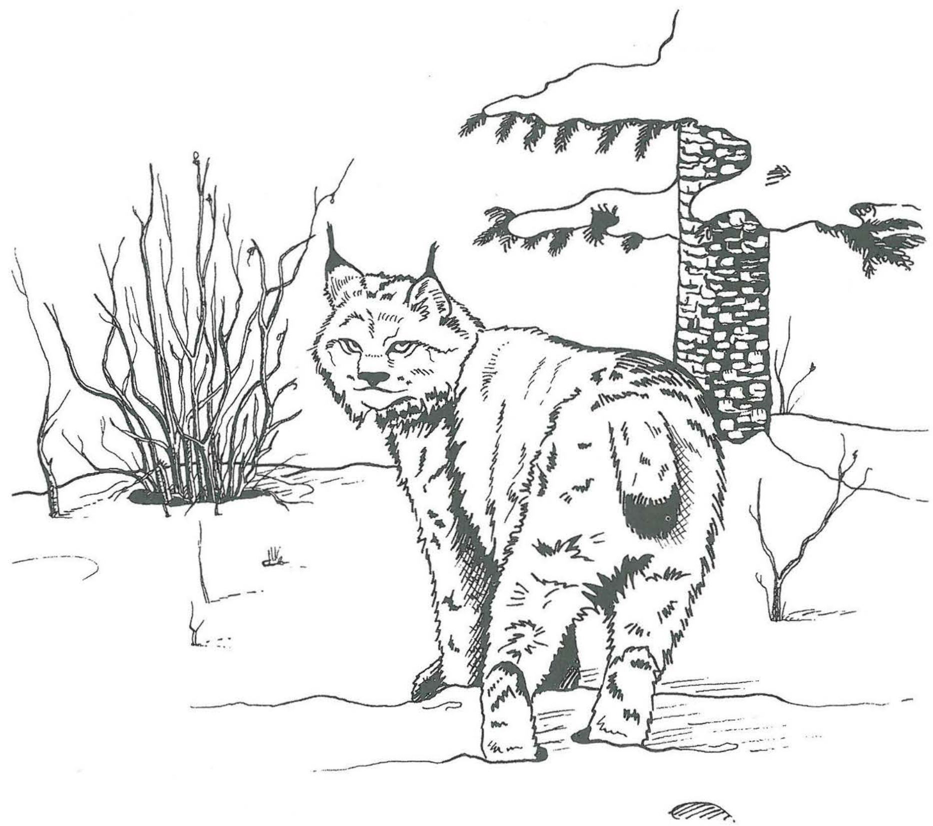
Conclusions and Future Directions

CHARLES J. KREBS, RUDY BOONSTRA, STAN BOUTIN,
& A. R. E. SINCLAIR



The Kluane Region of the boreal forest has been particularly well studied during this 10-year project, and we were fortunate to begin our project with a strong background of ecological research that had been carried out since the 1950s at the Arctic Institute of North America Kluane Research Station. The boreal forest is a large and diverse ecozone, and our studies have been done on one special part of it. This caution must form the background of all our conclusions. As scientists we will generalize to the boreal forests of North America, and we hope that our results will be found to apply in general to this ecozone from Alaska to Newfoundland. But, of course, we do not know if this is correct until further work has been done in many locations to look for generalities and for differences. Ecological research is both blessed and cursed by this dilemma of applicability as it sits midway between the elegant generality of physics and the complex special cases of sociology. We generalize our results as hypotheses for future evaluation.

We categorize our findings under two headings: *primary findings* are major results no one anticipated and are new to this project. *Secondary findings* are important results we or others had speculated about but for which there was no hard evidence when the study began in 1986. The division between these categories is somewhat arbitrary. Together they constitute the take-home message of this book.

20.1 Primary Findings

The food web of the Kluane boreal forest was known only in general when we started this study. We have described and quantified it precisely and have dissected its structure through a set of large-scale experiment that exceed in area and complexity any that have been applied to terrestrial ecosystems. The results summarized in the preceding chapters produced major results at all three trophic levels in this ecosystem.

20.1.1 Predator Trophic Level

Three major results were found at the predator level. First and most critical, we found that the boreal forest community is predominantly a top-down system in which the major changes are driven by the predator trophic level but with reciprocal effects operating at all trophic levels. Predators do not control all the species in the community, but the major influence across many species from hares to spruce grouse is predation, with red squirrels, mice, and voles being the major exception to this rule. Red squirrels are the only significant alternative prey available to predators in winter, and the fact that red squirrels and their predators are largely decoupled means that predators could not survive in the boreal forest in the absence of hare peaks.

Many ecologists have viewed boreal forest dynamics as a lynx–hare interaction, but we found that many predators in the boreal forest operate as a guild with redundancy. If any one of these predators were eliminated, little impact would be observed on ecosystem behavior because of this redundancy. Thus, lynx trapping has no impact on the ecosystem because other predators fill in the gaps. Predator redundancy, however, has its limits. Our predator exclosure results show clearly that avian predators cannot compensate completely for the absence of mammalian predators because snowshoe hare density rose in both areas from which mammalian predators but not avian predators were excluded.

We were surprised to find that, among the mammalian predators, coyotes acted as a specialist predator, much like lynx in this system. The coyote is the archetype of a generalist predator, and its success in North America has been often attributed to this generalist attribute. In the boreal forest, coyotes are constrained to operate as specialists, and they carry on successfully in that role. We found no similar result among the avian predators, which appear to be much more niche diversified.

20.1.2 Herbivore Trophic Level

Five major results were found at the herbivore level. First, snowshoe hares are a keystone species in the boreal forest. Hares account for the dominant biomass in these boreal systems, and we have quantified for the first time the relative biomass of all the main herbivores in this community. Many but not all of the ecological changes in this ecosystem are driven by snowshoe hares. If hares were eliminated, the boreal forest vertebrate community would largely collapse.

Hare dynamics seem to be driven by an interaction between predation and food supplies in a manner that results in most hares dying from predation and very few dying from starvation and malnutrition. We could find no evidence of malnutrition caused by food shortage at Kluane, in contrast to work on hares in Alberta by Keith et al. (1984). Nevertheless, hares impact both summer and winter food plants adversely so that the quality of food available to hares at the peak of the cycle is clearly less than that available in the low phase. The interaction of predation with food supplies may be mediated by predation risk, either through risk-sensitive foraging or through stress effects associated with high density.

The intense stress in snowshoe hares induced by predators was a major finding in this study (chapter 8). No one had applied the stress model to prey–predator interactions before the Boonstra and Singleton (1993) paper. Because we had experimentally manipulated populations, we were able to isolate the effect of predators on the levels of stress and show that it was not a simple food stress. This mechanism has great potential to explain the changes in reproduction that accompany the hare cycle.

We found that red squirrels are a poor alternative prey in the boreal forest. We had expected predators to turn to red squirrels after hares declined, but most predators moved off the study area or starved and thus fell to low numbers before some effectively switched to eating red squirrels. The impact of the hare decline on red squirrel numbers was thus nearly zero. Red squirrel dynamics respond more to cone crops of white spruce than to changes in predator numbers associated with the hare cycle.

Finally, both red squirrels and arctic ground squirrels were major predators of juvenile snowshoe hares during the first 10 days of life, whereas traditional hare predators such as lynx and coyotes were not. This trophic linkage of a "herbivore" eating another herbivore convolutes the food web and was a finding no one had expected. At present we do not know what impact these interactions might have on the hare cycle. Red squirrels and hares occur together virtually everywhere, whereas ground squirrels overlap hares only in a small part of the western boreal forest. Red squirrels may be the only hare predator in the system to show a strong type-3 functional response, and this could contribute to the ability of predators to stop the hare increase.

20.1.3 Plant Trophic Level

Three major results were found at the plant level. First, fertilization of the vegetation produced dramatic increases in plant growth of trees, shrubs, and grasses and forbs. The impact of this increased plant growth ranged from slightly positive for hares to negative for red squirrels and ground squirrels and slightly negative for red-backed voles. We do not know why these population reductions occurred, and our best guesses are that mushroom production was reduced under fertilization (red squirrels), that lupine populations collapsed (ground squirrels), or that perhaps berry production was reduced (voles). It was clear from the different responses of the fertilized plots and the food-addition plots that we could not move the boreal forest plant community very far by adding nutrients, at least in the sense of providing better habitat for the main herbivores in this system.

Protecting 4-ha plots from hare browsing over the 10 years of the study produced only small changes in the vegetation. Although hares remove significant amounts of shrub biomass at the peak of the cycle, the responses of shrubs, herbs, and grasses appear to be so slow that we cannot measure much change in only 10 years. We suspect that 50 years might be a better time frame for these exclosure studies. A larger impact on vegetation, particularly shrubs, seemed to occur when both hares were excluded and fertilizer was added, but this was not quantified. The suggestion is that hares may actually have counteractive effects whereby heavy browsing reduces shrub biomass, but high hare densities stimulate production through a nutrient pulse in the form of urine and feces.

The fire history of the Kluane region showed a time scale of fires over 500 years, with large differences between local areas. No one had expected this dramatic time scale for fire in this part of the boreal region. The time scale of fires in the Kluane regions is long, and perhaps 20–40 times the time scale of the hare cycle. Although the boreal forest in general is thought to be a fire dominated ecosystem, the herbivore impacts of hares and moose occur much more quickly, and herbivory should be added to fire and insect attacks as a major disturbance factor in this part of the boreal landscape.

20.2 Secondary Findings

In this section we summarize findings that are less global than those discussed above, as well as findings that confirm or confront ideas that have been previously presented in the boreal forest literature. Ecologists have developed a skeleton of food web theory for community dynamics (chapter 4), and in part of this section we summarize our findings that were expected from theory and either found or not found in the data from this study. The results summarized in the preceding chapters produced important secondary results at all three trophic levels.

20.2.1 Predator Trophic Level

Four specific results surprised us at the predator level. First, predators kill other predators, especially when hares are declining in abundance. Among both mammalian and avian predators, we were surprised by the amount of intraguild predation. Because this predation can operate to stabilize the predator trophic level, it is critical to document it in relation to cyclic events, and it becomes an important component of any modeling of this community.

We found that the lynx social system was unable to continue through the cyclic decline, in contrast to the great-horned owl social system. Because territoriality in both birds and mammals has a cost as well as a benefit, we can infer that at low hare densities lynx obtain no present or future benefit from defending a fixed territory. Great-horned owls, in contrast, remain on their territories without breeding through the cyclic low phase.

Predators did not respond to hot spots in prey density until the hare decline began in 1991. Predators defend territories that contain far more prey biomass than they can use for most of the hare cycle. Because predators of both mammals and birds can live through more than one hare cycle, territory defense may be oriented to the lean years rather than to the rich years.

Finally, predators surplus-killed through much of the hare cycle. Consequently, estimating the impact of predators on prey population through bioenergetic rules will seriously underestimate how much prey will be taken. Our ability to estimate predator foraging success directly and prey loss rates directly allowed us to determine biases from two directions. Previous studies have seriously underestimated predator offtake potential in boreal forest communities. When the strong functional responses are combined with the modest numerical responses shown by predators at Kluane, the magnitude of changes in killing power are equal to the magnitude of changes in hare density over the cycle.

20.2.2 Herbivore Trophic Level

Five specific findings should be highlighted at the herbivore level. First, the arctic ground squirrel showed a 10-year cycle entrained by predation spinning off from the snowshoe hare cycle. Because ground squirrels hibernate during winter and overwinter losses are constant, their dynamics are driven completely by summer events in this ecosystem. Both food and the social system (female philopatry) are important factors for arctic ground squirrel populations, but their effect was overridden by heavy predation from hare predators such as coyotes and great horned owls. Arctic ground squirrels are primarily mammals of open arctic tundra and rely on clear sightlines to detect predators. The boreal forest is much more marginal for them because of a susceptibility to predation.

Red-backed vole populations continued to show long-term cycles that peaked 2–3 years after the snowshoe hare peak. We postulate that this is driven by fluctuations in berry crops that react to the nutrient cycling that accompanies the snowshoe hare peak density, but this pattern is still a puzzle to us. Vole and mouse abundance in the Kluane ecosystem is low, and the rarity of marten in this system and the rarity of weasels seem to reflect this low average abundance of small mammals.

Red squirrels were the only herbivore to show stable populations throughout the study. This occurred despite extreme variation in spruce cone crops. We suspect that territory size in squirrels, like that of great horned owls, may be determined by periods of low food availability. Consequently, densities are fixed by territoriality. Abundant cone crops lead to increased production of young, but this does not translate into population increase because territories in good habitat are not compressed. Although we did not measure emigration, we suspect that juveniles produced during good years disperse to marginal habitats leading to much wider density fluctuations in these areas. Red squirrels declined in abundance on the fertilized areas relative to control. We were surprised by this decline, and only in the latter part of our study did we connect possible reduction in mushrooms under fertilization to the red squirrel decline. Because we did not quantify mushroom production during this study, this remains a hypothesis in need of testing.

The timing of low-phase cyclic dynamics in snowshoe hares was unchanged by any of the experimental treatments. We had expected the duration of the low phase to be reduced by one or more of the predator exclosure or predator exclosure + food-addition treatments, but the cyclic increase of 1994 began everywhere in our study area and in the rest of the Yukon at exactly the same time.

The reproductive decay in snowshoe hares that begins in the late increase phase and continues through the decline was mimicked in hares taken from the Yukon to Vancouver by Sinclair and raised under ideal conditions in the laboratory (Sinclair unpublished). This reproductive decay has been described by Cary and Keith (1979) and by us in field populations. We have been completely surprised by these findings. Sinclair's results show that the intrinsic reproductive schedule of a female hare seems to be programmed by early life so that it cannot be changed by later experience in favorable environments. This is the first evidence that intrinsic changes may be an essential feature of hare cycles, and it needs to be carefully replicated.

Spruce grouse show a 10-year cycle entrained by the hare cycle in spite of being at low density. Cycles in relatively rare species are not easy to measure, and we think that predators, spinning off from the hare cycle, drive these changes. The picture is probably the same for willow ptarmigan, but our data are less clear for them.

20.2.3 Plant Trophic Level

We highlight four results that were found at the plant level. First, white spruce did not respond to fertilization by changes in the timing of cone crops. In spite of additional growth and at least a slight increase in seed production, the years of high cone crops occurred simultaneously on control and fertilized areas. We presume that cone production is hard wired to climatic parameters (probably temperature and moisture related) and is not a flexible trait in white spruce.

Grasses and most herbs in the boreal forest are controlled primarily bottom-up by nutrients, with little impact top-down by herbivores. The impact of fertilization on herbs and grasses is species specific and long-term. A few herbs are highly selected by snowshoe hares and are strongly affected at the peak of the cycle. It is likely that in 10 years we have seen only transient dynamics of grasses and herbs in response to fertilization of vegetation, and that experiments of a time scale of 50 years or more will be needed to determine the equilibrium conditions for the boreal forest. Snowshoe hares rarely feed on grasses; only *Microtus* spp. feed regularly on them. If herbivory is of only minor importance to grasses and many herbs in this system, an equilibrium set by nutrient levels is possible.

Browsing by hares on willow and birch appears to stimulate shrub production. Heavy overgrazing at the peak of the cycle is followed by a rebound 2–3 years later. The unexpected result was that there was a net increase in shrub biomass over the 10 years of study, rather than an equilibrium between growth and offtake. Some effects through nutrient cycling are implicated, but we do not know the details of how this occurs, and the grazing cycle may be superimposed on a longer-term successional trend.

Secondary compounds in willows and birch seem to respond directly to hare browsing, as predicted by Bryant (1981). Adding fertilizer seemed to reduce the levels of secondary chemicals in shrubs, as predicted by Coley et al. (1985). These changes in the nutritional value of winter shrubs probably contribute to the reduction in hare body weight that occurs in the peak and decline phase of the cycle, but their relative importance is overwhelmed by increasing predation pressure in the Kluane system.

20.3 Opportunities for Further Work

The greatest value of the Kluane boreal forest project was that we could measure all the significant parts of the system in the same place at the same time. Joint studies like this reach levels of insight that are not additive but multiplicative and dependent on the mix and creativity of the people involved. Ours should be a model for further community studies. Nevertheless, we could not study everything in the ecosystem, and in this section we try to identify the main oversights we made in missing opportunities for studying elements that we now think are important pieces of the system dynamics. We recognize in retrospect five major specific opportunities for further work.

Mushrooms vary greatly in abundance from year to year. We began to census them only in 1993. There are years when mushrooms are very abundant in the boreal forest and many more years when mushrooms are difficult to locate. Mushroom crops are thus similar to white spruce cone crops in their irregularity and in their importance for the herbivores in the system. In particular, mushrooms are harvested by red squirrels and are eaten by arctic ground squirrels, voles, and mice. We did not anticipate the potential interference of fertilization with myccorhizae in the boreal forest and whether this might lead to reduced above-ground production of mushrooms for herbivores. These fungi may also be affected by the nutrient pulse associated with hare browsing at the peak of the cycle. This system would well repay study in the boreal forest.

We did not quantify the annual production of berries in our study area, and we now think they are critical for mice and vole population outbreaks. There are a variety of berry-producing shrubs in the Kluane regions from soapberry (*Shepherdia canadensis*) and bearberry (*Arctostaphylos uva-ursi*) to red bearberry (*Arctostaphylos rubra*), crowberry (*Empetrum nigrum*), and cranberry (*Vaccinium vitis-idea*). All these berry producers vary from year to year in productivity for unknown reasons possibly associated with temperature and precipitation levels. Soapberry is an important food of grizzly bears, and we suspect all these berries are important foods for many of the small mammals and birds in the system. We do not know the food habits of these species well enough, nor do we know how their population changes might tie into variations in berry production from year to year. This is an important gap in our understanding.

We were not able to include the larger vertebrates in our study. Moose, grizzly bear, black bear, Dall sheep, caribou, wolves, and wolverines are the main species we have only minimal information on. For the most part, wildlife ecologists study these large species as a separate system with little or no linkages to the snowshoe hare cycle or the smaller scale processes we have detailed in this book. This could well be a mistake because, for example, it does not allow us to cross-reference the predator–prey dynamics of wolves and caribou to the predator–prey dynamics associated with the hare cycle. These may well be two independent systems, but we cannot verify this by keeping studies of these species in two separate worlds. The problems of scale are not easy to overcome because of budget limitations, but we will never overcome these limitations as long as we think we can achieve complete understanding by ignoring half of the vertebrate community.

We concentrated our studies in the Kluane region, which has not had a significant forest fire for more than 70 years and has never had any industrial forestry. This provides good baseline data but does not allow us to answer specific questions about the impact of forest fires on the system, or more important, perhaps, what will happen to the hare cycle when industrial forestry fragments these boreal forests. We bring this out not because we had any possibility of addressing these important questions but because they are two of the three main disturbances that will affect these forests in the future. From 1994 to 1998, just as we were ending our studies, the spruce bark beetle killed approximately 30% of the older white spruce trees in the Kluane region. Insect attacks along with fire and logging must also be understood as a disturbance to the boreal system. Our intuition is that bark beetle kills are much less intrusive on this ecosystem than fire and logging, but this must be tested.

We did not leave in place any long-term experimental areas. Because of the termination of our research funding, we had to take down all our experimental fences after 10 years. The infrastructure required for a longer term of study was not readily available from any of our Canadian funding sources. We regret this. We are reminded of the moose exclosures at Isle Royale National Park in Lake Superior that have been in place for more than 50 years (McInnes et al. 1992), and we believe that similar exclosures in the Kluane area would be equally informative of ecosystem dynamics in 50–100 years. The major problem beyond land use is technical: such exclosures need frequent monitoring because of moose bungling and tree falls against the fence. To add a more interesting treatment of moose and hare exclosure would require more vigilance to keep hares out. We have no current way of funding or managing these kinds of long-term studies.

20.4 Unsolved Problems

There are three aspects of boreal forest dynamics that are as yet poorly understood. First, for the snowshoe hare cycle, which drives so much of this community, we do not understand exactly why there is an interaction between predation and food. There are two hypotheses that tie predation risk to this interaction, one suggesting a food linkage directly by a change in habitat selection (Hik 1995) and a second by Boonstra et al. (1998) suggesting an indirect link through stress caused by predation risk. We have rejected an alternative hypothesis by Bryant et al. (1985) that suggests a direct food-quality impact through secondary compounds and another alternative hypothesis by Keith et al. (1984) that suggests a direct food quantity impact through winter food shortage. We do not know if these alternative hypotheses apply to other regions in the boreal forest.

Our experimental addition of food and removal of predators has created the greatest disruption of the hare cycle of any experiment to date. However, some would maintain that the cycle escaped largely intact. This may be due to the fact that we could not remove all predators and hares liked to venture outside the fence or due to the fact that we missed some essential elements. There is considerable room for researchers with creative minds to overcome the shortcomings of our experiments and to test the robustness of our findings.

Second, we do not comprehend the spatial dynamics of the interactions highlighted in this book. Hare cycles are synchronous across all of western North America, which means that a predator cannot in general improve its chances of survival by moving to a new territory. We do not understand what drives these spatial dynamics. Red squirrels are strongly affected by cone crops, and we do not have a regional or provincial scale of understanding how cone crops vary from year to year. In southern and eastern parts of the boreal forest, plant productivity is higher and arctic ground squirrels are absent. Does this make any difference to how the system operates? Why does this synchronous and highly fluctuating community not go to extinction on occasion? What spatial scale is necessary to prevent extinction of the predators or the prey species in this system? Is conservation in northern Canada similar to conservation farther south? If we protect 12% of the boreal forest, will these community dynamics continue, or will the system collapse if it is reduced (for example) to half its present area? These are all long-term questions and the answers are critical for conservation in the north.

Third, we do not know the sensitivity of this boreal landscape to climate change. There are only two ways to determine this. First, if one knew exactly how climate will change, one could impose an experimental treatment similar in kind. For example, if rainfall is predicted to increase, one could irrigate a section of boreal forest and measure what changes in relation to unmanipulated plots. It is more difficult to do this with temperature and CO_2. Second, one could monitor the plant and animal communities of the boreal forest and measure time trends that might then be associated with measured climatic changes. This is certainly feasible, and the present study can be viewed as a start of a longer term monitoring program. The problem at present is that monitoring in the boreal forest is haphazard, unfunded, and not organized. The key issues of what to monitor, where to monitor, and how to monitor in a standard manner are all undirected. A long-term monitoring program must be coupled with experimental studies to follow up on ideas generated by the correlations that will appear between biological changes and weather trends. The fallacy regarding climate change is that correlation means causation.

20.5 Future Boreal Forest Research

We have completed one 10-year study of the vertebrate community in the southwestern Yukon, and we pause here to reflect on the future research agenda for the boreal forest. First, we recommend that a replicated study be carried out in another part of the boreal forest to test the generality of our conclusions. Ecologists are tempted always to generalize beyond the limits of their immediate data, and indeed they must do this or say nothing about how ecosystems work. But we should be humble enough to recognize that some conclusions are region specific.

Second, we recommend the immediate investigation of how logging and fire may impact the hare cycle, the dominant process structuring the vertebrate community. We need a rigorous before-and-after control–impact design (Green 1979) with suitable replication to answer these questions. The forestry precedent in southern regions is to cut the trees first and then to start to ask questions about impacts on biodiversity. We hope the managers of the Yukon boreal forest areas are more intelligent in their planning.

Third, we suggest a broad program based on adaptive management to ask what level of harvesting is sustainable for game species and furbearers in the boreal region. The government is in the process of promising subsistence hunting privileges to Native Americans in the north without sufficient information on what this means ecologically or the means to determine if it is sustainable. If fur trapping becomes a viable industry, we have no scientific guidelines for how much harvesting is sustainable in a fluctuating system. If snowshoe hares become an important game species, as they are now in Newfoundland, we do not have any guidelines about how much harvesting they can sustain without major impacts on abundance. We suggest a proactive program to determine these limits is more desirable than an a posteriori explanation 50 years from now of why lynx went extinct in the Yukon or Alaska. We emphasize that part of this program must be an attempt to determine the linkages between the large vertebrates and the small vertebrates in the boreal forest. Perhaps we can manage caribou in total ignorance of what snowshoe hares are doing or perhaps not. We assume ignorance is bliss at present, and we may learn the hard way that this is not a good way to manage boreal ecosystems. We should learn from the mistakes in the south and avoid repeating them in the north.

Fourth, in the longer term we need to compare the North American boreal forest with the Siberian boreal forest and the Fennoscandian boreal forest. We have at present little more than anecdotal information about the Siberian boreal forest, and it leads us to believe that it is similar to the Canadian boreal forest so that we would expect similar ecosystem dynamics. The Fennoscandian boreal forest, however, seems completely different. Mountain hares (*Lepus timidus*) are rare in Sweden and Finland (Angerbjörn 1989), and the boreal forest community seems dominated by the 3- to 4-year cycle of voles and lemmings (Hansson and Henttonen 1988, Danell et al. 1998). We do not know why Fennoscandian boreal forest community dynamics differ so completely from North American boreal forest dynamics, and the ecological reasons why one system is dominated by the keystone snowshoe hare while the other is dominated by several species of small rodents are completely unknown. In the global picture this is a key question for ecologists in the twenty-first century.

Literature Cited

Angerbjörn, A. 1989. Mountain hare populations on islands: effects of predation by red fox. Oecologia **81**:335–340.

Boonstra, R., D. Hik, G. R. Singleton, and A. Tinnikov. 1998. The impact of predator-induced stress on the snowshoe hare cycle. Ecological Monographs **68**:371–394.

Boonstra, R., and G. R. Singleton. 1993. Population declines in the snowshoe hare and the role of stress. General and Comparative Endocrinology **91**:126–143.

Bryant, J. P. 1981. Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees. Science **213**:1573.

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

Coley, P. D., J. P. Bryant, and F. S. Chapin III. 1985. Resource availability and plant antiherbivore defense. Science **230**:895–899.

Danell, K., T. Willebrand, and L. Baskin. 1998. Mammalian herbivores in the boreal forests: their numerical fluctuations and use by man. Conservation Ecology **2**(2):9.

Green, R. H. 1979. Sampling design and statistical methods for environmental biologists. Wiley, New York.

Hansson, L., and H. Henttonen. 1988. Rodent dynamics as community processes. Trends in Ecology and Evoltuion **3**:195–200.

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

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.

McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology **73**:2059–2075.