

Using experimentation to understand the 10-year snowshoe hare cycle in the boreal forest of North America

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Abstract

1. Population cycles have long fascinated ecologists from the time of Charles Elton in the 1920s. The discovery of large population fluctuations in undisturbed ecosystems challenged the idea that pristine nature was in a state of balance. The 10-year cycle of snowshoe hares (*Lepus americanus* Erxleben) across the boreal forests of Canada and Alaska is a classic cycle, recognized by fur traders for more than 300 years.
2. Since the 1930s, ecologists have investigated the mechanisms that might cause these cycles. Proposed causal mechanisms have varied from sunspots to food supplies, parasites, diseases, predation and social behaviour. Both the birth rate and the death rate change dramatically over the cycle. Social behaviour was eliminated as a possible cause because snowshoe hares are not territorial and do not commit infanticide.
3. Since the 1960s, large-scale manipulative experiments have been used to discover the major limiting factors. Food supply and predation quickly became recognized as potential key factors causing the cycle. Experiments adding food and restricting predator access to field populations have been decisive in pinpointing predation as the key mechanism causing these fluctuations.
4. The immediate cause of death of most snowshoe hares is predation by a variety of predators, including the Canada lynx (*Lynx canadensis* Kerr). The collapse in the reproductive rate is not due to food shortage as was originally thought, but is a result of chronic stress from predator chases.
5. Five major issues remain unresolved. First, what is the nature of the predator-induced memory that results in the prolonged low phase of the cycle? Second, why do hare cycles form a travelling wave, starting in the centre of the boreal forest in Saskatchewan and travelling across western Canada and Alaska? Third, why does the amplitude of the cycle vary greatly from one cycle to the next in the same area? Fourth, do the same mechanisms of population limitation apply to snowshoe hares in eastern North American or in similar ecosystems across Siberia? Finally, what effect will climatic warming have on all the above issues? The answers to these questions remain for future generations of biologists to determine.

KEYWORDS

boreal forest, food shortage, Kluane ecosystem, *Lepus americanus*, predation, sublethal stress, synchrony, travelling waves, Yukon

1 | INTRODUCTION

Population fluctuations have always captivated people partly because they can affect livelihoods as pest species that attack crops or as game animals that provide meat or furs. When Charles Elton discovered the detailed data compiled by the Hudson Bay Company on furs traded from different parts of Canada since 1673, he quickly realized that these data were at variance with the common belief in the stability of natural systems not subject to human disturbance. Elton began what has become a tidal wave of literature on population cycles and their causes and consequences for ecosystems. The natural variation in demography exhibited by cyclic populations has proven extremely useful for understanding the complex interplay between plants, herbivores and predators.

The 10-year cycle of snowshoe hares and their predators showed up clearly in fur returns from across Canada and Alaska, and presented itself as a test case for understanding one particular population cycle which had a 300-year history written in fur returns on a continental scale. The list of ecological factors that could produce a cycle was quickly identified since the mechanisms had to show a time-lag in their effects. Overgrazing and food shortage fits this profile, as does predation mortality, parasites and diseases. Other factors like sunspots were brought into the picture but quickly dismissed as potential agents because their temporal fluctuations did not match the snowshoe hare cyclic time-scale.

Early work by Green and Larson (1938) and Green, Larson, and Bell (1939) postulated that a stress disease they called "shock disease" was the cause of cyclic declines. This early work was dismissed as an artefact of studies done on hares in crowded laboratory rooms. But the general idea of Green and Larson (1938) that hares might suffer from some intrinsic ailment was dormant until 60 years later when it was brought back in studies of chronic stress (Boonstra, 2013) as described below.

In 1948, William Rowan, the Head of Zoology at the University of Alberta, declared that the 10-year cycle was the "outstanding problem of Canadian conservation." He stimulated Lloyd Keith to carry out a series of studies on the snowshoe hare cycle in Alberta, beginning his career with an early book on cycles (Keith, 1963). Lloyd Keith was convinced that the hare cycle was driven by two factors, food shortage in winter, which depressed reproduction, and predation in the decline phase. He and his students' research in central Alberta was the first to lay a firm quantitative foundation to the demography of the hare cycle (Keith, 1983; Keith & Windberg, 1978).

From this earlier research, we launched our research programme in 1976 in the Kluane Region of the Yukon. Previous research had laid out four clear hypotheses to test experimentally:

1. The hare cycle was caused by winter food shortage and the delayed recovery of winter browse damaged by excessive browsing by hares.
2. The hare cycle was caused by changes in food quality as a result of heavy browsing by peak hare densities which triggered an increase in secondary compound production by the plants.

3. The hare cycle was caused by heavy predation and the time-lag inherent in predator rates of population growth relative to that of the hares.
4. The hare cycle was caused by both food and predators, with food shortage at the peak followed by heavy predation in the decline.

Our approach consisted of obtaining detailed information on demographic parameters combined with measures of quantity and quality of hare food in the winter and estimates of kill rates of hare predators to test predictions following from each hypothesis. We went one step further, however, by experimentally manipulating food availability and predation rates. Our approach was not guided by a priori mathematical models because there was only limited empirical information to parameterize such models and the manipulations were the obvious ones based on the Lloyd Keith work.

2 | MATERIALS AND METHODS

All our studies on snowshoe hares were conducted by live trapping and radiocollaring of individuals. The details of these methods and those for radiotelemetry have been described in detail in Hodges et al. (2001). Population estimates of all the hare data presented here were calculated in DENSITY 4 and 5 (Efford, 2009). The major experiments are described in detail in Boutin et al. (2001), and much more detail about our general methods is given in Krebs, Boutin, and Boonstra (2001).

2.1 | Natural history of the snowshoe hare

Critical to understanding the population dynamics of snowshoe hares is knowledge of their life history and the constraints of their diet and habitat. These hares are the major herbivores in the boreal forest ecosystem, both in terms of biomass and of impact (Boonstra et al., 2016). We summarize the key features of their natural history here (see Hodges, 2000 for references). They are pure white in winter and brown in summer. All breeding takes place in summer, with a maximum of four litters being produced. Females breed synchronously and engage in post-partum insemination. The gestation period is 35–37 days, with the first litter (born in late May in the Yukon) averaging three leverets, the second five, and the third and fourth (if they have them) between three and five leverets. Young do not breed in their year of birth. Although the rare hare can live 7 years, most live very short lives (the average life span is 1 year), with almost all mortality being attributed to predation (Boutin, Krebs, Sinclair, & Smith, 1986; Hodges et al., 2001; Keith & Windberg, 1978; Murray, Keith, & Cary, 1998), and 70% of breeding females being yearlings. Virtually all avian and mammalian predators in the boreal forest eat hares (see the food web, Figure 6), with even the granivore and herbivore (red squirrels and Arctic ground squirrels respectively) eating hare leverets in summer. In winter, snowshoe hares are basically the only prey for predators to eat, since red squirrels are much less vulnerable due to reduced activity, ground squirrels hibernate, grouse are relatively rare

and small mammals live in the subnivean space below the snow. Hare diet in winter is largely restricted to the twigs of tall shrubs (dwarf birch *Betula glandulosa* and willow *Salix glauca*) and the ends of spruce branches available above the snowpack, but in summer includes forbs, grasses, leaves and some woody browse. The availability of browse in the winter is not only complex and dynamic as changing snow depth allows hares to access twigs at greater heights but it also makes twigs inaccessible as hares do not burrow into snow to access covered twigs (Keith, Cary, Rongstad, & Brittingham, 1984). Deaths during winter, even during the peak and decline, are not driven by starvation caused by absolute food shortage, but rather by increasing predation rates (Keith et al., 1984).

2.2 | Our experimental results

2.2.1 | Food addition experiments

In 1976, we decided to test the simplest hypothesis for hare cycles, that it was a result of winter food shortage. We set out three 10 by 10 grids (30-m spacing of live trap stations, 7.3 ha) for winter feeding of commercial rabbit chow (Krebs, Gilbert, Boutin, Sinclair, & Smith, 1986) for the period from 1977 to 1984. One of the two grids on islands was too difficult to provision in winter and we had to discard it. We had many problems with disturbances to feeding stations by bears and moose so these experiments were not perfect. They were, however, most consistent with the hypothesis that winter food shortage was not necessary for snowshoe hare declines because although the food addition served to increase density during the increase and peak phases, it failed to stop the hare decline. We were criticized for these feeding experiments because we used artificial high-quality rabbit chow as food and we pushed densities to above normal. To assess the validity of these criticisms we carried out another experiment of feeding hares in winter on natural food. Hares completely debark and consume the twigs of trees that blow down naturally. So we cut down large white spruce (*Picea glauca* (Moench) Voss) and aspen (*Populus tremuloides* Michx.) trees to feed hares on a 9-ha plot in winter (Krebs, Boutin, & Gilbert, 1986). Control and manipulated hare populations declined in unison with no measurable effect of the extra natural food provided in the decline (Figure 1). We decided that, while winter food is very important to hares, it was not the limiting factor in the Kluane boreal forest in these years. We also found that the proximate cause of virtually all the mortalities of our sample of radiocollared hares could be attributed to predation (Boutin et al., 1986) which matched the findings by Keith et al. (1984) studying a hare crash in Rochester, Alberta. Thus, we had two replicates of a hare crash pointing to predation as the causal agent.

2.2.2 | Food quality experiments

The second hypothesis postulating food quality as a driver of the hare cycle has been more controversial and difficult to test. Bryant (1981) showed that severe browsing in winter increased the level of toxic secondary compounds in four species of deciduous trees in Alaska and

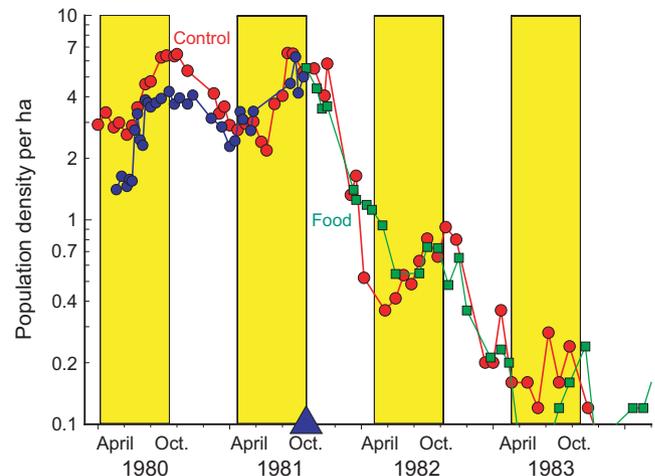


FIGURE 1 Natural feeding experiment on snowshoe hares at Kluane Lake, Yukon, during a population decline, 1981–1984. Two control trapping areas (red and blue symbols) were monitored until October 1981 when the feeding experiment began on one area (symbols) with winter feeding of felled white spruce and aspen trees (dark green symbols, Krebs, Boutin, et al., 1986). Feeding continued during the following three winters with no effect on the rate of population decline

that the carry-over of severe browsing could influence the snowshoe hare cycle via food quality. Fox and Bryant (1984) postulated that increases in secondary plant chemicals after heavy browsing resulted in high levels for 2–3 years after browsing damage, and this time delay could be a delayed density-dependent factor in generating hare cycles via changes in food quality. Sinclair, Krebs, Smith, and Boutin (1988) tested the secondary plant chemistry hypothesis by measuring phenols and resins in winter food plants over one hare cycle. They found that, contrary to the predictions of this hypothesis, secondary compounds decreased from the increase phase to the peak phase and into the decline of the hare cycle. While secondary chemicals had a strong influence on food choice by hares (Rodgers & Sinclair, 1997), food quality did not appear to be a limiting factor for hare population fluctuations. The complexities of plant secondary compound effects on herbivores urges caution in reaching this conclusion (Torregrossa & Dearing, 2009) and more research is needed in other parts of the boreal forest.

2.2.3 | Food addition and predator reduction experiments

It is always possible that a combination of factors determines population growth rates, hence, during the next cycle (1986–1996) we decided to manipulate both food and predation. We fed three larger live trapping grids (20 × 20 trap points, 30-m spacing, 32.5 ha) continuously year-round with commercial rabbit chow spread by a fertilizer spreader (Boutin et al., 2001). We surrounded one of these grids with a 2-m-high electrified fence around 1 km² to keep mammalian predators out. We could not keep avian predators out, so this was a predator reduction experiment, not a complete predator removal

manipulation. We built a second electrified fence around another area to try to measure the impact of mammalian predator removal alone. We fertilized two other large areas (1 km²) with commercial NPK fertilizer to test the bottom-up model of regulation. All these experiments are described in detail in Krebs et al. (2001).

The results surprised us (Krebs et al., 1995) and a synopsis of these 10-year experiments is illustrated in Figure 2. Feeding hares approximately tripled population density but did not affect the decline (as illustrated earlier in Figure 1). Density increase in feeding areas was largely by immigration rather than by increased reproductive success. The largest effect occurred on the combined food + predator reduction area, where densities reached about 11 times the control values at the cyclic peak. Statistically this shows an interaction between food and predation. But this was a puzzle because we could not detect any indication that winter food supplies were insufficient on control areas (Hodges, Boonstra, & Krebs, 2006; Hodges, Stefan, & Gillis, 1999). Population declines in hares are the result of severely decreased survival rates during the crash and one of our objectives with our experiments was to see if we could maintain survival rates to prevent the decline. Although we improved survival on all our treatments, the maximum effect was seen on the combined food + predator reduction area (Figure 3) where survival rates were high enough to maintain densities at peak control levels well after the other areas had crashed.

As with our studies of the previous cycle we found that the proximate cause of virtually all adult hare mortality was predation. Thus, the evidence continued to build for predation rather than food shortage as being a necessary driver of the hare cycle. Our experiments proved conclusively that high-quality food could not keep hares from the jaws and talons of their predators nor did hares die of starvation when protected from predators.

Our experimental approach to testing the role of food and predation in the hare cycle has been criticized on several fronts. Logistics

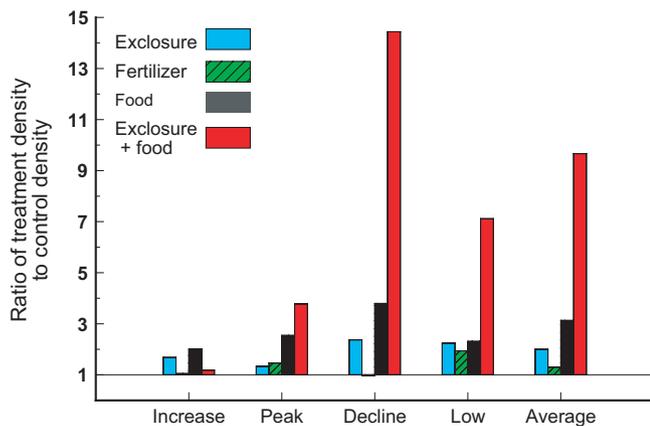


FIGURE 2 Ratio of population densities for the four experimental treatments to average control population densities at the same phase of the hare cycle. If there is no treatment effect, we expect a ratio of 1.0. During the peak and decline phases, the mammalian predator exclosure doubled density, food addition tripled density, and the combined treatment of food addition and predator reduction increased density 11-fold

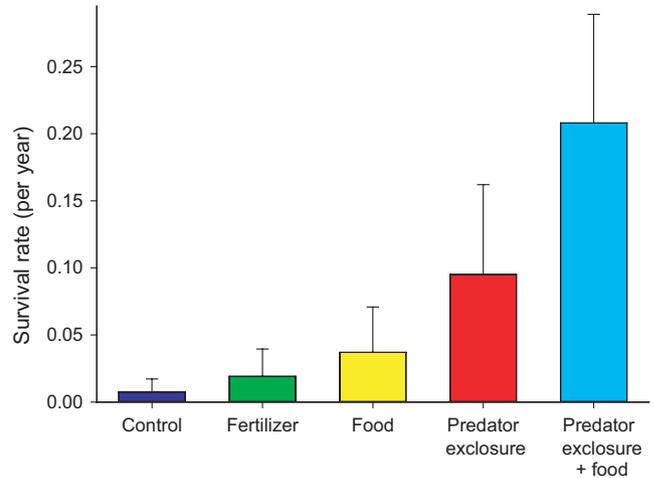
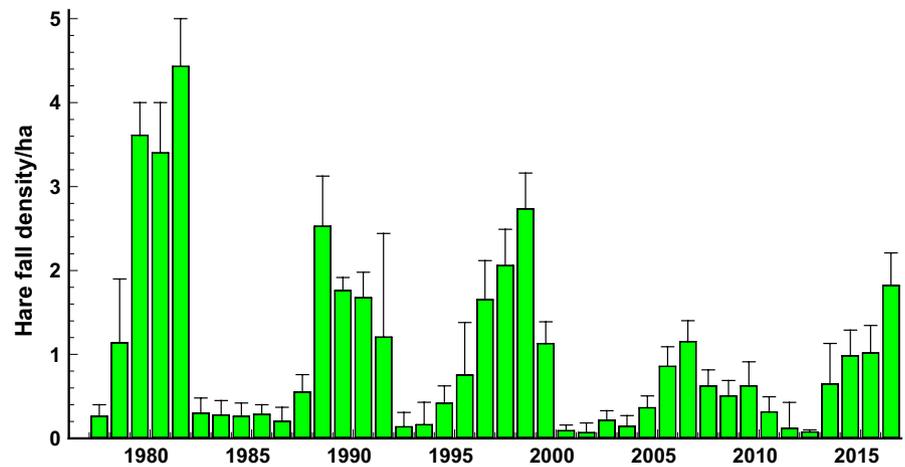


FIGURE 3 Annual survival rates (95% CL) for adult snowshoe hares with radiocollars during the decline phase of the cycle from autumn 1990 to autumn 1992. Sample sizes ranged from 197 to 278 individuals for these estimates (After Krebs et al., 1995)

prevented us from replicating the important mammalian predator removal treatment. We were faced with a dilemma; replicate the predator fence or add the interaction treatment of food supplementation and predator exclosure. We did have multiple contemporary control populations plus the detailed demographic information collected in previous cycles as context to compare our experimental results but a purist would argue that the major differences we observed could have been due to unknown inherent differences between control and experimental sites. Only further replication will resolve this issue. We also could not control hare or predator movements in and out of our treatment areas which affected density and survival estimates (Turchin, 2003). We allowed hares to move freely in and out of the predator fences and food supplemented areas from fear of creating a “fence effect” but we fenced areas three times the size of our trapping grids to try to prevent dispersal out of the fence. Many of our radiocollared animals still moved outside of the fence where they were killed by predators. It is also likely that predators spatially aggregated where our treatments created high hare densities, especially as the population decline continued.

We have continued to monitor three control grids since the major project of 1986–1996 ended, so that we now have a 41-year record of snowshoe hare numbers in this part of the Yukon. Figure 4 illustrates the sequence of hare densities for control areas at Kluane. There has been an irregular but observable trend to lower and lower peak hare densities over the period from 1976 to 2016. Traditional knowledge from Kluane First Nations people reported to us that the 1970–1971 peak was even higher than the 1980–1981 peak. The continued decline in hare peak numbers over this time has been accompanied by a continual increase in birch and willow shrubs that are the basis of the winter hare diet. Grabowski (2015) showed that standing biomass of dwarf birch approximately doubled between the 1987–1994 sampling period and 2014, while grey willow (*Salix glauca* L.) increased about 50% in biomass during that time. The cause of increased shrub growth was probably a mixture of reduced overwinter hare browsing, increasing light levels caused by white spruce tree mortality from the

FIGURE 4 Snowshoe hare autumn population density (per ha) on control trapping grids, 1977–2016. Upper 95% confidence limits are shown. There has been a gradual but slightly uneven decline in peak densities since the 1981 peak [Colour figure can be viewed at wileyonlinelibrary.com]



spruce bark beetle (*Dendroctonus rufipennis* (Kirby)) outbreak (Berg, Henry, Fastie, De Volder, & Matsuoka, 2006) and a warming climate. From 1985 to 2016 in the Kluane area May average temperatures have been increased 1.5°C, and mean June to August temperatures have increased 0.3°C (data from Haines Junction Meteorological Station, Environment Canada). Early winter temperatures (October to December) have increased slightly (0.44°C) in these 31 years, while late winter average temperatures (January to March) have increased 2.8°C. Thus, the climate in the Kluane area is warming but the warming is uneven with slight summer warming and stronger winter warming, all compounded by high variability from year to year.

2.2.4 | Alternative hypotheses for the decline in reproductive rates

Cary and Keith (1979) had shown in an elegant study that hare reproductive output collapsed over the cycle but the collapse began 2 years prior to hare peak density and continued through the decline phase. Stefan and Krebs (2001) repeated these observations for Kluane hares. The problem then became how to explain a collapse in reproductive rates in the absence of observable food limitation. Either we had insufficient information on access to food or food quality, or some other process reduced reproductive rates. Boonstra and Singleton (1993) and Boonstra, Hik, Singleton, and Tinnikov (1998) found that hares were severely stressed during the population decline and postulated that stress was both the proximate cause of the reproductive collapse and the long-term cause of the low phase (acting through maternal effects), and that a likely source of stress was the action of predators searching for hares to consume. This suggestion arrived at a critical time because new non-invasive methods had been developed to measure stress in wild mammals without having to regularly collect blood samples (Sheriff, Dantzer, Delehanty, Palme, & Boonstra, 2011).

The hypothesis that predator-induced stress caused the reproductive collapse was tested experimentally and observationally by Sheriff, Krebs, and Boonstra (2009, 2010, 2011), who measured stress levels by means of both plasma cortisol levels and their faecal metabolites. Four criteria had to be confirmed before this hypothesis could be tentatively accepted: (i) hares are sensitive to stress caused

by predation risk; (ii) increased maternal stress results in a decrease in reproduction; (iii) maternal stress is inherited from mothers to offspring; and (iv) offspring from stressed mothers also produce fewer offspring. The first three of these predictions have been confirmed. Breeding females were most stressed during summers of peak predator numbers, stressed females produced fewer offspring and the offspring of stressed females also were also stressed (Figure 5), so that the continuation of reproductive failure was carried from generation to generation by maternal effects. We still need to show that high predator-induced stress causes a failure to produce late summer litters 3 and 4, and that offspring from stressed mothers actually have high stress levels when they themselves breed.

The exact mechanism by which maternal stress programmes offspring is not yet known. It does not appear to be due to genetic changes (Sinclair, Chitty, Stefan, & Krebs, 2003). Changes in gene expression have been found (Lavergne, McGowan, Krebs, & Boonstra, 2014) and the most plausible hypothesis is that these changes are linked to epigenetic changes in expression of key regulatory genes, especially those affecting the stress axis (Ho & Burggren, 2010). One of the central enigmas of the hare cycle is the 2–5-year low phase

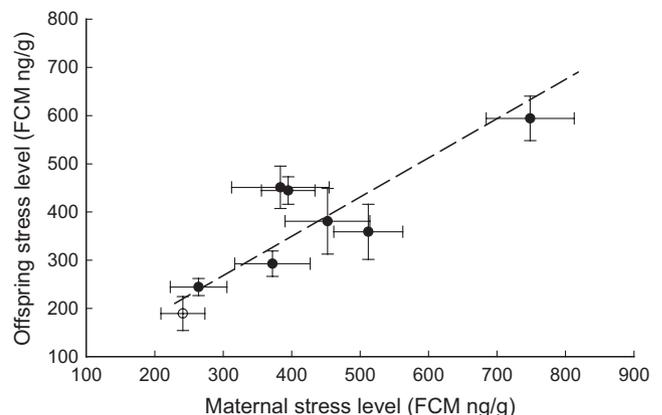


FIGURE 5 Maternal inheritance of stress levels from females to offspring. Each point is from the litter of a single female ($n = 8$) measured over the increase to decline phase of the cycle, ± 1 SE (After Sheriff et al., 2010; Figure 2)

following the decline (Figure 4). If there is stress-induced maternal programming of offspring that persists into adulthood, this could explain the low phase. But why does it last a variable length of time and what causes the females eventually to return to their highly fecund state? We suspect, but do not know, that the epigenetic changes may take time to dilute out of the population. Sheriff, McMahon, Krebs, and Boonstra (2015) found that the length of the low phase was a function of the severity of the decline phase, suggesting that the more severe the predation risk, the greater the epigenetic signature, and by extension, the more generations required to remove that signature. This working hypothesis remains to be tested. An alternative hypothesis by Tyson, Haines, and Hodges (2010) suggests that the prolonged low phase of the cycle may be due to the special role that great horned owls may play as predators during this phase. The cycle low and the factors that trigger the return to increase remain the least well-studied components of the hare cycle.

2.2.5 | Alternative hypotheses for the decline in survival rates

There are many predators that feed on snowshoe hares from “herbivores” like red squirrels (*Tamiasciurus hudsonicus* (Erxleben)) and grizzly bears (*Ursus arctos* (L.)) to more specialized carnivores like Canada lynx (Figure 6). The result of this food web is that few hares die of old age, and for about 95% of hares the immediate cause of death is predation (Boutin et al., 1986; Hodges et al., 2001). But the cycle is often mislabelled and modelled as a hare–lynx cycle, and there is a need to consider models that consider multiple predators as well as multiple prey species (Tyson et al., 2010).

Two alternative explanations for declines in hare survival are that parasites or diseases reduce the condition of hares, thus allowing predators to deliver the coup de grâce. There is as yet no good evidence that this explanation operates in the Kluane system (Sovell, 1993).

Keith, Cary, Yuill, and Keith (1985), Keith, Keith, and Cary (1986) carried out an extensive study of helminth parasites of snowshoe hares in central Alberta. Five parasite species were prominent in the hare population but there was no indication that prevalence affected any reproductive parameters of the hare population over the population cycle. Murray, Cary, and Keith (1997) reduced nematode prevalence experimentally in hares during 2 years to determine if parasitism increased vulnerability to predation. Virtually all hares in their study died from predation, and they found a significant increase in predation on untreated hares relative to treated ones, which suggested that there might be an interaction between parasitism and predation.

In the Kluane area there has been no evidence found of high mortality in snowshoe hares directly from diseases or parasitism, so the only potential link may be through increasing vulnerability to predators. The role of pathogens in the system is as yet unexplored. More research is needed on the role of parasites and pathogens in hare cycles, although our Kluane studies would suggest that these effects would be small. In the same manner, we and others like Murray et al. (1997) have found almost no deaths in hares that could be ascribed to starvation (Hodges et al., 2006). Hare populations decline in the presence of superabundant food, as shown in Figure 1.

2.2.6 | Synchrony in snowshoe hare cycles

There remains a widespread belief that snowshoe hare cycles occur in synchrony across all North America. This is not correct, as was pointed out long ago by Chitty (1950). The reality is much more interesting. Smith (1983) analysed the questionnaire data of the Snowshoe Rabbit Enquiry of the 1930s and 1940s and suggested that hare peaks followed a travelling wave (Figure 7) with delays up to 4 years in peak numbers across Canada.

To determine if a travelling wave is currently occurring, Krebs et al. (2013) gathered the existing survey data of snowshoe hares from

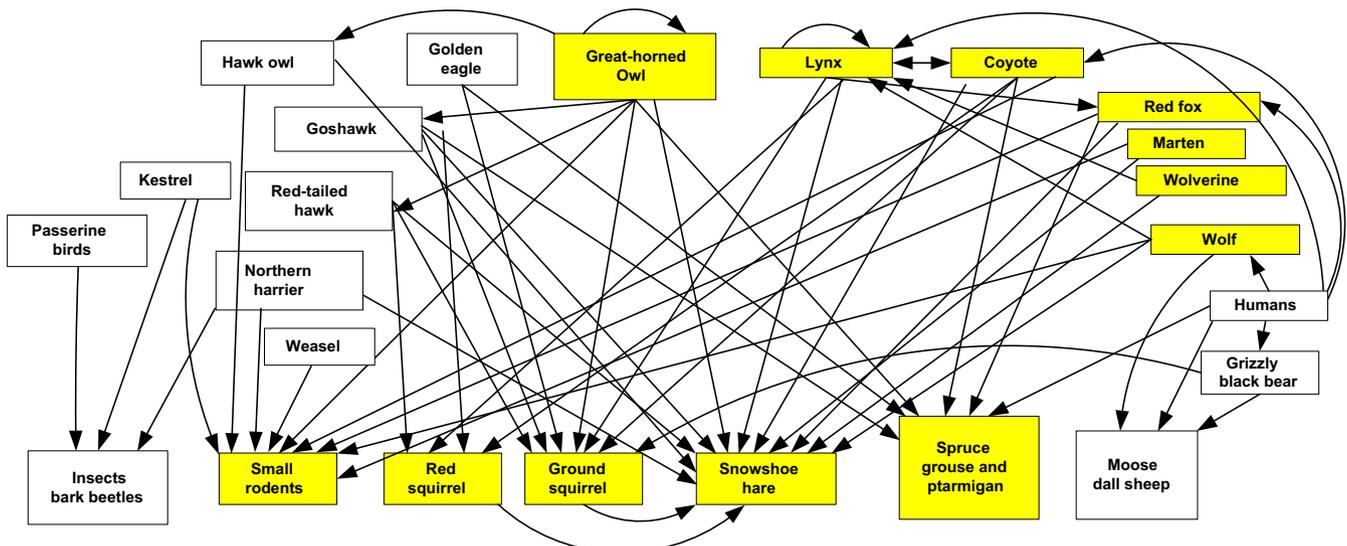


FIGURE 6 Herbivore and carnivore food web for major species in the Kluane Yukon terrestrial ecosystem. Species shaded in yellow are the main species for which we have quantitative data. Occasional diet items are not shown in this diagram [Colour figure can be viewed at wileyonlinelibrary.com]

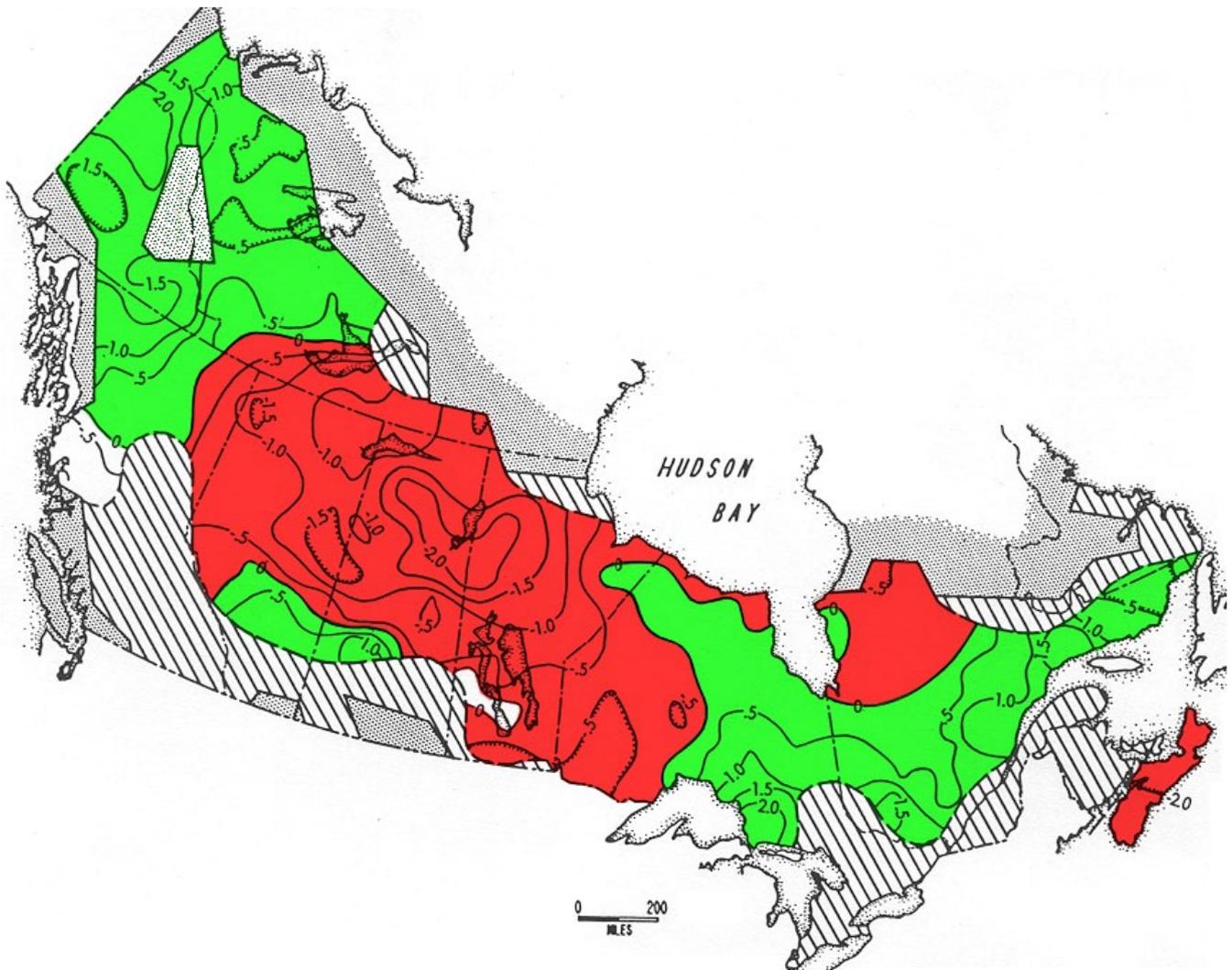


FIGURE 7 Synchrony in snowshoe hare cycles across Canada from 1931–1948, as measured by questionnaires (Chitty, 1950). The average peak phase across Canada was scaled as 0.0, and the contour lines indicate peaks occurring earlier than average (red, negative contours) or later than average (green, positive contours). During this period hare peaks were reached earliest in the central boreal region of northern Saskatchewan and Manitoba (After Smith, 1983)

central British Columbia, Yukon, Northwest Territories and Alaska from 1970 to 2012. No extensive data were available from central and eastern Canada. The western part of the travelling wave described by Smith (1983) from trapper questionnaire data in the 1930s and 1940s still exists (Figure 8). The reason for this travelling wave is not yet clear. The best suggestion is that it results from the movements of surplus predators in search of higher prey abundance as the snowshoe hare population collapses (Sherratt, 2001). We know from collared animals that lynx move in all directions up to 1100 km from their point of original capture (Mowat, Poole, & O'Donoghue, 2000) (Figure 9). Row et al. (2012) showed that Canada lynx were essentially panmictic across all 6000 km of the Canadian mainland, suggesting widespread dispersal on a continental scale.

If patterns of synchrony are indeed driven by mobile predators, we are still left with needing an explanation of why the cycle seems to “start” in central Saskatchewan and radiate outwards (Figure 8). We have no idea why this might be.

2.2.7 | Variable amplitude in snowshoe hare cycles

A final general observation about 10-year cycles has been that they are highly variable in amplitude (Krebs et al., 2014). Some hare peaks are very high (super-peaks) and show obvious signs of extensive browsing on winter shrubs, and other peaks are nearly invisible to the casual observer (Figure 4). Understanding the problem of amplitude variation is a landscape issue with all the problems of studying events that are spatially extensive (Lewis, Hodges, Koehler, & Mills, 2011). On a small scale, Ginzburg and Krebs (2015) explored the possibility that snowshoe hare cycle amplitude was defined by the minimal abundance of hare predators in the low phase of the cycle. Because all the predators of hares increase more slowly than hares, hares will escape heavy predation losses for a longer phase of increase, thus reaching higher densities until the predators catch up. Hence, the lower the density of predators during the low phase, the greater the peak hare density and the more browsing damage. This hypothesis works for

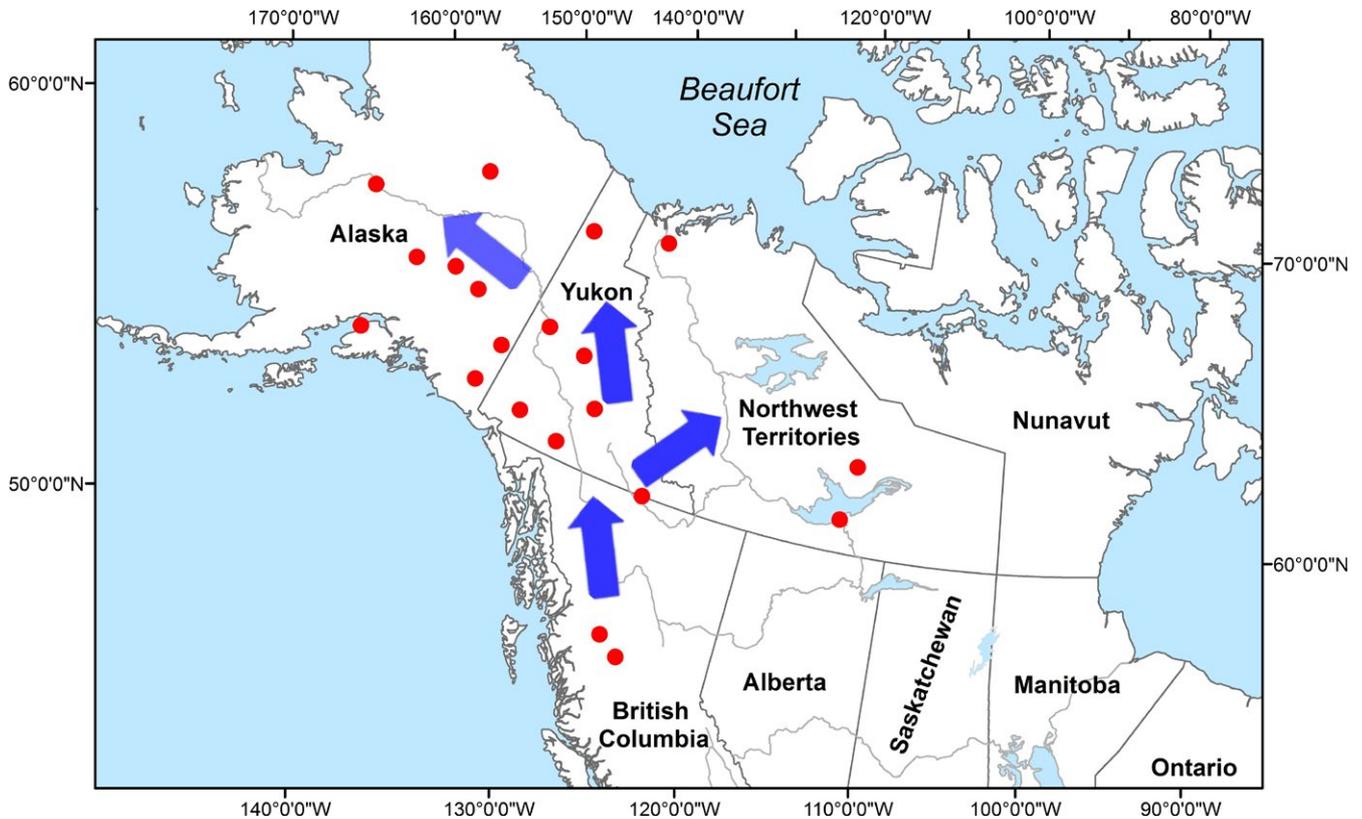


FIGURE 8 A travelling wave of peak snowshoe hare abundance in northwestern North America during the period from 1970 to 2012. Red dots indicate sites with quantitative data on hare abundance. Blue arrows indicate approximate travelling wave with each additional arrow from south to north indicating a 1–2 year time-lag in the arrival of peak numbers (Data from Krebs et al., 2013) [Colour figure can be viewed at wileyonlinelibrary.com]

Kluane hare populations but needs to be tested in other parts of the hare's geographic range.

The effect of habitat patchiness on hare cyclic amplitude offers another explanation of super-peaks. Extensive forest fires, for example, may produce optimal hare habitat over large areas. If what is optimal for hares is much less optimal for predators, this could affect the overall predation pressure during the population increase phase. In a similar manner if parasites vary in abundance in areas fragmented by fires, a reduction in parasite prevalence might allow better reproductive success and survival (Murray et al., 1998).

2.2.8 | Hare cycles in eastern North America and eastern Eurasia

All our activities have been focused in western North America and we do not know the degree to which they apply to the boreal forest of eastern North America, but we expect that they do. The 10-year cycle is dominant in the boreal forest of Canada and across Siberia but in the boreal forest of northern Europe 3–4-year cycles of voles dominate community processes. Boonstra et al. (2016) explained these striking differences as being climatically driven (Figure 10). Temperatures in the former are 15–20°C colder in winter. This directly affects the vegetation that can occur on the two areas—tall shrubs (birch and willow) are adapted to severe cold and shallow snows of winter and dominate in western North America, whereas a luxurious dwarf shrub layer

(*Vaccinium* spp.) is adapted to the mild temperatures and deep snows and dominates in northwestern Eurasia. Ultimately the occurrence of the 10-year cycle in the boreal forest of North America is driven bottom-up by severe winter climate. That being the case, we predict that severity of the winter climate will maintain the tall shrub vegetation as one progresses eastward across the continent (hence the declining tree line as one progresses eastward) and that 10-year cycles are expected to occur throughout these boreal forest regions. In Eurasia, the western regions are heavily influenced by warm air masses and maritime climate from the Atlantic. However, east of the Ural Mountains, we expect a severe continental climate (analogous to that in northern Canada) across Siberia and with it a change in the vegetation to favour tall shrubs in the understorey and 10-year hare cycles. The evidence, based on fur returns over relatively short time periods of ~20 years, is suggestive, but consistent with this prediction. Bulmer (1984) concluded that the mountain hare appeared to have a cycle length of 8 years in the Komi region just west of the Urals, and of 11 years in the far east of Siberia in the Yakutia region. In both cases, the peak in the European lynx returns lagged 1–2 years behind the hare peak.

2.3 | Models of the hare cycle and alternative approaches

Turchin (2003) formulated several criticisms of our experimental work, the most notable being that our predictions and analyses were not

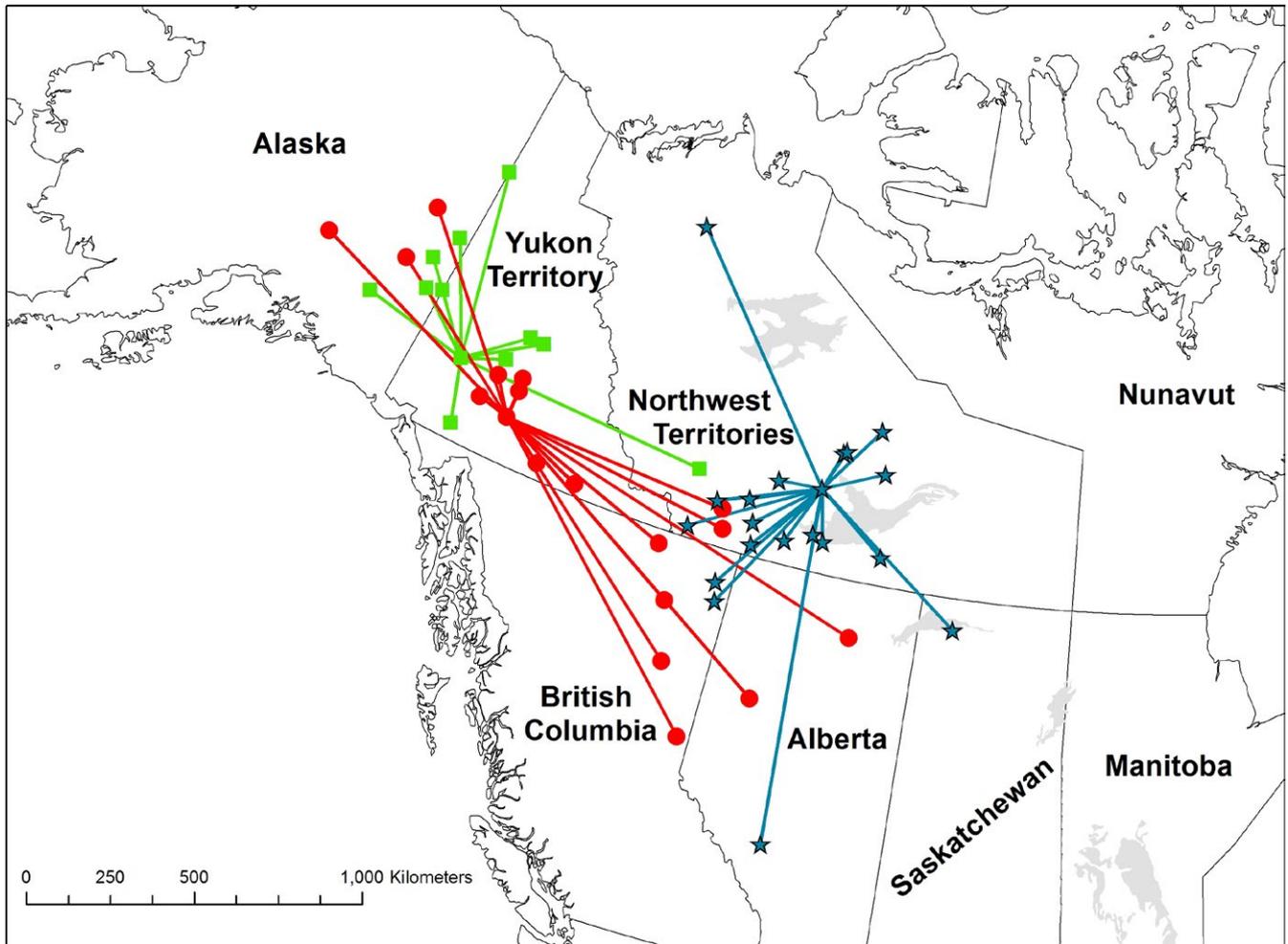


FIGURE 9 Dispersal movements recorded from radiocollared Canada lynx from the point of capture in the Yukon and Northwest Territories to the point of death due to fur trapping. A maximum straight line movement of 1,100 km has been recorded (After Mowat et al., 2000) [Colour figure can be viewed at wileyonlinelibrary.com]

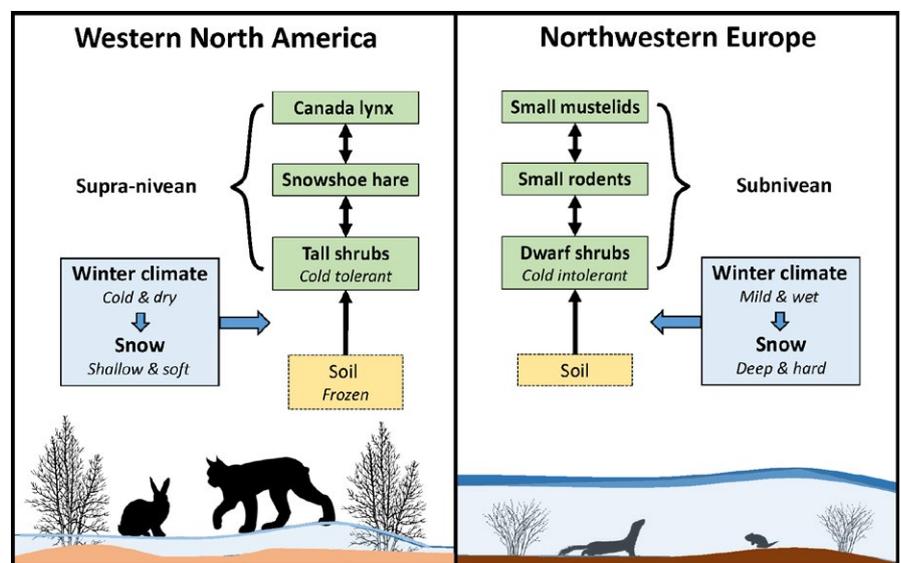


FIGURE 10 A proposed explanation for how winter climate—acting mainly through temperature and snow quantity—give rise to the different vegetation and food web dynamics found in the boreal forests of western North America and northwestern Europe (From Boonstra et al., 2016) [Colour figure can be viewed at wileyonlinelibrary.com]

theoretically informed by any sort of mathematical model; something he considered to be essential when dealing with systems driven by complex nonlinear dynamics. The essence of the argument is captured by

King and Schaffer (2001) when they state that “qualitative differences in behaviour can result from quantitative differences in parameter values” such that “the articulation of alternative verbal hypotheses and their

evaluation by strong inference—the conventional biological approach—may be doomed from the outset”. We interpret this to mean that depending on circumstances, our experimental treatments might point to the importance of one factor, whereas in another cycle they could point to an alternative factor even though the underlying mechanisms for the cycle remain consistent. The only way to evaluate this argument is with replicated studies on different hare cycles. This has been done now for 45 years at Kluane Lake and our work was based on pioneering experiments and studies by Lloyd Keith and his colleagues in Alberta (Keith et al., 1984). The result of these replicate studies is that the demography and proximate causes of mortality of the cycles studied are consistent, so that a single set of mechanisms should be sought as an explanation.

Attempts to model the hare cycle have been surprisingly few (summarized in Korpimäki & Krebs, 1996). Early models published by Fox and Bryant (1984) and Trostel, Sinclair, Walters, and Krebs (1987) served as background for our experimental manipulations, but large gaps in the empirical information needed to parameterize the sorts of models suggested by Turchin (2003) limited their utility. King and Schaffer (2001) constructed a standard trophic interaction model linking vegetation, hares and predators (Turchin, 2003) and parameterized it using the empirical findings from Rochester and Kluane. The model could produce cycles that were similar in period and amplitude to empirical observations and it was also able to reproduce results of the Kluane experiments. King and Schaffer (2001) analyses led them to the following conclusion: “Regardless of the relative importance of predation and starvation in a given locale, the model predicts that although resource limitation is responsible for arresting the increase phase of the cycle, it is increasing predation mortality that brings about the crash.” The King and Schaffer model has been criticized as being “overfitted” because of the large number of parameters involved (Ginzburg & Jensen, 2004). In addition, the key link to vegetation in the model was created by a standard density dependence relationship between hare condition and reproduction or mortality. There was no consideration of the non-consumptive effects of predation on hare reproduction hypothesized by Boonstra et al. (1998) as an alternative to resource limitation as an explanation of reproductive changes.

All in all, empirical studies and mathematical models are important tools for testing factors important in the hare cycle. We do not agree with Turchin (2003) that systems should be modelled before proceeding with empirical studies and experiments. Both methods need to inform the other. We have been frustrated by the lack of testable predictions stemming from modelling papers (but see King and Shaffer for an exception) and we have pointed out some of the frustrations modellers have with our empirical analyses. In the end, the conclusions of the modelling work were not vastly different from our empirical work or the statistical modelling of Stenseth, Falck, Bjørnstad, and Krebs (1997) but more linkage between various approaches is needed.

3 | DISCUSSION

When the 10-year cycle of snowshoe hares was first described about 100 years ago by biologists, there were a multitude of hypotheses

suggested about what the cause of these cycles could be. The list of possible mechanisms for population changes is very large, starting with climate, food supplies, predation, parasitism, disease and an array of social factors like territoriality and infanticide. Each of these general mechanisms can then be broken down into a series of alternatives. For example, food shortage as a general limiting factor could operate in summer or winter, involve juveniles or adults, could involve food quality as well as quantity, and be involved with secondary chemicals in the food plants. If we take only the five broad categories above, we can calculate that there are 31 combinations of these, each one of which is a distinct hypothesis. Faced with this impossible agenda, ecologists must use natural history insights to reduce the hypotheses to a manageable level. Given this reduction in possible mechanisms, we must test each hypothesis experimentally in the field. We have focused on food and predation as the two most likely main processes driving hare population dynamics. Since in this case each experimental test must be carried out for 10 years, progress cannot be rapid.

There are two shortcuts to do this difficult, bottom-up experimental work. First, one could build a mathematical model of the cycle and compute the consequences of the assumptions made in the model. This is an attractive top-down methodology but, in our case, despite extensive modelling by many ecologists, little light was shed on the actual mechanisms causing the cycle until we did our manipulations at Kluane Lake. The reason for this is twofold. Many models contain parameters that cannot possibly be measured in natural systems. Secondly, a whole host of simplifying assumptions must be made to avoid an infinite regress in model building. The result has been that a host of models exist for cyclic population dynamics, virtually none of which are useful in guiding experimental studies in natural systems.

A second shortcut in ecological studies has been to utilize laboratory populations in microcosms to mimic nature. While this is a useful strategy for many systems, it does not work for mammal or bird populations both because of scale and of lack of complexity and realism. The dispersal of individuals is a critical process for many populations, and in every moderate size microcosm it is difficult to permit dispersal dynamics and habitat selection as would occur in natural ecosystems. Home ranges of snowshoe hares vary from about 2 ha to 7 ha depending on sex and density (Boutin, 1984), so that holding hares in small enclosures risks potential artefacts. The most misleading early episode for snowshoe hares was the conclusion of Green et al. (1939) that shock disease caused hare declines (Chitty, 1959).

Both the food and the predator hypotheses are difficult to test for field populations unless clear hypotheses are stated with explicit predictions and unless experimental manipulations are carried out. This is perhaps the major advance of our work over the last 40 years—that experimental design is critical for population studies and manipulations can be done at relevant spatial scales. But the other crucial thing here is that we had to look inside the black box that is the animal to look for mechanisms that might explain the reproductive changes in the hare cycle from studies of stress physiology.

3.1 | Next steps

We now have information in the literature on three to five complete snowshoe hare cycles from only two study areas in the boreal forest. To date, the basic patterns seem consistent; predation is a prime driver of the cycle, but there are four important areas for future research.

1. The Kluane experiments need to be repeated and improved upon. There is a clear need for geographic expansion of studies to other regions of the boreal forest and further replication.
2. The mechanism behind the decrease in hare reproduction in the late increase, peak and crash needs to be precisely nailed down. The current hypothesis of an indirect, non-consumptive effect of predation via the stress axis needs further testing.
3. The cyclic low and early recovery remains as the most poorly understood part of the cycle. At least two hypotheses now exist to explain the low phase and models could be useful in testing ideas as

to the magnitude and mechanism of how maternal effects could act and disappear during the low.

4. New technologies like proximity radiocollars are available to follow the spatial location and activity of hares and their predators, and should provide better insight into both the consumptive and non-consumptive effects of predators on hare demography.

4 | CONCLUSIONS

The early knowledge of snowshoe hare cycles helped to move the scientific consensus away from the idea that nature was in a state of balance, which was disturbed only by humans or perhaps angry deities. It took ecologists until about 1950 to begin to take seriously the question of why natural populations fluctuated, and what we could do about them if they damaged our livelihoods. Snowshoe hares

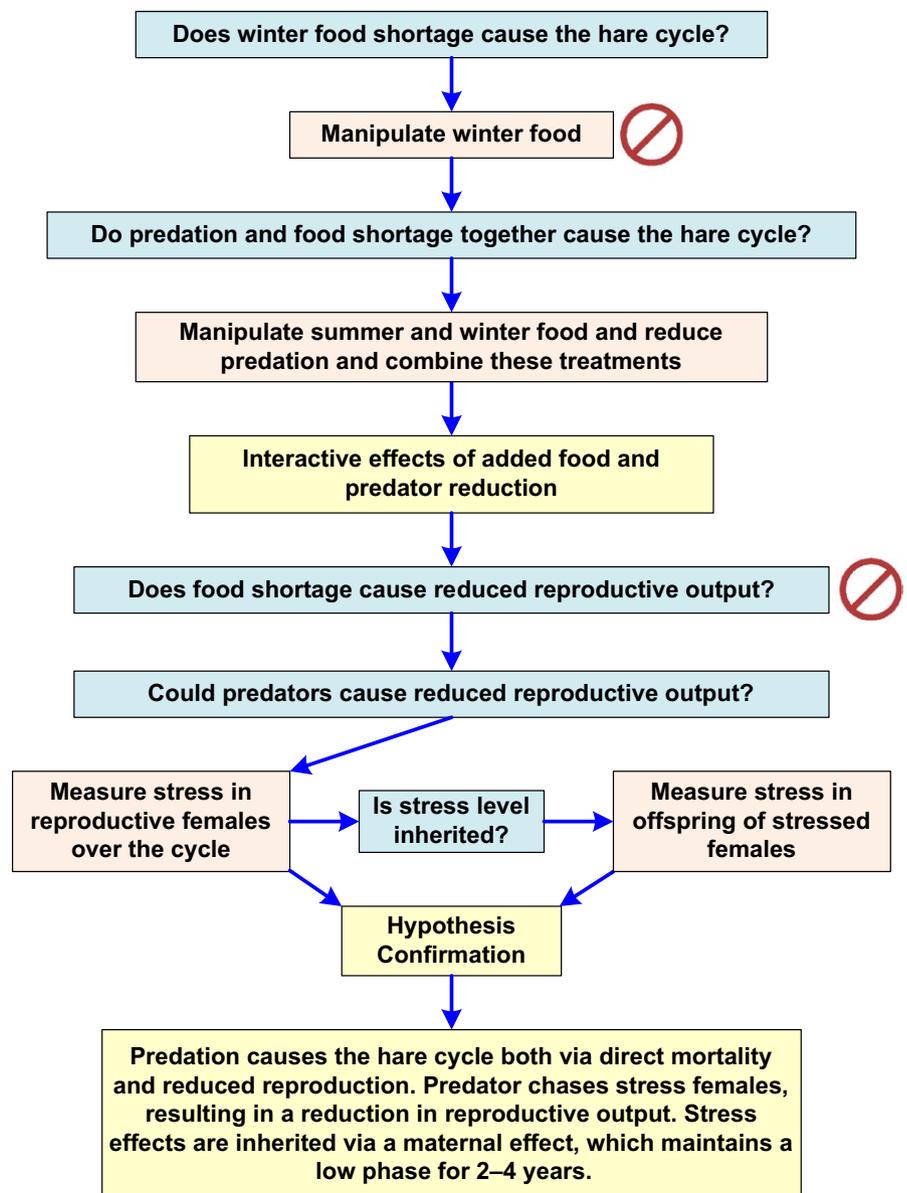


FIGURE 11 Flow chart of the 40 years of research that have allowed us to develop a comprehensive view of the ecological mechanisms behind the 10-year cycle of snowshoe hares in the Yukon. The negative symbols indicate no effect of the proposed factor [Colour figure can be viewed at wileyonlinelibrary.com]

were an early bellwether of ecosystem fluctuations that needed to be understood in northern landscapes. As such they became a classical Canadian ecological icon that appears in the beginning of almost every biology textbook.

We have achieved a tentative explanation of what causes snowshoe hare cycles (Figure 11). That is progress in our view. But we recognize that all scientific conclusions are tentative no matter how extensive the study. In our case, we draw the sweeping conclusion that the cause of snowshoe hare population cycles across all of the boreal forests of Canada, Alaska and Siberia are caused by predation acting directly on mortality and indirectly on a landscape of fear producing chronic stress in breeding females. We have no idea if this sweeping generalization is correct, and can only wait for additional studies of hares across this vast region to test our conclusions. We fully subscribe to the concept of science as “conjecture and refutation,” and there is still much to do to test our understanding of boreal forest ecology.

We have gradually expanded our view from population ecology to community and ecosystem ecology of the Yukon boreal forest. The interactions between the components of the boreal forest community need to be described and understood before we can hope to predict how climate change will alter these interactions. We would suggest that detailed studies of movement patterns of the major predators—coyotes (*Canis latrans* Say), lynx, great horned owls (*Bubo virginianus* Gmelin) and goshawks (*Acciper gentilis* L.)—in this ecosystem will help us to tie what happens locally to the extensive forests of northern North America. There is a major gap in the few current studies of plant dynamics within this ecosystem, both from the point of view of plant–herbivore interactions and that of plant succession during a time of rapid climate change. These issues are long-term problems with which science deals poorly. If understanding the hare cycle was a 40-year problem, with many questions yet unanswered, the community and ecosystem issues in the boreal forest are 100- and 200-year problems at a time when the science funding time frame is 3–5 years. We need to ask ourselves what the ecologists of the year 2100 will wish we had done now to advance the understanding of natural systems. A fair question with no simple answer.

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AUTHORS' CONTRIBUTIONS

All authors contributed to the field research and to the writing of this synthesis paper.

DATA ACCESSIBILITY

The snowshoe hare population data presented here are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.684s1> (Krebs, Boonstra, & Boutin, 2017). These data include the metadata, phases of the population cycle, capture–recapture data for all the control grids live trapped, fence+food mark–recapture data, population estimates for control grids and for the natural feeding experiment.

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