What Drives the 10-year Cycle of Snowshoe Hares?

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In 1831 the manager of a Hudson's Bay Company post in northern Ontario wrote to the head office in London. The local Ojibway Indians were starving, he reported, because of a scarcity of "rabbits," and they were unable to trap for furs because they spent all their time fishing for food (Winterhalder 1980). These shortages of so-called rabbits, which apparently occurred approximately every 10 years, are regularly mentioned in Canadian historical documents from the 18th and 19th centuries. Those rabbits were in fact snowshoe hares (*Lepus americanus*), and their 10-year cycle is one of the most intriguing features of the ecology of the boreal forest.

Ten-year cycles were first analyzed quantitatively when wildlife biologists began to plot the fur trading records of Hudson's Bay Company during the early 1900s. The Hudson's Bay Company, established in 1671, kept meticulous records of the numbers of furs traded from different posts spread across Canada. The most famous time series drawn together from those records was that of Canada lynx (Elton and Nicholson 1942; Figure 1). The lynx is a specialist predator of snowshoe hares, and the rise and fall in lynx numbers mirrors, with a slight time lag, the rise and fall of snowshoe hare populations across the boreal region.

The spectacular cycles of snowshoe hares and their predators have captured the attention of biologists as well as historians. These cycles are highlighted in virtually all ecology texts and are often cited as one of the few examples of Lotka-Volterra predator–prey equations, a simple model which shows never-ending oscillations in the numbers of predators and their prey. Cycles seem to violate the implicit assumption of many ecologists that there is a balance in nature, and anyone living in the boreal forest would be hard pressed to recognize a balance among the boom and bust in nature's economy. The challenge to biologists has been to understand the mechanisms behind these cycles, which has not been easy. One cycle lasts 10 years, and few PhD students or researchers wish to take 10 years to obtain $n = 1$. Fortunately,

THE TEN-YEAR CYCLE OF SNOWSHOE HARES—ONE OF THE MOST STRIKING FEATURES OF THE BOREAL FOREST—IS A PRODUCT OF THE INTERACTION BETWEEN PREDATION AND FOOD SUPPLIES, AS LARGE-SCALE EXPERIMENTS IN THE YUKON HAVE DEMONSTRATED

over the last 40 years ecologists working in Alberta, the Yukon Territory, and Alaska have put together an array of studies that have resolved most, but not all, of the enigmas behind these cycles (Keith 1990, Boutin et al. 1995).

To understand any fluctuating population, one must first know in detail the mechanisms of changes in births, deaths, and movements that are the proximate causes of the changes in numbers. Before we describe these details, we should note that these 10-year hare cycles tend to occur in synchrony across broad regions. Indeed, hares across most of Canada and Alaska reached a peak in 1997–1999 during the most recent cycle. We explain the reasons behind this synchrony below, but let us note here that movements of hares cannot explain these population changes via immigration or emigration. Movements on a local level might be important, but at the regional level all populations rise and fall in unison. Population changes must be driven by changes in births and deaths.

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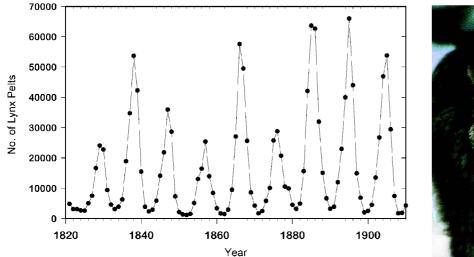
Figure 1. Canada lynx fur returns from the Northern Department of the Hudson's Bay Company from 1821 to 1910. The Northern Department occupied most of western Canada. The cycle for these data averages 9.6 years. Data are from Elton and Nicholson (1942). Photo: Mark O'Donoghue.

Reproductive and survival changes

Snowshoe hares can have three or four litters over a summer, with five leverets on average in each litter. All hares begin to breed in spring when they are 1 year old, so age at sexual maturity is a constant. If reproductive rates are to vary, only litter size or the number of litters can change. Lloyd Keith and his students at the University of Wisconsin, working in central Alberta, supplied the first detailed description of the way in which hares change their reproductive rate over a 10-year cycle (Cary and Keith 1979). Reproductive output reaches its peak very early in the phase of population increase, when females are producing 16–18 young per summer. It then begins to fall rapidly while numbers are still rising; it reaches a nadir in the year of the density peak or 1–2 years thereafter, during the decline phase of the cycle. The response of reproductive output to hare density seems to lag 1–2 years, so that, as shown in Figure 2, for example, the lowest repro-

ductive output occurred in 1973, 2 years after the density peak of 1971. We found a similar but not identical pattern of response in hares in the southwestern Yukon. The reproductive rate at the cyclic peak in the Yukon was about two-thirds of the maximum, compared with one-half of the maximum in the Alberta peak. But reproduction in both areas was minimal in the decline phase (about one-third of maximum reproduction) and highest in the early increase phase of the 10-year cycle (Stefan 1998, Hodges 2000).

Changes in mortality rates are the other driver of changes in hare numbers over the cycle. At Kluane Lake in the Yukon we measured survival rates of hares with radio collars during two population cycles. Additional data on survival of hares over two cycles in central Alberta was obtained through mark-and-recapture methods and radiotelemetry (Keith 1990). The pattern of change for adult hare survival is shown in Figure 3. Adult survival rates begin to drop slowly
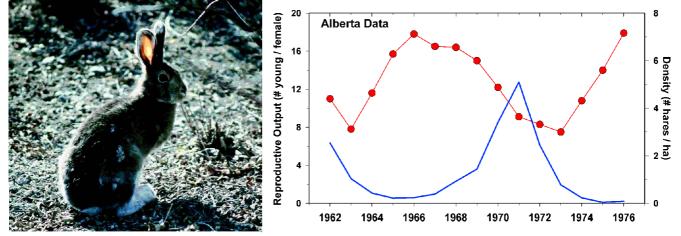

Figure 2. Changes in the annual reproductive output of female snowshoe hares in the Rochester area of central Alberta, 1962–1976. Reproductive output was measured in autopsy samples. Data from Cary and Keith (1979). Photo: Alice Kenney.
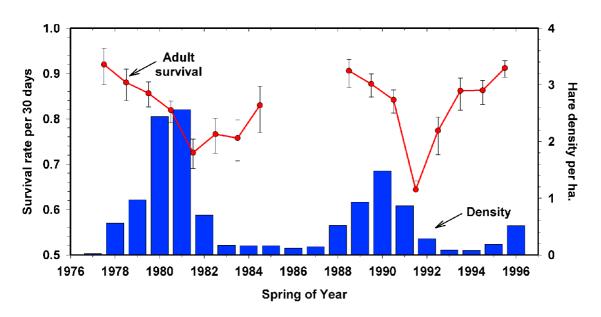
Figure 3. Changes in adult hare survival rates over the 10-year cycle at Kluane Lake, Yukon, from 1977 to 1996. Hare density (histogram) in spring of year t is plotted along with survival rates averaged from spring of year t to t+1 for radio-collared hares in control areas. Too few hares were captured in 1985–1987 to estimate survival accurately.

as the population increases to a peak but then drops dramatically for 1 to 2 years, part of the cause of the collapse in population numbers (Krebs et al. 1986, Hodges 2000a). Once low numbers are reached, adult survival rates improve slowly but do not reach the maximum until 4 to 5 years after the peak.

Juvenile survival can be broken down into preweaning survival for the first 30 days of life, and postweaning survival from 30 days to 1 year of age the following April. Postweaning survival follows the pattern already illustrated in Figure 3 for adult hares. Preweaning survival is more difficult to measure, and we have data only from the Yukon for this stage of the life cycle. We caged pregnant hares caught in the wild when they were near term and then radio-tagged the leverets immediately after birth when the cage was removed. Figure 4 shows that survival is very poor in this early stage. Relatively high survival occurs only in the first 2 to 3 years of the increase phase, and survival is already low before peak hare density is reached. Preweaning survival remains low in the peak and at least 2 years into the decline phase, and the lowest survival occurs near the end of the decline when hare density is already very low (Stefan 1998).

The demographic pattern of the hare cycle is remarkably clear and

consistent. Lloyd Keith and colleagues found the same changes in central Alberta cycles that we found in southwestern Yukon cycles (Keith and Windberg 1978). The key finding is that both reproduction and survival rates begin to decay in the increase phase of the cycle, 2 years before peak densities are reached. Maximal reproduction and highest survival rates occur early in the increase phase of the cycle. By the late increase phase, reproduction has already slowed and survival rates of both adults and juveniles are falling.
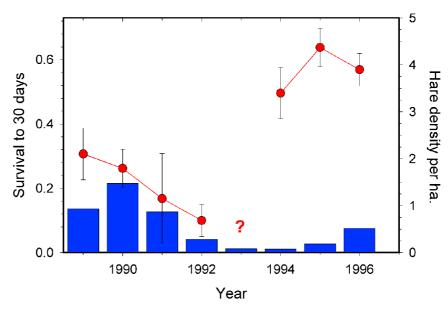

Figure 4. Preweaning survival of snowshoe hares over a population cycle at Kluane Lake, Yukon Territory. Leverets were radio-tagged at birth and followed for 30 days. It was impossible to obtain any juveniles in the summer of 1993. Hare density in spring is shown by the histogram.

Both reproduction and survival rates continue to fall for 2 to 3 years after the peak of the cycle, and over the low phase they start to recover to high values.

Causes of the cycle

What causes these changes in reproduction and survival? There are three main factors that seem most likely to cause hare cycles: food, predation, and social interactions. In addition to these single-factor explanations, two multifactor explanations have been suggested, one involving food and predation, and the other—the most complex hypothesis—involving all three factors.

Many other factors might affect snowshoe hare cycles, but these seem more likely to be modifying influences than primary causes. Disease and parasitism are two ecological factors that might affect hare populations but do not seem to be an essential cause of cycles. Parasite loads, for example, might cause hares to be in poor condition and therefore more susceptible to predators. Lloyd Keith and his students surveyed hare parasite loads for many years in Alberta and concluded that none of the many parasites of the hares caused much direct mortality (Keith et al. 1985). Experimental work with antihelminthics in field populations of hares either had no measurable impact on reproduction and survival (Sovell and Holmes 1996) or produced minimal effects (Murray et al. 1997). The conclusion is that disease and parasites may affect some hare populations sporadically (see reports in Chitty 1948, 1950, for example), but they cannot be an essential cause of cycles.

The food hypothesis is attractive because it can explain both why reproduction changes over the cycle and why survival might change as well. There are two variants of the food hypothesis. First, hares may run out of food and starve, or, second, the quality of the food may decline. Because hares eat a variety of green plants in the summer, no one has considered food shortage in summer to be an important factor. Winter food plants are the small terminal twigs of willow, birch, and small trees, as well as other shrubs; most studies have concentrated on the possibility that winter foods are limiting to hares (Keith et al. 1984). Like all herbivores, snowshoe hares have preferred winter foods and may browse a large fraction of these preferred plants at the peak of the cycle.

There is little evidence from our Yukon studies that overall food quantity is limiting at any time. We measured food abundance over the cycle by quantifying edible forage and we assessed consumption rates of marked twigs. Consumption increased markedly during the peak (Smith et al. 1988, Hik 1995, Krebs et al. 2001), with 80% to 90% of the available bog birch being consumed. However, only 20% to 40% of the grey willow—the dominant shrub in the area—was consumed, thus indicating that food was not limiting at any time in the cycle. If the absolute abundance of food were limiting, we should have found hares that had starved, but only about 3% of the hare mortalities could be directly attributed to starvation.

Alternatively, food quality could change over the cycle. John Bryant at the University of Alaska suggested one attractive qualitative food hypothesis based on secondary chemicals: Shrubs and small trees can fight back against browsers by increasing their content of secondary chemicals such as tannins and resins, which deter digestion in herbivores (Bryant 1981). Indeed, experimental browsing of shrubs in Alaska has shown that the plants can respond to damage by increasing their secondary chemical defenses (Bryant et al. 1985). The key question is whether these plant changes can influence the hare cycle.

To answer this question, we conducted five food-addition experiments during two hare cycles in the southwestern Yukon. In four we provided high-quality rabbit chow without limit to hares; in the fifth experiment we added high-quality natural food to a declining hare population (Krebs et al. 1985, 1995, Sinclair et al. 1988). The response of hares to rabbit chow is classic: Hares move into the food-addition areas and their density increases approximately two- to threefold in comparison with control areas. But once the density increases on the food-addition areas, the hare cycle continues unchanged. Hares decline in number at the same time and at the same rate on the food areas as on unmanipulated controls.

Artificial food-addition experiments have been criticized because the added food is high quality and not natural. We tried to address this criticism by supplying natural food to one declining hare population. Tony Sinclair and Jamie Smith had shown that snowshoe hares largely avoided small white spruce trees because the needles contain camphor (Sinclair and Smith 1984, Rodgers and Sinclair 1997). Consequently, small spruce seedlings were the least preferred food in cafeteria trials with hares. But foliage from large white spruce trees with branches beyond the reach of hares contain no camphor, and these branches become highly preferred food when supplied in a cafeteria trial. This observation was dramatically verified when a large white spruce tree was blown over by a windstorm: Hares devoured the fallen branches. We therefore decided to feed a population of hares through a decline by cutting down white spruce trees and thus providing natural, highly preferred food to a collapsing hare population.

Stan Boutin and Scott Gilbert did this experiment over three winters, with the results shown in Figure 5. The extra natural food produced no detectable effect on the rate of population collapse. The failure of this extra food to affect the hare population decline was shown clearly on five areas in two cycles in the southwest Yukon. Such results imply that food shortage by itself is not the explanation for the hare cycle. Whatever secondary chemical changes occur in winter food plants, they are at most a contributing factor, not the primary cause of the hare collapse.

Another way of approaching the possible role of food in hare cycles is to improve the quality of the vegetation by adding nutrients in fertilizer. We ran this experiment from 1987 to 1996 on two areas in the southwestern Yukon, each
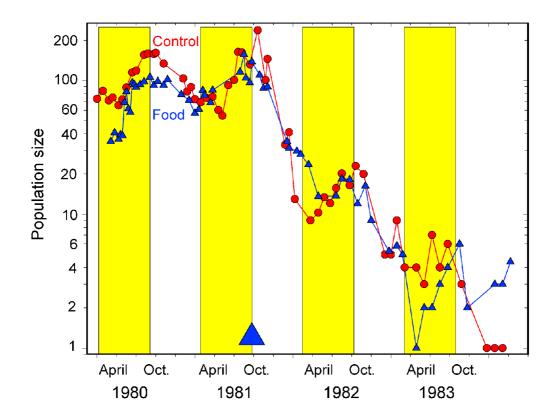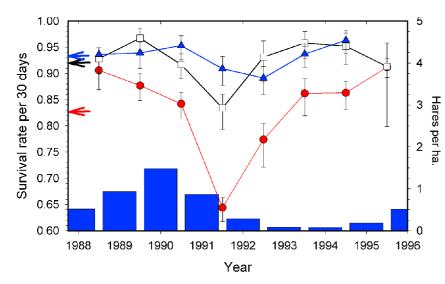
Figure 5. Changes in snowshoe hare numbers on control (1050, red) and food-supplemented (blue) areas during the population decline of 1981–1983 at Kluane, Yukon. The natural feeding experiment was begun in October 1981 (blue triangle). Summer months are shaded yellow. Data are from Krebs et al. (1985).

1 km². On each area we added NPK fertilizer each spring to increase the availability of soil nutrients. Boreal forest soils are typically impoverished in nutrients, particularly nitrogen, and nutrients added through fertilizer are immediately taken up by plants. We measured plant responses to nutrient additions and found large increases in individual plant growth in grasses, shrubs, and trees (Turkington et al. 1998). None of this plant improvement resulted in more snowshoe hares on the fertilized areas, relative to the controls; we therefore concluded that the dynamics of the hare cycle cannot be changed by nutrient additions to the ecosystem. The message seemed to be repeated: The hare cycle is not driven primarily by plant–herbivore interactions.

The predation hypothesis is the next most likely explanation for the hare cycle. In our studies with radio-collared hares, the immediate cause of death of 95% of the hares was predation by a variety of predators, the main ones in the Yukon being lynx, coyotes, goshawks, and great horned owls (Rohner and Krebs 1996, O'Donoghue et al. 1997). Few hares died with signs of malnutrition, and those that did starve were found more often in the increase and peak phases rather than in the decline (Hodges 2000a). In contrast to adult hares, leverets are killed by a variety of small raptors, such as boreal owls, red-tailed hawks, kestrels, and hawk owls, and by small mammals, particularly red squir-

rels and ground squirrels. Of the leverets with radio tags, 81% died because of predation (O'Donoghue 1994). These observations of natural history support the contention that predation by a variety of birds and mammals plays an important role in the hare cycle.

For mammalian predators in winter, we used snow tracking to monitor density changes and kill rates of lynx and coyotes. All hare predators showed strong numerical changes that lagged behind the hare cycle 1–2 years (Boutin et al. 1995). In addition, both lynx and coyotes killed more hares per day in the peak and decline phases than during the increase. These kill rates were well above previous estimates and well in excess of energy demands. Surplus killing seems to be a characteristic feature of these predators.

To test the predation hypothesis, we excluded mammalian predators from two areas by constructing electric fences in the Yukon, each 1 km². We also attempted to exclude avian predators from smaller areas inside the electric fence by means of fish netting and monofilament fishing line strung in trees, but these proved impractical and ineffective. The fence was permeable to hares and other small mammals, which could move in and out at will. In one fenced area we also added food, so we had a combined treatment manipulating predation pressure and food supplies (Krebs et al. 1995). Because of the size of the exclosures and the main-

Figure 6. Changes in survival rates of snowshoe hare numbers on control and fenced areas during the population cycle of 1988–1996 at Kluane, Yukon. The arrows show the mean survival rate for each treatment. The survival rate per 30 days is averaged over each year, with 90% confidence limits, for radio-collared hares.

tenance they required, we were unable to replicate these fence treatments.

The main impact of the electric-fence predator exclosures was to increase the survival rate of radio-collared hares. Figure 6 shows that the collapse in survival that normally occurs in the peak and decline phases of the cycle was nearly eliminated by the exclusion of mammalian predators. There is a slight decrease in survival during the decline phase with the combined predator exclosure and food treatment, but the impact of additional food on survival during the decline is small. The mortality rate is almost entirely driven by predation.

Two further conclusions follow from these experiments. Inasmuch as avian predators had access to the two predator exclosures, avian predation by itself is not sufficient to explain the changes in survival rates. There is a slight reduction in survival inside the predator exclosures during the decline (Figure 6), and this is a measure of the impact of bird predation by itself on hare survival. Since many species of predators are involved in causing the collapse in preweaning, juvenile, and adult hare survival, we cannot pinpoint the role of any individual predator species. In particular, the snowshoe hare cycle is not strictly a lynx–hare cycle, as many textbooks claim, and if the lynx is removed from the predator community—as it is on Anticosti Island in the St. Lawrence River in eastern Canada—the hare cycle continues unchanged because of predator compensation (Stenseth et al. 1998).

If we can explain the changes in mortality rates by predation, how can we explain the changes in reproduction that accompany the cycle? We have attacked this question experimentally by providing hares on two open areas with supplemental food year-round. We measured annual reproductive output for female hares by multiplying pregnancy rates and average litter sizes for each of the summer litters and summing these for each breeding season. Figure 7 summarizes our data. Reproductive output at Kluane Lake was severely reduced in the decline phase, as Lloyd Keith (Cary and Keith 1979) found in Alberta (Figure 2). Adding
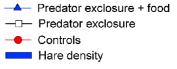
food during the peak of the cycle in 1989 and 1990 had no impact on reproductive output (O'Donoghue 1994). However, during the decline phase in 1991 and 1992, the predator exclosure plus food treatment caused a dramatic increase in reproductive output over that found in control hares (Hik 1995, Stefan 1998). Because we were unable to obtain these reproductive data on food addition sites in 1991 and 1992, we do not know if it is the additional food or the exclusion of mammalian predators, or a combination of these factors, that produced the results shown in Figure 7.
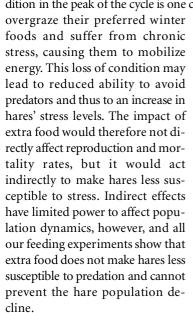
Indirect effects

How might predator exclusion affect reproductive output? There has been much interest in the indirect effects of predators on prey (Lima 1998). One way in which predators might cause a decline in reproductive output is by stressing hares through high rates of encounter and repeated unsuccessful attacks during the peak and decline phases (Boonstra et al. 1998a). Chronic stress has many direct detrimental effects on mammals, including reduction in reproductive rate, mobilization of energy reserves, and increased susceptibility to diseases and parasites. Stress effects may also be indirect and long term, affecting adult brain function (Lupien and McEwen 1997) and offspring viability and behavior (Matthews 2000). Figure 8 illustrates these ideas for a hypothetical hare cycle in which predation pressure causes chronic stress. Unfortunately, we have not yet been able to measure stress levels through an entire hare cycle, but the data we have from declining and low populations is consistent with this hypothetical scheme.

What is the role of high-quality food in the hare cycle? Population density increased on areas provided with supplemental food. Hares on the areas provided with supplemental food did not lose weight over winter and in general were in better body condition than control hares. Food quality clearly limits body condition and population density in hares. In addition to these direct effects, changes in food quality could have subtle indirect effects on hares, contributing to chronic stress and making them more or less

Figure 7. Reproductive output of female snowshoe hares over a population cycle at Kluane Lake, Yukon. The blue line shows hare density in control populations. Supplemental food (green bars) does not affect reproductive output at the peak of the cycle, but in the decline phase of 1991 and 1992 high reproductive output was sustained on the experimental area fenced from mammalian predators and provided with supplemental food (red bars). We were unable to measure reproductive output in every year for all treatments, and thus we do not know for the critical decline years of 1991 and 1992 whether reduced reproductive output is caused by food or predation or both.

able to avoid predators, parasites, and disease (Hik 1995, Boonstra et al. 1998a, Hodges et al. 1999). Poorer body condition in the peak of the cycle is one consequence when hares overgraze their preferred winter foods and suffer from chronic stress, causing them to mobilize energy. This loss of condition may lead to reduced ability to avoid predators and thus to an increase in hares' stress levels. The impact of extra food would therefore not directly affect reproduction and mortality rates, but it would act indirectly to make hares less susceptible to stress. Indirect effects have limited power to affect population dynamics, however, and all our feeding experiments show that extra food does not make hares less susceptible to predation and cannot prevent the hare population decline.

Another possible source of stress for hares is social interactions. Snowshoe hares are not particularly good candidates for social regulation of population size, and most hypotheses about hare cycles have ignored the social dimension

(Krebs 1986). Hares are not territorial, and aggression seems to be restricted to males competing in mating chases and to females resisting attentive males. There are no records of in-

Figure 8. The chronic stress hypothesis as an explanation of the changes in reproduction that accompany the snowshoe hare cycle. Chronic stress is postulated to arise from signs of predator abundance (odor, visual sightings, tracks, unsuccessful chases), and is thus related to predator densities. According to this hypothesis, any physiological measure of chronic stress, such as cortisol levels, should be maximal late in the decline phase of the hare cycle. The immune system would also be compromised because of chronic stress. We do not yet know whether this hypothesis is the correct explanation for the reduced reproduction that occurs during the hare cycle.
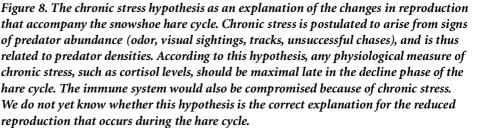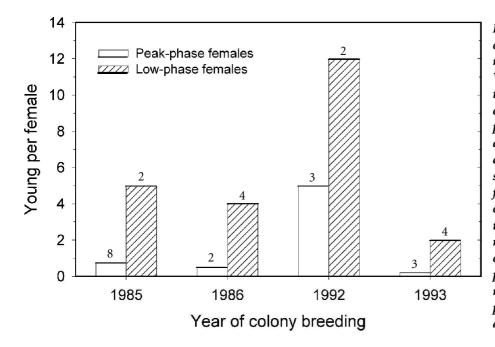
Figure 9. The annual reproductive output of snowshoe hare females maintained in a colony at Vancouver. Individual females were taken from field populations and classified by the state of the field population at the time of initial capture. For 4 years there were enough females to compare simultaneously the population of females taken from the peak phase of the cycle with those taken from the low phase. Low-phase females maintain a lifetime reproductive output much greater than peak-phase females; these lab results mimic the observed changes in field populations. Numbers above bars are numbers of females.

fanticide in hares, and without territoriality and infanticide there would seem to be little room for social interactions to play a role in population dynamics.

Nevertheless, there remain some puzzles. One is the lack of an explanation for the low phase, which follows the decline and lasts 2–4 years (Boonstra et al. 1998b). A second puzzle is evidence implicating the role of maternal effects in reproductive performance. Tony Sinclair maintained a laboratory colony of hares for 14 years in Vancouver to test for impacts of secondary chemicals on food choice. Females were maintained in individual cages with high-quality food and were treated for potential parasites. Hares in captivity regularly live 5–7 years, much longer than they live in nature. Therefore the colony at times consisted of a mixture of females trapped live in the Yukon from peak populations and from low populations. Figure 9 compares the reproductive output in captivity of these two groups of hares (A.R.E. Sinclair, personal communication, 1999). Hares taken from low populations maintained a lifetime reproductive output more than double that of hares taken from peak populations, suggesting that female hares are already programmed for their reproductive success early in life, and no matter how fine an environment is provided, they cannot change.

These results are completely serendipitous: This was not a planned comparison, females could not be matched for age, and this reproductive measurement was not the reason the colony was maintained. There was no correlation in these colony data between the reproductive output of mothers and daughters, suggesting that this effect was not a genetic. A planned comparison of colony hares should be carried out to see whether the effect can be verified in another population. At present, these results must be considered unproven, but tantalizing.

We are now close to understanding the snowshoe hare cycle. The 10-year cycle is a result of the interaction between predation and food supplies, but of these two factors, predation is clearly the dominant process. The impact of food is felt largely in winter and it is mostly indirect. Hares do not usually die directly of starvation or malnutrition—the immediate cause of death is virtually always predation. But food quality and quantity affect body condition and in this way may predispose hares to predation, increased parasite loads, and higher levels of chronic stress. These indirect effects of predation and food are the probable cause of reduced reproductive output. Hares in peak and declining populations must trade off safety and food, and these behavioral tradeoffs define the dynamics of the decline (Hik 1995, Hodges 2000b). The result is a time lag in both the indirect effects and the direct effects of predation, which causes the cyclicity. The low phase of the cycle is the combined result of continuing predation mortality and slowly recovering reproductive potential.

Synchrony in the hare cycle

Not only do snowshoe hare numbers fluctuate in 10-year cycles, but these cycles tend to occur in synchrony across much of the boreal forests of Canada and Alaska. Synchrony is not absolute, however; different regions within Canada can drift out of phase. Smith (1983) used questionnaire data on snowshoe hare abundance from 1931 to 1948 to measure synchrony across Canada (Figure 10). He concluded that there was a large area of cyclic synchrony in northern Manitoba and Saskatchewan that was 2 years ahead of "average," and areas in southern Ontario and Quebec that were up to 2 years later than average for this time period. Populations in the Yukon were also up to 2 years later than average. In some sense, the peak of the hare cycle for this time period was like a traveling wave in a pond, with the center in the middle of the boreal forest. The result of this kind of traveling wave is that synchrony falls off with distance, as shown
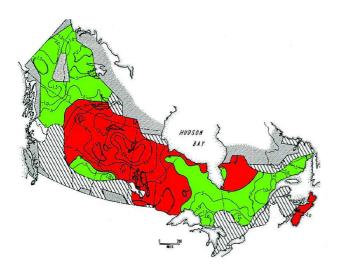
Figure 10. Synchrony in snowshoe hare cycles across Canada, 1931–1948, as measured by questionnaires (Chitty 1948, 1950). The average peak phase across Canada was scaled as 0.0, and the contour lines indicate peaks occurring earlier than average (red, negative contours) or later than average (green, positive contours). During this period, hare peaks were reached earliest in the central boreal region of northern Saskatchewan and Manitoba (Smith 1983).

in Figure 11 for lynx fur return data from the Canadian provinces for the period 1920–1987 (Ranta et al. 1997).
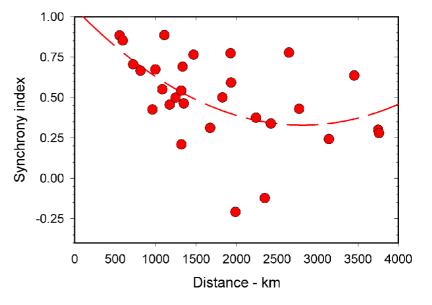
Because Canada lynx fur harvests are highly correlated with snowshoe hare numbers, the fur trading records of the Hudson's Bay Company have been used extensively to analyze synchrony in the 10-year cycle (Stenseth et al. 1999, Haydon and Greenwood 2000). Regions across Canada showed a higher degree of synchrony in the 19th century than during the 20th century, for reasons that are not clear. Within Canada, Stenseth et al. (1999) showed, there were three broad regions within which the lynx cycle was simi-

larly structured (Figure 12). These three regions coincided with the climatic zones defined independently from the North Atlantic Oscillation (NAO), a climatic oscillation similar to the El Niño in the Pacific Ocean. The reasons for these correlations are not clear, though Stenseth et al. (1999) suggest that the changing snow levels associated with the NAO might affect the hunting efficiency of lynx.
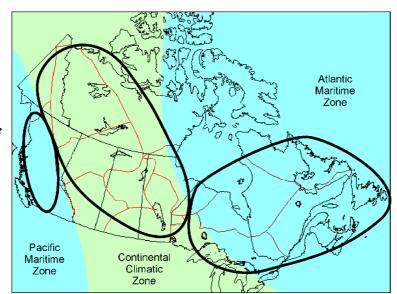
What ecological factors might cause synchrony across large geographic regions? Two general models for synchrony can be suggested, one driven by weather and one by dispersal movements. The most famous model to synchronize the hare cycle across North America is the weather model related to the sunspot cycle (Sinclair et al. 1993). Sunspots and hare numbers are highly correlated for three time periods during the past 250 years: 1751–1787, 1838–1870, and 1948–1986, which were all periods of high-amplitude sunspot fluctuations (Sinclair and Gosline 1997). Because sunspots affect broad weather patterns, it is possible that sunspots might, through weather, entrain snowshoe hare cycles across the continent when solar activity is unusually high. The main problem with this explanation is that there is at present no mechanism for sunspot-affected weather patterns to translate into demographic impacts on hares. All our studies in the Yukon suggest the predominant role of predators in driving the hare cycle. As mentioned above, Stenseth et al. (1999) suggested an indirect impact of snow depth on hunting success of mammalian predators as one way in which synchrony might be coordinated, but there are no data to test this suggestion. There is also a problem in reconciling the global nature of sunspot activity with the local variations in synchrony shown in Figure 10.

Dispersal movements would appear to be the more likely explanation for synchrony. Hares disperse on a local scale of a few kilometers (Gillis 1997, Hodges 2000b), so hare movements seem incapable of affecting synchrony except on a local scale. Predator movements are more likely the key element causing synchrony within the boreal region. Long-range

Figure 11. Synchrony among pairs of provinces in Canada for lynx fur return data from 1920 to 1987. The geographic midpoint of each province was used to calculate the distance between provinces. The synchrony index is the simple correlation coefficient between the pairs of provinces. Synchrony falls off with distance and then rises again because British Columbia and the Yukon as well as eastern Canada tend to peak 2–3 years later than the average of central Canada. The dashed line is a simple polynomial regression. Data from Statistics Canada, as used by Ranta et al. (1997).

Figure 12. Climatic regions (shaded) within Canada, defined by the North Atlantic Oscillation. The large circles define the three regions within which the lynx cycle is most structurally similar. These regions fit within the independently defined climatic zones. Stenseth et al. (1999).

dispersal movements of radio-collared lynx have been described in several studies (Mowat et al. 2000). Documented dispersal movements up to 1100 km have been recorded, with 15 movements greater than 500 km. These dispersal movements were detected only because the dispersing lynx were caught by fur trappers, and thus constitute a biased (truncated) set of true dispersal movements. Houston (1978) reported similar data for movements of great horned owls, with 36 banded owls moving 265 to1415 km before being shot, trapped, or found dead. These data for great horned owls and lynx indicate the potential for predator dispersal to synchronize hare cycles over large areas of the boreal forest region (Ydenberg 1987, Ims and Steen 1990). If predators move from food-poor to food-rich regions on a scale of 1000 km, they could readily bring local regions into synchrony in the general pattern shown in Figure 10. The predator-dispersal hypothesis for synchrony of hare cycles is attractive because it is parsimonious, since predation plays such an important role in driving the hare cycle through its direct effects on hare mortality and its indirect effects on hare reproduction.

Lynx, which have been declared a threatened species in the continental United States, and the dynamics of its interaction with snowshoe hares in states with southern boreal forests, such as Montana, are in critical need of study (Ruggiero et al. 2000). If hare populations are synchronized regionally by predator movements, the fragmentation of hare and lynx habitat in the southern parts of Canada and in the northern United States could break the ebb and flow of these linkages. The present shortage of genetic information on the geographic structure of both snowshoe hare populations and lynx populations needs to be remedied to define these spatial issues more clearly for conservation.

Conclusions

Lotka and Volterra were partly correct when they guessed that the snowshoe hare cycle was a predator–prey oscillation, but they missed the critical point that the cycle can be understood only by analyzing three trophic levels rather than two. The hare cycle is produced by an interaction between predation and food supplies, and its biological impacts ripple across many species of predators and prey in the boreal forest.

The boreal forest is one of the great ecosystems of the earth, and the 10-year snowshoe hare cycle is one of the most striking features of this ecosystem. After 70 years of questionnaire research, time series analyses, and field experiments, we have a good understanding of the dynamics behind the hare cycle and the importance of predation and food supplies in regulating that cycle. The snowshoe hare is a critical species in the boreal forest: If it should disappear, many species of predators would go with it, and the structure of the plant community would be altered substantially.

The boreal forest ecosystem and the 10-year cycle in snowshoe hares are clearly resilient to a variety of natural disturbances, from forest fires to short-term climatic fluctuations, but it is unclear whether they can withstand the changes that humans impose without collapsing. The impact of directional climate change on the boreal forest community will probably be less in the short term than the impact of forestry and other human activities such as oil and gas exploration. We should explore the limits of resilience of the snowshoe hare cycle as forest harvesting extends north into the boreal forest, lest we compromise this fascinating system.

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