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Snowshoe hare demography during a cyclic population low

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Summary

1. Snowshoe hare (*Lepus americanus* Erxleben) populations were studied in south-west Yukon during the low phase of the 10-year population cycle. Food availability and predator abundance were manipulated in a factorial design to determine the importance of each factor in hare dynamics during this phase.

2. Food was abundant during the low phase, and snowshoe hares were not food limited.

3. Survival of hares was higher than at any other phase of the cycle, and predators were scarce, but >75% of hare deaths resulted from predation.

4. Food addition resulted in higher hare densities and better body condition than on control sites. There were no observable effects of food addition on population rate of increase, recruitment, survival or age structure.

5. Mammalian predator reduction resulted in higher hare densities, higher survival, better body condition and an older age structure. Relative to control populations, recruitment was lower and population rates of increase similar.

6. The joint manipulation of food addition + predator reduction had greater positive effects on hare density and body condition than either single factor manipulation. Survival was better than on control sites, and the age structure was older than on control sites. Population rates of increase were similar, but recruitment was higher on the control areas.

7. We conclude that snowshoe hare dynamics at the low of the cycle are dominated by the interaction of food and predation. Risk of predation also had indirect effects on snowshoe hare age structure and body condition.

Key-words: body condition, food addition, population density, predator reduction, survival.

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Introduction

For decades, ecologists have known that snowshoe hares exhibit an 8- to11-year cycle in abundance, with hare densities changing 20–200 fold (Green & Evans 1940; Elton & Nicholson 1942; Keith & Windberg 1978; Finerty 1980; Keith *et al.* 1984). The hare cycle is broadly synchronous across the boreal and northern temperate forests of North America (Smith 1983; Sinclair *et al.* 1993; Sinclair & Gosline 1997), and is associated with predictable changes in reproduction and survival (Keith 1990). The underlying mechanisms causing these changes in survival and reproduction have been much debated. To form a cycle of the appropriate duration, there needs to be a density-dependent lag of 1–3 years in one or both of these factors (Finerty 1980; May 1981; Royama 1992). Hare densities remain low for 2–4 years, with apparent lags in vegetative regrowth and predator numbers, indicating that the dynamics during the low phase may be crucial to the generation of the cycle.

The main hypotheses proposed to explain the dynamics of the cycle involve trophic interactions: food–hare, hare–predator or food–hare–predator. Changes in plant quantity or quality, resulting from heavy browsing during hare population peaks, may create the necessary time lag as plants regrow lost

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biomass or adjust their chemical defences (Pease, Vowles & Keith 1979; Bryant 1981; Fox & Bryant 1984). Changes in predation pressure may be sufficient to cause the cycle as predators respond functionally and numerically (Trostel *et al.* 1987; Krebs *et al.* 1992; O'Donoghue *et al.* 1997). There are two forms of the food–hare–predator hypothesis. The Keith hypothesis states that food shortage in the winter of peak densities initiates the decline phase, then predation continues the high mortality that characterizes the decline phase (Keith 1974, 1990). Alternatively, recent evidence from the Yukon suggests that both food supply and predation are integral to the population dynamics of hares at all stages of the cycle (Krebs *et al.* 1995; Krebs, Sinclair & Boutin 1996).

Despite these potential explanations, hare population dynamics during the low phase are still poorly understood (Boonstra & Singleton 1993; Hik 1994, 1995; Krebs *et al.* 1995), partly because previous studies have focused on the transition from peak densities to low densities (Keith & Windberg 1978; Wolff 1980, 1981; Keith 1990; Hik 1995). Furthermore, food availability is apparently high during the low phase of the cycle, and predator numbers low, both of which should promote high hare survival; reproduction is also good during this phase (Smith *et al.* 1988; Keith 1990; Boutin *et al.* 1995; Krebs *et al.* 1995). Direct effects of food limitation or predation alone are therefore seemingly insufficient to explain the length of the low phase. Several authors have speculated that predation risk produces indirect effects on nutrition, body condition and reproduction of hares during the low phase of the cycle, and that these indirect effects may be sufficiently large to create the extended duration of this phase (Wolff 1980, 1981; Boonstra & Singleton 1993; Hik 1994, 1995; Krebs 1996).

In this paper, we provide experimental tests of these hypotheses for the low of the cycle (see also Table 1). If the low of the cycle is extended because of a food–hare interaction, then addition of high quality food should cause an earlier increase than that observed for hare populations without supplemental food. This earlier increase could result from increased fecundity because of better nutrition or it could be a result of higher survival if starvation or predation deaths were reduced by the abundance of food [see McNamara & Houston (1987) and Sinclair & Arcese (1995) for the difficulty in separating starvation and predation deaths]. If, instead, a hare–predator interaction causes the dynamics of the low phase, then hare populations protected from predators should have a shorter low phase than their control counterparts. The mechanism here is likely to be increased survival. Finally, if dynamics during the low phase of the cycle result from an interaction of all three trophic levels, then the joint manipulation of predation risk and food availability should have greater effects on fecundity, survival, density and duration of the low phase than does manipulation of either single factor.

For the low phase of the 10-year cycle, the purposes of this study were therefore: (i) to describe demographic parameters of the hares; (ii) to quantify food availability and predation pressure; (iii) to test experimentally the trophic level hypotheses for this phase by manipulating food and predation; and (iv) to examine the indirect effects of predation on hare body condition, age structure and recruitment. We used control, food addition, predator reduction and food addition + predator reduction manipulations established by the Kluane Boreal Forest Ecosystem Project by summer 1988 (Krebs *et al.* 1992; Krebs *et al.* 1996) to address these questions.

Methods and materials

STUDY AREA AND TREATMENTS

This research focuses on the years 1993–96, encompassing the low phase of the 10-year cycle, and is part of a long-term examination of community organization conducted by the Kluane Boreal Forest Ecosystem Project (Krebs *et al.* 1992). The study area is in south-western Yukon near Kluane Lake (60°57′N, 138°12′W), in a broad, glacial valley about 900 m above sea level. The 350 km^2 study area comprises predominantly white spruce [*Picea glauca* (Moench) Voss] forest on the valley floor, but extends up the slopes into the alpine tundra of the Ruby Range to the north-east and the Kluane Range to the south-west. The valley floor has occasional pockets of aspen (*Populus tremuloides* Michx.) and poplar (*P. balsamifera* L.), multiple small lakes, and several swampy areas. Grey-leaved and felt-leaved willow (*Salix glauca* L., *S. alaxensis* Coville), bog birch (*Betula glandulosa* Michx.) and soapberry [*Shepherdia canadensis* (L.) Nutt] are common, both in the swamps and as understorey in the spruce forests.

The study reported here used seven 34-ha treatment areas which the Kluane Boreal Forest Ecosystem Project established before or during 1988 (Krebs *et al.* 1992, 1995). Three areas were unmanipulated controls. Two areas (food) were provisioned *ad libitum* with commercial rabbit feed (minimum 16% crude protein) spread along four 570 m cutlines. One area (fence) was contained within a 1 km^2 electric and chicken wire fence which excluded the main terrestrial predators, lynx (*Lynx canadensis* Kerr) and coyote (*Canis latrans* Say). Part of the trapping area inside the fence (10 ha) was covered with monofilament line strung through the trees to deter goshawks (*Accipiter gentilis* L.), Harlan's hawks (*Buteo jamaicensis* Gmelin) and great horned owls (*Bubo virginianus* Gmelin). The final treatment (food + fence) was a combination of food addition and fence but had no monofilament.

Snowshoe hares were trapped on each of these areas every March and October for population estimates. Sporadic trapping occurred at other times to maintain the number of radio-collared hares for estimates of

Table 1. Predicted effects of trophic manipulations on snowshoe hare dynamics during the low phase. Statements are relative to the control populations. Food limitation could be either an absolute shortage of available biomass, or a shortage of food low in secondary compounds. The predation hypothesis refers to mortality effects alone, or to mortality and indirect effects of risk on hare behaviour and physiology. Statements in bold indicate the most likely mechanism for numerical change, while those in regular type might change in the direction indicated or might not differ from control populations. For the interaction hypothesis, the food addition + predator reduction treatment should have greater impact on hare dynamics than either single factor manipulation, as indicated by the + signs

Manipulation	Food limitation	Predation	Interaction
Food addition	Increase earlier density higher –growth rate higher –survival better **–recruitment higher** **–condition better** –mean age lower	Increase same density same –growth rate same –survival same –recruitment same –condition same –mean age same	Increase earlier density higher –growth rate higher –survival better **–recruitment higher** **–condition better** –mean age lower
Predator reduction	Increase same density same –growth rate same –survival same –recruitment same –condition same –mean age same	Increase earlier density higher –growth rate higher **–survival better** –recruitment higher –condition better –mean age higher	Increase earlier density same –growth rate higher **–survival better** –recruitment higher –condition better –mean age higher
Food addition + predator reduction	Increase earlier density higher –growth rate higher –survival better **–recruitment higher** **–condition better** –mean age lower	Increase earlier density higher –growth rate higher **–survival better** –recruitment higher –condition better –mean age higher	Increase earlier + density higher + –growth rate higher + **–survival better +** **–recruitment higher +** **–condition better +** –no age prediction

survival. Eighty-six Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, WI) were spaced in four trapping lines across 34-ha grids; the effective trapping area was 60 ha. Traps were baited in the evening with alfalfa (and rabbit feed on the food addition areas) and checked the following morning at first light. Each hare was identified with a Monel No. 3 eartag (National Band and Tag Co., Newport, KY). For every capture, recordings were made of eartag, location, sex, reproductive condition (males: abdominal or scrotal testes; females: lactating, pregnant or not pregnant), length of right hind foot, and weight. Some hares were radio-collared with 40 g radio-collars (Lotek, Newmarket, ONT), which were equipped with mortality sensors that doubled the pulse rate when the collar did not move in 4 h.

DENSITY, POPULATION RATE OF CHANGE, AND RECRUITMENT OF SNOWSHOE HARES

Hare densities were estimated every March from three to seven nights of trapping per area. Population sizes for each treatment grid were derived as the average of jack-knife estimates from program CAPTURE (Otis *et al.* 1978; Boulanger & Krebs 1994) and Jolly–Seber estimates (Seber 1982). The Jolly–Seber and CAPTURE estimates were similar and highly correlated ($r = 0{\cdot}96$) for snowshoe hares, and both give the same results; the mean of the two is presented here for simplicity. The annual recruitment rates were estimated as the geometric mean (averaged from spring to spring) of Jolly–Seber dilution rates (Krebs 1989). The annual finite rate of increase was calculated as N_{t+1}/N_t.

SURVIVAL RATES OF SNOWSHOE HARES

Snowshoe hare survival rates were estimated based on radio-collared hares. Each hare's mortality date was defined as the day after it was last known to be alive, unless the state of the corpse or sign at the death site indicated a more recent death. We censored records for hares for which time of death could not be determined to within 2 weeks, and for hares that had incomplete records as a result of accidental death (trap death, road kill), radio-collar failure, or loss of radio signal because of dispersal. For these cases, the censoring date was the last date on which the hare was known to be alive. It was assumed for these cases that most loss of radio signals was not a result of deaths of the hares and destruction of the radios. Hares that originated on the fence and food + fence treatments but died outside of the fences were censored on the last date that they were known to be inside the fences. If hares survived beyond the time interval under exam-

ination, their censoring date was the last day of the interval. Survival rates were calculated in Statistica (StatSoft 1995) using Cox's proportional hazard model (Cox & Oakes 1984). Survival rates did not fit the assumptions of any of the parametric survival models, therefore leading us to use this semi-parametric approach.

WINTER FOOD AVAILABILITY

In May–June of 1995, five to ten transects were conducted on each treatment area to estimate the standing biomass of shrubs. Along each 90- to 180-m transect, all willow and birch bushes within a 2-m wide belt were measured for number of stems >5 cm, basal circumference and maximum height. These values were converted into estimates of standing crop biomass for each area, using regressions calculated from a sample of 76 birch bushes and 104 willow bushes that were measured, cut and weighed (all regressions had r^2 values of $>0{\cdot}90$; C.J. Krebs, A.R.E. Sinclair and W. Hochachka, unpublished data). These estimates are expected to be constant from year to year because most changes in vegetation occur for twigs <5 mm diameter (A.R.E. Sinclair and C.J. Krebs, unpublished data).

The proportion of standing biomass comprising small twigs (<5 mm diameter) was assessed annually. Every May, bushes were cut down on ≈ 50 1-m^2 plots on two control areas, one food area and the food + fence area; for each shrub species, biomass of >5 mm twigs and <5 mm twigs was recorded. In 1994 and 1995, 20 individual bushes each of birch and willow were cut down on the other control and food sites, and on the fenced site.

Biomass of large twigs was calculated as (a·stem^2 + b·circumference·height)/(2·transect length), where a and b are fitted constants. This value is in units of g wet weight m^{-2}, and was converted to kg dry weight ha^{-1}, using 0·55 as the ratio of dry weight to wet weight (A.R.E. Sinclair and C.J. Krebs, unpublished data). Small twig biomass was then calculated as (small weight/total weight)·large weight/[1 − (small weight/total weight)·large weight], where *small weight* and *total weight* were from annual clip plots and *large weight* from the belt transects. Confidence intervals were derived from the confidence intervals of the clip plot data.

FOOD AVAILABILITY PER HARE

The above calculations provide estimates of the standing amount of food left in early May, before leaf-out and summer growth. As such, values represent yearly minima of available small twigs. The amount of browse available per hare at the end of winter was estimated by dividing the available kg ha^{-1} of small twigs (willow and birch combined) by the March density of hares for each site. Although twigs are differentially available, depending on snow height and whether branches are bent over by snow, hares were observed tunnelling in the snow to expose buried twigs; they also bit through thick stems to obtain smaller twigs that they could not reach directly. Therefore most twigs are available to hares.

PREDATOR NUMBERS IN THE STUDY AREA

Predator densities were studied by other researchers affiliated with the Kluane Boreal Forest Ecosystem Project. Numbers of great horned owls, goshawks and Harlan's hawks were assessed in the spring and summer, using playback techniques, sightings and records of owl hootings (F.I. Doyle unpublished data, Rohner & Doyle 1992; Doyle & Smith 1994; Boutin *et al.* 1995; Rohner 1996). Raptor censuses were conducted intensively within a 100 km^2 core study area. Lynx and coyote numbers were determined through the course of each winter (November–March), by a combination of trapping, track transects and records of coyote howling (Boutin *et al.* 1995; O'Donoghue *et al.* 1997).

CAUSES OF DEATH OF SNOWSHOE HARES

Radio-collar frequencies were monitored a minimum of three times a week from the Alaska Highway, using a large antenna mounted on a vehicle. When mortality signals were heard, project personnel located the radio-collar by using handheld receivers and yagi or H antennas (Telonics, Mesa, AZ). At each site of death, information on predator tracks, feathers, scat, whitewash, hare remains and manner of eating were collected. These clues combined to provide identification of the cause of death (C. Doyle & C.J. Krebs, unpublished protocol). Corpses found intact were collected for necropsy.

Conservative criteria were used for determining the cause of death. If all of the evidence present at a site indicated a particular predator species, the kill was assigned to the predator. If, however, most of the evidence indicated a particular species but there were inconsistencies or the evidence was scanty, the death was classified as 'unknown predator'. Similarly, if the evidence for predation rather than nonpredation was poor, the death was assigned to the conservative category of 'unknown death'. It was assumed that the distribution of causes for 'unknown deaths' was similar to that for known deaths.

CONDITION OF SNOWSHOE HARES

Condition of female hares in the spring was estimated as observed weight/predicted weight, where predicted weight was derived from an equation relating weight and skeletal size: weight (g) = 1·97 + right hind foot length (mm)$^{1{\cdot}48}$. The parameters were derived from 171 female hares from control sites caught in the springs

of 1989–96 (K.E. Hodges, C.I. Stefan, E.A. Gillis, unpublished paper). The index indicates relative condition, with a value of one indicating the hare is in average condition relative to the female population at large (O'Donoghue & Krebs 1992; Krebs & Singleton 1993).

AGE OF SNOWSHOE HARES

Snowshoe hares can have up to four litters in a summer, and parturition dates are synchronized between females (Keith 1990; O'Donoghue & Boutin 1995). Therefore juvenile hares trapped in summer could be assigned to one of the four litter groups, based on their weight and right hind foot length. Juveniles caught in the autumn were often adult weight, so all hares caught for the first time in the autumn were classified as juveniles of unknown litter unless they could be identified as third or fourth litter. We aged all hares one year on January 1st.

Results

DENSITY AND POPULATION RATE OF CHANGE

Snowshoe hare populations were generally at their lowest densities in the springs of 1993 and 1994 (Fig. 1). Hare populations on all treatments declined from 1992 to 1993. From 1993 to 1994, two control populations and the food + fence population declined but populations on the other sites increased. All populations increased annually thereafter, with the exception of a decline on the fenced site from 1995 to 1996. The annual rate of increase in 1995–96 was much higher than in the preceding 3 years (Fig. 2). Because spring densities were lowest from 1993 to 1995, and rates of increase either below one or generally close to it, these years will be considered as the low phase. The increase phase will be considered to have started with summer breeding in 1995.

With the exception of the fence treatment in 1996, all manipulations resulted in increased density, but no manipulated population increased earlier than the control populations. From 1993 to 1995, the food addition site had densities $\approx 4{\cdot}2$ times higher than control areas, the fence manipulation had densities $\approx 2{\cdot}5$ times higher, and the food + fence manipulation had densities $\approx 10{\cdot}9$ times higher. In 1992–93 and 1993–94, annual rates of increase were similar for all treatments. In 1994–95, two control populations had higher rates of increase than elsewhere, and in 1995–96 populations on the fence and food + fence treatments had lower rates of increase than did the food and control populations.

RECRUITMENT AND SURVIVAL OF SNOWSHOE HARES

Recruitment rates generally increased on control sites during the low phase of the cycle (Fig. 3), but two control populations had their recruitment rates reduced during the first year of population increase (1995–96). In both food areas, recruitment was lowest in 1994–95. The fence and food + fence manipu-

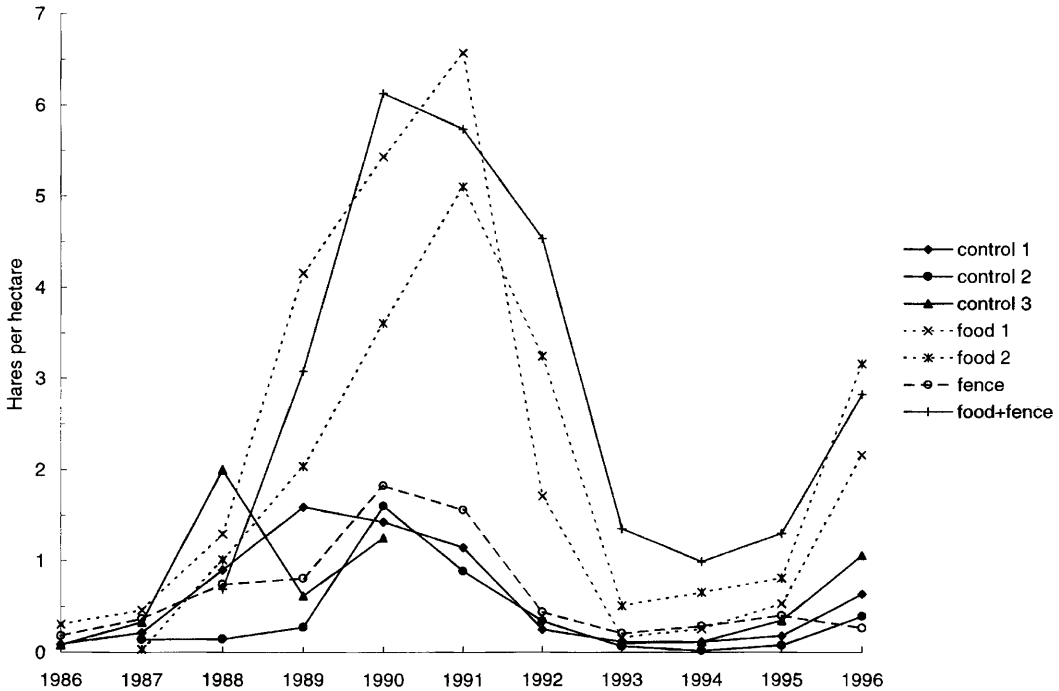

Fig. 1. Spring snowshoe hare densities through a population cycle near Kluane Lake 1986–96. This study commenced in March 1993, and continued until April 1996, encompassing the low and early increase phases of the cycle.

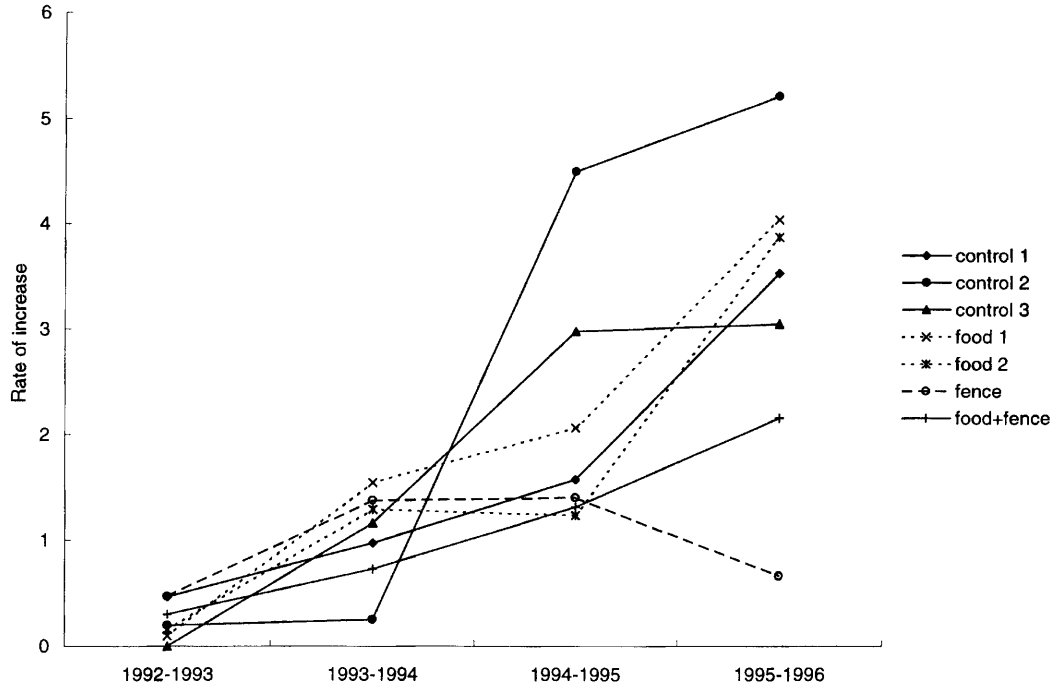

Fig. 2. Annual rate of increase of snowshoe hares. These rates were calculated as N_{t+1}/N_t, from spring to spring. Values lower than one indicate a declining population.

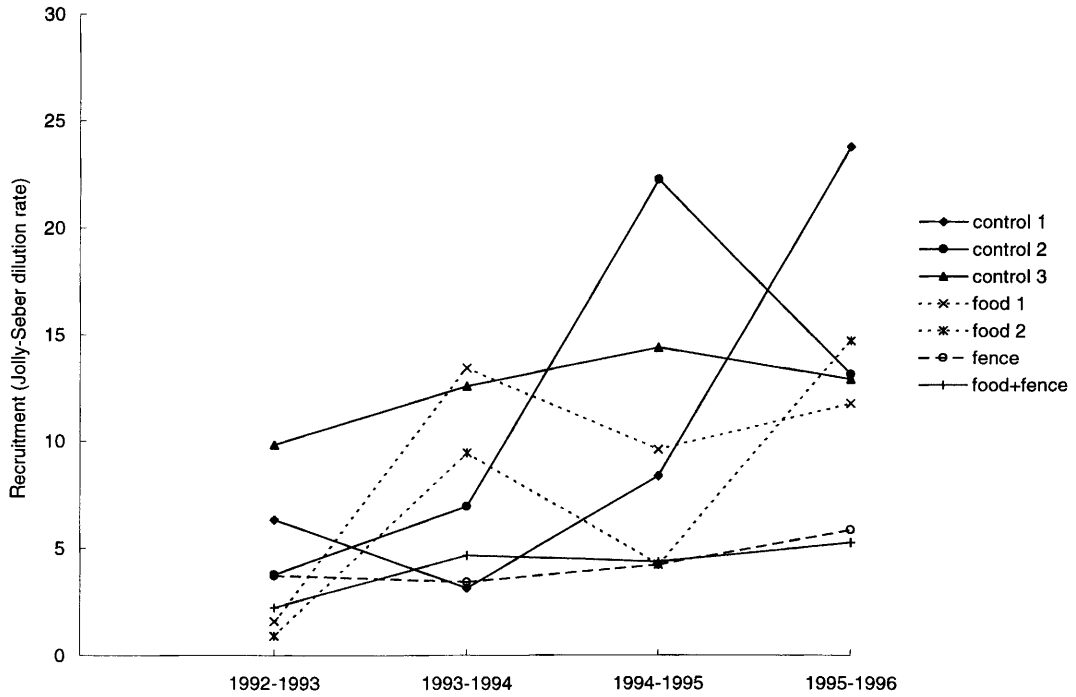

Fig. 3. Recruitment rate of snowshoe hares. The values are geometric means of Jolly–Seber dilution rates, calculated from spring to spring. The values are $N_{\text{actual}}/N_{\text{predicted}}$, with $N_{\text{predicted}}$ derived from estimation of what the population would have been had no animals been added to it (through immigration or birth).

lations had little change in recruitment rates. Control populations generally had higher recruitment rates than did the manipulated populations, but in all years some of the control populations were similar to the food populations. Both the food and control populations had higher recruitment rates than the fence or food + fence populations.

Treatment and year effects on survival were tested with Cox's proportional hazard model (Cox & Oakes 1984). Sex was never a significant effect in any analysis

and was dropped from the main analysis. Year, treatment and interaction effects were all highly significant (all $P < 0{\cdot}001$). These differences arose because of different year effects on the various treatments. Control hares had higher survival in 1995–96 than in previous years (Fig. 4). Hare survival on the fence treatment did not change through time, and hare survival on the food + fence treatment was lower in 1995–96 than in previous years. Hares on the food treatment had lower survival rates in 1993–94 than in later years.

If we combine survival over all years, control hares had the lowest annual survival rate, 0·22 (95% C.L. 0·16–0·29). Hares on food treatments survived somewhat better, with annual survival of 0·29 (0·21–0·40). Hares inside the fence and food + fence treatments had the much higher annual survival rate of 0·47 (0·40–0·56, and omitting 1995–96 on the food + fence because of the coyote on that area).

FOOD AVAILABILITY

Small twigs were plentiful during the low phase in hare numbers (Table 2), with willow consistently more abundant than birch. There was no clear pattern of increase or decrease in willow and birch biomass through the years of low hare densities. At the end of every winter, the amount of willow and birch remaining could have fed the existing hare population for another entire winter (Fig. 5). Although food per hare was lowest on the food + fence treatment, there was still ample food left there, considering especially that the calculation of food per hare is an underestimate as it does not include other food plants or growth of plants in summer.

PREDATOR NUMBERS

The summer adult raptor populations remained similar through the low phase, but lynx and coyote numbers showed more interannual variation (Table 3). There were 1–2 pairs of goshawks in each summer, 9–10 pairs of Harlan's hawks and 10–11 pairs of great horned owls. Both lynx and coyote numbers were lowest in the final period of the low phase (5–6 coyotes, 8–9 lynx) and both increased slightly in numbers by the first winter of snowshoe hare increase. Predator densities were therefore low but fairly consistent throughout the cyclic low phase, despite the large change in hare densities (Fig. 5).

CAUSES OF DEATH FOR SNOWSHOE HARES

Predation accounted for 75–100% of the deaths of adult hares on control sites (Table 4). The other treatments had similar proportions of predation deaths, except for the food + fence treatment, which had slightly elevated numbers of nonpredation deaths. Lynx and coyotes were responsible for most of the predation deaths (≈65%) on the food and control areas. Goshawks and owls accounted for only 9–21% of predation deaths on these sites (the remainder of predation deaths were due to mustelids or were

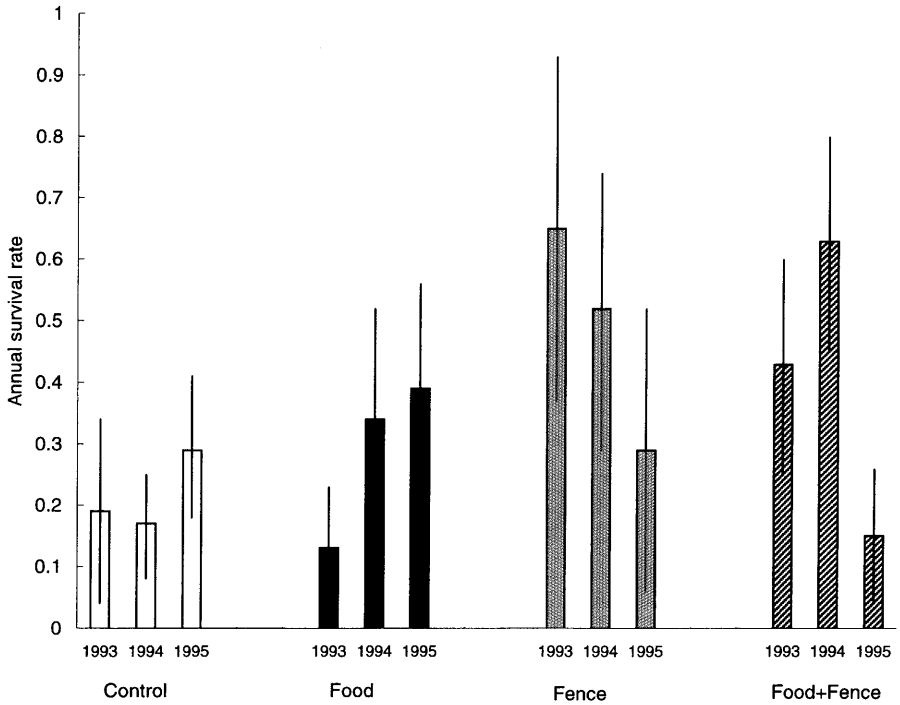

Fig. 4. Annual survival rates of radio-collared snowshoe hares. Rates are Kaplan–Meier estimates calculated from 1 April to 31 March. Bars indicate mean survival, and lines are 95% confidence limits derived from Greenwood's standard error (Pollock *et al.* 1989). Usually at least 10 hares were radio-collared per treatment at any given time.

Table 2 Food availability for snowshoe hares: biomass of birch and willow. Values are kg ha^{-1} (dry weight), mean (95% CI). Large twigs are >5 mm diameter and small twigs are <5 mm diameter. Values were derived from estimates of standing biomass (belt transects) and the ratio of small twigs to total biomass (clip plots). Biomass of large twigs is thought to be similar from year to year (A.R.E. Sinclair & C.J. Krebs, unpublished data)

	Large biomass (all years)	Small twig biomass			
		1993	1994	1995	1996
Birch					
Control 1	2	2	1 (0·2–3)	0	0
Control 2	71	32 (28–36)	33 (29–37)	22 (6–47)	55 (37–80)
Control 3	7	?	26 (15–55)	17 (12–27)	?
Food 1	371	?	220 (143–324)	217 (148–307)	?
Food 2	394	?	76 (46–135)	74 (46–135)	?
Fence	620	?	258 (147–406)	605 (357–1022)	?
Food + fence	240	45 (43–46)	84 (82–87)	112 (77–157)	110 (82–143)
Willow					
Control 1	1811	627 (460–820)	419 (406–431)	441 (317–579)	420 (255–614)
Control 2	2094	434 (353–522)	376 (358–395)	430 (343–522)	366 (310–425)
Control 3	238	?	499 (329–814)	118 (76–171)	?
Food 1	1322	?	729 (443–1125)	732 (496–1038)	?
Food 2	394	?	336 (218–511)	693 (448–1139)	?
Fence	1919	?	462 (292–660)	800 (549–1108)	?
Food + fence	2591	556 (537–577)	411 (400–422)	618 (465–788)	547 (396–699)

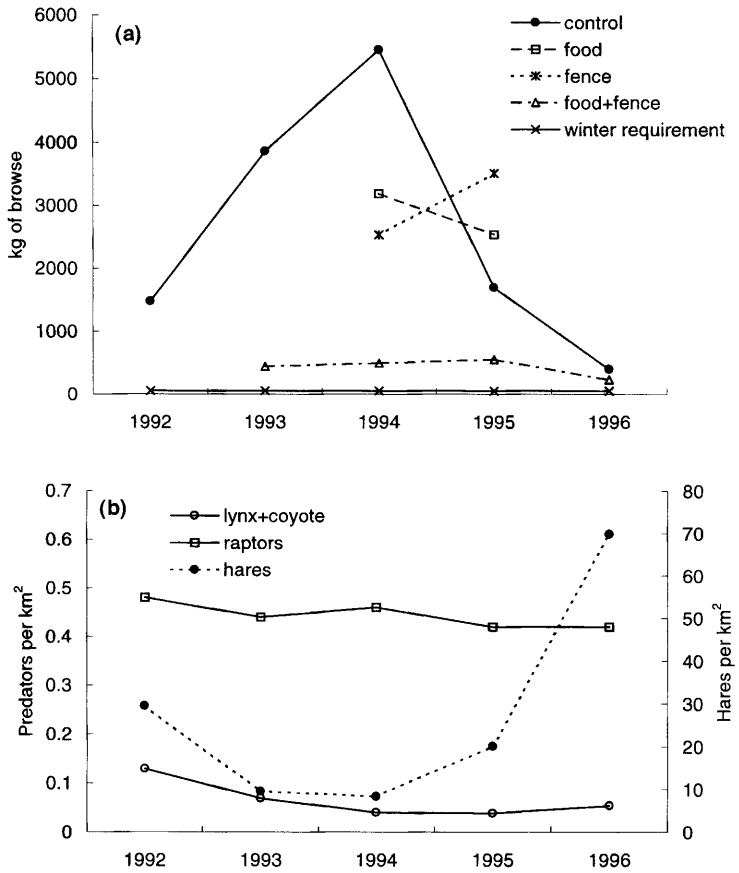

Fig. 5. Food and predator densities. (a) Woody browse available per hare at end of winter. The four treatment lines indicate availability, as kg browse of <5 mm twigs per hare. Biomass was assessed in May of each year, and hare densities in March. The winter requirement line indicates that ≈54 kg of browse are needed per hare per winter, based on a 180-day winter and the estimate of Pease *et al.* (1979) that a hare needs 300 g (fresh weight) daily. (b) Predator densities. –○– represents the density of lynx + coyotes; –□– indicates the combined density of goshawks + Harlan's hawks + great horned owls; and --●-- indicates the average density of hares from the three control sites.

Table 3. Predator numbers at Kluane during the low and early increase phases of the snowshoe hare cycle. Raptor numbers represent pairs of breeding birds in 100 km^2, and mammal numbers represent individuals in 350 km^2. Data from F.I. Doyle (unpublished data), Boutin et al. 1995, and O'Donoghue et al. 1997. Raptor numbers were assessed in summer, and mammal numbers in winter

	1992	1993	1994	1995	1996
Summer					
Great Horned Owl (*Bubo virginianus*)	14	10	11	10	10
Goshawk (*Accipiter gentilis*)	1	2	2	1	1
Harlan's Hawk (*Buteo jamaicensis*)	9	10	10	10	10
Winter					
Coyote (*Canis latrans*)	17	9	5	6	7
Lynx (*Lynx canadensis*)	28	15	9	8	12

unidentifiable). On the fence and food + fence sites, raptors caused 51–89% of the predation deaths. In the winter of 1995–96 a coyote inside the food + fence manipulation was responsible for 37% of total predation mortality on this site during the 3-year study period.

BODY CONDITION

Female snowshoe hares on the unmanipulated control sites were in below average condition in the first year of the low and the first year of the increase (Fig. 6). Female hares on all treatments were in better average condition than females on control sites, and hares on the food and fence treatment were in better condition than hares on the food addition sites (two-way ANOVA, treatment $F_{3,318} = 15{\cdot}0$, $P < 0{\cdot}001$, followed by Tukey post hoc tests). Annual effects were statistically indetectable (two-way ANOVA, year $F_{3,318} = 0{\cdot}90$, NS), but the interaction of treatment and year was significant ($F_{9,318} = 4{\cdot}38$, $P < 0{\cdot}001$). The interaction term may be due to three anomalous years: control hares were in poorer condition in 1993 than in later years, and in 1996 fed hares were in better condition and hares on the food + fence site in poorer condition than in previous years.

AGE STRUCTURE

On control sites, yearling hares composed 83·3–89·3% of the breeding population during the low of the cycle; in 1996, the first year of increase, yearlings composed 89·6% of the population (Table 5). On all four treatments, proportion of yearlings increased and mean age decreased through the 3 years of the low. For both the fence and food + fence treatments, yearlings comprised a smaller fraction of the breeding population than on the control sites, and both mean age and maximum age were higher than for control populations.

Discussion

THEORIES FOR DYNAMICS OF THE LOW PHASE

The competing trophic models for dynamics of the snowshoe hare cycle are that food alone is limiting (food limitation), that predation alone is limiting (predation limitation), or that the two interact—continually or sequentially—to limit hare populations. The bulk of evidence suggests both food and predation contribute to cyclic dynamics (Keith & Windberg 1978; Keith 1990; Krebs *et al.* 1995, 1996). Two questions remain: whether the interaction is sequential or continuous, and whether predation affects hare demographics primarily as a mortality agent (the predation interaction hypothesis) or also affects condition and fecundity indirectly (the risk interaction hypothesis).

Keith's sequential food-predation hypothesis states that predation is limiting but food adequate during the low phase (Keith *et al.* 1977; Keith & Windberg 1978). Keith & Windberg (1978) suggested that the increase phase did not begin until predation mortality declined, as a result of the numerical lag in predator populations (Keith *et al.* 1977). Although malnutrition (resulting from limited food supply) increased both starvation and predation deaths (Keith *et al.* 1977; Pease *et al.* 1979; Keith 1990), during low phases hares appeared not to be malnourished (Keith & Windberg 1978; Keith 1990). For the low phase, the sequential food-predation hypothesis and the predation interaction hypothesis are the same, because both do not expect food to affect population dynamics at this time.

In contrast, predation may also affect prey indirectly through the stress of chases or predator avoidance, and limitation of foraging time or locations. Behavioural trade-offs between safety and food are common in small mammals (e.g. Brown *et al.* 1988; Desy, Batzli & Liu 1990; Lima & Dill 1990; Lagos *et al.* 1995), and have been shown for hares during other phases of the cycle (Gilbert & Boutin 1991; Hik 1994, 1995; Rohner & Krebs 1996). According to this argument, the low phase can be explained as a result of behavioural trade-offs by hares, which can affect body condition, physiology, fecundity and both starvation and predation deaths (Boonstra & Singleton 1993; Krebs 1996). For the risk interaction hypothesis, food and predation are both essential to population dynamics because they will determine the behavioural trade-offs and the consequences thereof.

EVIDENCE OF FOOD LIMITATION?

The evidence presented here negates the idea that winter food was limiting to hares during the low phase

Table 4. Causes of death of snowshoe hares. Each timespan includes deaths from 1 April to 31 March. Values are percentages of the hares dead of each cause. Kills classified following Doyle *et al.* (unpublished data). *Unk-pred* includes known weasel, marten and eagle predations, and kills for which the predator could not be specified. *Non-pred* deaths are those with no sign of predation. *Unknown* deaths had inadequate sign to determine cause of death. The *outside fence* category includes hares from all years which originated inside a fence but died outside the fence. The *% predation* estimates deaths as a result of predation: the first value is predations/(known + unknown deaths) and the second value is predations/(known deaths)

	Coyote	Lynx	Owl	Goshawk	unk-pred	non-pred	unknown	*n* deaths	% predation
Control									
1993–94	42·1	21·1	0	5·3	10·5	0	21·1	19	78·9–100·0
1994–95	36·4	7·3	1·8	7·3	21·8	0	25·5	55	74·5–100·0
1995–96	22·0	24·4	4·9	19·5	17·1	2·4	9·8	41	87·8–97·3
Food									
1993–94	32·4	16·2	2·7	2·7	13·5	0	32·4	37	67·6–100·0
1994–95	14·3	28·6	0	0	14·3	0	42·9	21	57·1–100·0
1995–96	15·8	26·3	5·3	10·5	31·6	0	10·5	19	89·5–100·0
Fence									
1993–94	0	0	50·0	25·0	0	0	25·0	4	75·0–100·0
1994–95	0	0	54·5	9·1	9·1	0	27·3	11	72·7–100·0
1995–96	0	0	0	30·0	70·0	0	0	10	100–100
Outside fence	0	20·0	20·0	0	40·0	0	20·0	10	80·0–100·0
Food + fence									
1993–94	0	0	11·1	22·2	33·3	16·7	16·7	18	72·2–81·3
1994–95	0	9·1*	27·3	18·2	36·4	0	9·1	11	90·9–100·0
1995–96	39·3†	0	0	3·6	42·9	10·7	3·6	28	85·7–88·9
Outside fence	2·8	19·4	5·6	5·6	30·6	2·8	33·3	36	63·9–95·8

* A lynx was temporarily inside the fence; it killed only one radio-collared hare.
† A coyote was inside the fence from at least 9 November 1995 to 5 January.

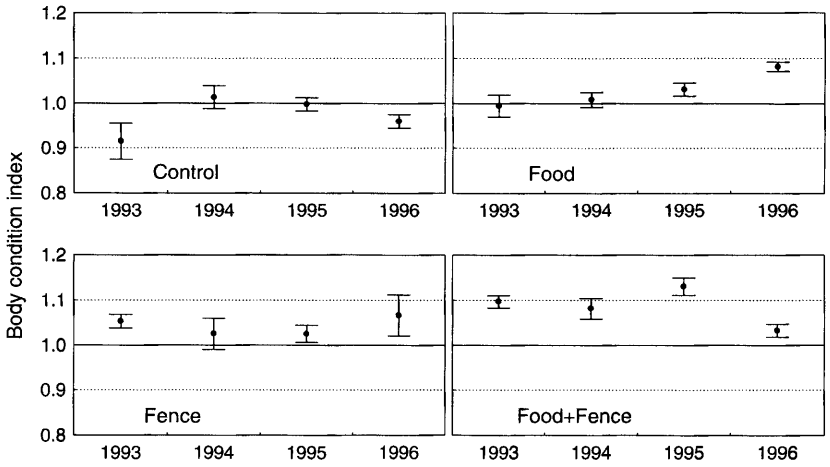

Fig. 6. Body condition of female snowshoe hares in spring. Values are mean ± SE. The condition index is observed weight/predicted weight, with predicted weight derived from the average relationship of skeletal size to weight. Values are relative and 1 indicates average condition. Each mean represents 2–92 hares (× = 20·8).

(see Table 6). Food density was high, and availability of birch and willow per hare was much higher than the food required per hare; hares also ate spruce and soapberry. Even if there were some changes in the secondary compound content of these species as a response to heavy browsing from hares at peak densities (Fox & Bryant 1984; Sinclair *et al.* 1988), willow has high digestibility and low phenolic and resin content, making it an adequate diet for hares (Sinclair *et al.* 1988). Winter food supply was not limiting during the low phase.

This pattern of abundant food affirms previous research at Kluane, which has not demonstrated food shortage for hares (Krebs *et al.* 1986; Sinclair *et al.* 1988). Food shortages have been observed at peaks of hare cycles in Alberta (Pease *et al.* 1979; Keith 1990)

Table 5. Spring age structure of snowshoe hares during the low phase of the cycle. All hares were aged a year on 1 January, so a population composed entirely of the previous summer's young would have a mean age of 1·0. Percent young is the percentage of the population aged one

	Hares caught	Mean age: years ± SE	Percent young	Age of oldest hares
Control				
1993	12	1·17 ± 0·11	83·3	2
1994	14	1·21 ± 0·16	85·7	3
1995	28	1·11 ± 0·06	89·3	2
1996	106	1·11 ± 0·03	89·6	3
Food				
1993	20	1·55 ± 0·21	70·0	4
1994	26	1·35 ± 0·19	84·6	5
1995	53	1·08 ± 0·05	94·3	3
1996	213	1·15 ± 0·03	87·3	4
Fence				
1993	10	1·70 ± 0·30	60·0	3
1994	15	1·53 ± 0·27	73·3	4
1995	24	1·33 ± 0·18	79·2	5
1996	5	1·60 ± 0·25	40·0	2
Food + fence				
1993	52	1·87 ± 0·12	38·5	4
1994	39	1·72 ± 0·17	64·1	4
1995	36	1·36 ± 0·13	75·0	4
1996	71	1·42 ± 0·11	74·7	6

Table 6. Synopsis of snowshoe hare demography during the cyclic low phase. Population rate of increase, survival and recruitment were calculated from spring to spring 1993–94, 1994–95 and 1995–96. Density, condition and mean age were calculated for March of each year.

(a) Treatment effects. Values are relative to control populations for the 3 years of the low phase combined. The final column indicates which trophic level hypothesis was supported. The + signs indicate more effect than on single factor treatments

	Food	Fence	Food + fence	Hypothesis supported
Density	Higher	Higher	Higher +	Interaction
Increase rate	Similar	Similar	Similar	None supported
Survival	Similar–higher	Higher	Higher	Predation
Recruitment	Similar–lower	Lower	Lower	None supported
Condition	Better	Better	Better +	Interaction
Mean age	Similar	Higher	Higher	Predation

(b) Comparison with other phases of the cycle. Values are from control sites and are relative to the general pattern of the low phase. Survival and increase rate data from Krebs *et al.* 1995, 1996, and unpublished data; condition and age data from K.E. Hodges, C.I. Stefan and E.A. Gillis, unpublished paper. Recruitment indices varied too much in each year and between sites to offer a clear or consistent pattern

	Increase	Peak	Decline
Increase rate	Higher	Lower	Lower
Survival	Similar	Lower	Lower
Condition	Poorer	Better	Poorer
Mean age	Similar	Higher	Higher

and experimentally created populations of food-short hares showed that malnourished hares have low body weights, lose weight over winter and commonly die of starvation (Vaughan & Keith 1981). At Kluane, there were no starvation deaths during the low phase, again confirming that hares were not food-limited during this phase. Food addition did result in better body condition and higher hare densities, but neither survival nor reproduction were affected (Stefan 1998).

EVIDENCE OF PREDATION LIMITATION?

There were few predators during the low phase of the cycle, and little reproduction by the predators (O'Donoghue *et al.* 1997). In contrast to Keith *et al.* 1977) data, which showed marked changes in predator density in each year of the low phase, at Kluane predator densities declined and then remained low for several years. Hares on control sites had an annual mortality rate of 71–83%, and despite the scarcity of predators at Kluane, more than three-quarters of these deaths were caused by predators. On the fence and food + fence sites most of the predation was by raptors, but the increased proportion of avian kills did not compensate for the lack of mammalian kills. The survival data thus support the predation hypothesis, because the reduction of predators resulted in higher annual survival rates, while food addition did not.

EVIDENCE FOR INTERACTING EFFECTS OF FOOD AND PREDATION

The higher hare densities on all treatments relative to controls may indicate that dynamics were affected by a food–predation interaction. But these treatment sites were not established *de novo* at the start of the low phase; the treatments began during the previous increase phase. It could be that higher treatment populations during the low phase are the result of higher populations during the peak and decline phases, rather than the result of differing demographic rates during the low phase. But even if that is the case, densities at those times support a food–predation interaction hypothesis (Krebs *et al.* 1995, 1996).

Additionally, the body condition and age structure changes on the manipulated sites support the interaction hypothesis. Although older hares tend to be in better condition than yearlings (Keith 1990; K.E. Hodges, C.I. Stefan, E.A. Gillis, unpublished paper), condition and age were independently affected by the manipulations. The same condition patterns also occur when condition alone of older adults is examined, and when age structures were similar between a control population and a treatment population, the treatment hares were in better condition (K.E. Hodges, C.I. Stefan, E.A. Gillis, unpublished paper). If predation risk alone affected age and condition, food supplementation should not have resulted in better body condition of hares.

INDIRECT EFFECTS OF PREDATION

Predation risk affected condition and age structure, as the fenced population illustrates. As additional confirmation, the food + fence treatment showed a reduction in condition—to the level of that of the control hares—in 1996. In November 1995, a coyote entered the fence; in January 1996, food addition was halted because the coyote was still inside and experimental integrity was already effectively destroyed. Snowshoe hare condition decreased rapidly after these changes.

Changes in condition and age structure did not, however, appear to lead to increased recruitment. The recruitment indices are based on trapping data, and thus it is impossible to distinguish the effects of fecundity, juvenile survival and dispersal on the estimates. Condition does not appear to affect fecundity (K.E. Hodges, C.I. Stefan, E.A. Gillis, unpublished paper), but over-winter weight loss influences fecundity (Keith & Windberg 1978; Cary & Keith 1979; Keith 1990). It is still unclear whether age and condition changes are simply side-effects of reduced predation risk, or whether they are integral to cyclic changes of fecundity (Cary & Keith 1979).

CONCLUSIONS AND FURTHER DIRECTIONS FOR RESEARCH

The evidence from the cyclic low phase at Kluane refutes the food limitation, predation limitation and sequential food–predation hypotheses for hare population dynamics. Food was not limiting and the reactions of the fenced populations should not have occurred if the food hypothesis were true. Population responses on the food addition areas should not have occurred under the predation hypotheses, but the predicted differences in survival between the fenced and unfenced populations did occur. The data are consistent with the risk interaction hypothesis. The observed treatment effects on density, condition, age structure and survival support this hypothesis, and the changes in condition and age structure show that predation has indirect as well as direct effects on hare populations.

Several issues remain unresolved. Knowledge of both fecundity and juvenile survival would be helpful, especially because four litters are born during the low phase (Cary & Keith 1979; Stefan 1998) and because juvenile survival may be crucial to hare population dynamics (Keith & Windberg 1978; Krebs *et al.* 1986; Keith 1990; Gillis 1997). Population dynamics of animals with short generation times and short lifespans are more likely to be sensitive to changes in recruitment than is the case for animals that are longer-lived (Lebreton & Clobert 1991), so understanding

the factors influencing juvenile recruitment would be helpful. During the low phase of the cycle, fecundity is high (Cary & Keith 1979; Stefan 1998) and Gillis (1997) found that first- and second-litter juveniles survived as well as adults during the early increase phase, but that third- and fourth-litter juveniles survived less well. It is difficult to reconcile those apparent trends towards increase with the observed numerical pattern of a several year low phase.

Although the evidence supports the risk interaction hypothesis, the food + fence manipulation did not have a shorter low phase than the control areas. This inability to change the timing of the cycle could result from the small (1 km^2) size of the fenced area and even smaller food addition area, the ability of hares to disperse out of the relatively high density food + fence area, or an insufficient change in food availability or predation risk.

One crucial issue is whether the differing densities reflect the dynamics that occurred earlier in the cycle, or dynamics that occur during the low phase of the cycle. Control populations had similar survival to the food populations, and higher recruitment, both of which counter the observed numbers and suggest that the density differences resulted from the history of the manipulated populations. The relatively low recruitment on treatment areas may also be an artefact of the elevated densities, rather than a population-level response to food and predation. In order to derive a truer sense of the effects of food and predation on demography during the low phase, these manipulations should be introduced at the end of the decline phase.

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