Trophic Dynamics of the Boreal Forests of the Kluane Region

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ABSTRACT. The trophic dynamics of the Yukon boreal forest have been under investigation at the Kluane Lake Research Station since 1973. We monitored and conducted experiments on the major species in this ecosystem, except the large mammals (for logistic reasons). The central problem has been to determine the causes of the 9–10 year cycle of snowshoe hares, and to achieve this we carried out several large-scale experiments manipulating food supplies, predator pressure, and soil nutrient availability to test hypotheses that food, predation, or habitat quality regulate populations. The hare cycle is driven top-down by predators, and most hares die because they are killed by predators. Predators also cause stress in female hares, and the stress response seems to be responsible for the loss of reproductive potential in the decline and low phases of the hare cycle. Many of the specialist predators and some herbivores in this ecosystem fluctuate with the hare cycle. Arctic ground squirrels do, but red squirrels do not, being linked closely to white spruce seed masting years. Small rodents fluctuate in numbers in two patterns. Red-backed voles and four species of *Microtus* voles have a 3–4 year cycle that seems to be driven by food supplies and social behaviour. Deer mice, in contrast, have fluctuated dramatically in the 38 years we have monitored them, but not cyclically. White spruce seed production varies with temperature and rainfall, but was not affected by adding nutrients in fertilizer. Global warming and reduced hare browsing in the last 20 years have helped to increase the abundance of shrubs in these forests. It will be challenging to predict how this system will change as climatic warming proceeds, because even closely related species in the same trophic level respond differently to perturbations. We recommend continued monitoring of the major species in these boreal forests.

Key words: boreal forest, snowshoe hares (*Lepus americanus*), red-backed voles (*Myodes rutilus*), *Microtus* spp., Arctic ground squirrels (*Urocitellus parryi*), red squirrels (*Tamiasciurus hudsonicus*), grouse, fertilization, predation

RÉSUMÉ. La dynamique trophique de la forêt boréale du Yukon fait l'objet d'une étude à la station de recherche du lac Kluane depuis 1973. Nous avons fait des expériences et surveillé les espèces importantes de cet écosystème, sauf en ce qui a trait aux principaux mammifères (pour des raisons de logistique). Le problème central a consisté à déterminer les causes du cycle de 9 à 10 ans du lièvre d'Amérique. Pour ce faire, nous avons effectué plusieurs expériences à grande échelle dans le cadre desquelles nous avons manipulé les disponibilités alimentaires, la pression exercée par les prédateurs et la disponibilité en nutriments dans le sol afin de mettre à l'épreuve les hypothèses selon lesquelles la nourriture, la prédation ou la qualité de l'habitat régularisent les populations. Le cycle du lièvre est dicté par les prédateurs de haut en bas, et la plupart des lièvres meurent parce qu'ils sont tués par les prédateurs. Par ailleurs, les prédateurs sont une source de stress chez les lièvres femelles, et la réaction au stress semble responsable de la perte de capacité de reproduction dans la phase du déclin et la phase basse du cycle du lièvre. Grand nombre des prédateurs spécialistes et certains herbivores de cet écosystème fluctuent en fonction du cycle du lièvre. C'est le cas du spermophile arctique, mais ce n'est pas le cas de l'écureuil roux, car il est étroitement lié aux années de paisson de graines d'épinette blanche. Le nombre de petits rongeurs fluctue en fonction de deux modèles. Le campagnol à dos roux et quatre espèces de campagnols *Microtus* ont un cycle de trois à quatre ans qui semble dicté par les disponibilités alimentaires et le comportement social, tandis que la souris sylvestre a connu d'énormes fluctuations pendant les 38 années qui ont fait l'objet d'une surveillance, sans toutefois afficher de cycles. La production de graines d'épinette blanche varie en fonction des températures et des chutes de pluie, mais n'a pas été influencée par l'ajout de nutriments au fertilisant. Le

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réchauffement planétaire et le broutage réduit des lièvres ces 20 dernières années ont aidé à accroître l'abondance d'arbustes dans ces forêts. Il sera difficile de prévoir comment ce système changera au fur et à mesure du réchauffement climatique, car même les espèces étroitement liées du même niveau trophique réagissent aux perturbations de manière différente. Nous recommandons la surveillance continue des principales espèces de ces forêts boréales.

Mots clés : forêt boréale, lièvre d'Amérique (*Lepus americanus*), campagnol à dos roux (*Myodes rutilus*), *Microtus* spp., spermophile arctique (*Urocitellus parryi*), écureuil roux (*Tamiasciurus hudsonicus*), tétras, fertilisation, prédation

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INTRODUCTION

The boreal forest comprises about 25% of the world's closed canopy forests. In North America, it stretches from the Pacific to the Atlantic, covering more than five million square kilometres. Compared with temperate and tropical forests, the boreal forest is a relatively simple ecosystem— the plants are nutrient-limited by nitrogen, the forests are disturbance driven by fire, and the whole system runs on a slow time scale due to low temperatures and short growing seasons (Chapin et al., 2006).

In 1973, we began work at the Kluane Lake Research Station by surveying the small rodents in the region of Kluane National Park. This early research showed that small rodent biodiversity was among the highest in North America (14 species, with 11 under 50 g in mass) because it is a zoogeographical tension zone between the Alaskan-Siberian fauna and southern Canadian species (Krebs and Wingate, 1976). We realized early on that the dominant mammalian species in this forested ecosystem was the snowshoe hare (*Lepus americanus*), which showed its classic 9–10 year cycles. Our attention changed from small rodents to snowshoe hares (*Lepus americanus*) and ultimately to trying to decipher the vertebrate population dynamics of the boreal forest ecosystem. In this paper, we review our findings by trophic level and provide a historical view of how our research thinking developed. We chose the Kluane region for this research because of the facilities of the Kluane Lake Research Station.

Snowshoe Hares

For 35 years we have been monitoring the density of snowshoe hares on control areas in the Kluane region (Fig. 1). The 9–10 year hare cycle has continued throughout this time, with some variation in the peak hare density and the duration of the low phase of the cycle.

During the 1970s, the dominant view of the hare cycle was that it was caused by food shortage in winter (Keith, 1983; Fox and Bryant, 1984). Two alternative hypotheses were that it was driven by predation or that it was caused by social interactions. We rejected the social interactions hypothesis because hares are not territorial and show no significant spacing behavior (Boutin, 1984).

In 1976, we began a winter feeding experiment on three study grids in the Kluane area, predicting that if winter food shortages were the dominant factor driving changes in numbers, one could reverse the decline by feeding the hares with high-quality food during the winter. From 1976 to 1984, we carried out this experiment with a negative result: fed areas and control areas declined at the same time and at the same rate (Krebs et al., 1986a). We tested at the same time whether this result was an artifact of artificial food (rabbit chow) by feeding natural food (white spruce [*Picea glauca*], aspen [*Populus tremuloides*]) at the peak of the cycle (Fig. 2), but even so we failed to prevent the decline (Krebs et al., 1986b). Adding food early in the cycle increased the carrying capacity two- to threefold, so more hares were present on feeding sites by the cyclic peak, but declines occurred on both fed and control sites at the same time and at the same rate. By 1983, it seemed highly unlikely to us that food shortage explained very much of the cyclic dynamics, and we postulated that winter food shortage was not necessary for cyclic snowshoe hare declines.

If winter food was not the determining factor in hare declines, predation appeared to be the most likely second candidate, which suggested to us that we needed a much wider project covering predator-prey dynamics, as well as food plant studies. In 1986, we began a set of large-scale manipulations that lasted 10 years (Krebs et al., 2001). On 1 km^2 blocks of boreal forest, we (1) manipulated food supplies by providing artificial feed (commercial rabbit chow), (2) reduced mammalian predation by the use of an electric fence, (3) manipulated both food supplies and mammalian predation by a second electric fence, and (4) increased plant productivity by fertilizing two blocks of forest. The results were spectacular (Fig. 3). When used separately, food addition and mammalian predator exclusion each increased hare density above control values, but the combination of food addition and predator exclusion produced hare densities of 10 times the control values (Krebs et al., 1995). We concluded that the hare cycle was driven by an interaction of predation and food supplies.

For virtually all hares, the immediate cause of death is predation (Boutin et al., 1986; Hodges et al., 2001). But this fact presented another puzzle: how does the interaction of food and predation influence hare dynamics? In particular, Cary and Keith (1979) had shown clearly that reproductive output changed dramatically in hares at the peak and decline phases of the cycle (Fig. 4), and we have confirmed this pattern in our area (Stefan and Krebs, 2001). But we had shown by our feeding experiments that this reproductive collapse was not caused by food shortage. The solution to this dilemma was provided by Boonstra et al. (1998),
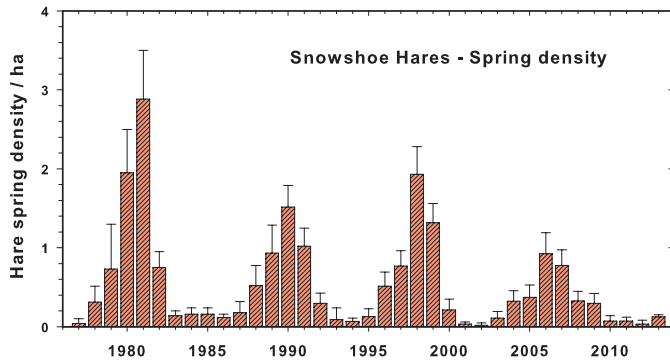
FIG. 1. Changes in population density of snowshoe hares on unmanipulated areas of the Kluane boreal forest. Error bars are 95% confidence limits. (C. Krebs, unpubl. data.)
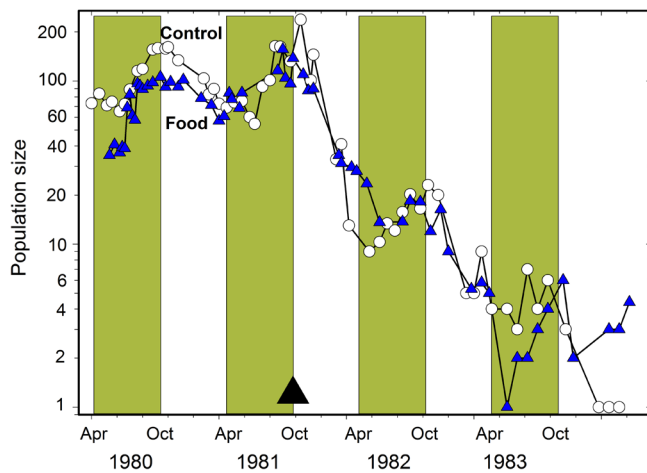

FIG. 2. A natural feeding experiment on a declining snowshoe hare population. The large triangle marks the start of the experiment in early winter 1981. White circles represent the control sites, and blue triangles, the fed sites. The white columns represent the winter (October 1 to March 31) and the shaded columns represent summer (April 1 to September 30). The x-axis ticks are spaced at 5-week intervals. The population decline was unaffected by additional food. (Modified from Krebs et al., 1986b.)

who postulated that stress was the proximate cause of the reproductive collapse, and that a likely source of stress was the action of predators searching for hares to consume.

The hypothesis that predator-induced stress caused the reproductive collapse was tested experimentally and observationally by Sheriff et al. (2009, 2010, 2011), who measured stress levels by means of both plasma cortisol levels and their fecal metabolites. Stressed females produced fewer offspring, and these offspring of stressed females also produced fewer offspring, so that the continuation of reproductive failure was carried from generation to generation by maternal effects. These results emphasize the "landscape of fear" world in which snowshoe hares exist.

The inference from all this work on snowshoe hares is that the hare cycle is driven by the direct and indirect effects of predation through direct killing and through stress from predators hunting hares (Sheriff et al., 2011). Further work is underway to replicate and test the details of the indirect components of the stress model (see Boonstra et al., 2014).
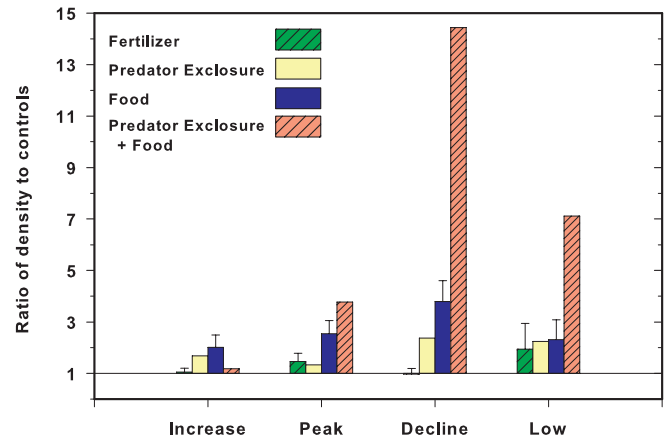

FIG. 3. The impact of four large-scale manipulations on snowshoe hare density at Kluane Lake, 1986–96. All experiments were carried out on 1 km² plots. The ratio of density is scaled to no effect of a treatment when the ratio is 1.0. The combined mammalian predator exclosure plus food addition experiment produced the most dramatic experimental effect, particularly in the decline and low phases of the cycle. Error bars are 95% confidence limits. (Data from Hodges et al., 2001.)
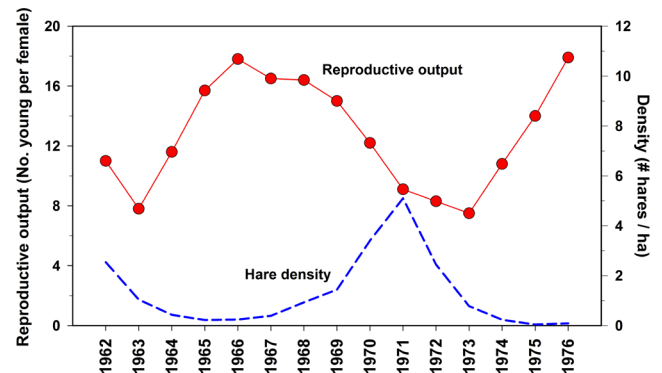

FIG. 4. Reproductive collapse associated with the snowshoe hare cycle in Alberta from 1962 to 1976. The dashed line shows hare density, and black dots represent reproductive output over the entire breeding season. A similar collapse in reproductive output occurred in hares at Kluane Lake. (Data from Cary and Keith, 1979.)

Small Mammals

Two rodent species are typically dominant in Yukon boreal forests. Red-backed voles (*Myodes rutilus*) and deer mice (*Peromyscus maniculatus*) typically comprised more than 90% of captures in snap traps and live traps. Four species of *Microtus* are less common. Fluctuations in the two dominant species are dramatically different. Red-backed voles show a 3−5 year cycle (Fig. 5a), while deer mice had two periods of high density about 25 years apart (Fig. 5b). In particular, deer mice were nearly absent from all trapping areas from 1989 to 2003 but have since recovered to high numbers.

Feeding experiments during summer increased the density of both red-backed voles and deer mice two- to three-fold (Gilbert and Krebs, 1981). This increase resulted largely from immigration into the fed areas because
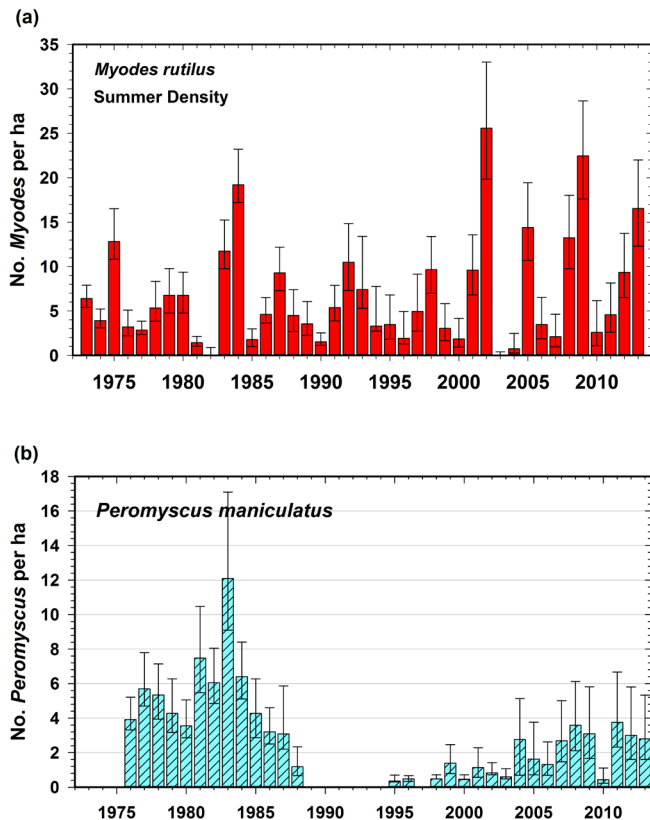
FIG. 5. Spring densities of (a) red-backed voles, (b) deer mice at Kluane, 1976 to 2011. Error bars are 95% confidence limits. Red-backed voles have a 3–4 year cycle, while deer mice had two high-density periods about 25 years apart. These species are the two dominant rodents in the Kluane boreal forest. (C. Krebs, unpubl. data.)

summer adult survival was not improved by feeding. Schweiger and Boutin (1995) followed this work with a winter feeding experiment to test the prediction that winter food supplies limited overwinter survival. In the first winter of feeding, immigrants moved into the feeding grid and increased the population density temporarily, but when the spring breeding season began, numbers on control and food grids became similar. Overwinter survival was higher on the food grids, but higher survival did not translate into higher numbers at the start of spring breeding. Schweiger and Boutin (1995) concluded that social processes associated with territoriality drove changes in numbers during the breeding season, so that high densities could not be produced by supplemental winter feeding.

For most of the period of study, small mammal predators were rare, and thus red-backed vole numbers were probably driven by a combination of social processes and food supplies (Boonstra and Krebs, 2006). We have no simple explanation for the changes in deer mouse numbers. Disease as a factor is not likely, as any disease is unlikely to have been propagated through a 15-year period of very low densities in deer mice from 1989 to 2003. Microtine-specialist predators (least weasels [*Mustela nivalis*], ermine [*M. erminea*]) were few during many years of this low period, and no obvious change in seed production occurred throughout

this period. All the correlations between marten (*Martes americana*) and weasel density indices and *Peromyscus* and *Myodes* numbers are positive rather than negative, suggesting that mouse numbers control predator numbers, rather than vice versa.

Microtus numbers are low in the Kluane boreal forest, and the limited data we have suggest a 3–4 year cycle with peak populations that have been exactly in phase with the red-backed vole peaks from 1987 to 2009. This synchronization of cycles could indicate a climate link or a plant production link between these populations.

None of the large-scale snowshoe hare manipulation experiments described above had any positive effect on vole and mouse numbers. There is a suggestion of a negative effect on the fertilized grids, where red-backed vole numbers were on average about 30% below control values. This effect could involve the reduction in the number of plant species when fertilized (see Turkington et al., 2014).

Red Squirrels

Red squirrels (*Tamiasciurus hudsonicus*) are the third most abundant mammalian herbivore in the Yukon boreal forest, comprising on average about 16% of the vertebrate biomass (Krebs et al., 2001). Their numbers have been fluctuating since 1987 (Fig. 6). A peak in numbers occurred from 1999 to 2001, and a low from 2003 to 2005 was followed by some recovery. The peak was associated with a high white spruce cone crop year in 1998, and the low, with poor spruce cone production during those years. The dynamics of red squirrel populations are driven by the resource pulses created by the seed crops of white spruce. However, unlike most consumers in these types of resource pulse systems, red squirrels appear to have the ability to anticipate cone crops (Boutin et al., 2006). Females increase both litter size and the number of litters in mast years and thus produce a substantially larger number of juveniles, the majority of which recruit into the population. The increased cone production in mast years occurs in time for the juveniles to take advantage of the cone crop late in the summer, but the adult females have produced all their offspring before the cone crop matures. Thus the increased energy expenditure required by adult females to produce more young is not fueled by mast seed. We think adult females practice a conservative reproductive strategy in most years, producing many fewer juveniles than is energetically possible, but then in mast years achieve their maximum reproductive capacity. This reproductive strategy appears adaptive because with no vacant territories, there is little pay-off in producing more young in non-mast years and most juveniles die. This fierce competition is relaxed in a mast year, and the extra juveniles produced can recruit into the population (Boutin et al., 2006).

Masting in plant species is thought to be an adaptation to seed predators whereby trees starve predators in non-mast years and "swamp" them in mast years, so that more seeds escape predation. The squirrels' ability to anticipate mast
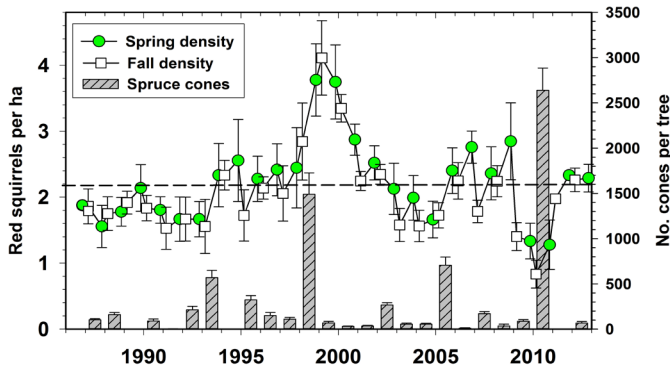
FIG. 6. Average spring and fall densities of red squirrels in relation to white spruce cone crops at Kluane Lake, 1987 to 2012. Error bars represent 1 standard error. The dashed line indicates average squirrel density. Data points represent averages of five red squirrel study areas. (S. Boutin, unpubl. data.)

years reduces the effectiveness of this strategy, but only to a degree. We have measured the functional response of squirrels harvesting cones in mast and non-mast years. In mast years, the number of cones stored by each squirrel does not exceed about 8500, even though as many as 300 000 cones may be available on some individuals' territories. On average, only 10% of the available cones were harvested in mast years in contrast to non-mast years, when the proportion hoarded was closer to 40%. Squirrels clearly are satiated in mast years, and this limitation on their harvest leads to greater seed escape in those years (Fletcher et al., 2010).

One of the interesting findings from the red squirrel research has been the observation that red squirrels are important predators of juvenile snowshoe hares during the first two weeks of the hares' life (O'Donoghue, 1994). Red squirrels killed between 20% and 47% of 170 radio-collared juvenile hares. We do not yet have a good quantitative estimate of how this predation by red squirrels changes over the hare cycle and might affect snowshoe hare population changes, but the finding does add another potentially important dimension to trophic dynamics in this part of the boreal forest.

Arctic Ground Squirrels

Arctic ground squirrels (*Urocitellus parryi*) are interesting because the Kluane region is the only part of their geographic range in which they occur in boreal forest habitats, primarily in meadows interspersed within the forest. Typically this squirrel is an Arctic and alpine species, and in the Kluane area it occurs in high abundance in alpine areas (Hik et al., 2001; Donker and Krebs, 2011). Ground squirrels in this area hibernate for eight to nine months of the year, from August-September to April, so they are not a part of the winter vertebrate community and thus not food to sustain the predators in winter.

In the boreal forest, ground squirrel numbers closely follow the snowshoe hare cycle (Fig. 7), and predation in
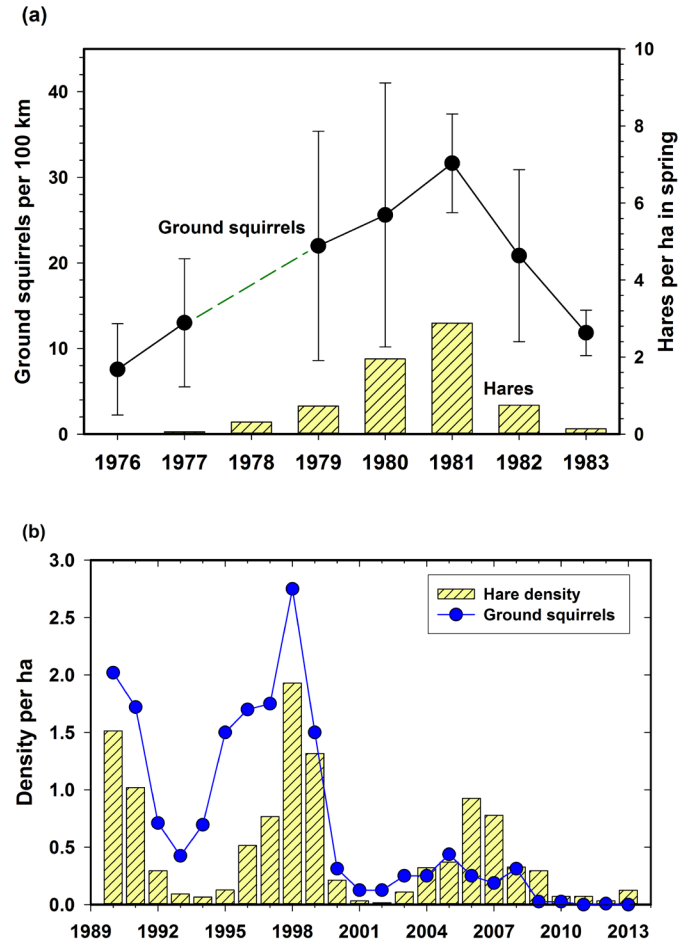

FIG. 7. Arctic ground squirrels in boreal forest: (a) Road counts from 1976 to 1983. (b) Density estimates from 1990 to 2013. Error bars are 95% confidence limits. Two ground squirrel study areas averaged for these data. (C. Krebs, unpubl. data.)

summer seems to be a limiting factor (Karels et al., 2000; Boonstra et al., 2001). Burrow selection appears to be the key to survival in ground squirrels: individuals in burrows in open areas, where potential predators were clearly visible, were more likely to survive (Karels and Boonstra, 1999). This observation seems to be a potential key to understanding why ground squirrels since 2001 have remained at very low densities. Increased shrub growth has been correlated with climatic warming in this part of Yukon, so that visibility from potential burrow sites within the forest has been greatly reduced by the increase in plant biomass and cover. This reduced visibility may be the reason for the current low densities of ground squirrels within the forest, compared to high densities in the alpine zone (Boonstra et al., 2001; Donker and Krebs, 2012).

Arctic ground squirrels are a major predator of juvenile snowshoe hares in our study area, where they occur together in forest habitats (O'Donoghue, 1994). Arctic ground squirrels killed between 11% and 29% of 170 radio-collared juvenile hares. As with red squirrels, we do not know how much this mortality may affect the hare cycle.

Other Herbivores

Many other herbivores exist in the Kluane boreal forest and we have not been able to study them in detail. We have data on two species groups.

Two forest grouse and three ptarmigan species are present in the Shakwak Valley at Kluane (Martin et al., 2001). Forest grouse are rather evenly distributed across the boreal forest. Spruce Grouse (*Falcipennis canadensis*; 85% of forest grouse biomass in summer) are associated with conifer forest, and Ruffed Grouse (*Bonasa umbellus*) with deciduous patches. Forest grouse represent less than 1% of the biomass of herbivores at the snowshoe hare high, but about 5% to 6% at the hare low (Martin et al., 2001). Forest grouse and ptarmigan cycle in the Kluane system, and hare predators seem to drive their population changes. Spruce and Ruffed Grouse begin their cyclic decline 6 to 12 months before the hares' decline, and this decline appears to be driven by predation during winter. They remain low in years of low hare abundance because of avian predation on juvenile birds over winter, as indicated by high fecundity and survival of juveniles to independence in fall but no recruitment of younger birds to the breeding population in the following years (Martin et al., 2001). Unlike several of the other herbivores that hibernate, grouse remain active year-round, and populations tend to form flocks in winter. Willow Ptarmigan (*Lagopus lagopus*) breed in the subalpine, but in winter they move down into the boreal forest, where they are subject to predation mostly from raptors (Hannon and Gruys, 1990; Martin et al., 2001). The overlap of forest and tundra grouse increases the reliability of the winter food supply to predators, and the concentrations of all grouse in winter may be vital to maintaining low densities of several avian predators during the hare low.

The Kluane study was the first to report a potential cycle in Spruce Grouse that was in synchrony with the hare cycle, in which grouse showed at least a 75% decline in spring population size (Martin et al., 2001). Spruce Grouse in Kluane also differed in several life history parameters from other populations studied. Grouse at Kluane were about 5% to 6% larger and heavier, had higher clutch sizes, and differed in several breeding displays from populations in southern and eastern Canada and Alaska (Ellison and Weeden, 1979; Boag and Schroeder, 1992; Martin et al., 2001: Table 11.2). Another important finding on Spruce Grouse has been that there are specific feeding trees that Spruce Grouse harvest to the exclusion of other spruce trees (Mueller, 1993). We were not able to unravel the chemistry of this preference; it is a problem waiting to be studied further.

In general, we have considered insects as constituting a very small role in the trophic dynamics of the Yukon boreal forest. This belief was interrupted by a spruce bark beetle (*Dendroctonus rufipennis*) outbreak that began in our study area in 1990 (Berg et al., 2006). Spruce bark beetles kill trees by burrowing in the phloem of the inner bark and damaging fluid transport tissues in the tree. By analyzing tree rings, Berg et al. (2006) were able to show that spruce bark beetle outbreaks in the Kluane region were very rare events in the last 250 years. They attributed this fact to the cold temperatures in the Kluane area and suggested that climate change could increase the frequency of beetle outbreaks at Kluane. During the peak of the 1990–2010 outbreak, from 1997 to 2000, we found a maximum of 30% to 35% of white spruce with diameter at breast height (DBH) of more than 10 cm were attacked by bark beetles in a given year (Fig. 8). In 2000 (C. Krebs, unpubl. data), after the outbreak began to decline, the cumulative percentage of killed spruce trees on eight sites monitored ranged from 0% to 41%, with a median of 14% dead white spruce trees with DBH above 10 cm per site, including tree deaths from all causes (but mostly from spruce bark beetles). The immediate effect of spruce tree mortality is most visible in seedeaters such as red squirrels, small rodents, and crossbills, but we have not yet been able to quantify these effects in the short time since the beetle outbreak stopped. Over the long term, secondary succession is filling in the forest, but we may require 50 or more years of monitoring to see the full impact of the spruce bark beetle on community dynamics.

We have insufficient data on songbirds and other small herbivores. The few data we have are available in Smith and Folkard (2001).

Predators

At the same time that we were studying hares, we obtained detailed data on the major predators in this ecosystem: lynx (*Lynx canadensis*), coyotes (*Canis latrans*), Great Horned Owls (*Bubo virginianus*), and other smaller predators (Boutin et al., 1995; Rohner, 1995; O'Donoghue et al., 1997). All of these predators fluctuate with hare numbers, but respond with a time lag because of their lower reproductive rates (Fig. 9). This finding was consistent with the predictions of models that demand delayed density-dependence to generate cycles in predator-prey systems.

Lynx and coyotes are the major mammalian predators of hares, squirrels, and small rodents in this ecosystem. Wolves (*Canis lupus*) are present in relatively low numbers because of the relatively low densities of their main prey, moose (*Alces alces*) and caribou (*Rangifer tarandus*), which we did not study. Both lynx and coyotes behaved as specialist predators, responding both numerically and functionally to hare densities. In the Kluane area, these predators eat almost nothing but snowshoe hares when they are available, but change their diet to squirrels and small rodents during the low population density phase of the hare cycle (O'Donoghue et al., 1998).

The Great Horned Owl is the major bird predator of hares, and like the lynx, it fluctuates with hare numbers, but with a time lag because of its low reproductive rate (Rohner, 1995, 1997). Figure 10 shows the density of nesting Great Horned Owls from 1987 to 2011. These owl data mirror the lynx and coyote data in showing a delayed, density-dependent response to hare density. One important difference with
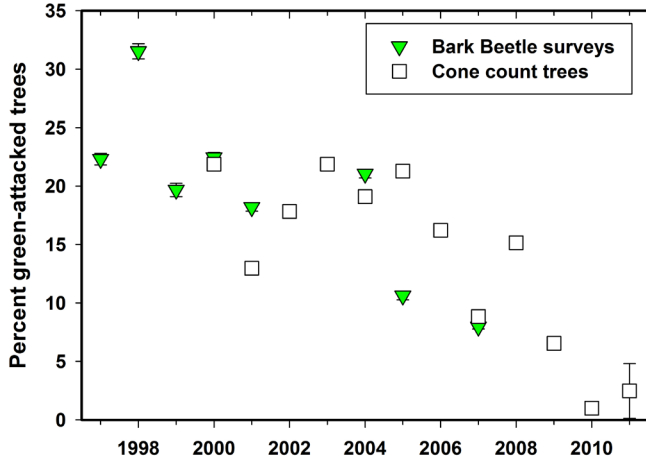
FIG. 8. Percentage of white spruce trees attacked by the spruce bark beetle during the 1990s outbreak.
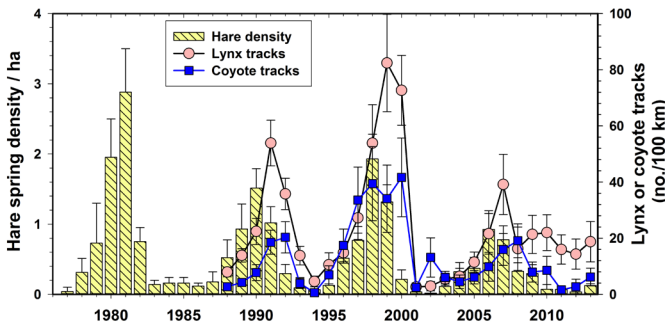

FIG. 9. Coyote and lynx tracks in relation to snowshoe hare density in the Kluane region. Snow tracking in winter provides a good index of predator densities. Error bars are 95% confidence limits. (C. Krebs, unpubl. data.)
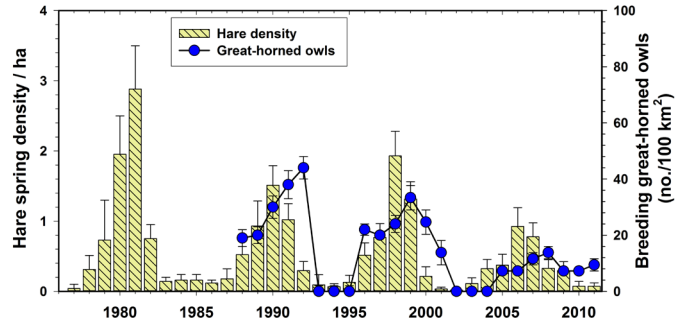

FIG. 10. Great Horned Owl population changes in relation to the snowshoe hare cycle at Kluane. Owl estimates are based on spring hooting surveys and include only breeding pairs. Error bars are 95% confidence limits. (C. Rohner and E. Hofer, unpubl. data.)
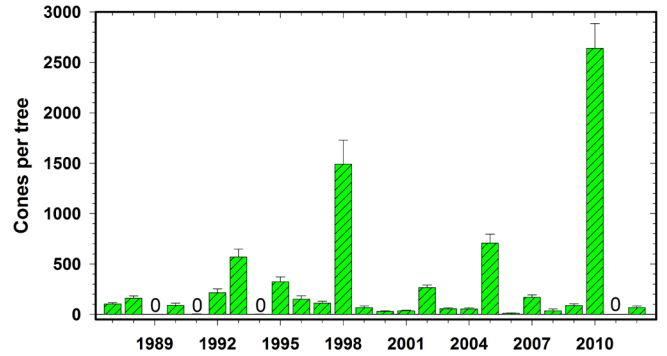

FIG. 11. White spruce cone counts in the Kluane area, 1986 to 2011. Cone counts are carried out on an average of 700 trees each year. Counts were corrected to be whole tree estimates using the method of LaMontagne et al. (2005). Error bars are 95% confidence limits. (Modified from Krebs et al., 2012.)

Great Horned Owls is that there is a "surplus" or floating population that is difficult to census (Rohner, 1997). These surplus individuals do not defend territories, but they do consume snowshoe hares, so they are an important component of the predator community, comprising up to 40% of the total density of owls at the peak of the hare cycle.

Since 2000, there have been significant changes to the predator community in the Kluane region. Marten, previously nearly unknown in this area of Yukon, have become common; ermine have increased in abundance; and cougars (*Puma concolor*), although currently scarce, have colonized the area. By continued monitoring, we hope to determine the impact of these changes on the vertebrate community.

Tree and Shrub Dynamics and Production

We have monitored white spruce seed production and shrub growth at Kluane since 1987, and we will briefly summarize what we have found.

White spruce is the dominant tree in the Kluane boreal forest. Like many northern conifers, it has highly variable mast years (Fig. 11). Since 1987, major mast years have occurred in 1998 and 2010 and moderate mast years in 1993 and 2005. The conventional wisdom (Juday et al., 2003) is

that major mast years in white spruce are limited by five thresholds that must be passed in order to have a successful cone crop in year t: 1) Sufficient growth reserves from previous years, so there cannot be two large cone crops in a row; 2) Warm temperatures and a drought stress signal in midsummer of year $t-1$, when bud primordia form; 3) A lack of pruning of reproductive shoots from snow and wind in winter; 4) Warm temperatures in the spring of year t to promote pollen and cone bud maturation; and 5) Lack of frost and heavy rain in spring of year t to allow pollination.

The anecdotal, less detailed model for good cone crops is warm dry weather in year $t-1$ to induce the cone crop and again in year t to produce the cone crop (Zasada et al., 1992).

We tested this five-threshold model for white spruce cone crops with 26 years of data from Kluane and rejected it because it explained very little of the variation in our data (Krebs et al., 2012). Our statistical model explained 54% of the variation in cone crops from July and August temperatures of years $t-1$ and $t-2$ and May precipitation of year $t-2$. The model gave no indication of a periodicity in cone crops (autocorrelation analysis, 26 years, all $p > 0.35$), and years of large cone crops were synchronous over the Kluane

region with few exceptions. The surprising result for Kluane is that weather conditions two years prior to the cone crop seem to be the most significant predictors of large cone crops.

White spruce appears to be responding to climatic warming in the Kluane region. Boonstra et al. (2008) showed that on control plots, growth-ring widths increased from 1986 to 1997, a time during which average early summer temperature was increasing on average by 0.14°C per year. We have yet to update this study of ring widths in control trees since 1997.

Two shrubs dominate in the Kluane region, grey willow (*Salix glauca*) and dwarf birch (*Betula glandulosa*), and snowshoe hares, as well as moose, feed on them. We measured relative growth rates in these shrubs by collecting terminal twigs 5 mm in diameter from 460 willows and 330 birch trees each year from 1987 to 2008. Growth rates varied dramatically from year to year (Fig. 12). There is no correlation between the annual growth rate indices of these two shrubs. Two variables affect these growth indices: weather and the amount of browsing by snowshoe hares in winter (Smith et al., 1988). For dwarf birch, hare browsing is the major driver of annual growth (browsing stimulates growth), but this is not the same for willow, which is not so heavily browsed and presumably responds more to changes in temperature and rainfall. There is a very slight positive time trend in the annual growth rate indices of these shrubs over the 21 years of data, but this trend is not significant. We can thus find no strong signature of climatic warming in these measures of shrub growth.

Correlations with Broad Climatic Indices

We have explored our time series to look for evidence of cross-correlations with the broad-scale Pacific Decadal Oscillation (PDO). We have not published these details because they are uniformly non-significant statistically. Our search for climatic correlations has been successful only with local variables of monthly temperature and precipitation (spruce cones, ground berries, mushrooms). One reason for our lack of success could be that our time series are too short. Any correlations that might be found with large-scale oscillations like the PDO have to be tied to mechanisms working within the ecosystems of Kluane, as Morrison and Hik (2007) have done. More exploration of climatic effects is clearly needed.

CONCLUSIONS

Whither trophic dynamics research in the boreal forests at Kluane? Three major problems stand out for further research. The amplitude of the snowshoe hare cycle has apparently been diminishing over the last 30 years (Fig. 1), and this trend could be a signature of climate change. We do not know that this is the case, and regardless of the current fervor over blaming climate change for everything, we
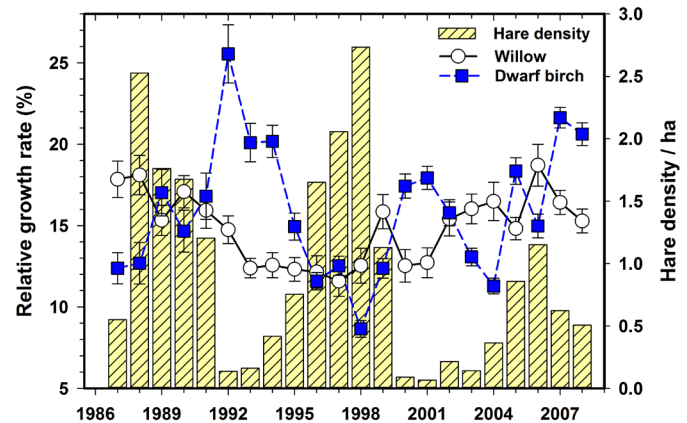
FIG. 12. Relative growth rates of 5 mm diameter twigs of grey willow and dwarf birch at Kluane, 1987 to 2008. Error bars are 95% confidence limits. (C. Krebs, unpubl. data.)

need to know the mechanisms behind these changes. They could be caused by a collapse of regional synchrony and the associated movements of predators out of declining hare populations. Alternatively, the declining amplitude of the hare cycle could be caused by changes in the abundance of generalist predators, or changes in the hunting success of lynx and coyotes. A second major problem has been our inability to link processes in the boreal forest with those in alpine environments. We now know, for example, that Arctic ground squirrels have gone nearly extinct in the boreal forest, while they remain at high abundance in the alpine areas just above the valley forests. Certain components of the biomass from various trophic levels move seasonally from the boreal forest to the alpine areas, but the role of these movements in affecting the vertebrate community has not been determined. Finally, we need another large-scale study of predator dynamics in another location in this ecosystem to test ideas that have arisen from our major project. We do not have a good understanding of how snow conditions affect the hunting success of terrestrial or avian predators, and if climatic models are approximately correct, snow conditions will change in the coming years.

Beyond these large-scale issues, a host of other questions needs to be investigated. The Kluane boreal forest is an ecosystem of oscillations in hares, mice, plant production, and predator numbers. Whether and how these oscillations interact is an important issue for further research. Porcupine (*Erethizon dorsatum*) populations in this region come and go in a cycle of approximately 20 years, and no one has any information on why this might be. Deer mice have a strange long-term pattern that we do not understand at all. We have assumed that the trophic dynamics we have described operate independently of the large mammal component of the vertebrate community—moose, wolves, grizzly bears (*Ursus arctos*) and black bears (*U. americanus*), caribou, and Dall sheep (*Ovis dalli*). A large-scale study of all these species, large and small, would be desirable to test this assumption. We have very little information on insects in this part of the boreal zone, and we suspect they

may become more common and affect both plant dynamics and insectivore abundance. We know almost nothing about nutrient dynamics in the soil, and our fertilization studies and rainfall addition studies have raised numerous questions about nutrient cycles in this part of the boreal forest (see Turkington et al., 2014). We need to continue the monitoring study begun in 1973 to provide a continuous record of the response of key ecosystem components to changes over time. Changes in trophic dynamics, even within a relatively simple ecosystem like this one, are impossible to predict as the climate shifts. Field experiments are necessary to test these ideas because models will not provide the answers we need.

The bottom line is that a host of large- and small-scale studies need attention. This conclusion is not surprising, since ecological studies typically generate more questions than they answer.

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