Yellowstone National Park. 1997. Yellowstone's northern range: complexity and change in a wildland ecosystem. National Park Service, Mammoth Hot Springs, Wyoming. 148 pages.

Zeigenfuss, L.C., F.J. Singer, S. Williams and T.L. Johnson. 2002. Influence of herbivory and water additions to willow communities on elk winter range. *Journal of Wildlife Management*, in press.

STAN BOUTIN, CHARLES J. KREBS, RUDY BOONSTRA AND
ANTHONY R.E. SINCLAIR

14

The role of the lynx–hare cycle in boreal forest community dynamics

Snowshoe hare (*Lepus americanus*) and lynx (*Lynx canadensis*) populations show 9- to 11-year cycles throughout the boreal coniferous forests of Canada and Alaska. Lynx cycles, recorded in Hudson Bay trapping records covering many decades, have been analyzed by population ecologists interested in understanding the mechanisms underlying the cycle (Royama 1992, Ranta et al. 1997). Long-term records of hare cycles are less common but there have been two major field programs that have measured demographic changes over at least one full cycle. This includes the work based at Rochester, Alberta by Lloyd Keith and co-workers (Keith et al. 1984, Keith 1990) and our work based at Kluane, Yukon (Krebs et al. 1986, Sinclair et al. 1988, Krebs et al. 1995). These field studies have established the demographic mechanisms that drive changes in hare numbers and have tested mechanistic hypotheses about factors that stop population increase and cause the hare population decline (Keith 1990, Krebs et al. 2001*b*).

It is clear that the lynx and hare are tightly linked (Royama 1992, Stenseth et al. 1998). Lynx show strong functional and numerical responses to changes in hare density (Keith et al. 1977, O'Donoghue et al. 1998). In turn, the dominant proximate cause of hare mortality is predation (Keith et al. 1984, Boutin et al. 1986) with lynx being one of a suite of hare predators. Statistical analyses of time series data suggest that lynx cycles can be explained by a two trophic level interaction whereas hare cycles require a three trophic level interaction (Stenseth et al. 1997). This simple representation masks a rich set of hypotheses concerning the details of trophic interactions and the role that this predator–prey cycle plays in the broader forest community. Over the past 25 years our research team at Kluane has attempted to test hypotheses explaining hare cycles and to place the hare cycle in the broader boreal forest community. The work is unique in that it has combined the case study approach similar to the studies of Serengeti (Sinclair and Arcese 1995), Yellowstone (Houston 1982) and Bialowieza (Jedrzejewska and Jedrzejewski 1998) with large-scale experiments designed to test hypotheses about community organization.

In this chapter we focus on how the hare cycle affects the forest community including its vegetation, vertebrate herbivores, and predators as revealed by the Kluane research. We will address the following questions:

1. How many species and what processes are affected by the lynx–hare cycle?
2. Are trophic levels limited by bottom-up or top-down effects?
3. Is the lynx or hare a keystone species?

We take advantage of the major natural perturbation caused by the cycle to study the response of the community. In addition, we performed large-scale experiments designed to alter each trophic level and monitored how these alterations affected other trophic levels. The boreal coniferous forests of Canada and Alaska represent some of the largest tracts of natural forest left in the world but this is changing rapidly as commercial forestry and oil and gas development press northward. We will end by discussing how these human-caused changes might affect the lynx, hare, and their associated community.

Study area and approach

Details for the Kluane study area and the methods used can be found in Krebs et al. (2001*b*). The 350 km² study area was located in the southwestern Yukon at the base of a broad glacial valley. The forest was roughly an equal mix of willow (*Salix glauca*) shrub communities and mature open and closed (>50% canopy cover) white spruce (*Picea glauca*). The dominant shrubs were willow (*Salix glauca*) and dwarf birch (*Betula glandulosa*). All of the communities were of fire origin but there have been no fires in the past 50 years and over 90% of the forest is more than 100 years old. There has been no commercial forestry in the study site, which is bisected by a single major road, the Alaska Highway.

The northern location and relatively high elevation of the Kluane area creates a highly seasonal environment with below average productivity. The growing season does not begin before the third week of May and killing frosts occur as early as mid August. The timing of arrival of snow is highly variable and accumulation is normally around 1 m. Snowmelt is usually not complete before mid May.

We have been studying snowshoe hares at Kluane since 1977 and the work we describe here occurred from 1986 to 1996. There were two basic components: description of the vertebrate food web, including standing biomass and energy flow, and experimental manipulation of trophic levels. For the first component we used live-trapping and mark-recapture to estimate the abundance of snowshoe hares, deer mice (*Peromyscus maniculatus*) and voles (*Clethrionomys rutilus*, *Microtus* spp.), red squirrels (*Tamiasciurus hudsonicus*) and Arctic ground squirrels (*Spermophilus parryii*.) We did not estimate moose (*Alces alces*) density, but it was low (0.12/km², Gasaway et al. 1992). Lynx and coyote (*Canis latrans*) densities were estimated by a combination of snow track transects, intensive snow tracking, and radiotelemetry monitoring of individuals. We followed changes in relative abundance of other predators including red fox (*Vulpes vulpes*), wolf (*Canis lupus*), wolverine (*Gulo gulo*), and weasel (*Mustela* spp.) by snow track transects but we did not estimate their abundance. We used a combination of telemetry monitoring of prey and snow tracking of predators to estimate kill rates by predators. Marten (*Martes americana*) and fisher (*Martes pennanti*) were absent from our study area.

We performed a series of large-scale experiments designed to "kick" each trophic level (see Krebs et al. 2001*b* for details). We fertilized the forest each spring with nitrogen, phosphorus, and potassium to pulse the plant trophic level. Addition of rabbit chow ad libitum was used to increase the herbivore trophic level (hares, ground squirrels, mice, and voles). We erected a large (1 km²) predator exclosure by using chickenwire combined with electric wires to stop predators from digging under or climbing over the fence. All small herbivores, including snowshoe hares, could move freely through the fence. We also erected a small hare exclosure. Finally treatments were combined to produce a food addition plus predator exclusion treatment and a hare exclusion plus fertilization treatment. These treatments are summarized in Table 14.1.

Changes in the vertebrate food web over the cycle

During our study snowshoe hares underwent a typical cycle whereby they increased to peak autumn densities of 2–3 hares/ha in 1989 and 1990 and dropped to 0.01–0.1 hares/ha in 1993 (Boutin et al. 1995, Krebs et al.

Table 14.1. *Experimental treatments used in the Kluane Boreal Forest Ecosystem Project, 1986–1996*

Treatment	Replicates	Details
Food addition	2	Commercial rabbit chow supplied year round ad libitum, spread over 35 ha
Mammalian predator exclosure	1	Electric fence and chickenwire around 1 km²
Predator exclosure + food addition	1	Electric fence around 1 km² plus rabbit chow spread on central 35 ha
Fertilization	2	Nitrogen, phosphorus, potassium added each spring on 1 km²
Hare exclosure	1	4 ha
Hare exclosure + fertilizer	1	4 ha inside fertilizer replicate

1995, Hodges et al. 2001). The amplitude (minimum spring to maximum autumn densities) was roughly 20- to 40-fold. The peak densities of hares observed at Kluane were relatively low compared to other studies (Hodges et al. 2001). Figure 14.1A shows the standing biomass of the vertebrate herbivore community over the cycle. There are three important things to note. First, hares dominated the vertebrate herbivore biomass at the cyclic peak, comprising 65% of the total biomass. This dropped to about 10% during the low. Over the entire cycle, hares represented roughly 50% of the standing herbivore biomass. Second, total herbivore biomass varied roughly three fold over the cycle. Finally, apart from hares, red squirrels and ground squirrels were the only substantial alternative herbivore biomass available to predators. Because ground squirrels hibernate for eight months of the year, red squirrels are the only alternative prey from September to April. Mice and voles were never >5% of the vertebrate herbivore community (Boonstra et al. 2001*b*).

Predator biomass roughly doubled over the cycle with lynx and coyote being the predominant species (Fig. 14.1B). Fox, wolf, and wolverine were occasional visitors but we think that fox occupied the alpine areas and avoided the valley because of coyotes (O'Donoghue et al. 2001). One pack of wolves passed through our study area occasionally but their numbers were low. During the low phase, great horned owls (*Bubo virginianus*) and red-tailed hawks (*Buteo j. harlani*) equaled the biomass of lynx and coyotes.

Complete food web linkages are outlined in Krebs et al. (2001*a*). Hares were the dominant component of the diet of lynx, coyotes, and owls even during the low phase of the cycle (O'Donoghue et al. 1998, Rohner et al. 2001). All of the predators consumed grouse, voles, ground squirrels, and red squirrels. Hares browsed all of the shrubs and trees in the study area but birch was the preferred species (Smith et al. 1988). Birch comprised roughly 10% of the shrub biomass and it was not present on all of our study sites (Krebs et al. 2001*c*). Hares tended to feed on twigs <5 mm in diameter (Pease et al. 1979, Smith et al. 1988) and these made up roughly 10% of the standing shrub biomass (Krebs et al. 2001*c*).

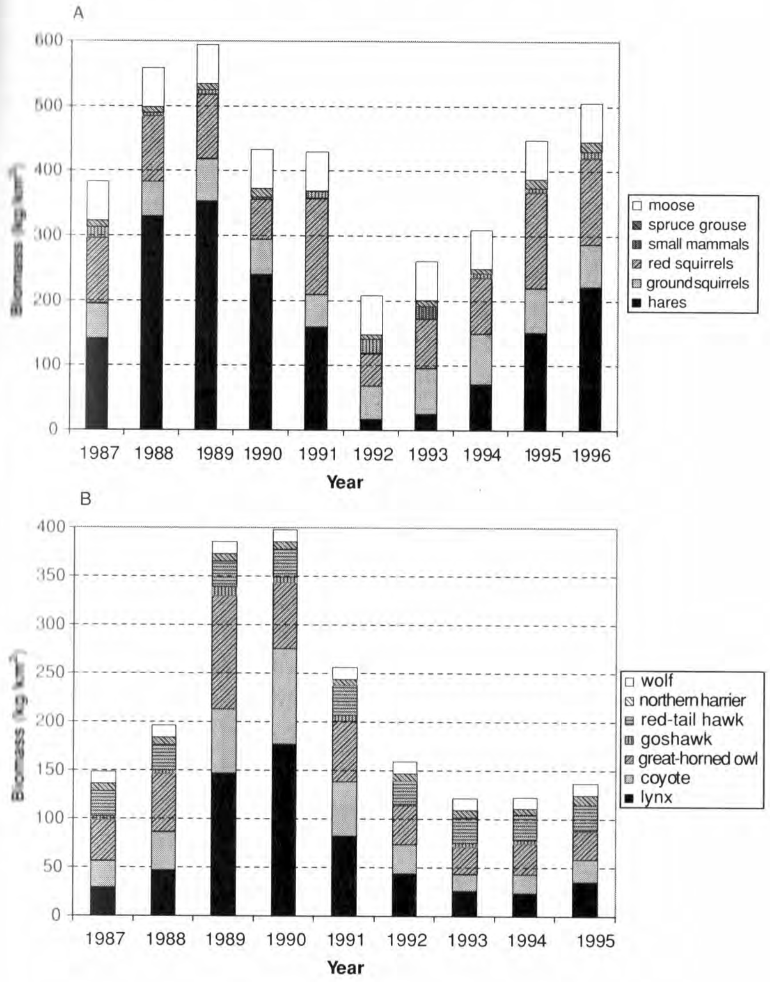

Fig. 14.1. Autumn biomass of vertebrate herbivores (A) and predators (B) at Kluane Lake in 1987–1996.

The plant trophic level

Effects of nutrients

We expected the plant trophic level to be strongly limited by nutrient availability as control sites had extremely low nitrogen values (0.97 ppm, Turkington et al. 1998). Fertilization had strong positive effects on grass and herb growth and biomass (Turkington et al. 1998). Fertilization increased the growth of small willow twigs (<5 mm) by 30% overall (Fig. 14.2). Birch showed similar increases except for the food addition treatment, where they were lower. There were similar increases on the hare exclosure plus fertilization plot, and even higher growth rates on the food addition plot and the predator exclosure plus food plot (Krebs et al. 2001*c*). Growth rates of birch peaked in 1992 on control sites whereas willow tended to decline to the low point of the hare cycle (Krebs et al. 2001*c*). Standing biomass of small twigs and shrubs reached their highest levels in 1992 and there was no difference in relative standing crop on fertilizer versus control grids.

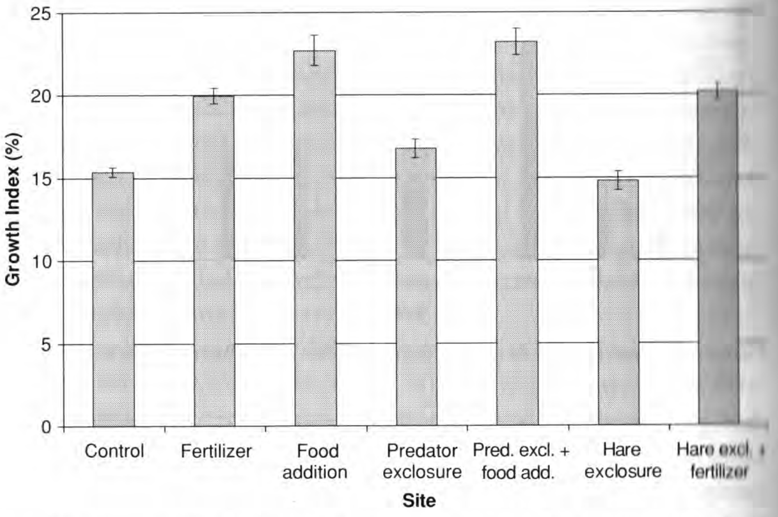

Fig. 14.2. Average growth index (%) of small twigs (<5 mm) of gray willow (*Salix glauca*) on each of the study treatments, with 95% confidence limits. The average was calculated over 1988–1995. The growth index was calculated as:

$$\frac{\text{Dry weight of current annual growth on 5-mm twig}}{\text{Dry weight of complete 5-mm twig}}$$

Effects of herbivores

There was little evidence that mammalian herbivores in the Kluane system affected the composition or abundance of herbs and grasses present (John and Turkington 1995, Turkington et al. 2001). In the case of shrubs, the impact was somewhat different. Browse rates of hares were monitored by following the fates of a tagged sample of twigs. Browsing of birch twigs rapidly increased to >50% in the late increase phase of the cycles and was as high as 80% at the peak and early decline (Fig. 14.3A). Once the hare numbers had crashed, virtually none of the twigs were clipped (Krebs et al. 2001*c*). The pattern of browsing on willow was similar but the percentage clipped on control areas was never >20% (Fig. 14.3B). During high hare densities, birch could not compensate for the loss of twigs due to hare browsing and twig biomass was less than one-fifth that of the previous year (Fig. 14.3A). In contrast, willow was able to fully compensate for the increased clipping by hares.

The density of hares was increased by 5- to 11-fold on the food addition and food addition plus predator exclusion grids (Krebs et al. 1995), and this led to a substantial increase in browse rates of willow. These levels were such that willow was not able to compensate and biomass was reduced. Averaged over the entire cycle, biomass of twigs on the predator exclosure plus food addition treatment was one-third that of controls (Sinclair et al. 2001). Hares had a significant effect on birch during the peak but browsing decreased rapidly thereafter such that total biomass actually increased to a peak in 1992. Browsing by hares on willow had little effect on standing crop. Overall, biomass of shrubs showed a clear cycle but, contrary to expectation, biomass increased from the start of the study to a peak in 1991 and 1992 before declining again (Krebs et al. 2001*c*).

The herbivore trophic level

Effects of plants

Herbivores had relatively little effect on the primary producer trophic level but can the same be said for the effect of plants on herbivores? Growth of grasses, herbs, and shrubs was increased roughly 30% by fertilizing (Krebs et al. 2001*c*, Turkington et al. 2001) but this did not result in higher herbivore biomass (Fig. 14.4). Ground squirrels and red squirrels actually declined on the fertilizer plots whereas meadow voles increased by 40% (Boonstra et al. 2001*b*). Food supplementation produced much stronger

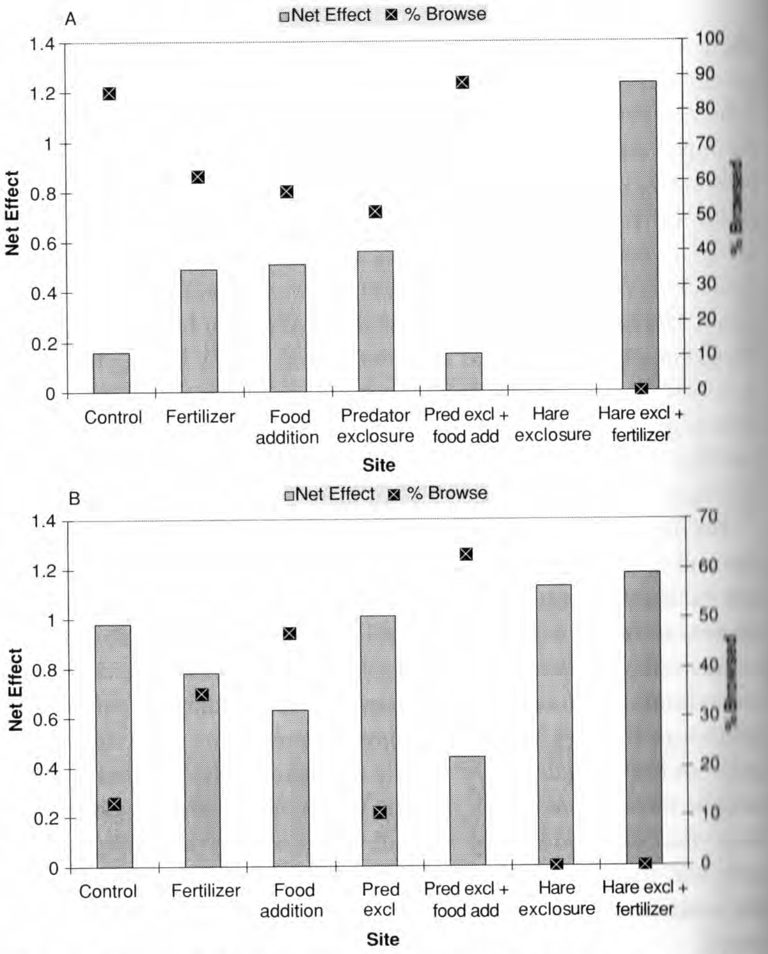

Fig. 14.3. Percentage of bog birch (*Betula glandulosa*) (A) and gray willow (*Salix glauca*) (B) browsed by hares in 1990–1991. The net effect of winter browsing is also shown and was calculated as $(1 - h)(1 + g)$ where h = biomass loss to herbivory and g = growth rate (see Sinclair et al. 2001 for details). Values <1 represent when browsing exceeded growth.

effects than did fertilization. Hare and ground squirrel densities increased 2- to 5-fold on average and this produced an average biomass increase over the cycle of 2.3-fold (Fig. 14.4). In the case of hares, much of the population increase was due to immigration (Krebs et al. 2001*a*). Red squirrels, mice, and voles showed no response to the food addition (Boonstra et al. 2001*a*,*b*).

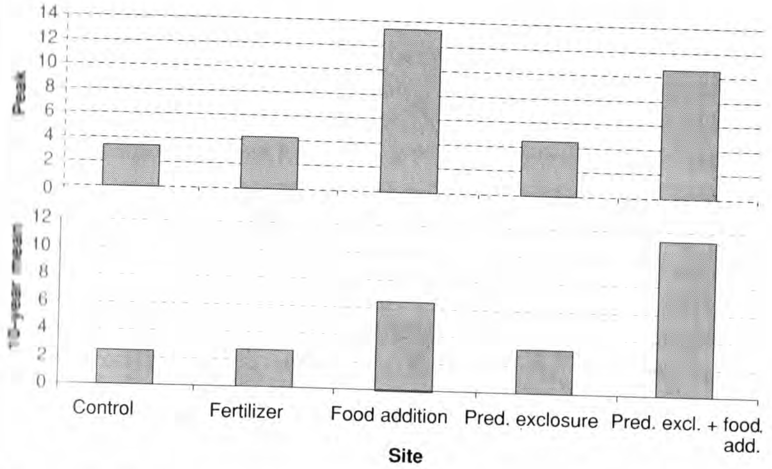

Fig. 14.4. Total herbivore biomass (kg/ha) on experimental treatments in the year of peak biomass and as a mean from 1987 to 1996.

Effects of predators

Predation was a dominant limiting factor for the herbivore trophic level. We recorded 866 mortalities of radiocollared hares on grids excluding the fenced areas (Hodges et al. 2001). Cause of death could be identified in roughly 85% of these cases and >90% of these were attributed to predation. Lynx and coyotes were responsible for 65% to 75% of these mortalities. Figure 14.5 shows the percentage of the autumn hare population removed by lynx and coyotes over winter as determined by radiotelemetry monitoring of hares and calculation of the functional and numerical response of lynx and coyotes from snowtracking. Losses as assessed by telemetry were consistently higher than those determined by snowtracking and both techniques have potential biases (see O'Donoghue et al. 2001). If true losses fell between the two estimates it is clear that lynx and coyote removed a substantial portion of the hare population during the peak and early decline. During the hare low, predators removed 10% to 40%.

We also followed the fates of juvenile hares during their first month of life by radiotelemetry. Mortality rates were high during this period but the striking finding was that lynx and coyotes took very few of these

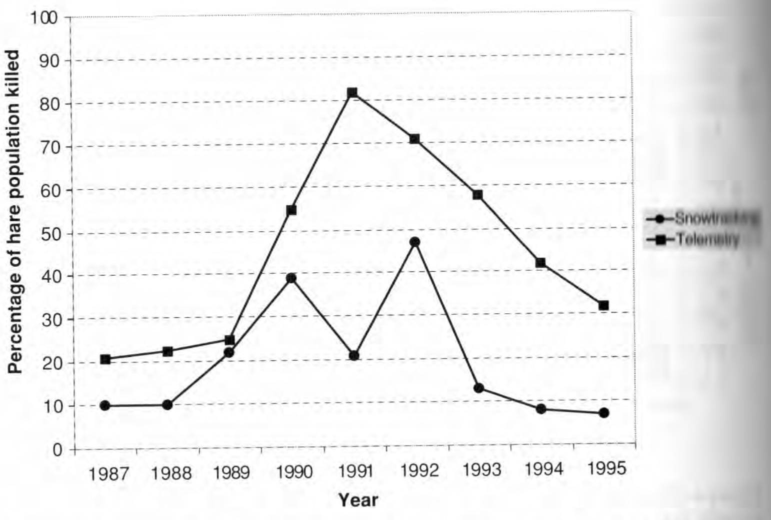

Fig. 14.5. Estimated total impact of predation by coyotes and lynx during winter (October through April) on snowshoe hares from 1987–1988 through 1995–1996 at Kluane. Estimates from snowtracking combined functional and numerical responses of the predators while estimates from telemetry used mortality rates of radiocollared hares.

small animals. Instead red squirrels and ground squirrels were the primary predators. When hares were abundant, up to 40% of the young leverets were killed by squirrels (O'Donoghue 1994, Stefan 1998, Hodges et al. 2001).

We also monitored the fates of ground squirrels and red squirrels via radiotelemetry. Ground squirrels were monitored from 1992 to 1995 and of 130 mortalities, 96% were due to predation (Hubbs and Boonstra 1997, Boonstra et al. 2001*a*). Lynx and coyote were responsible for only 20% to 30% of these losses with the rest caused by raptors. Red squirrels were also taken by coyotes and lynx but losses had little effect on red squirrel densities (Stuart-Smith and Boutin 1995). Winter losses were never >5% (O'Donoghue et al. 2001).

Exclusion of lynx and coyotes improved hare survival significantly during the population peak and early decline but this resulted in a relatively small increase in hare density (Hodges et al. 2001). This was partially due to the fact that hares could move freely through the fence. Once they left the enclosure, they suffered losses equal to hares living outside of the fence.

The combined treatment of food addition plus predator exclusion produced the largest increase in herbivore biomass. The increase over the controls was 6-fold over the entire cycle (Fig. 14.4) and levels reached as high as 18 kg/ha in the spring of the last year of the study. This compared to an average of 2.48 kg/ha for controls.

Linkages between herbivores

We were interested in whether other herbivores were influenced by the hare cycle either indirectly through predator switching or possibly through direct competition. Changes in ground squirrels, forest grouse (spruce grouse: *Falcipennis canadensis*, ruffed grouse: *Bonasa umbellus*), willow ptarmigan (*Lagopus lagopus*), and muskrats (*Ondatra zibethicus*) were directly correlated with changes in hare numbers and these species declined in synchrony with hares (Boutin et al. 1995, see also appropriate chapters in Krebs et al. 2001*b*). Redbacked and meadow vole numbers were inversely correlated with hare numbers (Boonstra et al. 2001*b*). Red squirrel numbers were largely unaffected by changes in hare numbers (Stuart-Smith and Boutin 1995, Boonstra et al. 2001*a*).

The predator trophic level

Effects of herbivores

It is clear that predators had a strong influence on some but not all of the herbivores in the system. The large changes in hare densities over the cycle had a strong influence on both lynx and coyotes. With the exception of the extreme cyclic low, hares represented virtually 100% of the winter diet of both predators (O'Donoghue et al. 1998). Even when hares were very scarce, they still comprised >50% of the biomass of kills. Red squirrels made up as much as 40% of the lynx diet in 1 year of the low but they were never >13% of the coyote's diet (O'Donoghue et al. 1998). Coyotes and lynx made many kills of small mammals in 1 year but mice and voles never formed a large component of the biomass consumed.

The number of lynx and coyotes tracked hare densities with a 1-year lag (Fig. 14.6). Lynx peaked at 17/100 km^2 and coyotes at 9/100 km^2. The amplitude of change was 7.5-fold for lynx and 6-fold for coyotes. Predators declined rapidly in the second winter of the hare crash (1991–1992). This was due to a combination of complete recruitment failure (no tracks of family groups) and relatively high emigration. In 1992–1993 winter survival of lynx plummeted to less than 10% (O'Donoghue et al. 1997, 2001). During this time, a number of lynx were killed by other predators including wolves, wolverine, and another lynx (O'Donoghue et al. 2001). In

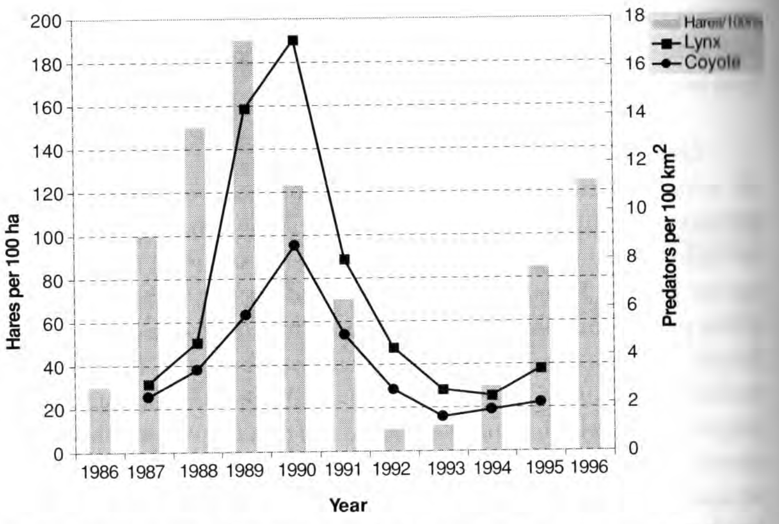

Fig. 14.6. Estimates of densities of snowshoe hares (mean of autumn and late winter estimates) and coyotes and lynx (early winter) for 1986–1997.

contrast, few coyotes died in our study area but 13 of 21 collared animals dispersed. Lynx and coyote populations did not begin to increase until hare numbers began to increase. Family groups did not reappear until 1995–1996.

The results at Kluane are consistent with findings from other northern studies over roughly the same time period. In south central Yukon, Slough and Mowat (1996) found a 10- to 17-fold change in lynx numbers with peak densities of 50/100 km². In the Northwest Territories, Poole (1994) observed a 10-fold change and peak densities of 30/100 km². In both of these areas coyotes were largely absent. These studies and observations of the previous population cycle at Kluane (Ward and Krebs 1985) also reported high emigration rates of lynx during the hare crash. In north central Alberta, lynx and coyote densities varied 3- to 4-fold, with lynx numbers peaking at 10/km² and coyotes at 44/100 km² (Keith et al. 1977, Todd et al. 1981).

Competitive interactions

Both coyotes and lynx relied heavily on snowshoe hares during our study. The question is how do these two similar-sized carnivores co-exist on a relatively limited resource base? Lynx have long been viewed as a snowshoe hare specialist. Coyotes are relative newcomers to the boreal forest and they are considered to be generalists (O'Donoghue et al. 2001). This was not the case at Kluane. Overlap in diet and habitat use remained extremely high between lynx and coyotes even during the hare low. It seemed that the low diversity of alternative prey at Kluane led to coyotes having no alternative but to specialize on hares (O'Donoghue et al. 2001).

Community organization

In general, the Kluane study provides the following insights into the major processes that operate on the vertebrate community. The snowshoe hare dominates the vertebrate herbivore biomass and a broad suite of mammal and raptor species feed primarily on hares. Hares, in turn, inhibit the growth of their main winter food plants, willow and birch, during the hare peak. This effect is short-lived and there appears to be some stimulation of shrub growth one to two years after the hare peak. It appears that the hare is regulated from both above and below with the predator–hare interactions being stronger than the vegetation–hare interactions. These findings are in accordance with statistical time-series analyses (Royama 1992, Stenseth et al. 1997). Predators, on the other hand, are regulated from below (Stenseth et al. 1997). The hare cycle appears to create cycles in most of the small herbivores present either through predators switching to alternative prey as hares decline or through stimulation of berry production through increased nutrient cycling (Boutin et al. 1995, Boonstra et al. 2001*b*). The notable exception to this is the red squirrel whose populations do not appear to be coupled to hares. Red squirrels represent the only alternative prey available to predators in winter.

The Kluane study was designed to test a number of hypotheses related to the regulation of each trophic level (Sinclair et al. 2000, 2001). The focus was on whether the size (biomass) of each level was controlled by bottom-up (White 1978, 1984, Polis and Strong 1997), top-down (Hairston et al. 1960, Menge and Sutherland 1976), or reciprocal effects (Power 1984, Benndorf and Horn 1985). Our results suggest that there is not one pure model that applies to all trophic levels. Instead, we found strong reciprocal effects at the upper trophic levels. Hares and the main predators in the system (lynx, coyote, great horned owl) were tightly linked with predators limiting hare numbers and vice versa. The reciprocal interaction was weaker between herbivores and vegetation. Although hares had some effect on the small twig biomass of the most preferred shrub species, they had little overall effect on the total biomass or species composition of any of the major vegetation compartments. Vegetation was limited by bottom-up nutrient availability.

Despite the fact that we increased vegetation production by 30% through fertilization, we saw very little increase in herbivore biomass. In contrast, food addition to herbivores led to a 3-fold increase overall. We attribute these results to the fact that laboratory rabbit chow represented a major increase in quality as well as quantity of food for hares and ground squirrels. Fertilization served to increase the quantity and quality (Sinclair et al. 2001) of natural vegetation only slightly and this was not enough to overcome other limitations on the hare population. Hares are capable of reaching much higher densities in other habitat types. For example, Slough and Mowat (1996) recorded hare densities twice as high as ours in regenerating pine (*Pinus contorta*) stands some 300 km from the Kluane study site. It would take many years of fertilization at the Kluane site to produce these sorts of hare densities because of the slow response of the plants to increased nutrients.

A 3-fold increase in herbivore densities with food addition did not lead to major changes in shrub vegetation. Although birch could not compensate for the higher browsing during the peak and early decline, it quickly recovered thereafter. It was only when hare densities were pushed to even higher levels and were maintained at or above peak control densities over an entire cycle (food addition plus predator exclusion, Fig. 14.4) that shrub biomass showed significant declines. It appears that chronic high hare densities would be required to change shrub cover in these hare-dominated systems.

Despite overwhelming evidence that predation is the proximate cause of mortality of most herbivores in the Kluane system, and population declines in part are due to lower survival, we did not observe a large increase in herbivore density on the mammalian predator exclusion grid. This was partially due to the fact that avian predation compensated somewhat for the reduced mammalian predation (Hodges et al. 2001). More importantly though, hares moved out of the predator exclosure when their numbers reached high densities (Hodges et al. 2001). We do not know why this occurred, but it may have been that hares were driven to forage more widely to find patches of unbrowsed birch or willow (Hik 1995).

Lynx and coyotes relied heavily on snowshoe hares even during the population crash. In fact, they had few options, as red squirrels represented the only alternative prey during winter. This situation appeared to trigger long-range emigration by lynx and possibly coyotes after the hare crash. This phenomenon has been observed a number of times (Ward and Krebs 1985, Poole 1994, Slough and Mowat 1996, O'Donoghue et al. 2001) and is a unique feature of the boreal forest created by the hare cycles.

Finally, we could not disrupt the hare cycle completely. Single-factor manipulations altered the amplitude of the cycle but only the combination of food addition plus predator exclusion affected both the amplitude and timing of the hare decline. We were able to maintain hare densities at or above peak control levels from 1989 to 1995 on the food addition plus predator exclusion treatment. However, the cycle was still apparent although the amplitude was reduced to a 5-fold change as opposed to 20- to 40-fold changes on controls. It appears that feedbacks between the vegetation–herbivore–predator trophic levels make it difficult to disrupt the cycle completely (see also Royama 1992). The Kluane work did not address the reasons for the broad scale synchrony observed in the long-term Hudson Bay lynx trapping records and snowshoe hare questionnaires (see Ranta et al. 1997).

Is the hare or lynx a keystone species?

Although the concept of keystone species has become overused (Mills et al. 1993), we think that it is applicable in the case of the snowshoe hare for the following reasons. Hares represent the main food for many of the predators in the boreal forest and the elimination of hares would lead to extinction of lynx and coyotes and great horned owls. None of the resident predators were capable of successful recruitment during the hare crash despite expanding their diet to consume alternative prey. A more appropriate test of the keystone species idea would be to replace hare biomass with an equivalent amount of alternative herbivores. Although this is logistically impossible, we can do the thought experiment. Replacing hares with equivalent amounts of moose or ground squirrels would still lead to the elimination of lynx, coyotes and owls because moose are too big to be killed and ground squirrels are unavailable during winter. The situation would be unlikely to change as well if hare biomass were to be converted into red squirrels. Although both lynx and coyotes hunted red squirrels more often during the hare low, they took only a small percentage of the available population. Red squirrels are active for only a small portion of the day during winter, particularly when temperatures are very low. For the majority of time, they are safely hidden in nests that are inaccessible to the main predators. Voles are likely too small for them to be efficient prey items for lynx and coyotes. Capture rates would have to be two orders of magnitude higher to produce the energetic returns obtained from hunting hares. Grouse seem like the only alternative prey that might function as a substitute for hares. Spruce grouse densities in our study were intermediate (50/km^2) relative to published records (Boag and Schroeder 1987, 1992, Martin et al. 2001). Grouse made up a small portion of the diets of lynx and coyotes at Kluane (O'Donoghue et al. 2001) but there is no information available in the literature to indicate whether these predators could specialize on grouse if grouse numbers were increased substantially.

Besides having a major influence on the persistence of predator populations, the hare cycle also acts to entrain cycles in five of the seven other herbivores in the Kluane system (Boutin et al. 1995). In the case of ground squirrels, grouse, ptarmigan, and probably muskrats, this appears to result from predator switching as hares, the primary prey, decline in numbers. Vole numbers appear to cycle in an inverse fashion relative to hares and one hypothesis is that this may be due to a time-lag between increased nutrient cycling from high hare densities and berry production in dwarf shrubs (Boonstra et al. 2001*b*).

It seems that hares possess some unique features that are not easily substituted by other herbivores in the system. Can the same be said for lynx and other predators? This does not appear to be the case. The predator–hare interaction is an important driver of the hare cycle (Keith et al. 1984, Krebs et al. 1995) but it seems that the key predators, lynx, coyote, and great horned owl, are highly interchangeable (Stenseth et al. 1997). The long-term hare studies by Keith and co-workers in central Alberta occurred where lynx were relatively scarce and coyotes were the dominant predator (Keith et al. 1977, Todd and Keith 1983). Great horned owls were partially able to compensate for the exclusion of lynx and coyotes at our Kluane site (Hodges et al. 2001). It seems that removal of any one of these species of predator would not lead to a change in the hare cycle and associated parts of the community.

Is the snowshoe hare a keystone throughout its range? Unfortunately, information on the role that hares play in community dynamics of the montane western coniferous forests of British Columbia and the northwestern U.S. is limited (see Hodges 2000 for a review). However, information on population densities suggests that hare numbers may continue to cycle in the southern part of their range but at less than half of the densities observed in their northern range (Hodges 2000). Because of this, it is

likely that the hare's influence on the community is diminished. In fact, it has been suggested that the presence of lynx in the southern montane portion of the hare's distribution is primarily due to periodic immigration into these areas from more northerly regions following hare crashes (Thiel 1987, Mowat et al. 2000, see also Schwartz et al. 2002).

It has been suggested that the hare cycle is diminished in the southern part of its range because more and more of the available habitat is of lower quality and a broad suite of generalist predators do not allow hare densities to build to levels observed during peaks in the north (Keith et al. 1993). Experiments in western montane forests are required to test this hypothesis but it is likely that lynx and snowshoe hare are secondary components of a more diverse vertebrate community in this region.

Potential effects of human activities

The large tracts of northern coniferous forests in Canada and Alaska are undergoing changes through a variety of human activities: large-scale commercial forestry, widespread oil and gas exploration, and encroachment of agriculture from the south. How resilient are lynx–hare cycles to these activities? We could not completely stop the hare cycle with our relatively small-scale experiments and it is clear that the boreal forest and hare cycles have experienced large-scale natural disturbances such as fire many times in the past. Hare densities are likely higher in young forest and in areas with high shrub cover. Intensive forest management designed to reduce shrub density to favor rapid regeneration of conifer will likely be detrimental to hare and lynx populations. New forest-management approaches designed to approximate patterns of regeneration following natural disturbance such as fire are much less likely to have these negative effects.

Broad changes in the average age of forest cover could possibly affect the amplitude of the cycles but it is unlikely to alter the cycles themselves. The Kluane study suggests that major changes in the hare–predator interaction would be required for this to occur. Conventional forestry leaves a pattern of alternating cut and uncut forest that creates a relatively high amount of edge habitat. It is possible that this could affect the hunting success of predators but not to the degree that the cycle would be disrupted. Hare cycles do disappear near the southern boundary of the species' range and studies by Keith and Bloomer (1993) suggest that this may be due to changes in the proportion of hare habitat versus non-hare habitat. As the amount of useable habitat declines, the probability of hares being killed by a suite of generalist predators in the unfavorable habitat increases. When these rates become high enough the cycle is actually stopped and hares never reach peak densities. It is possible that this could occur in other parts of the hare's range if large tracts of forest were to be converted to unforested areas through agriculture or oil sands mining. However, if the predominant vegetation cover in a region continues to be forest this seems unlikely.

As industrial activities increase in the north, so does the amount of linear corridor development. This in turn, increases public access. These sorts of changes could affect lynx by creating trapper access to refuge areas. Lynx are easily trapped and the numbers of lynx have been greatly reduced in the southern part of their range through habitat loss and heavy trapping pressure. Slough and Mowat (1996) suggested that high numbers of lynx remain in the Yukon despite extensive trapping because large refugia exist. This scenario can change rapidly as oil and gas exploration creates many kilometers of seismic lines that become access routes for trappers. Although these changes may affect lynx negatively, it is likely that they will favor coyotes. Coyotes have expanded their distribution into the boreal forest and it is likely that this has been aided, if not precipitated, by industrial expansion. In the Yukon, coyotes are not widely distributed and they tend to be concentrated in areas where there are major roads. It appears that the hare cycle is robust to relative changes in predator species composition. Whether it would persist if lynx were to disappear completely is another question.

Summary

As mammalian ecologists, it was not hard to be occupied with the lynx–hare cycle when we began our study of the Kluane system. Virtually all of the vertebrate community is linked to the hare in a direct or indirect fashion. The Kluane study has helped to establish the hare–lynx cycle in the broader context of the boreal forest community. The snowshoe hare is the dominant vertebrate herbivore in this system and changes in its numbers have strong effects up the trophic web with lesser effects down the web. Hare cycles directly determine cycles in most vertebrate predators, which indirectly creates cycles in other herbivores through shared predators. Hares do not have major effects on vegetation except on selected species during peak densities. Hares function as a keystone species, and lynx, coyotes, and great horned owls would disappear in the absence of hares. In contrast, it appears that members of the predator guild are highly interchangeable. The Kluane work has provided insights into the strength of the various trophic relationships and their robustness to experimental perturbation. The experiments we conducted were large scale as far as experiments go, but they were very small scale relative to the changes that are about to unfold in the world's northern forests. The lynx–hare cycle has proven to be remarkably robust but it is crucial that ecologists continue to monitor this vertebrate complex as the large experiment of industrial development unfolds on the landscape. There is still much to be learned about this fascinating system.

Acknowledgments

We wish to thank all of the workers and colleagues who participated in the Kluane Project. We thank Dennis Murray and J. David Brittell for helpful comments. Finally we thank Cathy Shier and Ainsley Sykes for support in preparation of the manuscript.

Literature cited

Benndorf, J. and W. Horn. 1985. Theoretical considerations on the relative importance of food limitation and predation in structuring zooplankton communities. Pages 383–396 *in* W. Lampert, editor. *Food Limitation and the Structure of Zooplankton Communities*. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, Germany.

Boag, D.A. and M.A. Schroeder. 1987. Population fluctuations in spruce grouse: what determines their number in spring? *Canadian Journal of Zoology* **65**:2430–2435.

Boag, D.A. and M.A. Schroeder. 1992. Spruce grouse (*Dendragapus canadensis*). *In* A. Poole, P. Stettenheim and F. Gill, editors. *The Birds of North America*. The Academy of Natural Sciences, Philadelphia, The American Ornithologists' Union, **No. 5**. Washington DC, USA.

Boonstra, R., S. Boutin, A. Byrom, T. Karels, A. Hubbs, K. Stuart-Smith, M. Blower, and S. Antpoehler. 2001*a*. The role of red squirrels and Arctic ground squirrels. Pages 179–214 *in* C.J. Krebs, S. Boutin, and R. Boonstra, editors. *Vertebrate Community Dynamics in the Kluane Boreal Forest*. Oxford University Press, New York, New York, USA.

Boonstra, R., C.J. Krebs, S. Gilbert, and S. Schweiger. 2001*b*. Voles and mice. Pages 215–239 *in* C.J. Krebs, S. Boutin, and R. Boonstra, editors. *Vertebrate Community Dynamics in the Kluane Boreal Forest*. Oxford University Press, New York, New York, USA.

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.

Boutin, S., C.J. Krebs, R. Boonstra, M.R.T. Dale, 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, V.O. Nams, 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.

Gasaway, W.C., R.D. Boertje, D.V. Grangaard, D.G. Kelleyhouse, R.O. Stephenson, and D.G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs* **120**:1–59.

Hairston, N.G., F.E. Smith, and L.B. Slobodkin. 1960. Community structure, population control and competition. *American Naturalist* **94**:421–425.

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. 2000. Ecology of snowshoe hares in southern boreal and montane forests. Pages 163–206 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires, editors. *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder, Colorado, USA.

Hodges, K.E., C.J. Krebs, D.S. Hik, C.I. Stefan, E.A. Gillis, and C.E. Doyle. 2001. Snowshoe hare demography. Pages 141–178 *in* C.J. Krebs, S. Boutin, and R. Boonstra, editors. *Vertebrate Community Dynamics in the Kluane Boreal Forest*. Oxford University Press, New York, New York, USA.

Houston, D.B. 1982. *The Northern Yellowstone Elk: Ecology and Management*. MacMillan, London, United Kingdom.

Hubbs, A.H. and R. Boonstra. 1997. Population limitation in Arctic ground squirrels: effects of food and predation. *Journal of Animal Ecology* **66**:527–541.

Jedrzejewska, B. and W. Jedrzejewski. 1998. Predation in vertebrate communities: the Białowieża primeval forest as a case study. *Ecological Studies*. Volume 135. Springer Verlag, Berlin, Germany.

John, E. and R. Turkington. 1995. Herbaceous vegetation in the understory of the boreal forest: does nutrient supply or snowshoe hare herbivory regulate species composition and abundance? *Journal of Ecology* **83**:581–590.

Keith, L.B. 1990. Dynamics of snowshoe hare populations. Pages 119–195 *in* H.H. Genoways, editor. *Current Mammalogy*. Plenum Press, New York, New York, USA.

Keith, L.B. and S.E.M. Bloomer. 1993. Differential mortality of sympatric snowshoe hares and cottontail rabbits in central Wisconsin. *Canadian Journal of Zoology* **71**:1694–1697.

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., 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., S.E.M. Bloomer, and T. Willebrand. 1993. Dynamics of a snowshoe hare population in fragmented habitat. *Canadian Journal of Zoology* **71**:1385–1392.

Krebs, C.J., B.S. Gilbert, S. Boutin, A.R.E. Sinclair, and J.N.M. Smith. 1986. 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., S. Boutin, R. Boonstra, A.R.E. Sinclair, J.N.M. Smith, and 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., R. Boonstra, S. Boutin, and A.R.E. Sinclair. 2001*a*. What drives the 10-year cycle of snowshoe hares? *BioScience* **51**(1):25–35.

Krebs, C.J., S. Boutin, and R. Boonstra, editors. 2001*b*. *Vertebrate Community Dynamics in the Kluane Boreal Forest*. Oxford University Press, New York, New York, USA.

Krebs, C.J., M.R.T. Dale, V.O. Nams, A.R.E. Sinclair, and M. O'Donoghue. 2001*c*. Shrubs. Pages 92–115 *in* C.J. Krebs, S. Boutin, and R. Boonstra, editors. *Vertebrate Community Dynamics in the Kluane Boreal Forest*. Oxford University Press, New York, New York, USA.

Martin, K., C. Doyle, S. Hannon, and F. Mueller. 2001. Forest grouse and ptarmigan. Pages 240–260 *in* C.J. Krebs, S. Boutin, and R. Boonstra, editors. *Vertebrate Community Dynamics in the Kluane Boreal Forest*. Oxford University Press, New York, New York, USA.

Menge, B.A. and J.P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. *American Naturalist* **110**:351–369.

Mills, S.L., M.E. Soulé, and D.F. Doak. 1993. The keystone-species concept in ecology and conservation. *BioScience* **43**(4):219–224.

Mowat, G., K.G. Poole, and M. O'Donoghue. 2000. Ecology of lynx in northern Canada and Alaska. Pages 265–306 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires, editors. *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder, Colorado, USA.

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

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., S. Boutin, D.L. Murray, C.J. Krebs, E.J. Hofer, U. Breitenmoser, C. Breitenmoser-Wuersten, G. Zuleta, C. Doyle, and V.O. Nams. 2001. Coyotes and lynx. Pages 275–323 *in* C.J. Krebs, S. Boutin, and R. Boonstra, editors. *Vertebrate Community Dynamics in the Kluane Boreal Forest*. Oxford University Press, New York, New York, USA.

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.

Polis, G.A. and D.R. Strong. 1997. Food web complexity and community dynamics. *American Naturalist* **147**:813–846.

Poole, K.G. 1994. Characteristics of an unharvested lynx population during a snowshoe hare decline. *Journal of Wildlife Management* **58**:608–618.

Power, M.E. 1984. Depth distributions of armoured catfish: predator-induced resource avoidance? *Ecology* **65**:523–528.

Ranta, E., V. Kaitala, and J. Lindstrom. 1997. Dynamics of Canadian lynx populations in space and time. *Ecography* **20**:454–460.

Rohner, C., F.I. Doyle, and J.N.M. Smith. 2001. Great horned owls. Pages 339–376 *in* C.J. Krebs, S. Boutin, and R. Boonstra, editors. *Vertebrate Community Dynamics in the Kluane Boreal Forest*. Oxford University Press, New York, New York, USA.

Royama, T. 1992. *Analytical Population Dynamics*. Chapman & Hall, London.

Schwartz, M.K., L.S. Mills, K.S. McKelvey, L.F. Ruggiero, and F.W. Allendorf. 2002. DNA reveals high dispersal synchronizing the population dynamics of Canada lynx. *Nature* **415**:520–522.

Sinclair, A.R.E. and P. Arcese, editors. 1995. *Serengeti II: Dynamics, Management and Conservation of an Ecosystem*. University of Chicago Press, Chicago, Illinois, USA.

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.

Sinclair, A.R.E., C.J. Krebs, J.M. Fryxel, R. Turkington, S. Boutin, R. Boonstra, P. Seccombe-Hett, P. Lundberg, and L. Oksanen. 2000. Testing hypotheses of trophic level interactions: a boreal forest ecosystem. *Oikos* **89**(2):313–328.

Sinclair, A.R.E., C.J. Krebs, R. Boonstra, S. Boutin, and R. Turkington. 2001. Testing hypotheses of community organization for the Kluane ecosystem. Pages 407–436 *in* C.J. Krebs, S. Boutin, and R. Boonstra, editors. *Vertebrate Community Dynamics in the Kluane Boreal Forest*. Oxford University Press, New York, New York, USA.

Slough, B.G. and G. Mowat. 1996. Lynx population dynamics in an untrapped refugium. *Journal of Wildlife Management* **60**:946–961.

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.

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

Stenseth, N.C., W. Falck, O.N. Bjørnstad, and C.J. Krebs. 1997. Population regulation in snowshoe hare and Canadian lynx: asymmetric food web configurations between hare and lynx. *Proceedings of the National Academy of Sciences of the United States of America* **94**:5147–5152.

Stenseth, N.C., W. Falck, K.S. Chan, O.N. Bjørnstad, M. O'Donoghue, H. Tong, R. Boonstra, S. Boutin, C.J. Krebs, and N.G. Yoccoz. 1998. From patterns to processes: phase and density dependencies in the Canadian lynx cycle. *Proceedings of the National Academy of Sciences of the United States of America* **95**:15430–15435.

Stuart-Smith, A.K. and S. Boutin. 1995. Predation on red squirrels during a snowshoe hare decline. *Canadian Journal of Zoology* **73**:713–722.

Thiel, R.P. 1987. The status of Canada lynx in Wisconsin, 1865–1980. *Wisconsin Academy of Sciences, Arts and Letters* **75**:90–96.

Todd, A.W. and L.B. Keith. 1983. Coyote demography during a snowshoe hare decline in Alberta. *Journal of Wildlife Management* **47**:394–404.

Todd, A.W., L.B. Keith, and C.A. Fischer. 1981. Population ecology of coyotes during a fluctuation of snowshoe hares. *Journal of Wildlife Management* **45**:629–640.

Turkington, R., E. John, C.J. Krebs, M.R.T. Dale, V.O. Nams, R. Boonstra, S. Boutin, K. Martin, A.R.E. Sinclair, and J.N.M. Smith. 1998. The effects of NPK fertilization for nine years on boreal forest vegetation in northwest Canada. *Journal of Vegetation Science* **9**:333–346.

Turkington, R., E. John, and M.R. Dale. 2001. Herbs and grasses. Pages 69–91 *in* C.J. Krebs, S. Boutin, and R. Boonstra, editors. *Vertebrate Community Dynamics in the Kluane Boreal Forest*. Oxford University Press, New York, New York, USA.

Ward, R.M.P. and C.J. Krebs. 1985. Behavioural responses of lynx to declining snowshoe hare abundance. *Canadian Journal of Zoology* **63**:2817–2824.

White, T.C.R. 1978. The importance of a relative shortage of food in animal ecology. *Oecologia* **3**:71–86.

White, T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* **63**:90–105.