure + Food					
1989	92	1.05 ± 0.02	94.6	2	54.3
1990	219	1.17 ± 0.03	83.1	3	43.6
1991	185	1.56 ± 0.05	55.1	3	43.2
1992	135	1.50 ± 0.07	68.9	4	54.5
1993	52	1.87 ± 0.12	38.5	4	65.4
1994	39	1.72 ± 0.17	64.1	4	46.2
1995	36	1.36 ± 0.13	75.0	4	55.6
1996	71	1.42 ± 0.11	74.7	6	56.5

These values are derived from trapping censuses conducted in March–April of each year. Hare ages were assigned on the basis of the size, weight, reproductive characteristics, and time of year when each hare was first caught. On January 1, we added a year to each hare's age. We do not report 1988 data because we would not have been able to age older hares accurately because of the lack of several years of prior trapping. Percent young is the percentage of hares in March that were born in the previous summer.

8.3.4 Survival Rates

Estimates of survival rates of adult hares were lowest during the decline (in 1991–1992, 30-day survival was 0.64, for an annual survival of 0.5%; figure 8.6) and highest during the increase phase (in 1988–1989 and 1995–1996, 30-day survival was 0.91, for an annual survival of 32%). Hares on the fertilizer treatments had survival patterns similar to hares on control sites. Hares on food addition sites had particularly low 30-day survival (0.70, 0.62) during the decline, but had slightly higher survival than control hares did during the other years. Hares on both the predator exclosure and predator exclosure + food treatments had higher survival (corrected for hares leaving the fences) than hares not protected from predators. Each of the fenced treatments had only one year when 30-day hare survival was lower than 0.90. On the predator exclosure the lowest survival was 0.83 in 1991–1992, and on predator exclosure + food the lowest survival was 0.89 in 1992–1993. In both cases, these were the years with the greatest decline rate. Hares on control sites had 30-day survival rates higher than 0.90 in only 2 years (1988–1989, 1995–1996), both of which were years of population increase.

Preweaning survival rates of leverets until 30 days varied among litter groups, among years, and among treatments (table 8.4). In most years on control areas, leverets born in the second litter of the year had lower survival than leverets born in other litters. Survival was low and variable at peak hare densities, lowest during the decline, and high during the increase phase. Survival rates did not differ between control and food addition areas, except in 1995 when survival was 12–44% lower on the food addition grids. In 1992, a decline year, none of the radio-tagged leverets on control areas survived. In contrast, leverets on the predator exclosure + food grid had survival rates of 0.21–0.43 in this year, which are still low compared with the survival rates observed during the increase phase on control sites (0.37–0.71). Throughout the cycle, of the leverets that were killed, 70% died in their first week of life and 23% in the second week.

Postweaning juvenile survival was measured in one year (1995–1996) of the increase phase (Gillis 1999). Juveniles born in the first two litters had survival rates similar to adults, but juveniles born in the third and fourth litters had poorer survival (table 8.5). During this year, food addition had no statistically noticeable effect on juvenile survival.

Table 8.3 Parturition data for snowshoe hares.

	Control							
	1988	1989	1990	1991	1992	1994	1995	1996
Mean Birth Date								
Litter 1	24 May ± 0.6	25 May ± 0.7	24 May ± 0.6	29 May ± 1.1	31 May ± 3.0	12 May ± 0.8	22 May ± 2.4	22 May ± 0.7
	(6)	(8)	(14)	(7)	(6)	(11)	(6)	(12)
Litter 2	30 June	2 Jul ± 0.9	26 Jun ± 0.7	6 Jul ± 0.7	6 Jul ± 4.5	18 Jun ± 1.0	20 Jun ± 1.3	27 Jun ± 0.9
	(1)	(13)	(27)	(11)	(2)	(9)	(9)	(14)
Litter 3	30 Aug ± 2.0	7 Aug ± 1.3	31 Jul ± 0.4)	—	—	25 Jul ± 1.2	28 Jul ± 1.4	2 Aug ± 0.6
	(3)	(7)	(19)			(10)	(8)	(13)
Range of Birth Date								
Litter 1	23 May–27 May	23 May–29 May	20 May–29 May	27 May–3 Jun	29 May–11 Jun	9 May–17 May	16 May–2 Jun	19 May–28 May
Litter 2	30 June	26 Jun–7 Jul	21 Jun–5 Jul	2 Jul–9 Jul	26 Jun–11 Jul	14 Jun–24 Jun	13 Jun–27 Jun	22 Jun–4 Jul
Litter 3	30 Jul–5 Aug	2 Aug–13 Aug	28 Jul–5 Aug	—	—	20 Jul–2 Aug	28 Jul–2 Aug	30 Jul–5 Aug
Pregnancy Rate %								
Litter 1	—	93.8 (32)	89.4 (67)	100 (7)	77 (9)	100 (14)	100 (17)	100 (29)
Litter 2	—	96.8 (31)	96.2 (52)	85 (13)	100 (9)	100 (8)	100 (17)	100 (21)
Litter 3	—	82.4 (34)	86.4 (50)	0 (13)	0[a]	100 (8)	100 (12)	100 (27)
Stillborn Rate								
Litter 1	—	0 (29)	7.3 (55)	0 (20)	0 (13)	3.1 (32)	0 (17)	0 (40)
Litter 2	—	7.7 (78)	4.5 (156)	30.4 (46)	0 (6)	0 (48)	1.6 (62)	6.3 (80)
Litter 3	—	6.3 (32)	13.6 (81)	—	—	4.7 (64)	8.9 (45)	1.3 (79)
Litter Size								
Litter 1	4.3 ± 0.21 (6)	3.6 ± 0.3 (8)	3.9 ± 0.2 (14)	3.3 ± 0.4 (7)	3.2 ± 0.2 (6)	3.2 ± 0.3 (11)	3.0 ± 0.5 (6)	3.6 ± 0.3 (12)
Litter 2	5 (1)	6.0 ± 0.4 (13)	5.8 ± 0.3 (27)	4.2 ± 0.6 (11)	4.5 ± 1.5 (2)	5.9 ± 0.4 (10)	6.9 ± 0.5 (9)	5.8 ± 0.3 (14)
Litter 3	6.0 ± 0 (3)	4.4 ± 0.4 (7)	4.3 ± 0.3 (19)	—	—	6.4 ± 0.3 (11)	5.6 ± 0.6 (8)	6.1 ± 0.5 (13)
% Females								
Litter 1	46.2 (26)	42.1 (19)	53.2 (47)	68.8 (16)	50.0 (12)	42.4 (33)	55.6 (18)	51.2 (41)
Litter 2	40.0 (5)	54.2 (72)	56.9 (144)	63.0 (46)	50.0 (6)	44.2 (52)	51.6 (62)	44.4 (81)
Litter 3	33.0 (18)	53.3 (30)	45.7 (70)	—	—	37.5 (64)	48.9 (45)	50.6 (79)

(*continued*)

Table 8.3 (*Continued*) Parturition data for hares on food and predator exclosure + food treatments.

	Food			*Predator Exclosure + Food*	
	1989	1990	1995	1991	1992
Mean Birth Date					
Litter 1	20 May ± 0.6 (8)	20 May ± 0.5 (26)	10 May ± 1.5 (6)	—	21 May ± 0.5 (15)
Litter 2	23 Jun ± 0.6 (17)	24 Jun ± 0.8 (28)	10 Jun ± 1.7 (5)	28 Jun ± 1.0 (9)	27 Jun ± 0.4 (18)
Litter 3	31 Jul ± 0.8 (15)	26 Jul ± 0.7 (22)	20 Jul ± 0.6 (5)	5 Aug ± 0.4 (6)	2 Aug ± 0.4 (19)
Range of Birth Date					
Litter 1	19 May–23 May	17 May–25 May	6 May–15 May	—	16 May–24 May
Litter 2	20 Jun–28 Jun	19 Jun–2 Jul	5 Jun–15 Jun	24 Jun–3 Jul	25 Jun–30 Jun
Litter 3	21 Jul–2 Aug	21 Jul–2 Aug	18 Jul–28 Jul	4 Aug–6 Aug	31 Jul–6 Aug
Pregnancy Rate %					
Litter 1	91.8 (73)	99.2 (119)	100 (27)	92.8[b]	92.8[b]
Litter 2	100 (67)	97.0 (67)	100 (19)	97.5[b]	97.5[b]
Litter 3	96.6 (58)	87.0 (77)	100 (15)	88.1[b]	88.1[b]
Stillborn Rate					
Litter 1	3.6 (28)	13.6 (86)	0 (25)	—	0 (55)
Litter 2	6.2 (114)	9.6 (135)	14.6 (41)	5.7 (70)	9.1 (132)
Litter 3	44.6 (72)	23.5 (119)	11.8 (34)	0 (28)	5.4 (111)
Litter size					
Litter 1	3.8 ± 0.4 (9)	3.7 ± 0.1 (26)	4.2 ± 0.4 (6)	—	4.1 ± 0.3 (15)
Litter 2	6.3 ± 0.5 (18)	6.1 ± 0.3 (27)	7.2 ± 0.4 (6)	7.8 ± 0.4 (9)	7.5 ± 0.3 (20)
Litter 3	4.8 ± 0.4 (16)	5.6 ± 0.2 (23)	5.7 ± 0.9 (6)	4.7 ± 0.6 (6)	5.9 ± 0.4 (20)
% Females					
Litter 1	47.6 (21)	56.8 (74)	56.0 (25)	—	37.0 (54)
Litter 2	57.4 (94)	43.8 (121)	50.0 (40)	50.7 (69)	50.4 (129)
Litter 3	62.5 (40)	49.5 (93)	46.9 (32)	66.7 (27)	51.4 (109)

Sample sizes are in parentheses. For stillborn rate and percent females, the sample sizes are numbers of leverets. For all others, sample sizes are numbers of adult females. Means are ± 1 SE.

[a] Although trapping data were not available for this litter, no third litter juveniles were captured later in the season.

[b] Pregnancy rates were not measured directly; these values were estimated from values for hares on food and control sites in 1989 and 1990 and used to calculate reproductive output in these years. Pregnancy rates were similarly estimated for control sites in 1988.

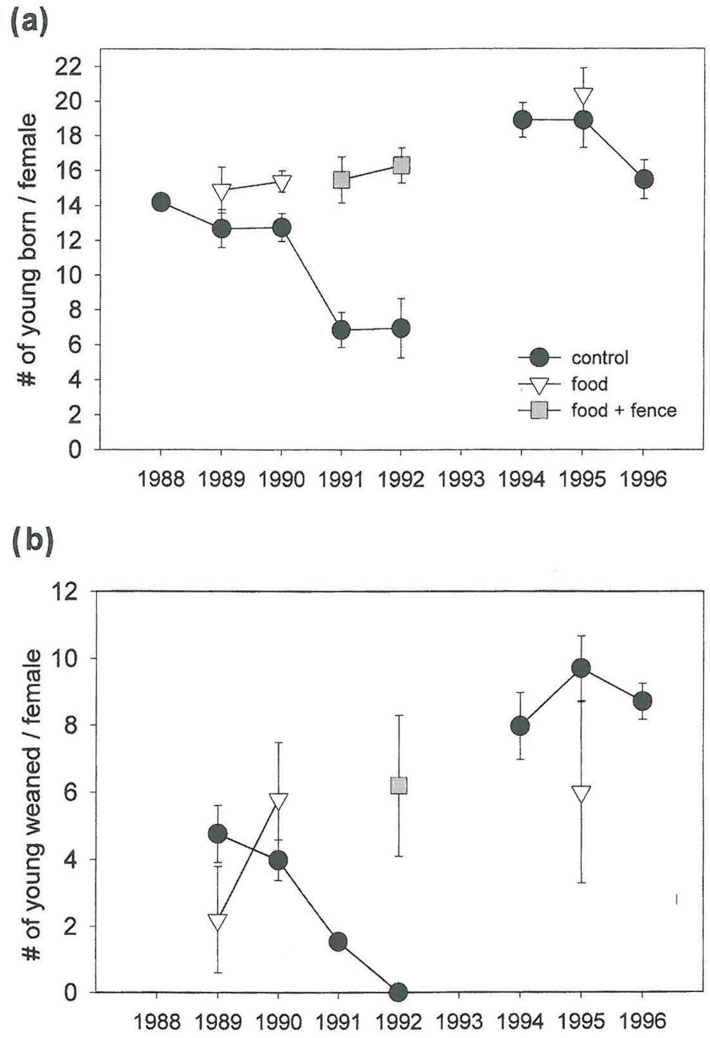

Figure 8.5 Snowshoe hare reproductive output and recruitment through the cycle. (a) Values are total young per female per summer, calculated from pregnancy rates and mean litter size per litter group. Litter 4 pregnancy rates and litter sizes for 1994 and 1995 were estimated based on values for last litters in other years, because the fourth litter was not measured directly. Pregnancy rates for control hares in 1988 and predator exclosure + food hares in 1991 and 1992 were based on averages for hares in 1989 and 1990 (see table 8.3). Standard errors were calculated from litter sizes. (b) Recruitment to 30 days. Values are calculated from reproductive output and survival to 30 days. For the food-addition grids in 1989, there was no survival estimate for litter 1, so we used the conservative value of survival of the second litter (0.15). This value is conservative because in most years hares in the second litters had lower survival than hares in first litters.

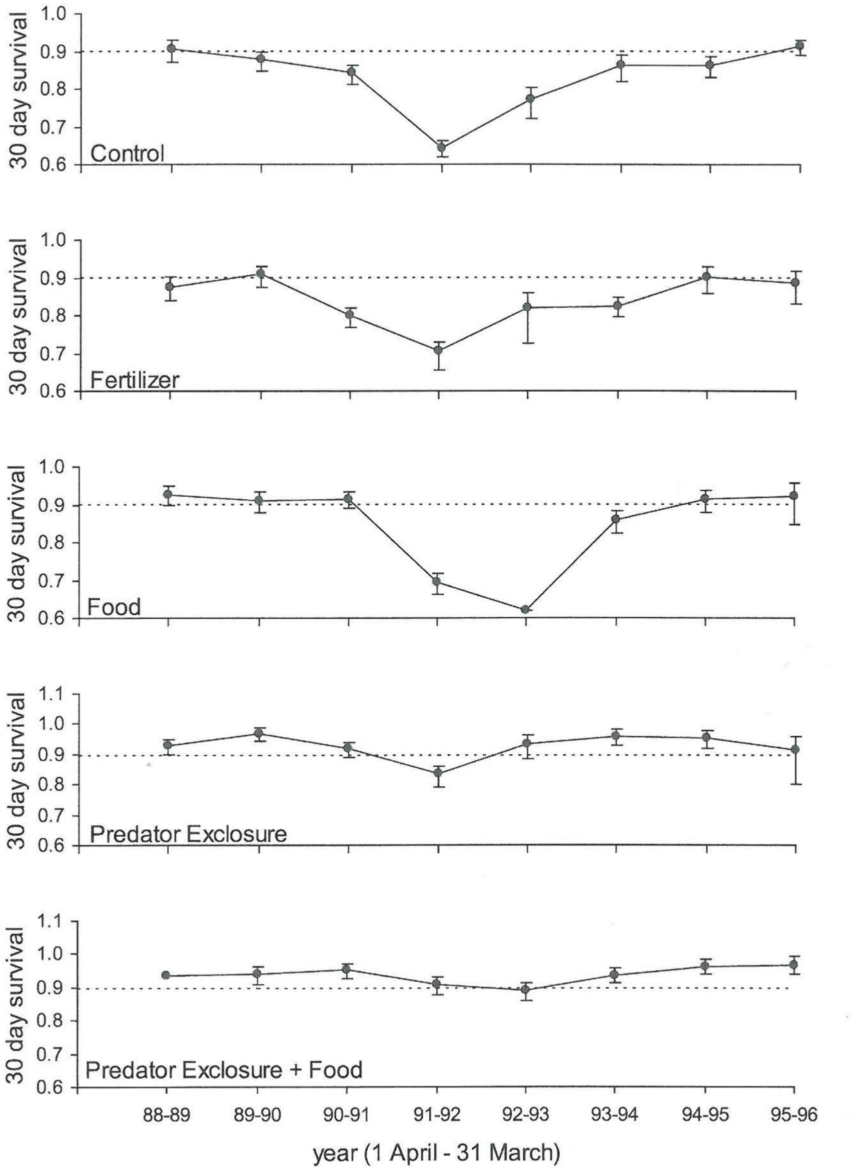

Figure 8.6 Adult snowshoe hare survival. Values are 30-day survival and 95% CLs (based on Pollock et al. 1989, equation 3); the line at 0.90 is given for comparison between treatments. A 30-day survival of 0.90 corresponds to an annual survival rate of 27.8%. Survival estimates were calculated from 1 April through 31 March. The point for fertilizer grids in 1995–1996 is based on the period 1 April to 29 February, since many radio collars were removed in the spring trapping census, making March survival estimates suspect. The 1995–1996 estimate for predator exclosure + food is based on the period 1 April–8 November, since a coyote inside the fence inflicted heavy mortality thereafter. Within each year, sample sizes were 42–168 hares (control), 26–131 (fertilizer), 44–114 (food), 25–113 (predator exclosure), and 35–94 (predator exclosure).

Table 8.4 Preweaning survival of snowshoe hares.

	1989	1990	1991	1992	1994	1995	1996
Control							
Litter 1	0.73 ± 0.13 (12)	0.27 ± 0.13 (11)	0.47 ± 0.12 (17)	0 (9)	0.50 ± 0.22 (27)	0.71 ± 0.11 (19)	0.61 ± 0.08 (39)
Litter 2	0.22 ± 0.09 (23)	0.13 ± 0.05 (41)	0 (21)	0 (4)	0.37 ± 0.08 (46)	0.61 ± 0.07 (49)	0.54 ± 0.06 (66)
Litter 3	0.18 ± 0.12 (11)	0.51 ± 0.11 (24)	—	—	0.66 ± 0.07 (50)	0.60 ± 0.09 (31)	0.56 ± 0.07 (61)
Food							
Litter 1	—	0.45 ± 0.10 (31)				0.49 ± 0.15 (14)	
Litter 2	0.15 ± 0.07 (28)	0.15 ± 0.07 (33)				0.17 ± 0.08 (22)	
Litter 3	0.15 ± 0.13 (15)	0.57 ± 0.11 (27)				0.48 ± 0.10 (28)	
Predator Exclosure + Food							
Litter 1				0.21 ± 0.11 (26)			
Litter 2				0.37 ± 0.09 (39)			
Litter 3				0.43 ± 0.09 (36)			

Kaplan-Meier techniques were used to estimate survival (± SE) of radio-tagged leverets from birth until 30 days old; hares were typically weaned between 4 and 5 weeks of age. The numbers of hares monitored are given in parentheses.

Table 8.5 Survival rates of postweaning juvenile hares.

	Control			*Food*		
	n	30-Day Survival	95% CL[a]	*n*	30-Day Survival	95% CL
Litter 1	16	0.93	0.86–0.97	8	0.85	0.00–0.94
Litter 2	13	0.95	0.88–0.99	9	0.94	0.84–0.99
Litter 3	18	0.78	0.00–0.86	10	0.89	0.00–0.98
Litter 4	4	0.41	0.00–0.89	8	0.75	0.00–0.87

These data were collected from radio-tagged animals in 1995–1996, during the population increase. Survival is estimated by the Kaplan-Meier estimator.

[a] We calculated 95% confidence limits using Greenwood's standard error (Pollock et al. 1989).

Simple Leslie matrix models of the demography of the cycle indicate that 30-day survival rates of postweaning hares must be above ~0.90 for the population to increase (figure 8.7). Above that survival rate, preweaning juvenile recruitment (number of leverets surviving to 30 days per female per year) has a strong impact on the rate of increase, but it seems that survival of hares >28 days old is the critical parameter for determining

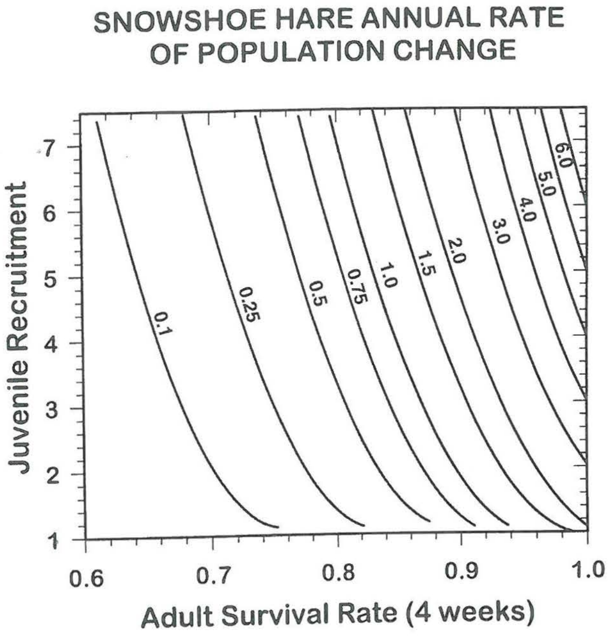

Figure 8.7 The impact of survival and recruitment on the annual rate of population change. The survival axis is 28-day survival of hares older than 30 days (i.e., postweaning juvenile and adult survival combined). Juvenile recruitment is measured as number of leverets alive at 30 days per mother per year. The rates of population increase were calculated using a simple Leslie matrix model, and they indicate that population growth basically occurs only when monthly survival is >0.90.

whether populations will increase or decline. This interpretation is supported by a recent analysis of the 1995–1996 increase data, which suggests that the numeric changes in the cycle predominantly result from changes in juvenile and adult survival, followed by leveret survival and reproductive output (Haydon et al. 1999).

8.3.5 Causes of Death

In most years, >90% of the adult snowshoe hares that died were killed by predators (table 8.6). On control areas, some hares died of nonpredation causes (e.g., starvation, injury) during the peak and decline years, but no control hares died of nonpredation causes during the low phase. Similar patterns of predation mortality were observed on all other treatments except predator exclosure + food; this treatment had some nonpredation deaths in all years except one year of the low phase, and the predation deaths are consequently 5–10% lower than on control sites. The fences were permeable to hares; throughout the cycle, 31.2% of radio-collared predator exclosure hares and 35.4% of predator exclosure + food hares died outside the fences. We excluded these deaths in calculating survival rates and causes of death for these treatments.

Mammalian predators, mainly coyotes and lynx, were responsible for 65–75% of the predator-caused deaths of adult hares on unfenced treatments (figure 8.8), whereas raptors, mainly great horned owls and goshawks, killed 70–80% of the predator-killed hares inside the fences. Although about 15% of deaths were identifiable only as predation and another 15% were completely unknown as to the cause of death, we expect that the causes of these deaths were distributed in a similar fashion. It is possible that great horned owl kills were less likely to be identified than were kills by other predators because owl kills have fewer diagnostic characteristics. Across all treatments and all years, only 18 kills were positively identified as due to other predators: 4 hares were killed by wolves, 2 by marten, 2 by wolverine, 2 by weasels, 1 by a bald eagle, 1 by a Harlan's hawk, and 6 by hawk owls. Five of the 6 hawk owl deaths occurred in February and March 1991 on control 1. Additionally, the fences were not completely effective at keeping out mammalian predators; over all the years 12.4% and 7.8% of deaths of radio-collared hares on predator exclosure and predator exclosure + food, respectively, were due to lynx before the lynx left the fences. The predator exclosure + food treatment had a coyote for about 3 months during winter 1995–1996, and more than half of the hare deaths on this treatment in the entire year were due to this one animal.

Adult hares on control sites had seasonal sources of mortality (figure 8.9). Most of the coyote kills (65%) were in October and November, and of these, 55% were cached whole rather than eaten immediately. Lynx, goshawks, and great horned owls made 70–75% of their kills of adult hares between December and May. Most hares (56%) that died of nonpredation causes died in February and March; <20% of nonpredation deaths occurred between June and November. These patterns may be slightly biased because 51% of the hares for which we could not identify a cause of death died during the summer. This bias is unlikely to be large, because only 26% of hares died during the summer, and we successfully identified the cause of death for 34% of these hares.

Like adults, postweaning juvenile hares mainly died of predation (table 8.7). On control sites, mammalian predators killed more juveniles than did raptors (12 and 3, respectively), and no nonpredation deaths were observed. On food sites, mammalian predators

Table 8.6 Causes of deaths of adult snowshoe hares.

	Deaths from known predators				*Deaths from all causes*						
Grid/Year	Coyote	Lynx	Goshawk	Owl	Mammal	Raptor	Unidentified predator	Nonpredation	Unknown	% Predation	No. Dead
Control											
1988–1989	16.7	0	11.1	0	22.2	27.8	11.1	22.2	16.7	73.3	18
1989–1990	19.4	9.7	9.7	3.2	29.0	16.1	16.1	9.7	29.0	86.4	31
1990–1991	4.3	10.0	14.3	11.4	15.7	42.9	7.1	11.4	22.9	85.2	70
1991–1992	43.3	14.2	3.9	10.2	58.3	17.3	9.5	0	15.0	100.0	127
1992–1993	13.9	19.4	11.1	8.3	41.7	22.2	13.9	0	22.2	100.0	36
1993–1994	42.1	15.8	5.3	0	57.9	10.5	5.3	0	26.3	100.0	19
1994–1995	40.8	6.1	8.2	2.0	55.1	14.3	16.3	0	14.3	100.0	49
1995–1996	22.5	15.0	12.5	5.0	50.0	22.5	12.5	2.5	12.5	97.1	40
Fertilizer											
1988–1989	0	15.8	5.3	5.3	15.8	26.3	26.3	5.3	26.3	92.9	19
1989–1990	8.3	8.3	4.2	4.2	33.3	16.7	29.2	0	20.8	100.0	24
1990–1991	8.3	30.6	22.2	12.5	41.7	38.9	5.6	6.9	6.9	92.5	72
1991–1992	22.9	20.0	4.3	8.6	55.7	14.3	14.3	1.4	14.3	98.5	70
1992–1993	7.7	30.8	15.4	0	38.5	15.4	23.1	0	23.1	100.0	13
1993–1994	22.2	11.1	11.1	22.2	33.3	33.3	0	0	33.3	100.0	9
1994–1995	6.3	6.3	6.3	6.3	18.8	12.5	37.5	0	31.3	100.0	16
1995–1996	11.1	27.8	0	0	44.4	11.1	11.1	5.6	27.8	92.3	18
Food											
1988–1989	16.7	8.3	0	8.3	33.3	8.3	16.7	8.3	33.3	87.5	12
1989–1990	4.5	0	4.5	4.5	18.2	31.8	31.8	4.6	13.6	94.7	22

(continued)

Table 8.6 (*Continued*)

Grid/Year	Deaths from known predators: Coyote	Lynx	Goshawk	Owl	Deaths from all causes: Mammal	Raptor	Unidentified predator	Nonpredation	Unknown	% Predation	No. Dead
1990–1991	24.2	15.2	9.1	9.1	45.5	18.2	15.2	3.0	18.2	96.3	33
1991–1992	26.4	12.5	12.5	1.4	48.6	13.9	15.3	1.4	20.8	98.2	72
1992–1993	28.6	14.3	3.6	7.1	50.0	10.7	21.4	3.6	14.3	95.8	28
1993–1994	38.7	22.6	3.2	3.2	61.3	6.5	16.1	0	16.1	100.0	31
1994–1995	17.6	29.4	0	0	52.9	0	11.8	0	35.3	100.0	17
1995–1996	10.0	30.0	10.0	0	45.0	10.0	25.0	0	20.0	100.0	20
Predator exclosure[a]											
1988–1989	0	21.4	0	0	21.4	0	35.7	7.1	35.7	88.9	14
1989–1990	0	11.1	11.1	22.2	11.1	33.3	22.2	11.1	22.2	85.7	9
1990–1991	0	7.4	14.8	14.8	7.4	59.3	11.1	3.7	18.5	95.5	27
1991–1992	0	17.0	13.2	39.6	17.0	56.6	7.6	7.6	11.3	91.5	53
1992–1993	0	20.0	20.0	20.0	20.0	70.0	10.0	0	0	100.0	10
1993–1994	0	0	20.0	60.0	0	80.0	0	0	20.0	100.0	5
1994–1995	0	0	12.5	50.0	12.5	62.5	25	0	0	100.0	8
1995–1996	0	0	27.3	9.1	0	45.5	36.4	9.1	9.1	90.0	11
Predator Exclosure + Food[a]											
1988–1989	0	30.0	0	0	30.0	0	50.0	10.0	10.0	88.9	10
1989–1990	0	15.4	0	0	23.1	15.4	15.4	7.7	38.5	87.5	13
1990–1991	0	7.1	35.7	0	7.1	57.1	14.3	14.3	7.1	84.6	14
1991–1992	0	9.7	32.3	9.7	9.7	51.6	16.1	9.7	12.9	88.9	31
1992–1993	0	6.9	13.8	20.7	6.9	62.1	17.2	6.9	6.9	92.6	29
1993–1994	0	0	17.6	11.8	0	52.9	23.5	5.9	17.7	92.9	17
1994–1995	0	9.1	18.2	27.3	9.1	72.7	9.1	0	9.1	100.0	11
1995–1996	53.6	0	3.6	0	53.6	10.7	14.3	14.3	7.1	84.6	28

Each time span includes deaths from 1 April through 31 March. Values are percentages of hares dead of each cause. "Owl" refers to great horned owls. Hares killed by marten, weasels, wolves, eagles, hawk-owls, and Harlan's hawks are included in the "mammal" and "raptor" categories as appropriate. Percent predation is calculated out of deaths for which cause of death was positively determined (i.e., excluding "unknown" deaths).

[a] On several occasions, mammalian predators were inside the fences for time periods of hours to days. Lynx were the most common.

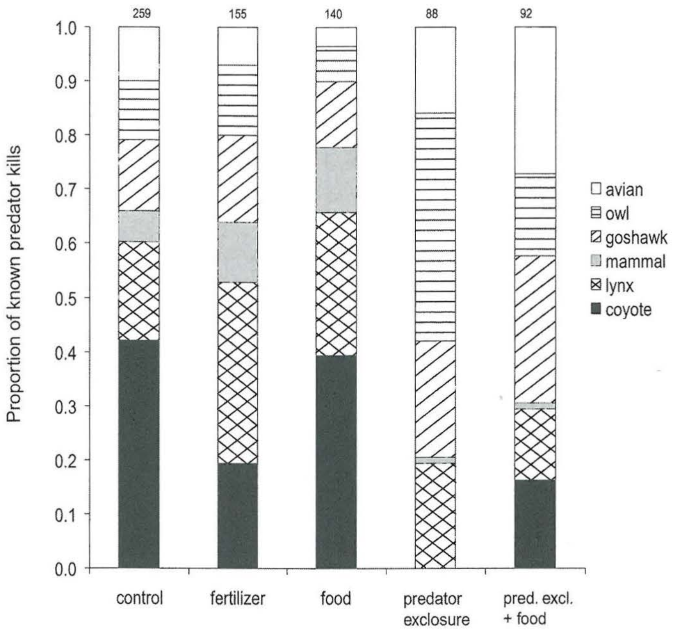

Figure 8.8 Predation deaths of adult snowshoe hares. All predator-caused deaths from 1 April 1988 to 31 March 1996 are included. Sample sizes for each treatment are at the top of each bar. *Avian* kills include kills made by bald eagles, hawk owls, and Harlan's hawks, plus hares killed by a raptor but for which the species of raptor could not be determined. *Mammal* kills include kills made by martens, weasels, wolverines, and wolves, plus kills for which the species of mammalian predator could not be determined. The mammalian kills on the two fenced grids are due to individual lynx and coyote that were inside the fences.

and raptors killed 7 and 6 juveniles, respectively, and 2 hares died of natural nonpredation causes. Juvenile mortality patterns were also seasonal, with most of the kills by raptors and coyotes occurring before November (Gillis 1999).

Leverets were killed by a different suite of predators (table 8.8). We observed no lynx or coyote kills of leverets. Red and ground squirrels were responsible for up to a third of leveret mortalities on control areas and food addition sites. On the predator exclosure + food grid during the decline, great horned owls and ground squirrels were the main predators (each responsible for 13% of all deaths), and we suspect that the high loss rate of leverets (27%) was due to great horned owls or other raptors carrying the animals off the grid and out of telemetry range. Most nonpredation deaths (abandoned/exposed) of leverets occurred during the decline phase (84% and 25% of deaths in 1991 and 1992, respectively; the next highest proportion of non-predation deaths on control areas was 3% in 1995).

Habitat structure and spatial patterning of predators affected the kill patterns that we observed. Coyotes hunted more frequently at either end of the Shakwak Trench than in the middle, affecting the kill patterns of adult snowshoe hares. The predator exclosure + food treatment had less dense spruce cover, scattered old trees, and exceptionally high densities of ground squirrels but comparatively low densities of red squirrels. For the lev-

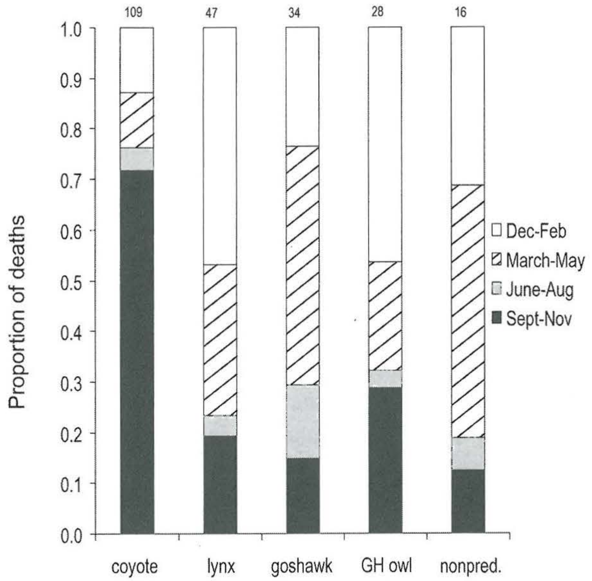

Figure 8.9 Seasonality of hare mortalities. Each bar indicates all the deaths of control hares for which cause of death could be determined for the period 1 April 1988 to 31 March 1996. Sample sizes for each mortality type are given above the bars.

Table 8.7 Causes of mortality for postweaning juvenile hares.

Cause of Death	Control	Food
Lynx	23.1 (6)	11.8 (2)
Coyote	7.7 (2)	23.5 (4)
Great horned owl	0 (0)	11.8 (2)
Goshawk	11.5 (3)	11.8 (2)
Unidentified mammal	15.4 (4)	5.9 (1)
Unidentified raptor	0 (0)	11.8 (2)
Unidentified predator	26.9 (7)	11.8 (2)
Total predation	84.6 (22)	88.2 (15)
Nonpredation	0 (0)	11.8 (2)
Unknown	15.4 (4)	0 (0)
No. of mortalities	26	18[a]
No. radio collared	49	35

These data were collected from radio-collared animals in 1995–1996, during the population increase. Animals were radio collared shortly after weaning and monitored until the following spring. Causes of mortality are presented as percentages of total deaths.

[a] One hare killed by a hunter was excluded from the analyses; percentages are based on 17 mortalities.

Table 8.8 Causes of deaths of leverets.

Cause of Death	Control							Food			Predator Exclosure + Food
	1989	1990	1991	1992	1994	1995	1996	1989	1990	1995	1992
Red squirrel	20.0 (6)	20.4 (11)	4.0 (1)	12.5 (1)	35.6 (16)	14.3 (5)	30.5 (22)	15.6 (5)	23.1 (12)	0 (0)	3.7 (2)
Arctic ground squirrel	13.4 (4)	13.0 (7)	0 (0)	0 (0)	0 (0)	17.1 (6)	8.5 (6)	9.4 (3)	7.7 (4)	15.4 (6)	13.0 (7)
Short-tailed weasel	0 (0)	0 (0)	0 (0)	0 (0)	20.0 (9)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Unidentified small mammal	0 (0)	0 (0)	0 (0)	25.0 (2)	6.7 (3)	5.7 (2)	6.9 (5)	0 (0)	0 (0)	5.1 (2)	3.7 (2)
Great horned owl	3.3 (1)	0 (0)	0 (0)	0 (0)	2.2 (1)	20.0 (7)	0 (0)	0 (0)	1.9 (1)	18.0 (7)	13.0 (7)
Goshawk	3.3 (1)	5.6 (3)	0 (0)	0 (0)	0 (0)	2.9 (1)	5.6 (4)	0 (0)	3.8 (2)	5.1 (2)	1.8 (1)
Boreal owl	0 (0)	0 (0)	0 (0)	0 (0)	6.7 (3)	0 (0)	1.4 (1)	0 (0)	0 (0)	0 (0)	0 (0)
Harlan's hawk	0 (0)	0 (0)	0 (0)	0 (0)	2.2 (1)	0 (0)	0 (0)	3.1 (1)	0 (0)	0 (0)	0 (0)
American kestrel	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.8 (1)
Unidentified raptor	0 (0)	0 (0)	0 (0)	12.5 (1)	13.3 (6)	2.9 (1)	4.2 (3)	0 (0)	0 (0)	12.8 (5)	18.5 (10)
Carcass or radio in tree	40.0 (12)	27.8 (15)	0 (0)	0 (0)	4.4 (2)	22.8 (8)	26.3 (19)	34.4 (11)	15.4 (8)	12.8 (5)	18.5 (10)
Unidentified predator	0 (0)	25.9 (14)	12.0 (3)	12.5 (1)	0 (0)	5.7 (2)	4.2 (3)	12.5 (4)	23.1 (12)	20.5 (8)	24.2 (13)
Total predation	80.0 (24)	92.6 (50)	16.0 (4)	62.5 (5)	91.1 (41)	91.4 (32)	87.6 (63)	75.0 (24)	75.0 (39)	89.7 (35)	98.2 (53)
Unknown	20.0 (6)	5.6 (3)	0 (0)	12.5 (1)	8.9 (4)	5.7 (2)	9.6 (7)	25.0 (8)	23.1 (12)	0 (0)	0 (0)
Abandoned/exposure	0 (0)	1.8 (1)	84.0 (21)	25.0 (2)	0 (0)	2.9 (1)	2.8 (2)	0 (0)	1.9 (1)	10.3 (4)	1.8 (1)
No. lost	4	4	8	1	15	11	10	6	10	9	27
No. of mortalities	30	54	25	8	45	35	72	32	52	39	55
No. radio tagged	46	76	38	13	123	99	166	42	93	64	101

The values are percentages of all mortalities of hares from birth until 30 days old. "Unidentified small mammal" deaths are deaths due to red squirrels, ground squirrels, or weasels, but for which the exact predator could not be determined. These data summarize kills for litters 1–3 in each year, except for 1991 and 1992, when hares had only two litters. Many of the "carcass or radio in tree" cases are probably due to red squirrel predation.

erets on this treatment, the low amount of red squirrel predation is probably due to this spatial pattern. Similarly, the nesting locations of raptors may have affected their contribution to hare mortality patterns. Of the raptorial kills of leverets that we observed, goshawk kills occurred only on controls 3 and 4, and the great horned owl kills occurred only on the two food grids and one off-grid site (Stefan 1998).

8.3.6 Immigration and Emigration

We assessed immigration rates by calculating the proportion of hares caught on a grid for the first time in each spring trapping session (including animals that had been caught previously on other grids). This index is problematic because it does not allow us to differentiate among resident hares from the area that were caught for the first time, hares that had immigrated since the previous autumn, and hares that were transient at the time of trapping. The food addition treatment had higher proportions of newly caught animals each spring than did all the other treatments, except during the low and increase phases when the fertilizer treatments had a higher proportion of newly caught hares (figure 8.10a). This pattern suggests that hares are attracted to the food. The fenced treatments had lower proportions of newly caught hares, possibly indicating that the fence or the relatively high hare densities within the fences acted as a deterrent to immigration.

Emigration was also difficult to assess because the experiment was not set up to study dispersal. As a very crude index, we consider the proportion of hares caught during only one trapping session. Hares on food addition areas were less likely to be caught multiple times than were hares on other treatments (figure 8.10b). On control sites, 54% of hares were caught in only one session, compared with 66% of the hares on food addition sites.

For the two fenced treatments, we could use one additional assessment of emigration: the proportion of radio-collared hares dying outside the fences. A greater proportion of hares left the fences as densities declined (figure 8.10c). This pattern could indicate two things—that more hares dispersed during this period, or that hares whose home ranges included both sides of the fence were more likely to be killed outside the fence during the decline phase. During the low phase, many of the animals that were later located outside fences had clearly left home ranges inside the fences (K. E. Hodges, unpublished data), which suggests that the decline pattern may similarly be due to dispersal. Furthermore, on the predator exclosure, the population decline from spring 1995 to spring 1996 is partially attributable to dispersal: of 19 hares that were radio collared in autumn 1995, 4 went through the fence (2 were trapped elsewhere, 2 died), and 3 hares moved from the trapping grid to a far corner of the entire fenced area; 7 radio-collared hares died on the trapping grid during the same period.

8.4 Impacts of Experimental Treatments

All treatments increased hare densities, although the effect of fertilization was minimal in relation to the large effects fertilization had on plant growth (see chapters 5 and 6). Food addition and excluding predators had their largest impacts during the decline with 3.8-fold and 2.4-fold increases in density, respectively. The simultaneous manipulation of predator exclosure + food also had the largest impact during the decline, with densities 14.4-fold higher than control densities. These treatment patterns are also observed when

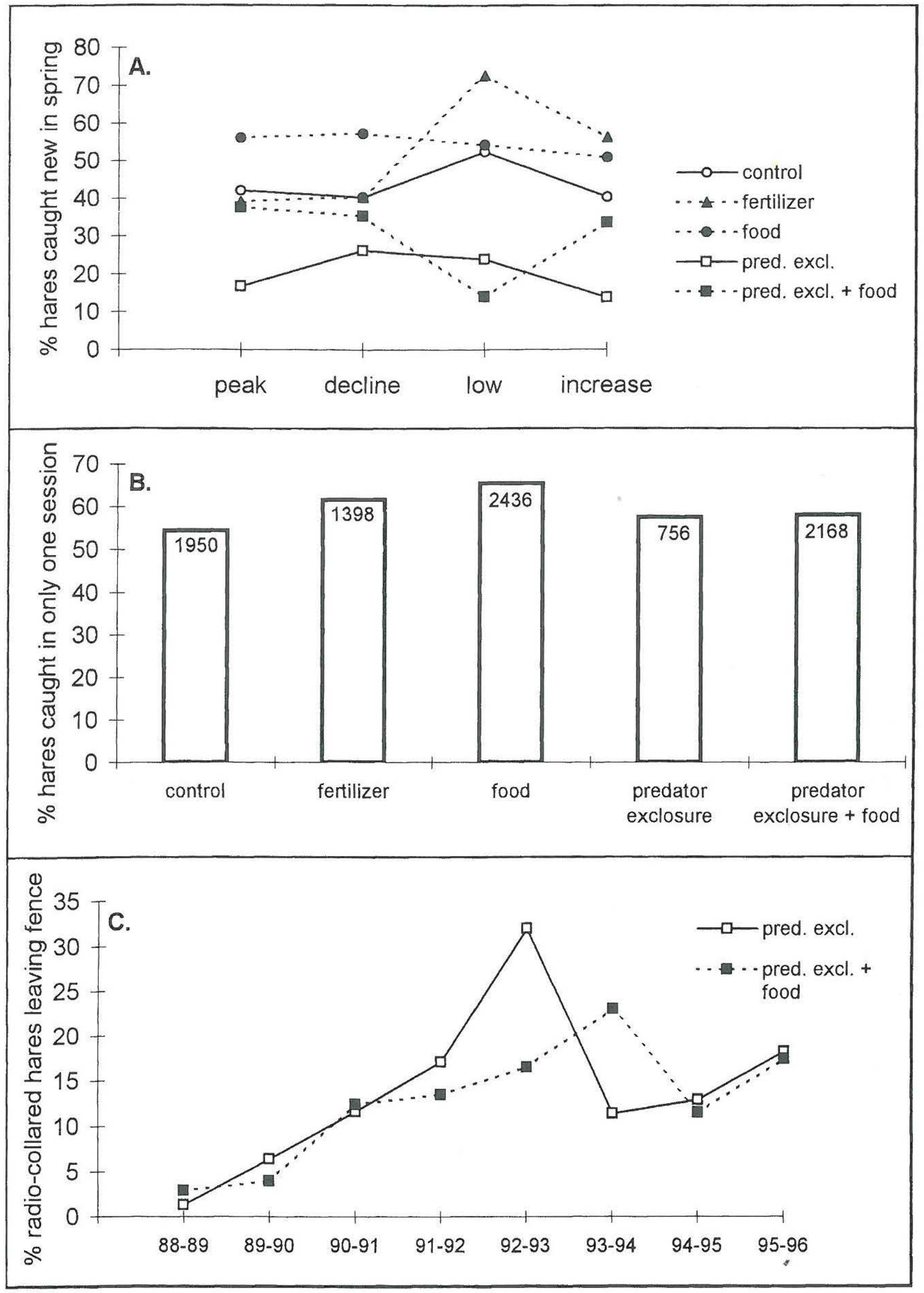

Figure 8.10 Indices of immigration and emigration of snowshoe hares. (A) Immigration, indexed as the proportion of hares caught each spring that were not previously captured on that grid. Proportions therefore include new hares and hares previously caught elsewhere. The increase phase includes the years 1994–1996; the trapping history was not deemed adequate to assess immigration during the first period of increase. (B) Proportion of hares caught during only one trapping session. The number of individual hares caught on each treatment are given in the bars. (C) Percentage of radio-collared hares leaving the fences within each year, 1 April–31 March. Through the entire cycle 31.2% or 62/199 hares left the predator exclosure, and 35.4% or 84/237 hares left the predator exclosure + food area. In the figure, the percentages are lower because the values are calculated as (*n* dead outside)/(*n* radio collared per year), and many radio-collared hares lived more than one year.

impacts are integrated across the entire cycle or examined in the other phases (CD-ROM frame 52).

This large impact indicates that food and predation interact in their effects on hare densities, because this magnitude is higher than the combined effects shown from the single-factor manipulations. The one caveat is that the manipulations were established during the increase phase, and hence for each phase the treatments had been in effect for a different length of time. The relative densities in each phase may therefore partly result from the length of time that each manipulation had been imposed.

The population rates of change also suggest that food and predation interacted in their impacts on hares. Hares on control areas, the fertilizer treatments, and predator exclosure had 2 years of severe decline and an additional 1 or 2 years of mild decline, whereas hares on food areas had only 2 years of severe decline. The hare population on predator exclosure + food had 2 years of mild decline, followed by only 1 year of severe decline. These patterns suggest that the predator exclosure + food manipulation altered the timing and pattern of the cycle, in addition to affecting hare densities throughout.

Clearly, the numeric changes are composed of the changes in reproduction, survival, and dispersal that occur during the cycle (table 8.9). Of these, juvenile survival, adult survival, and reproductive output are thought to be the major parameters contributing to cyclic numeric changes, both because of the sensitivity of the rate of increase to changes in these rates (figure 8.7; Haydon et al. 1999) and because of the observed magnitude of change in each of these parameters (Krebs et al. 1996, Stefan 1998). Understanding the cycle is therefore mostly an exercise in explaining why these demographic rates show the regular changes they do. Determining the effects of the experimental treatments on these parameters therefore allows a more sensitive test of cyclic mechanisms than does just looking at density and rate of population change. If an experimental manipulation changed either the magnitude or the timing of the changes in survival, reproduction, or dispersal, that would provide evidence that the factor manipulated is necessary for hare populations to cycle.

8.4.1 *Impacts on Hare Demography*

Hares on food addition sites had a total reproductive output similar to that of control hares, even though the onset of reproduction was slightly earlier in some years. Stillborn rates were higher for hares on food addition sites, which compensated for slightly higher litter sizes. Food addition did not improve the survival of leverets or juvenile hares, but adult hares on food addition sites survived slightly better than hares on control sites in peak years and slightly worse in decline years. Most of the increase in density on food addition sites relative to control areas resulted from movement of hares onto food sites, rather than from reproductive and survival rates in situ (see also Boutin 1984, Krebs et al. 1986b). Fertilization resulted in increased densities of natural food but did not change patterns of hare survival or rates of increase; there were small positive effects on hare density.

Hares inside the predator exclosure had higher survival rates than hares on control sites, but the cyclic patterns of change in survival and in density still manifested themselves. Unfortunately, we have no reproductive information for this treatment, but we suspect that reproduction on this treatment was similar to that on control areas. The predator exclosure treatment showed patterns of numeric change similar to those on the control areas,

Table 8.9 Summary of the effects the experimental treatments had on snowshoe hare demography during the cycle, for 1988–1996.

	Fertilizer	Food	Predator Exclosure	Predator Exclosure + Food
Attributes of Cycle				
Peak year	1990	1991	1990	1990
Low year	1993	1993, 1994	1993	1994
Spring density (minimum/maximum amount higher than controls)	1.0–1.9	2.0–3.8	1.3–2.4	1.2–14.4
Cyclic amplitude	46.9	24.7	8.8	6.2
Survival and Causes of Death				
Adult survival	Similar	Similar/lower	Higher	Higher
Juvenile survival	ND	Same in increase[a]	ND	ND
Leveret survival	ND	Same or lower[b]	ND	Higher in decline[c]
Predation deaths of adults (%)	Similar	Similar	Similar	Lower
Reproduction and Age Structure				
Litter 1 birth date	ND	Earlier by 4–12 days[b]	ND	Earlier by ~10 days in decline[c]
Litter number	ND	Same[b]	ND	Higher by one litter in decline[c]
Litter size	ND	Same[b]	ND	Higher in decline[c]
Total annual reproduction	ND	Same[b]	ND	Higher in decline[c]
Age structure	Same	Same	Older	Older
Dispersal				
Emigration (% single captures)	Higher	Highest	Higher	Higher
Immigration (% new in spring)	Same/ higher	Higher	Lower	Lower

ND indicates the parameter was not detrimental. Values are relative to the control. Multiple values indicate the range from replicate grids. Note that reproductive attributes and juvenile survival were only measured in some years.

[a] Juvenile survival was assessed in 1995–1996.

[b] Reproductive parameters were measured on food grids in only 1989, 1990, and 1995.

[c] Reproductive parameters for predator exclosure + food were measured in 1991 and 1992 only.

whereas the predator exclosure + food treatment did not. The two fenced treatments had similar survival rates, which suggests that the different reproduction on the predator exclosure + food treatment led to the changes in the cyclic dynamics. The similar dynamics between the predator exclosure and controls therefore indicates no difference in reproductive output.

The combined manipulation of food and predators altered both the magnitude and timing of the changes in reproduction and survival. Hares on the predator exclosure + food treatment did not show the collapse in reproductive output typical of the decline phase. Survival rates were uniformly high on the predator exclosure + food treatment throughout the cycle and did not show the reduction in survival seen on the other treatments (except predator exclosure). During the decline years on control sites, hares on this treatment remained at comparatively very high densities, and many hares went through the fences. This movement appears to be partially responsible for the decline in numbers on this treatment because reproduction and survival would have maintained a higher population in the absence of emigration. The decline was also partially due to low leveret survival in 1992 because of high predation rates by great horned owls.

8.4.2 *Causation of the Hare Cycle*

Our results show that the combined manipulation of food and predators had a much stronger impact on hare dynamics than did manipulation of either factor alone. The implication is that the food–hare (Bryant 1981, Fox and Bryant 1984) and hare–predator (Trostel et al. 1987) models are inadequate explanations of hare cyclicity. Instead, explanations of the hare cycle should focus on the analysis of the interactive effects of food and predation on hare dynamics. Studies at Kluane and elsewhere have indicated several promising approaches for analyzing the interactive effects of food and predation on the hare cycle (Wolff 1980, 1981, Sievert and Keith 1985, Sovell 1993, Hik 1994, Murray et al. 1997, 1998, Boonstra et al. 1998a, Hodges 1998). These approaches focus on hare behavior and physiology, thus emphasizing the ways individual hares are affected by food and predation.

The boreal forest is a mosaic of habitat types, and it is possible that modifications in hare habitat use patterns, movements, or foraging behavior in response to predation pressure could affect their diets, nutrition, survival, and perhaps fecundity (Dolbeer and Clark 1975, Wolff 1981, Hik 1994, Hodges 1998). Additionally, predators can cause hares stress through unsuccessful chases or by causing hares to change their behavior. These stress patterns change through the cycle as the number of predators varies, and the stress patterns lead to a number of physiological changes that might affect fecundity of hares or, through maternal effects, survival of the leverets (Boonstra et al. 1998a,b). Finally, levels of parasite infestation vary through the cycle, and parasites may affect hare behavior and physiology, leading to changes in fecundity or survival (Sovell 1993, Sovell and Holmes 1996, Murray et al. 1997, 1998).

8.4.3 *Efficacy of the Experimental Treatments*

The reliability of our demographic results depends partly on how effectively the treatments created food-rich and predator-poor areas. Food addition was popular among the fauna: moose, grizzly bears, ground squirrels, corvids, and microtines all ate the rabbit chow. For most of the year, we succeeded in spreading enough chow that hares had constant access to it, although we cannot be certain how much chow each hare obtained. During the spring thaw (~4 weeks) and periods of rain, the chow that was available became waterlogged and unpalatable. During the thaw, we were also unable to feed as regularly as during the rest of the year, which is problematic because that may be the time of year when hares are most nutritionally stressed due to the cumulative effects of overwinter browsing, the lack of new growth, and reproduction (mating chases and pregnancy). We made more effort to keep the predator exclosure + food addition treatment regularly fed during this period. Despite these problems, hares were routinely observed eating the rabbit chow, and there is evidence that it positively affected their nutritional intake and body condition (Hik 1994, Hodges 1998, Hodges et al. 1999b).

The fences were only partially effective. Raptors still had access to hares on the predator exclosure and predator exclosure + food grids. The monofilament on predator exclosure was not very effective at protecting hares: snow and trees damaged sections of monofilament, raptors were observed hunting beneath the monofilament, hares were killed underneath the monofilament, and many hares had home ranges that extended beyond the confines of the monofilament. Furthermore, the actual fences were not completely effective at excluding terrestrial predators, and there were some mammalian kills of hares on these treatments. Additionally, hares were able to go through the fences, and roughly one in three hares originally radio collared inside the fences died outside the fences. Despite these problems, these treatments did dramatically affect the hare populations within the fences: densities, rates of population change, survival rates, and causes of death were all different from those on the control sites. We therefore conclude that although the treatments were imperfect, they still reduced predation pressure enough to consider them effective.

8.4.4 *Experimental Scale and Methodological Concerns*

Hares' movement patterns may have differentially affected our density estimates for the various treatments because it is unclear what area the traps on each grid actually sampled. Although hare home ranges average about 10 ha, home range size and degree of overlap vary through the cycle and with the experimental treatments (Allcock 1994, Hik 1994, Hodges 1998). Hares with well-defined home ranges may also undertake forays of up to 1–2 km before returning to their home ranges (Hodges 1998). On the predator exclosure + food treatment, our density estimates were potentially underestimated because hares on the predator exclosure + food treatment had small home ranges (Hik 1994, Hodges 1998), so fewer hares living near the edge of the trapping grid were likely to be caught. In contrast, the food grids appeared to attract hares, and hares that spent most of their time off the grids may have made forays onto the food grids (K. E. Hodges unpublished data; see also Boutin 1984); this movement pattern could lead to overestimates of density, as hares that were only ephemerally present might have been trapped.

Understanding patterns of dispersal would also help in the intepretation of our results. Approximately 60% of captured hares were caught during only one trapping session, and it is difficult to know whether they were residents that avoided traps or transients that lived elsewhere. Additionally, our spring trapping sessions were just before or during the breeding season, which may have amplified hares' movements. The movement patterns of hares on the two fenced sites indicates that dispersal can affect the population dynamics of areas at least 1 km^2 in size.

Our survival estimates are likely to be underestimates (Haydon et al. 1999, C. J. Krebs and W. Hochachka unpublished data). The models of hare dynamics suggest that survival must be higher for the population growth rates seen during the increase phase. Empirically, the low survival estimates for the decline phase would yield much lower hare populations than we observed. There is some suggestion that trapping hares and perhaps radio collaring hares both affect survival negatively (C. J. Krebs and W. Hochachka unpublished data). Hare survival estimates from trapping data are much lower than radio telemetry estimates because of low trappability (Boutin and Krebs 1986), thus preventing the use of this alternative methodology.

In terms of the predator–prey interactions, the physical location of our hare grids with respect to raptor nests and coyote distribution may have affected both the survival rates and causes of mortality of hares on our trapping areas (Rohner and Krebs 1998, M. O'Donoghue unpublished data). In this case, our treatments were smaller than the patchiness of predator distributions.

8.5 Interactions with Other Species

Researchers have postulated that the cyclic decline is initiated because of food limitation (Pease et al. 1979, Keith 1990). Observations on shrubs and trees at Kluane indicate that sufficient food was available to hares throughout the cycle (see chapter 6; Smith et al. 1988). Additionally, few hares died of starvation (table 8.6), and patterns of hare body condition do not support the view that hares were nutritionally stressed during peak populations (Hik 1995, Hodges et al. 1999b). Hares on sites where food was added appeared to have heavy impacts on the vegetation, in that more twigs were browsed and more shrubs and spruce trees had bark stripped from them (see chapter 6; Hodges 1998), but the hares did not appear to be undernourished. Our estimates of available browse did not detect absolute food limitation at any time, but it is impossible to determine relative food limitation from examination of the plants (Hik 1995, Hodges 1998).

The herbivore community interactions were unexpected. Both ground squirrels and red squirrels exerted considerable predation pressure on leverets, possibly with a type-3 functional response (Stefan 1998). If squirrel-caused mortality is additive to other sources of mortality, leveret survival could easily have doubled without the presence of squirrels. Competitive interactions between hares and squirrels were either nonexistent or not obvious. The only food overlaps appeared to be in summer, when both hares and ground squirrels eat forbs. There potentially was moose–hare competition, in that moose and snowshoe hares both rely on woody browse through the winter, but moose densities were relatively low in the Shakwak Trench. Moose may have had an impact inside the predator exclosure fences; moose commonly broke through the fences and sometimes were inside for periods of several months. The size of the enclosures meant that this represented an unusually high density of moose for those time periods. Our indices of food abundance did not indicate food shortage on these treatments, however.

8.6 Conclusions

We conclude that the snowshoe hare cycle is caused by the simultaneous and interacting impacts of food supply and predation pressure on hares. There are clear changes in annual reproduction and leveret, juvenile, and adult survival; dispersal rates may change through the cycle as well. The single-factor manipulations resulted in changed densities and had some impacts on survival and perhaps reproductive output, but the overall cyclic pattern remained.

The combined manipulation of predator exclosure + food addition altered the timing and magnitude of changes in hare survival and reproduction, which, in turn, led to changes in the pattern of the numeric cycle. The extreme numeric decline was delayed for several years, perhaps because of high reproduction, until one year of particularly low survival coupled with high dispersal led to a dramatic numeric decline in this population. Future research should therefore focus on the ways in which food distribution and predation pressure interact in their effects on these demographic patterns. There are several potential behavioral and physiological pathways through which the impacts of food and predation pressure may affect hare densities.

Literature Cited

Allcock, K. 1994. Do predation risk and food affect the home ranges of snowshoe hares? BSc thesis, University of British Columbia, Vancouver.

Boonstra, R., D. Hik, G. R. Singleton, and A. Tinnikov. 1998a. The impact of predator-induced stress on the snowshoe hare cycle. Ecological Monographs **79**:371–394.

Boonstra, R., C. J. Krebs, and N. C. Stenseth. 1998b. Population cycles in small mammals: the problem of explaining the low phase. Ecology **79**:1479–1488.

Boutin, S. 1984. Effect of late winter food addition on numbers and movements of snowshoe hares. Oecologia **62**:393–400.

Boutin, S., B. S. Gilbert, C. J. Krebs, A. R. E. Sinclair, and J. N. M. Smith. 1985. The role of dispersal in the population dynamics of snowshoe hares. Canadian Journal of Zoology **63**:106–115.

Boutin, S., and C. J. Krebs. 1986. Estimating survival rates of snowshoe hares. Journal of Wildlife Management **50**:592–594.

Boutin, S., C. J. Krebs, R. Boonstra, M. R. T. Dale, S. J. Hannon, K. Martin, A. R. E. Sinclair, J. N. M. Smith, R. Turkington, M. Blower, A. Byrom, F. I. Doyle, C. Doyle, D. Hik, L. Hofer, A. Hubbs, T. Karels, D. L. Murray, M. O'Donoghue, C. Rohner, and S. Schweiger. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. Oikos **74**:69–80.

Boutin, S., C. J. Krebs, A. R. E. Sinclair, and J. N. M. Smith. 1986. Proximate causes of losses in a snowshoe hare population. Canadian Journal of Zoology **64**:606–610.

Bryant, J. P. 1981. The regulation of snowshoe hare feeding behaviour during winter by plant antiherbivore chemistry. *in* K. Myers and C. D. MacInnes (eds). Proceedings of the World Lagomorph Conference, pages 720–731. University of Guelph, Guelph, Ontario.

Cary, J. R., and L. B. Keith. 1979. Reproductive change in the 10-year cycle of snowshoe hares. Canadian Journal of Zoology **57**:375–390.

Dolbeer, R. A., and W. R. Clark. 1975. Population ecology of snowshoe hares in the central Rocky Mountains. Journal of Wildlife Management **39**:535–549.

Elton, C. S. 1924. Periodic fluctuations in the numbers of animals: their causes and effects. British Journal of Experimental Biology **2**:119–163.

Ernest, J. 1974. Snowshoe hare studies. Final Report, Alaska Department of Fish and Game, Juneau.

Finerty, J. P. 1980. The population ecology of cycles in small mammals. Yale University Press, New Haven, Connecticut.

Fox, J. F., and J. P. Bryant. 1984. Instability of the snowshoe hare and woody plant interaction. Oecologia **63**:128–135.

Gillis, E. A. 1999. Survival of juvenile snowshoe hares during a cyclic population increase. Canadian Journal of Zoology **76**:1949–1956.

Gillis, E. A., and C. J. Krebs. 1999. Natal dispersal of snowshoe hares during a cyclic population increase. Journal of Mammalogy **80**:933–939.

Haydon, D. T., E. A. Gillis, C. I. Stefan, and C. J. Krebs. 1999. Biases in the estimation of the demographic parameters of a snowshoe hare population. Journal of Animal Ecology **68**:501–512.

Hik, D. S. 1994. Predation risk and the 10-year snowshoe hare cycle. PhD dissertation, University of British Columbia, Vancouver.

Hik, D. S. 1995. Does risk of predation influence population dynamics? Evidence from the cyclic decline of snowshoe hares. Wildlife Research **22**:115–129.

Hodges, K. E. 1998. Snowshoe hare demography and behaviour during a cyclic population low phase. PhD dissertation, University of British Columbia, Vancouver.

Hodges, K. E., C. J. Krebs, and A. R. E. Sinclair. 1999a. Snowshoe hare demography during a cyclic population low. Journal of Animal Ecology **58**:581–594.

Hodges, K. E., C. I. Stefan, and E. A. Gillis. 1999b. Does body condition affect fecundity in a cyclic population of snowshoe hares? Canadian Journal of Zoology **77**:1–6.

Keith, L. B. 1974. Population dynamics of mammals. Proceedings of the International Congress of Game Biologists **11**:17–58.

Keith, L. B. 1981. Population dynamics of hares. *in* K. Myers and C. D. MacInnes (eds). Proceedings of the World Lagomorph Conference, pages 395–440. University of Guelph, Guelph, Ontario.

Keith, L. B. 1983. Role of food in hare population cycles. Oikos **40**:385–395.

Keith, L. B. 1990. Dynamics of snowshoe hare populations. *in* H. H. Genoways (ed). Current mammalogy, pages 119–195. Plenum Press, New York.

Keith, L. B., J. R. Cary, O. J. Rongstad, and M. C. Brittingham. 1984. Demography and ecology of a declining snowshoe hare population. Wildlife Monographs **90**:1–43.

Keith, L. B., A. W. Todd, C. J. Brand, R. S. Adamcik, and D. H. Rusch. 1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. Proceedings of the International Congress of Game Biologists **13**:151–175.

Keith, L. B., and L. A. Windberg. 1978. A demographic analysis of the snowshoe hare cycle. Wildlife Monographs **58**:1–70.

Krebs, C. J., R. Boonstra, S. Boutin, M. Dale, S. Hannon, K. Martin, A. R. E. Sinclair, J. N. M. Smith, and R. Turkington. 1992. What drives the snowshoe hare cycle in Canada's Yukon? *in* D. R. McCullough and R. H. Barrett (eds). Wildlife 2001: Populations, pages 886–896. Elsevier Applied Science, London.

Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. Science **269**:1112–1115.

Krebs, C. J., S. Boutin, and B. S. Gilbert. 1986a. A natural feeding experiment on a declining snowshoe hare population. Oecologia **70**:194–197.

Krebs, C. J., B. S. Gilbert, S. Boutin, A. R. E. Sinclair, and J. N. M. Smith. 1986b. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon, 1976–84. Journal of Animal Ecology **55**:963–982.

Krebs, C. J., A. R. E. Sinclair, and S. Boutin. 1996. Vertebrate community dynamics in the boreal forest of north-western Canada. *in* R. B. Floyd, A. W. Sheppard, and P. J. De-Barro (eds). Frontiers of population ecology, pages 155–161. CSIRO Publishing, Melbourne.

Murray, D. L., J. R. Cary, and L. B. Keith. 1997. Interactive effects of sublethal nematodes and nutritional status on snowshoe hare vulnerability to predation. Journal of Animal Ecology **66**:250–264.

Murray, D. L., L. B. Keith, and J. R. Cary. 1998. Do parasitism and nutritional status interact to affect production in snowshoe hares? Ecology **79**:1209–1222.

O'Donoghue, M. 1994. Early survival of juvenile snowshoe hares. Ecology **75**:1582–1592.

O'Donoghue, M., and C. M. Bergman. 1992. Early movements and dispersal of juvenile snowshoe hares. Canadian Journal of Zoology **70**:1787–1791.

O'Donoghue, M., S. Boutin, C. J. Krebs, and E. J. Hofer. 1997. Numerical responses of coyotes and lynx to the snowshoe hare cycle. Oikos **80**:150–162.

O'Donoghue, M., S. Boutin, C. J. Krebs, G. Zuleta, D. L. Murray, and E. J. Hofer. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology **79**:1193–1208.

O'Donoghue, M., and C. J. Krebs. 1992. Effects of supplemental food on snowshoe hare reproduction and juvenile growth at a cyclic population peak. Journal of Animal Ecology **61**:631–641.

Pease, J. L., R. H. Vowles, and L. B. Keith. 1979. Interaction of snowshoe hares and woody vegetation. Journal of Wildlife Management **43**:43–60.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management **53**:7–15.

Rohner, C., and C. J. Krebs. 1998. Response of great horned owls to experimental "hot spots" of snowshoe hare density. Auk **115**:694–705.

Royama, T. 1992. Analytical population dynamics. Chapman & Hall, London.

Sievert, P. R., and L. B. Keith. 1985. Survival of snowshoe hares at a geographic range boundary. Journal of Wildlife Management **49**:854–866.

Sinclair, A. R. E., C. J. Krebs, J. N. M. Smith, and S. Boutin. 1988. Population biology of snowshoe hares. III. Nutrition, plant secondary compounds and food limitation. Journal of Animal Ecology **57**:787–806.

Smith, J. N. M., C. J. Krebs, A. R. E. Sinclair, and R. Boonstra. 1988. Population biology of snowshoe hares. II. Interactions with winter food plants. Journal of Animal Ecology **57**:269–286.

Sovell, J. R. 1993. Attempt to determine the influence of parasitism on a snowshoe hare population during the peak and initial decline phases of a hare cycle. MSc thesis. University of Alberta, Edmonton.

Sovell, J. R., and J. C. Holmes. 1996. Efficacy of ivermectin against nematodes infecting field populations of snowshoe hares (*Lepus americanus*) in Yukon, Canada. Journal of Wildlife Diseases **32**:23–30.

Stefan, C. I. 1998. Reproduction and pre-weaning juvenile survival in a cyclic population of snowshoe hares. MSc thesis, University of British Columbia, Vancouver.

Trostel, K., A. R. E. Sinclair, C. J. Walters, and C. J. Krebs. 1987. Can predation cause the 10-year hare cycle? Oecologia **74**:185–192.

Vaughan, M. R., and L. B. Keith. 1981. Demographic response of experimental snowshoe hare populations to overwinter food shortage. Journal of Wildlife Management **45**:354–380.

Windberg, L. A., and L. B. Keith. 1976. Experimental analyses of dispersal in snowshoe hare populations. Canadian Journal of Zoology **54**:2061–2081.

Wolff, J. O. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. Ecological Monographs **50**:111–130.

Wolff, J. O. 1981. Refugia, dispersal, predation, and geographic variation in snowshoe hare cycles. *in* K. Myers and C. D. MacInnes (eds). Proceedings of the World Lagomorph Conference, pages 441–449. University of Guelph, Guelph, Ontario.