# Hares and Small Rodent Cycles: a 45-year Perspective on Predator-prey Dynamics in the Yukon Boreal Forest

**Charles J. Krebs**[1], **Rudy Boonstra**[2], **Alice J. Kenney**[3] **and B. Scott Gilbert**[4]

[1] Department of Zoology, University of British Columbia, Vancouver, B.C. V6T 1Z4 Canada, and Institute for Applied Ecology, University of Canberra, Bruce, ACT 2601

[2] Department of Biological Sciences, University of Toronto Scarborough, Toronto, Ontario M1C 1A4 Canada

[3] Department of Zoology, University of British Columbia, Vancouver, B.C. V6T 1Z4 Canada, and Institute for Applied Ecology, University of Canberra, Bruce, ACT 2601

[4] Renewable Resources Management Program, Yukon College, Whitehorse, Yukon Y1A 5K4

## ABSTRACT

Long-term research is required in ecology to determine patterns of population changes, to suggest limiting factors, and to determine if and how climate change is affecting populations and their communities. In the Kluane region of the Yukon we have monitored control populations of snowshoe hares, mice, and voles from 1973 to 2017 (the longest of any similar time series anywhere in North America) and here we ask what we have observed and learned from these time series. The amplitude of hare cycles may be decreasing over this period. In contrast, the 3-4-year cycles of red backed voles (*Myodes rutilus*) are becoming more dramatic and the amplitude of their peak years are increasing. Four species of *Microtus* voles fluctuated independently of red-backed voles prior to 1998, but their peak years became synchronous thereafter, with the dominant species changing from peak to peak. The deer mouse (*Peromyscus maniculatus*) fluctuated irregularly, completely disappearing from the catch for 5 years in the early 1990s. Weasels were rare for the first 25 years of small rodent changes and marten were absent, but since 2000 marten have colonized and both small predators have become more abundant. Predation drives the snowshoe hare cycle, but it is far from clear that it does so for the small rodents. We suspect that social behaviour is critical for vole cycles, but this supposition has not been tested experimentally. The boreal forests of Canada and Alaska support a boom-bust set of dynamics but the voles fluctuate independently and out of phase with the hares and there is no universal cause.

**Key words:** population cycles, boreal forest, snowshoe hares, mice, voles, Yukon

DOI: https://doi.org/10.7882/AZ.2018.012

## Introduction

Most ecologists are supportive of long-term research programs, and it is important to justify this support by asking what surprises have been discovered from long-term studies (Hughes *et al.* 2017). Here we concentrate on a 45-year time series for populations of snowshoe hares (*Lepus americanus*) and small rodents (*Myodes rutilus, Peromyscus maniculatus, and Microtus* spp.) in the Kluane region of the southwestern Yukon. The 9-10 -year cycle of snowshoe hares occurs across the boreal forest zone of Canada and Alaska, and most of our research has been on explaining the dynamics of this cycle (Krebs *et al.* 2018). The boreal forest is the largest ecosystem in Canada (~ half of its land mass) and in North America covers 5,120,000 km$^2$ (Kuusela, 1992). Cycles of small rodents have been observed at many locations across Canada and the USA but most studies have been too short to estimate long-term trends (Boonstra and Krebs 2012).

Long-term research has buried in it two objectives. First, to describe the patterns of change in populations or communities. This is its natural history element, and the general problem has always been that this is not considered science and hence not funded by granting agencies. The second objective is to determine the mechanisms behind the observed patterns, and this objective can be achieved in two ways. Experimental manipulations are the simplest way to get at mechanisms and are to be preferred if possible. Alternatively, in many cases careful observations can narrow the field of alternative hypotheses. Observations without manipulations are a weak form of inference but, presently we are limited to using simple observations to suggest mechanistic hypotheses that can be tested at a later time. A weakness of the observational approach is that it assumes constancy in the patterns being studied, and this problem is compounded in an era of changing climate. In this paper we use a mixture of experimental and observational studies to report the changes in the key mammal species and to suggest the mechanisms driving these changes in numbers of hares and small mammals in the Kluane region of the Yukon.

The mechanisms of population change are well understood, and a background of studies is available for narrowing our search for the most important mechanisms causing population change. For snowshoe hares the two main driving mechanisms have been food and predation, and we have been able to test these experimentally (Krebs *et al.* 2018). For the rodents we have much less experimental data and we rely instead on weak inference from natural history observations. Rodent populations can change because of weather, food supplies, interspecific competition, predation, disease, parasitism, or social interactions (Boonstra *et al.* 2001, Boonstra and Krebs 2006). For our northern populations discussed here, disease and parasitism have not been thought to be significant mechanisms causing populations to change in abundance, and we will ignore them in this paper because we have no relevant data. This is a conclusion specific to these northern rodents and must not be considered a general conclusion applicable to all small rodents in other ecosystems.

For snowshoe hares, our hypothesis is that changes in density are caused by predation and thus all changes in mortality and reproduction can be linked to predators. The alternative hypotheses are that food supplies, weather, or disease are major mechanisms causing population changes. Note that we begin with simple single-factor hypotheses because they are the easiest to reject, and not because they can explain everything about density changes.

For small rodents the search for mechanism is more complicated because social interactions can combine interactively with weather, food supplies, predation or disease to produce many two-factor hypotheses that must be tested (Wolff 1997; Boonstra and Krebs 2006; Sutherland and Singleton 2006; Krebs *et al.* 2007). In this paper we present observational data to make weak tests of the single factor weather, predation, and food hypotheses for mice and voles at Kluane.

## Methods

All population estimates were obtained from mark-recapture data from grid live-trapping. For hares from 1976 to 1984 we used 10 by 10 grids with 30 m spacing of live-traps. We discovered by that time that hare home ranges averaged 3-7 ha (Boutin 1984), and consequently we needed a larger trapping grid to reduce the edge effect. After 1984 we used 20 by 20 grids with 30 m spacing. Details of trapping methods are described in Hodges *et al.* (2001). We recalculated all our population density estimates using SECR methods described by Efford *et al.* (2009) and programmed by him in DENSITY 4 and DENSITY 5. When there were fewer than 7 individuals captured because of low density, we used the minimum number known alive along with the estimated average effective size of the area trapped (17 ha for 10 by 10 grids, 61 ha for 20 by 20 grids).

For small rodent trapping we used a standard 10 by 10 grid-size with 15 m spacing of live-traps. We used 100 Longworth live-traps per grid from 1976 to 1984 and thereafter 50 live-traps unless the rodents were at high density when we increased the number of live-traps to 100. Live-traps were left in the field all year round, locked open. We typically pre-baited the live-traps 2-4 days before the actual live-trapping.

Beginning in 2005 we recorded temperature at ground level over winter with duplicate Maxim Thermochron iButtons (DS 1921G-F5, https://www.maximintegrated.com/en/products/digital/ibutton.html ) that recorded temperature every 4 hours to obtain a measure of winter severity under the snow. Winter severity was measured by degree-days below -10°C. For each day temperature was measured every 4 hours and the measures < -10°C were then summed to give the total degree-day for that particular day.

The food web for the boreal forest ecosystem at Kluane is given in Boonstra *et al.* (2018). Details of predator-prey interactions in this ecosystem are given in Krebs, Boonstra and Boutin (2001), Krebs *et al.* (2014a), Chan *et al.* (2017), and Boonstra *et al.* (2018) with detailed analyses of data on predator abundance in the Kluane boreal forest.

## Results

### a) Snowshoe hares

Figure 1 shows the spring density for snowshoe hares from 1977 to 2017 averaged over 3 control grids. Densities in spring at the start of the breeding season ranged from a low of 0.04 to a high of 3 per ha. The median amplitude (high/low) for autumn hare density for all the data was 20-30-fold (Krebs *et al.* 2014b). There is a visual tendency for the peak spring density to decline from the 1970s to 2017. The 1971 peak at Kluane was judged by M. Hoefs (pers. comm.) to be very much higher than our 1981 peak, and local knowledge dating from the 1930s identified a hare peak that was so high that some overwintering horses in the area starved and had to be put down. Thus, there were likely peaks even higher than those we have observed. With five 9-10-year cycles our sample is suggestive of a declining peak density but not quite statistically significant (slope = -0.044, SE = 0.019, $p = 0.11$).

The mechanism behind cyclic hare demography is predation (details in Krebs *et al.* 2018). We manipulated food supplies both in winter and summer and while it enhanced local hare density (largely via immigration), fed populations declined at the same time and at the same rate as controls. Direct predation is the cause of death of >90% of snowshoe

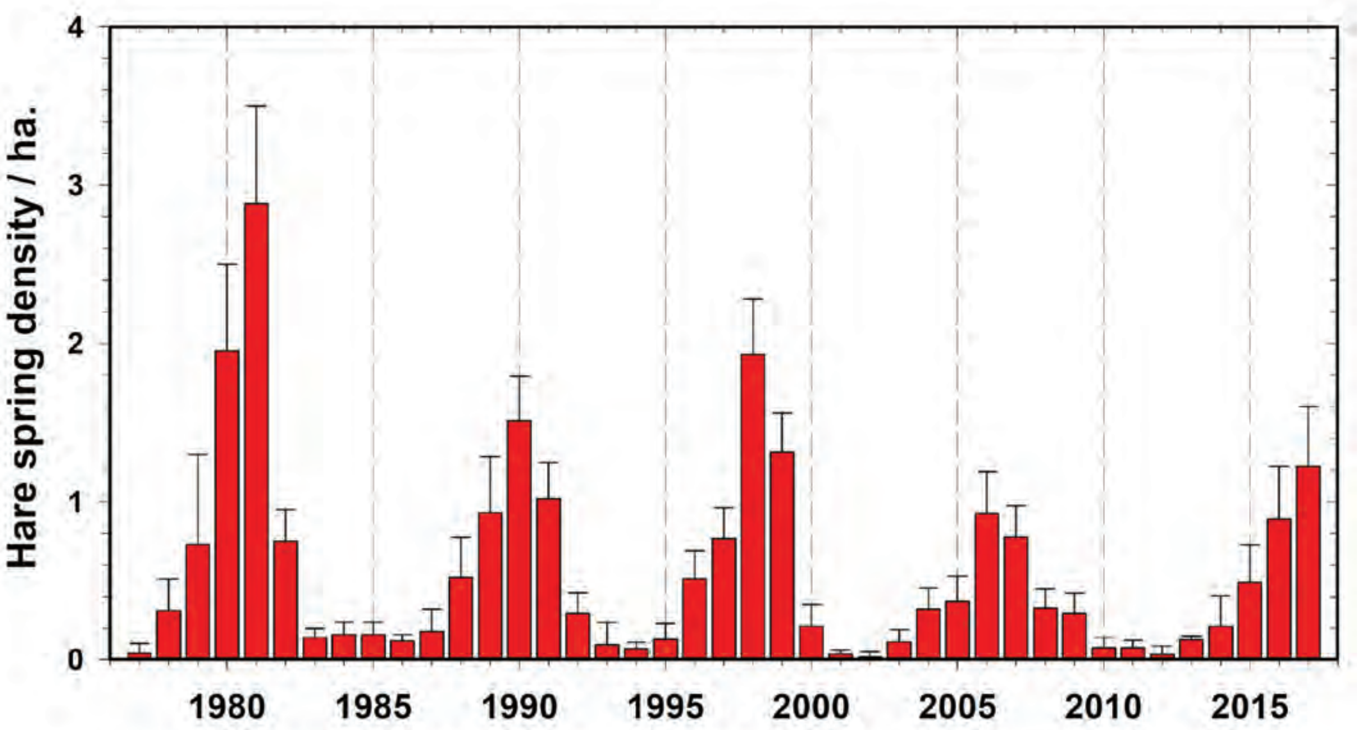

**Figure 1.** Average snowshoe hare density (per ha) on control grids in spring at the start of the breeding season, 1977 to 2017. Hares had been at peak density in 1971 just before we began working in the Yukon. Error bars are 95% confidence limits.

hares (O'Donoghue *et al.* 2001). More puzzling has been to explain why the reproductive rate of hares declines after the cyclic peak and remains low for several years. We initially thought this was due to food shortage, as postulated by Cary and Keith (1979), but feeding experiments showed that food shortage was not the direct cause of the decline (Krebs *et al.* 1986). Boonstra *et al.* (1998) suggested that the reproductive collapse of hares was stress-related, chronic stress arising from continued predator chases. Sheriff *et al.* (2009) confirmed this hypothesis, and subsequent work underway now is so far consistent with the view that reproduction in hares is highly sensitive to predator chases. DeAngelis et al. (2015) have suggested an alternative hypothesis for reproductive decline associated with changes in plant toxin levels but we do not have the detailed data needed to test this hypothesis.

Our long-term studies of snowshoe hares have allowed us to ask questions about changes in cyclic amplitude that might lead to cyclic collapse, to investigate how synchrony of hare cycles occurs at a landscape level (Krebs *et al.* 2013), and most importantly to discover the importance of chronic stress for mammalian reproduction in field populations. This has led further into investigations of how stress can reorganize the mammalian brain and the mechanisms behind reproductive maternal effects in mammals (Lavergne *et al.* 2014).

## b) Red-backed voles

The red-backed vole (*Myodes rutilus*) is the most common small rodent in the Kluane region, comprising on average about 65% of the rodent population (see Boonstra and Krebs 2012 for details of their natural history). There has been past controversy about whether or not this species shows 3-4-year population cycles in the boreal forest. Figure 2 shows that regular 3-4-year cycles seem to be the rule in the Kluane region. The pattern is suggestive of an increase in amplitude of *Myodes* cycles after the year 2000. Figure 3 provides a correlation with that timing. Weasels (*Mustela erminea*) are a major specialist small mammal predator and are common in western Eurasian boreal forests where they are associated with the cycles their small mammals undergo (Korpela *et al.* 2014) but weasels are uncommon in North American boreal forests. They have always been present in our study area and are caught in our live-traps but densities are low most of the time. From 1987-1996, on 15 live-trapping grids we caught only 9 weasels. Snow tracking data over this period recorded an index of their abundance (Fig 2 in Boonstra and Krebs 2006) and weasel tracks reached a peak once when red-back voles declined to a low, but we concluded that overall the expected inverse relationship between weasel abundance and red-back vole overwinter survival was weak. Marten (*Martes americana*) were effectively missing from this area of the boreal forest from 1973 to 2000 (Slough 1989). We saw no evidence of their presence from 1973 to 1986. Snow tracking began in 1987 and from 1987 to 2000 we scored 0.2 marten tracks per 100 km of snow tracking (12037 km tracked) and from 2001 to 2017 we scored an average of 20.2 marten tracks per 100 km of snow tracking (6040 km tracked). Small rodents are a major part of the diet of marten, and the pattern shown in Figure 3 suggests a higher amplitude of the *Myodes* cycle after 2000 coincident with the arrival of a major vole predator (average peak density before 2000 = 9.7/ha, after 2000 = 19.5/ha, $t$ = 4.84, $p$ < 0.01, $n$ =

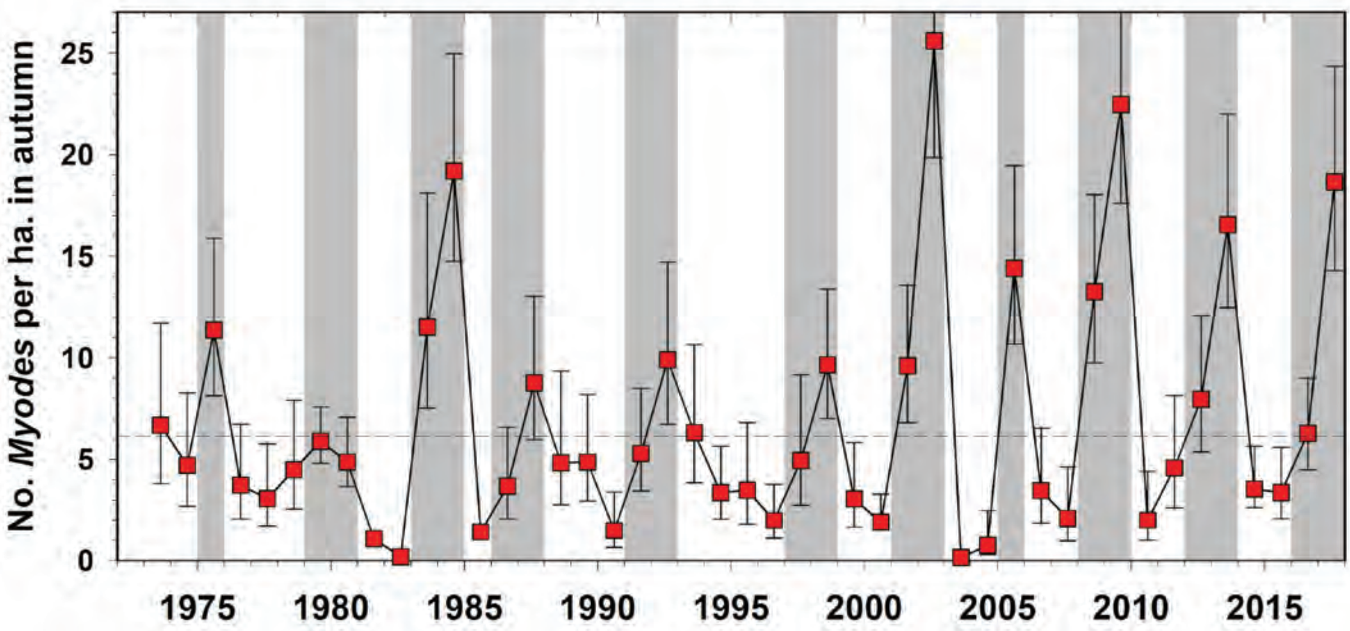

**Figure 2.** Changes in red-backed vole density (per ha) on control live-trapping grids in autumn at the end of the breeding season, 1973 to 2017. From 1973 to 1985 one or 2 grids were averaged. After 1985 three grids were averaged. Error bars are 95% confidence limits. Shading represents periods of peak abundance. The horizontal dashed line represents the average density over the entire period of study.

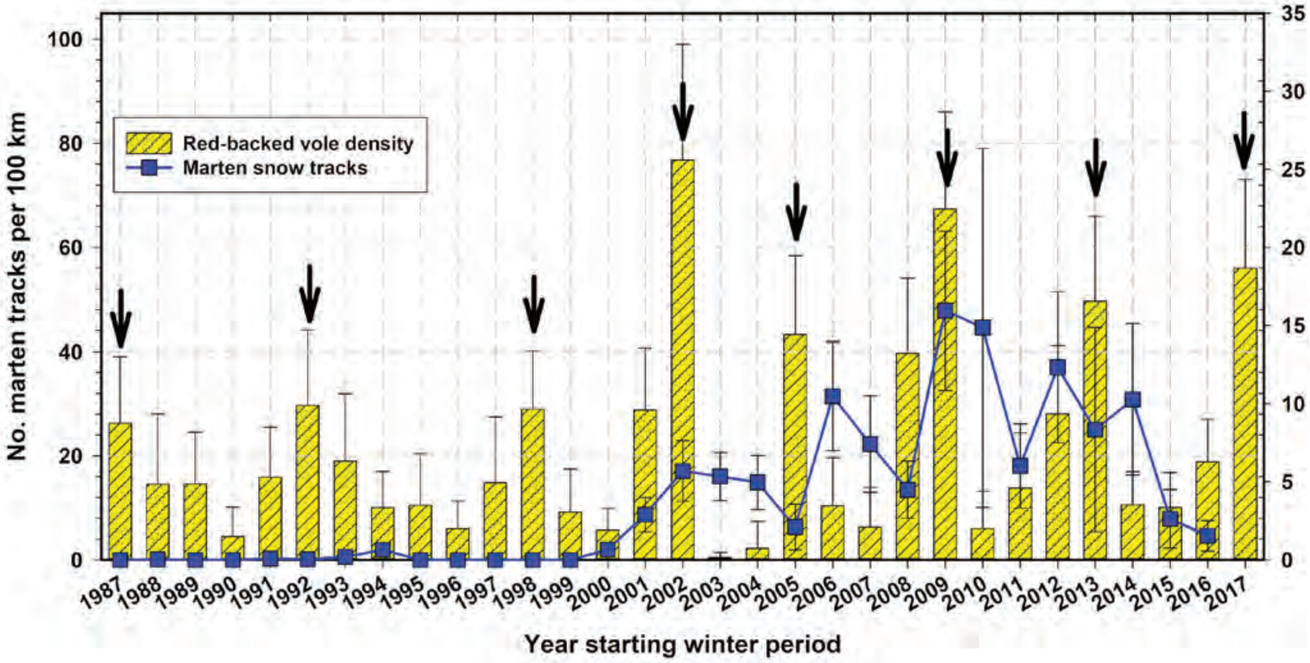

**Figure 3.** Average red-backed vole density (per ha) in autumn, and number of marten snow tracks counted on line transects in winter (1987 to 2017). Peak years for voles designated by arrows. Marten were virtually missing in this part of the boreal forest before 2001.

8 cycles). Thus marten presence and density changes may be a consequence, not a cause, of increased vole densities.

One of the common beliefs in small rodent population dynamics is that, in areas with winter snow cover, the severity of winter weather adversely affects population abundance (Fuller 1969). We have been able to test that with *Myodes* in the Kluane area with data from 2005 to 2017. In 2005 we began measuring ground level temperatures through the winter. Data were collected on the exact sites of our live-trapping grids. Figure 4 shows that the observed data is almost the exact converse of the prediction that more severe winters would cause a larger population decline over the winter months. *Myodes rutilus* can breed in winter (Boonstra and Krebs 2012) but we do not have winter live-trapping data for our area. We can see no support for the severe weather hypothesis.

There are two simple hypotheses about the control of *Myodes* densities that are not adequately tested. First,

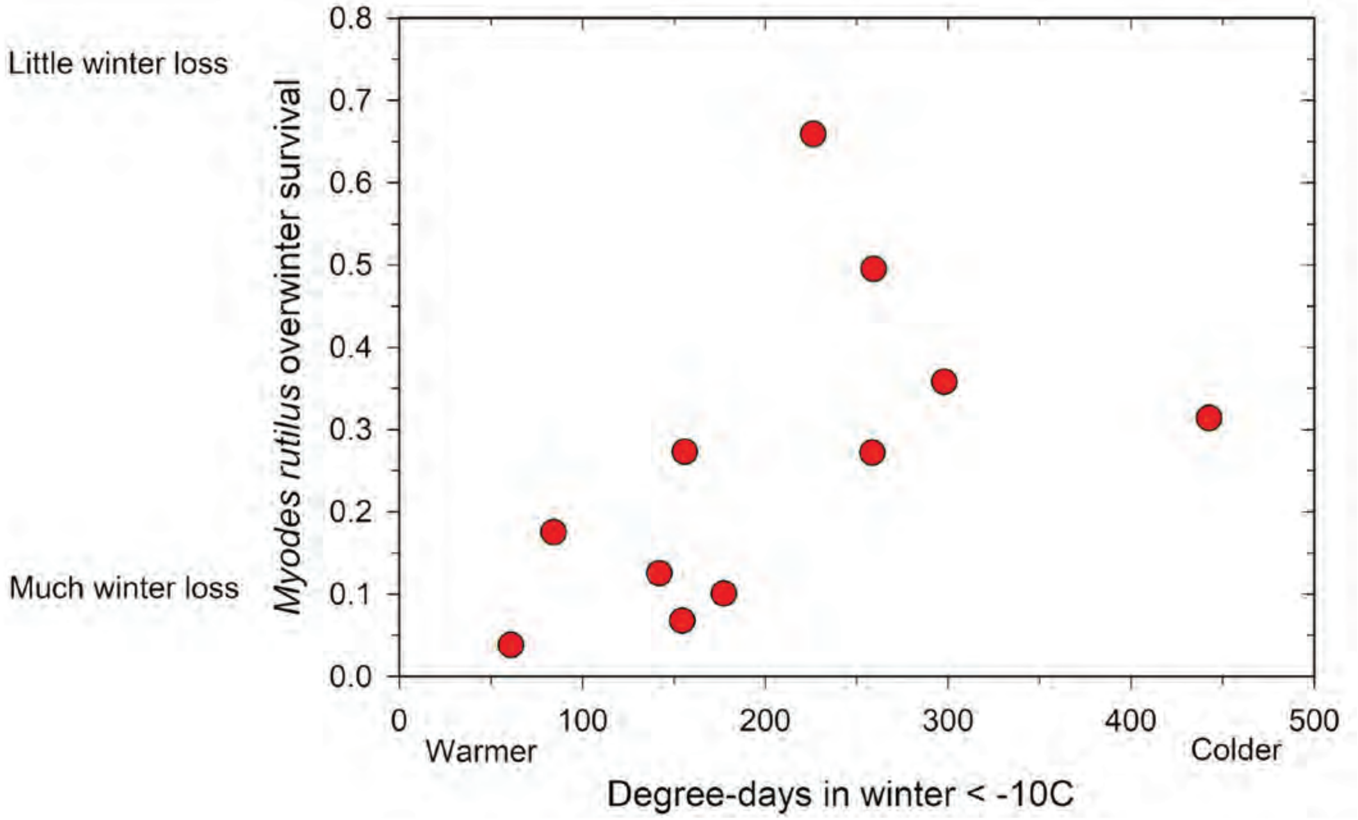

**Figure 4.** Overwinter survival of red-backed voles in relation to winter severity, 2005-2016. Winter severity is measured from November to March. Overwinter survival is estimated by (spring density of year ***t+1)***/ (autumn density of year ***t***). The prediction that more severe winters would reduce populations more is rejected for these data, and the converse is more likely to be correct.

in Krebs *et al.* (2010) we suggested that berry crops of crowberry (*Empetrum nigrum*) in year *t* were a good predictor of *Myodes* densities in year *t+1*. The addition of 8 years of data has rejected this statistical model (Krebs unpublished). We can find no model involving the measured berry crop of year *t*-1 that correlates with overwinter declines in density from the data available from 1997 to 2017. From these data, food as indexed by berry crops does not seem to limit *Myodes* numbers. A second hypothesis is that red-backed voles have the behavioral organization – female territoriality – in which spacing behavior can potentially limit breeding density, cause density-dependent inhibition of maturation of young of the year, and infanticide (Bujalska, 1973; Gilbert *et al.* 1986; Lambin and Krebs 1993; Mappes *et al.* 1995). We do not yet have the detailed studies of female territoriality and potential infanticide in *Myodes rutilus*, to test the social behaviour hypothesis for population changes.

## c) Deer mice

Deer mice (*Peromyscus maniculatus*) are common in the boreal forest of the Yukon. They are near the northern limit of their geographic range at this latitude and have been little studied. Figure 5 shows the observed density changes in deer mice on our control grids from 1976 to 2017. Two aspects of these density changes are notable. First, in autumn trapping from 1989 to 1995 not a single deer mouse was captured on 15 live-trapping grids. In spring trapping over that period only 2 deer mice were captured in 1993. Clearly deer mice did not go extinct over this period, but we have no explanation for this prolonged local absence. Second, after the 1989-95 hiatus, deer mice appeared to be on average less abundant than they were before 1989. This difference in average density was associated with two events. A major bark beetle outbreak in the 1990s in the Kluane region attacked 30-35% of mature white spruce trees (*Picea glauca*) and killed about 14% of them (Krebs *et al.* 2014a). While this bark beetle kill must have reduced white spruce cone production at least locally, we have no correlational evidence that white spruce seed production was associated with *Peromyscus* abundance. The correlation from 1995 to 2017 between *Peromyscus* spring abundance and spruce cone crops of the current or previous year are both non-significant ($r = 0.11$, $n = 23$). Thus, we have no evidence from white spruce seed crops that can explain the deer mouse patterns of changes in abundance. We know from removal experiments that adult female *Peromyscus* restrict the recruitment of juveniles via territorial behaviour (Galindo and Krebs 1987) but this type of social interaction could not lead to local extinction over a 5 year period. Galindo and Krebs (1985a) could find no evidence of competitive release of *Peromyscus* from interactions with *Myodes rutilus* and *Microtus pennsylvanicus*. Thus we do not know what caused the population changes for deer mice

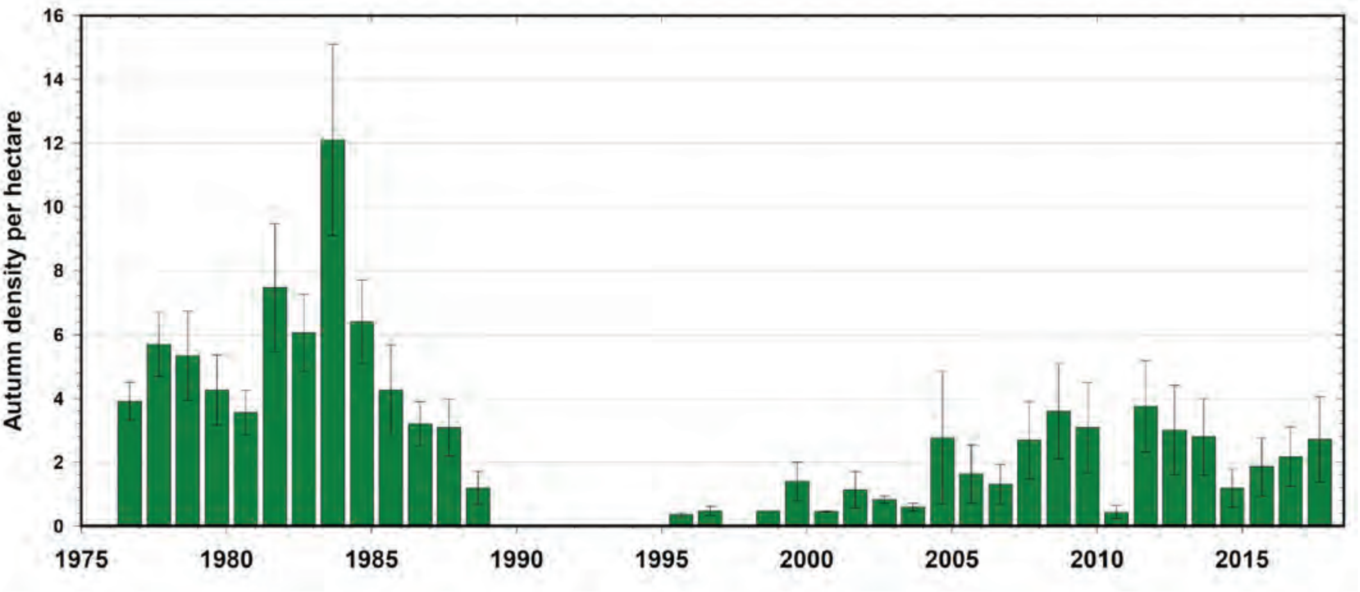

**Figure 5.** Average population density of *Peromyscus maniculatus* on control grids in autumn, 1976 to 2017. In spite of extensive trapping on 15 live-trapping grids (Boonstra *et al.* 2001) from 1989 to 1995 no *Peromyscus* were captured in autumn. Error bars are 95% confidence limits.

shown in Figure 5 but we do not think it is associated with interspecific competition between the common rodent species at Kluane Lake.

## c) Meadow voles

The last group of rodents that we have long-term data on are 4 species of *Microtus – M. oeconomus, M. pennsylvanicus, M. miurus, and M. longicaudus*. *M. longicaudus* is the largest of these voles but in our samples is relatively rare. All these *Microtus* are primarily herbivorous, eating both dicotyledon and monocotyledon leaves, stems, and roots; seeds make up a small proportion of the diet and insects are an insignificant component of the diet (see Boonstra *et al.* 2001 for references). The pattern of density changes since 1987 are shown in Figure 6. *Microtus* comprise about 15% of the small mammals in the Kluane boreal forest, and because they feed heavily on grass, they are distributed mostly in open spruce forest. While Figure 6 shows clear evidence of 3-4-year cycles, the dominant species of *Microtus* on our live-trapping grids varied with the year. However, from 1998 onwards the peaks in the *Microtus* group of species coincided with that of red-backed voles. There are only two explanations for the synchrony in species – either periodically severe weather is synchronizing their years of good and poor survival or predation is doing so. We reject the former but are not convinced of the latter. Thus, we need to investigate *Microtus* on a larger spatial scale to determine if we are simply looking at patch dynamics at too small a spatial scale of our 3 ha grids and at the same time carry out

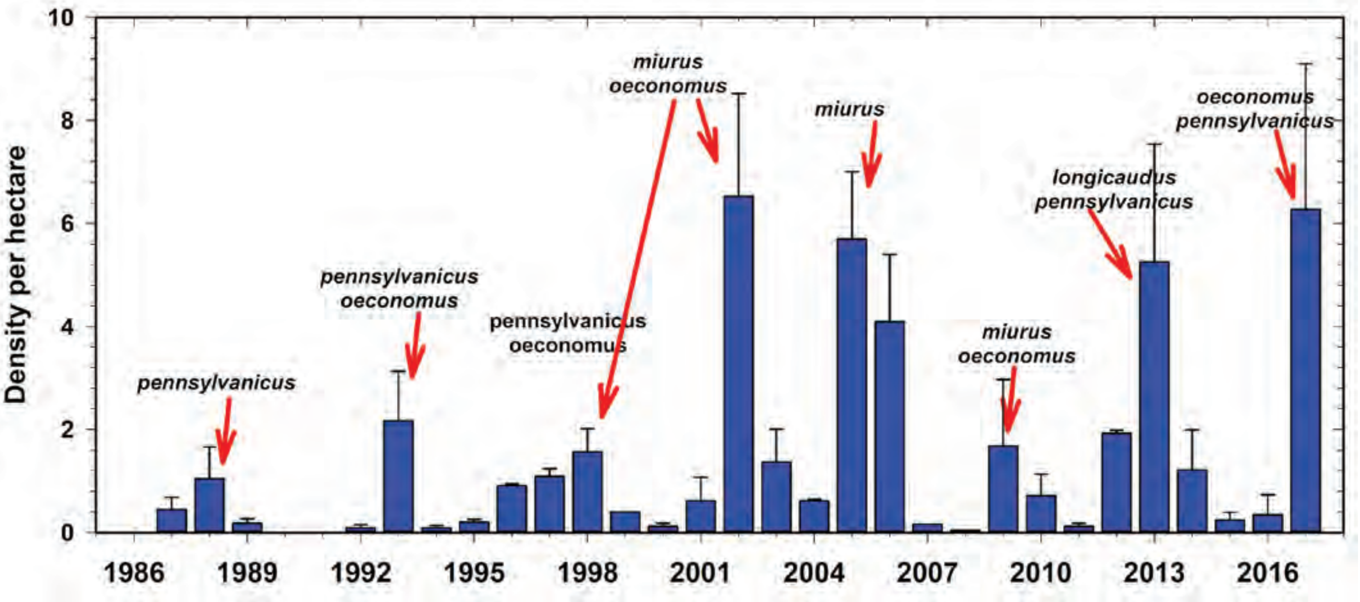

**Figure 6.** Average *Microtus* spp. density per ha on control grids in autumn from 1987 to 2017. There is strong evidence of a 3-4- year cycle but the dominant *Microtus* species at the peak changes from cycle to cycle. Error bars are 95% confidence limits.

predator exclosure experiments, targeting the mustelids. From our data *M. oeconomus* and *M. pennsylvanicus* are the most common of the *Microtus* species, but we have not investigated interspecific competition between these two microtines. Galindo and Krebs (1985b) could find no evidence that *M. miurus* responded to the removal of *M. oeconomus* by increasing in numbers or by expanding their habitat use. Interspecific competition for space is possibly involved among some of these *Microtus* species.

## Discussion

The major theme to emerge from these studies of small mammals in the boreal forest is that short-term studies of 2-4 years can give a misleading view of population dynamics. When we began these studies in the 1970s we did not know if any of the small rodent species showed periodic fluctuations. There was in the 1970s only one quantitative long-term study of the snowshoe hare cycle (Keith and Windberg 1978), and one of our objectives was to test Keith's ideas in a more pristine northern environment. At the time we began this work there was no clear consensus on climate change happening, or at what rate, and one of the values of long-term data is to set the background for possible future changes in ecosystems (Arcese and Sinclair 1997). Our data also clearly indicate that small mammal dynamics – in hares, mice or voles – in the boreal forests in the Yukon are undergoing predictable, repeated patterns, but that major changes are occurring. We do not clearly understand the causes of these changes nor the long-term trajectory. We think that climate change over the last 45 years is partly or largely behind these changes, and thus the need for continued monitoring of this changing ecosystem.

From the changes we have discovered over the last 45 years, we can suggest six critical questions to be investigated:

1. Will the peaks of the hare cycle continue to collapse, and if so by what mechanism? This is a critical question because hares are a main prey item in this food web. Can hare reproduction be reduced by plant toxins, as suggested by DeAngelis *et al.* (2015)?

2. What is the mechanism behind the change in amplitude of *Myodes* cycles after the year 2000, given the general belief that an increase in predator abundance should reduce the cyclic amplitude rather than increase it? A likely mechanism is an increase in plant productivity caused by an increase in summer temperatures.

3. What causes the odd pattern of *Microtus* cycles shown in Figure 6? A possible model is competition between *Microtus* species for the limited open grassy patches in the boreal forest, producing a lottery of who wins where. Larger trapping grids and more replicates could shed light on this issue, and competition for space among the *Microtus* species needs experimental investigation.

4. What factors can cause a pattern of disappearance of deer mice (Figure 5) for 5 years and what holds their density to such low numbers? Feeding experiments could address this issue and the possibility of competition for space among the rodent species. Another mechanism is the possible appearance of a disease, but we have no clue as to its identity.

5. Are the results of poorer overwinter survival of *Myodes* in warm winters (Figure 4) an artefact, given the general belief that cold winters should be detrimental to survival of voles and mice in the boreal forest?

6. Given the apparent greening of the arctic, will the average densities of all these herbivores increase over time? At least in the case of the arctic ground squirrel, the opposite seems to have happened (Werner *et al.* 2016).

Every scientific study raises more questions than it answers, and this is the way of scientific progress. If there is one overall limitation on our ecological understanding at the present time it is that our generalizations depend too much on short term studies. This shortcoming was recognized many years ago (Likens 1989), but the fact that much ecological research is carried out by graduate students doing a 2-5-year graduate degree means that we are limited in obtaining a long-term view of an ecosystem. This is changing slowly and our ecological wisdom has retreated from the simple universal theories of the 1970s to a more balanced view of the complexity of ecological interactions.

Ecology today is at a comparable stage of development as physics, chemistry and geology were in the 19th century. Technological progress is rapid but scientific progress is slow and it is the aim of long-term studies to develop the background to understanding how the ecological world works. It is no easy task.

## Acknowledgements

We thank the numerous field assistants who have collected the field data we have summarized here and the Natural Sciences and Engineering Research Council of Canada for financial support throughout these studies. We thank Andy and Carole Williams, Sian Williams and Lance Goodwin at the Kluane Lake Research Station for their assistance.

## Literature Cited

**Arcese, P., and Sinclair, A.R.E. 1997**. The role of protected areas as ecological baselines. *Journal of Wildlife Management.* **61**: 587-602. doi:10.2307/3802167

**Boonstra, R. and Krebs, C.J. 2006.** Population limitation of the northern red-backed vole in the boreal forests of northern Canada. *Journal of Animal Ecology* **75:** 1269-1284. doi: 10.1111/j.1365-2656.2006.01149.x

**Boonstra, R., and Krebs, C.J. 2012.** Population dynamics of red-backed voles in North America. *Oecologia* **138:** 601-620. doi:10.1007/s00442-011-2120-z

**Boonstra, R., Krebs, C.J., Gilbert, B.S., and Schweiger, S**. 2001. Voles and mice. Pp. 215-239. in Ecosystem Dynamics of the Boreal Forest: The Kluane Project. edited by C. J. Krebs, S. Boutin and R. Boonstra. Oxford University Press: New York.

**Boonstra, R., Hik, D., Singleton, G.R., and Tinnikov, A. 1998**. The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs* **68**: 371-394. doi: 10.1890/0012-9615(1998)068[0371:TIOPIS]2.0.CO;2

**Boutin, S. 1984**. Home range size and methods of estimating snowshoe hare densities. *Acta Zoologica Fennica* **171**, 275-278.

**Bujalska, G. 1973.** The role of spacing behaviour among females in the regulation of reproduction in the bank vole. *Journal of Reproduction and Fertility* (Supplement) **19:** 465–474.

**Cary, J.R., and Keith, L.B. 1979**. Reproductive change in the 10-year cycle of snowshoe hares. *Canadian Journal of Zoology* **57**: 375-390. doi: 10.1139/z79-044

**Chan, K. W., Boutin, S., Hossie, T. J., Krebs, C. J., O'Donoghue, M., and Murray, D. L. 2017**. Improving the assessment of predator functional responses by considering alternate prey and predator interactions. *Ecology* **98**: 1787-1796. doi:10.1002/ecy.1828

**DeAngelis, D. L., Bryant, J. P., Liu, R., Gourley, S. A., Krebs, C. J., and Reichardt, P. B. 2015**. A plant toxin mediated mechanism for the lag in snowshoe hare population recovery following cyclic declines. *Oikos* **124**: 796-805. http://dx.doi.org/10.1111/oik.01671

**Efford, M.G., Borchers, D.L., and Byrom, A.E. 2009**. Density estimation by spatially explicit capture-recapture: likelihood-based methods. Pp. 255-269 in Modeling Demographic Processes in Marked Populations. edited by D.L. Thomson, E.G. Cooch and M.J. Conroy. Springer: New York.

**Fuller, W.A. 1969.** Changes in numbers of three species of small rodents near Great Slave Lake, N.W.T. Canada, 1964–67, and their significance for population theory. *Annales Zoologici Fennici,* **6:** 113–144.

**Galindo, C. and Krebs, C.J. 1985a**. Habitat use and abundance of deer mice: interactions with meadow voles and red-backed voles. *Canadian Journal of Zoology* **63**: 1870-1879. doi: 10.1139/z85-278

**Galindo, C. and Krebs, C.J. 1985b**. Habitat use by singing voles and tundra voles in the southern Yukon. *Oecologia* **66**: 430-436.

**Galindo, C. and Krebs, C.J. 1987.** Population regulation in deer mice: the role of females. *Journal of Animal Ecology* **56**: 11-23. doi: 10.2307/4796

**Gilbert, B.S., Krebs, C.J., Talarico, D., and Cichowski, D.B. 1986.** Do *Clethrionomys rutilus* females suppress maturation of juvenile females? *Journal of Animal Ecology* **55**: 543–552. doi: 10.2307/4737

**Hodges, K.E., Krebs, C.J., Hik, D. S., Stefan, C.I., Gillis, E.A., and Doyle, C.E. 2001**. Snowshoe hare demography. Pp. 141-178 in Ecosystem Dynamics of the Boreal Forest: The Kluane Project. edited by C. J. Krebs, S. Boutin and R. Boonstra. Oxford University Press: New York.

**Hughes, B.B., Beas-Luna, R., *et al.* 2017**. Long-term studies contribute disproportionately to ecology and policy. *BioScience*. **67**: 271-281. doi:10.1093/biosci/biw185.

**Keith, L.B., and Windberg, L.A. 1978**. A demographic analysis of the snowshoe hare cycle. *Wildlife Monographs* **58**: 1-70.

**Korpela, K., Helle, P., Henttonen, H., Korpimäki, E., Koskela, E., Ovaskainen, O., Pietiäinen, H., Sundell, J., Valkama, J., and Huitu, O. 2014**. Predator–vole interactions in northern Europe: the role of small mustelids revised. *Proceedings of the Royal Society B: Biological Sciences* **281**(1797): 20142119. doi: 10.1098/rspb.2014.2119

**Krebs, C.J., Gilbert, B.S., Boutin, S., Sinclair, A.R.E., and Smith, J.N.M. 1986**. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon, 1976-84. *Journal of Animal Ecology* **55**: 963-982. doi: 10.2307/4427

**Krebs, C. J., Boutin, S., and Boonstra, R. 2001**. *Ecosystem Dynamics of the Boreal Forest: the Kluane Project*. Oxford University Press: New York.

**Krebs, C.J., Lambin, X., and Wolff, J.O. 2007**. Social behavior and self-regulation in murid rodents. Pp. 173-181 in Rodent Societies: An Ecological and Evolutionary Perspective, edited by J.O. Wolff and P.W. Sherman. University of Chicago Press: Chicago.

**Krebs, C.J., Cowcill, K., Boonstra, R., and Kenney, A.J. 2010**. Do changes in berry crops drive population fluctuations in small rodents in the southwestern Yukon? *Journal of Mammalogy* **91**: 500-509. doi: 10.1644/09-MAMM-A-005.1

**Krebs, C. J., Kielland, K., *et al.* 2013**. Synchrony in the snowshoe hare cycle in northwestern North America, 1970-2012. *Canadian Journal of Zoology* **91**: 562-572. doi:10.1139/cjz-2013-0012

**Krebs, C.J., Boonstra, R., Boutin, S., Sinclair, A.R.E., Smith, J.N.M., Gilbert, B.S., Martin, K., O'Donoghue, M., and Turkington, R. 2014a**. Trophic dynamics of the boreal forests of the Kluane Region. *Arctic* **67**: 71-81. doi:10.14430/arctic4350

**Krebs, C.J., Bryant, J., *et al.* 2014b**. What factors determine cyclic amplitude in the snowshoe hare cycle? *Canadian Journal of Zoology* **92**: 1039-1048. doi:10.1139/cjz-2014-0159

**Krebs, C.J., Boonstra, R., and Boutin, S. 2018**. Using experimentation to understand the 10-year snowshoe hare cycle in the boreal forest of North America. *Journal of Animal Ecology* **87**: 87-100. doi: 10.1111/1365-2656.12720.

**Kuusela, K. 1992.** The boreal forests: an overview. *Unasylva* **43,** 3–13.

**Lambin, X., and Krebs, C.J. 1993.** Influence of female relatedness on the demography of female Townsend's vole populations in the spring. *Journal of Animal Ecology* **62**: 536-550. doi: 10.2307/5203

**Lavergne, S.G., McGowan·, P.O., Krebs, C.J., and Boonstra, R. 2014**. Impact of high predation risk on genome-wide hippocampal gene expression in snowshoe hares. *Oecologia* **176**: 613-624. doi: 10.1007/s00442-014-3053-0

**Likens, G.E. (Ed.) (1989)**. 'Long-term Studies in Ecology: Approaches and Alternatives.' (Springer Verlag: New York). ISBN:0387967435

**Mappes, T., Ylonen, H., and Viitala, J. 1995**. Higher reproductive success among kin groups of bank voles (*Clethrionomys glareolus*). *Ecology* **76**: 1276-1282. doi:10.2307/1940934

**O'Donoghue, M., Boutin, S., *et al.* 2001**. Coyotes and lynx. Pp. 275-323 in Ecosystem Dynamics of the Boreal Forest: The Kluane Project. edited by C. J. Krebs, S. Boutin and R. Boonstra. Oxford University Press: New York.

**Sheriff, M.J., Krebs, C.J., and Boonstra, R. 2009.** The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. *Journal of Animal Ecology* **78**: 1249-1258. doi:10.1111/j.1365-2656.2009.01552.x

**Slough BG 1989.** Movements and habitat use by transplanted marten in the Yukon Territory. *Journal of Wildlife Management* **53:** 991–997.

**Sutherland, D.R. and Singleton, G.R. 2006**. Self-regulation within outbreak populations of feral house mice: a test of alternative models. *Journal of Animal Ecology* **75**: 584-594. doi: 10.1111/j.1365-2656.2006.01081.x

**Werner, J.R., Gillis, E.A., Boonstra, R., and Krebs, C.J. 2016**. You can hide but you can't run: apparent competition, predator responses and the decline of Arctic ground squirrels in boreal forests of the southwest Yukon. *PeerJ* **4**: e2303. doi:10.7717/peerj.2303

**Wolff, J.O. 1997**. Population regulation in mammals: an evolutionary perspective. *Journal of Animal Ecology* **66**: 1-13. doi: 10.2307/5959