

Population limitation of the northern red-backed vole in the boreal forests of northern Canada

RUDY BOONSTRA* and CHARLES J. KREBS†

*Centre for the Neurobiology of Stress, Department of Life Sciences, University of Toronto at Scarborough, 1265 Military Trail, Scarborough, ONT, M1C 1A4, Canada; and Department of Zoology, University of British Columbia, 6270 University Blvd, Vancouver, BC V6T 1Z4, Canada

Summary

1. Across the vast boreal forests of North America, no population cycles in *Clethrionomys* species occur. In Eurasia, by contrast, some *Clethrionomys* populations of the same species undergo regular 3–5-year cycles. We examined the effects of nutrients, food, competitors, predators and climate on population limitation in the northern red-backed vole (*Clethrionomys rutilus* Pallas) in the south-western Yukon to determine why this difference occurs.
2. From 1986 to 1996 we added food, reduced large mammal predators and excluded snowshoe hares (*Lepus americanus* Erxleben) from large plots and found that none of these manipulations affected red-backed vole abundance. Adding nutrients as nitrogen, phosphorus and potassium (NPK) fertilizer had a slight negative effect, probably acting through a reduction in dwarf shrub productivity caused by competition from grasses.
3. We monitored weasel populations directly through trapping and indirectly through snow tracking. Predation by these vole specialists was irrelevant as a limiting factor most of the time because voles in this area do not reach the densities needed to sustain weasel populations. Other boreal forest mammal and bird predators did not focus on red-backed voles. However, when red-backed vole populations increased in the forest and *Microtus* voles also increased in the meadows, weasel populations increased and may have temporarily depressed red-backed voles in winter.
4. We monitored one major potential food, white spruce seeds, but seed fall was not related to population changes in red-backed voles, even after mast years.
5. We assessed the impact of weather variables, and the average depth of the snow pack during winter (October–March) was correlated directly with vole demography, having both direct effects in that year and delayed effects in the following year.
6. Our long-term trapping data (1973–96) indicate that *Clethrionomys* populations fluctuated, with peaks following hare peaks by 2–3 years.
7. We propose that the key variable limiting these vole populations is overwinter survival, and this is a function of overwinter food from berries produced during the previous summer by dwarf shrubs. These shrubs may be stimulated by abundant moisture from winter snows or by periodic fertilization from large quantities of pellets produced at snowshoe hare peaks.

Key-words: dwarf shrub berry production, overwinter survival, snowshoe hare cycles, spruce seeds, pellet fertilization, weasel predation, winter snowpack.

Journal of Animal Ecology (2006) **75**, 1269–1284
doi: 10.1111/j.1365-2656.2006.01149.x

Introduction

Many populations of voles and lemmings in the northern hemisphere go through 3–5-year cycles in numbers. Their cause has been pursued vigorously for almost a century, generating numerous hypotheses and experimental tests

and ongoing controversy and debate. Their understanding continues to be highly relevant, as it addresses one of the central questions of population ecology – what are the factors that regulate numbers (Sinclair 1989)? To achieve regulation, density-dependent processes are critical to bring populations back to equilibrium density. However, some populations do not go through regular cycles nor do they maintain constant density. Understanding these populations and the processes governing their dynamics addresses a second major question of population ecology – what are the factors that limit numbers (Krebs 2002)? Population limitation simply refers to the factors that affect population growth rates.

Across the 5 million km² of boreal forests in North America, populations of red-backed voles (*Clethrionomys* spp.) do not cycle, though they occasionally increase to high numbers. Two species occupy these forests parapatrically. The northern red-backed vole occupies forests north of 60° latitude and the southern red-backed vole (*C. gapperi* Vigors) occupies the southern remainder. The absence of cycles in North America rests on good evidence. For the northern species, major population studies have been carried out in four areas of the boreal forest, some running for 10–20 years (central Alaska – West 1982; Whitney & Feist 1984; southern Yukon – Krebs & Wingate 1985; Gilbert *et al.* 1986; Gilbert & Krebs 1991; Boonstra *et al.* 2001; the southern Northwest Territories (NWT) – Fuller 1985; the northern NWT – Martell & Fuller 1979). Similarly for the southern species, major studies have been carried out in two areas (southern NWT – Fuller 1977, 1985; Manitoba – Mihok, Schwartz & Iverson 1985). Cheveau *et al.* (2004) have argued that *C. gapperi* cycles in the boreal forests of Québec, but the evidence is inferential and not based on solid, long-term population studies. In marked contrast, some red-backed vole populations in northern Eurasia, particularly those north of 60° latitude in Fennoscandia, have shown the characteristic microtine cycle (although recently they have become attenuated – Henttonen *et al.* 1987; Henttonen 2000; Hörnfeldt, Hipkiss & Eklund 2005).

In the southern Yukon three major peaks in the northern red-backed vole have occurred in the last 20 years (1973, 1984 and 1992, with additional modest vole peaks occurring in 1975 and 1987; Krebs & Wingate 1985; Gilbert *et al.* 1986; Gilbert & Krebs 1991; Boutin *et al.* 1995). The major ones coincided with the late decline or low phase of the snowshoe hare cycle. Four possible explanations can be suggested for this inverse relationship: **1.** Predation: red-backed voles may be acting as a buffer prey, such that when hares are abundant, so are their predators that also eat voles. These predators may be eating voles to such an extent during the hare peak and early decline that vole numbers are depressed (Erlinge *et al.* 1984), and only when the predator populations collapse after the hare decline can vole populations grow (Hansson & Henttonen 1985). In northern Fennoscandia, small mammal species show 3–5-year cycles in numbers and predators have been implicated in causing population

declines (Henttonen *et al.* 1987; Hanski, Hansson & Henttonen 1991; Korpimäki *et al.* 2002).

2. Competition: competition for food between hares and red-backed voles during the peak summers of hare abundance may seriously depress food supply for the voles. **3.** Nutrient release: high hare densities at the peak of their 9–10-year cycle cause high production of hare faeces which then fertilize the forest. Nutrients from the decay of these faeces are captured by plants critical to the diet of small mammals, particularly seed-bearing dwarf shrubs. The latter bear large crops of seeds when weather conditions are suitable and this results in a vole peak (variants of this hypothesis have been put forward for lemmings in the Arctic – Schultz 1969). **4.** Weather: the observed variation in vole numbers could be due to weather variables. Stochastic processes, operating principally through weather, may indirectly affect vole populations through their effect on seed or mushroom crops (Kalela 1962; Dyke 1971; West 1982) or may directly affect vole populations through negative effects on survival (e.g. low temperatures caused by insufficient snow cover; Fuller 1969; Martell & Fuller 1979; Whitney & Feist 1984).

In this paper we attempt to test these four hypotheses for red-backed voles in the southern Yukon by means of large-scale manipulations of nutrients, food supplies and predators in the boreal forest. Other details of these experiments have been reported elsewhere (Krebs, Boutin & Boonstra 2001a) and here we focus on the northern red-backed vole. This species occurs throughout the circumpolar boreal forests of the northern hemisphere from Canada westward through to Norway (Koshkina & Korotkov 1975; Fuller 1985; Henttonen *et al.* 1987). Young are born from May to September, remain non-reproductive in their year of birth (except for young from the first litters during low-density years) and breed the next year. Reproduction does not occur during winter (West 1982; Gilbert *et al.* 1986). Females give birth potentially to five to six consecutive litters (five to six babies/litter) during the short breeding season because of postpartum oestrus and a 20-day gestation period (Krebs & Wingate 1985).

Study site and methods

STUDY AREA

The study was located along the Alaska Highway within the valley of the Shakwak Trench east of Kluane Lake in the south-western Yukon Territory, Canada (60°57' N, 138°12' W). The boreal forest in this region is dominated by white spruce (*Picea glauca* Voss.), a shrub layer of soapberry (*Shepherdia canadensis* (L.) Nutt.), willows (*Salix* spp.) and dwarf birch (*Betula glandulosa* Michx.), and a ground layer of dwarf shrubs and herbs (*Arctostaphylos* spp., *Vaccinium* spp., *Geocaulon lividum* (Richards) Fern., *Empetrum nigrum* L.) and other forbs (Turkington *et al.* 2002). The average yearly temperature in the Kluane region is –3.83 °C and the mean

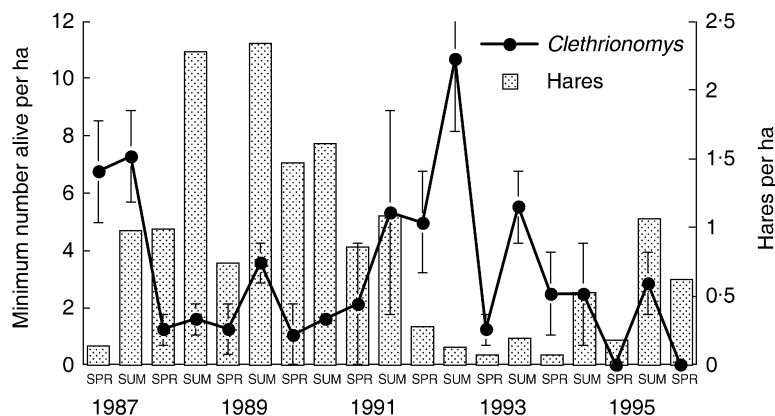


Fig. 1. Population changes of northern red-back voles on two control grids (means \pm SE) from 1986 to 96 in south-western Yukon near Kluane Lake. Population changes of snowshoe hares (histograms) on control grids are presented for comparison.

monthly temperatures for the warmest (July) and coldest (January) months are 13 °C and -22 °C, respectively (data from Burwash Landing Climatological Station 1967–96). The climate is classified as cold continental (Boutin *et al.* 1995), with snow typically covering the ground (mean depth 55 cm) from October to early May and July being the only frost-free month.

EXPERIMENTAL DESIGN

In addition to two control areas that were used to estimate variation in natural populations, we also monitored small mammals on grids within five, large-scale experimental treatments (for details, see Boutin *et al.* 2001; for grid locations, see Fig. 1 in Boutin *et al.* 1995), as follows.

1. Food addition: from 1988 to March 1996 *ad libitum* supplemental food (commercial rabbit pellets; 16% protein; Shur-Gain, Maple Leaf Foods Inc., Edmonton, Alberta, Canada) was added to two 36-ha areas (Food 1 and Food 2). Red-backed voles in the laboratory eat this food readily. Approximately 300 kg were distributed every 5–6 days throughout the entire year so that food availability would be continuous. Because pellets were broadcast with a fertilizer spreader along 570 m long feeder rows, interference from black bears (*Ursus americanus* Pallas), grizzly bears (*U. arctos* L.) and moose (*Alces alces* L.) was minimal.

2. Predator exclusion: a 1-km² area was enclosed within a 2.2 m high 8600 V electric fence in 1987 to keep out large mammalian predators (lynx *Lynx canadensis* L. and coyotes *Canis latrans* Say), but it was not a barrier to small mammal movement. The fence was effective at keeping out these mammalian predators (Krebs *et al.* 1995). The fence did not exclude the avian predators, but territoriality prevented high raptor densities on this treatment (Rohner & Krebs 1998), so fenced and unfenced hares faced similar raptor predation. Two small mammal grids were located within the enclosure, separated by 472 m at their nearest edge. On the first (called the predator enclosure), small mammals were protected only from large mammal predators. On the

second (called the predator enclosure + mono), small mammals were protected from avian predators as well by covering a 9 ha area with a barrier of nylon monofilament (2 m above ground spaced 45 cm apart, set up in the summer of 1988). The monofilament almost eliminated avian predation on ground squirrels that remained under the monofilament (Byrom 1997), but was not effective at eliminating avian predation on snowshoe hares (Krebs, personal communication) or on red squirrels (K. Stuart-Smith & S. Boutin, personal communication).

3. Predator enclosure + food addition: the above two treatments were combined on a 1-km² area in 1988 using the same protocols described above. Two replicate small-mammal grids were set up within this treatment, both of them straddling different feeder rows and separated by 400 m at their nearest point. Because of the difficulty in setting up and maintaining the monofilament barrier on the Predator Exclusion, one was not erected on this treatment and thus it excluded only larger mammalian predators.

4. Fertilizer addition: two 1-km² fertilizer sites had nitrogen, phosphorus and potassium (NPK) applied aerially from 1987 to 1994 (for details see Turkington *et al.* 1998). Over this period, a cumulative total of 120 g N, 20 g P and 10 g K were added to each m² on each of these sites. Fertilization strongly affected herbaceous vegetation (Turkington *et al.* 2002) and increased the growth rates of shrubs (Krebs *et al.* 2001b) and white spruce (Boonstra *et al.* unpublished data).

5. Snowshoe hare exclosures: two 4-ha² snowshoe hare exclosures were constructed in 1988 to assess how the absence of the dominant herbivore – hares – influenced small mammal dynamics. One exclosure was unmanipulated and the other was nested within one of the fertilizer treatments above to assess how the absence of hares and the addition of nutrients influenced small mammal dynamics. The exclosure walls were 3 m high to prevent both hares and moose from entering and constructed of 5 cm orange plastic-mesh construction-type fencing (L-77 Vexar, Dupont Canada, Toronto, Canada). To prevent hares from chewing through the fencing, we had to line it with 4 cm chicken wire mesh to a height of 1.5 m.

Ideally we would have liked to replicate all treatments, but this proved impossible for the predator enclosure and predator enclosure + food sites, owing to the high costs of maintaining 8 km of electric fencing on a nearly daily basis for a decade (see Boutin *et al.* 2001). Ecologists are caught in the tension between the manipulations necessary to understand large-scale ecological processes and the impossibility of replicating large manipulations (Carpenter *et al.* 1995; Schindler 1998; Oksanen 2001). Our control sites sampled a wide range of natural variation within our study area, increasing the likelihood that differences on the treatments were due to our manipulations.

LIVE-TRAPPING PROCEDURES

We monitored vole populations on 12 live-trapping grids (2.81 ha, 100 trap points arranged in a 10 × 10 pattern, 15.24-m interval between points) from 1987 to 1996. Grid size was determined to be optimal based on two criteria. First, earlier work in the valley (Gilbert & Krebs 1981; Gilbert *et al.* 1986) had found this size to be adequate to assess population processes of small mammals. Secondly, it was the largest we could handle given the need to prebait and trap simultaneously all live-trapping grids twice per summer (Boonstra *et al.* 2001). All small mammal grids were either nested within or immediately adjacent to the hare trapping grid or in the middle of the experimental treatment in comparable open spruce habitat with well-developed shrub and herb layers. Longworth live-traps were placed at every other trap point for a total of 50 traps and each trap was covered with a board to protect the trap from sun and rain. Traps remained permanently on the grids for the entire study and were locked open between trapping sessions; thus, voles were habituated to them. Because of disturbance of the traps by red squirrels and Arctic ground squirrels on 10 of the 12 grids in 1987, traps were placed within a wire mesh cage in 1988 that permitted entry of small mammals, but not of the squirrels.

Population censuses were conducted twice each year: the first, to obtain overwinter survival and spring densities prior to reproduction, occurred over a 1.5-week period starting in mid- to late May just after snowmelt and before young from the first litter were entering the traps. The second, to obtain summer population growth, occurred in late August–early September. Prior to a population census, all traps were prebaited for 1 week with a handful of oats. During a census, traps were baited with oats and a slice of apple; cotton stuffing was provided for warmth. They were set in the evening of the first day and checked three times: by 09.00 h the next morning, by 20.00 h the next evening, and by 09.00 h the second morning, when all traps were locked open. Voles were marked with fingerling fish eartags, and at each capture we recorded tag number, mass (g) and reproductive condition [males: testes scrotal (breeding) or abdominal (non-breeding); females: perforate or non-perforate vagina, lactating or not, pubic symphysis closed, slightly open or open, and obviously pregnant].

WEASEL ABUNDANCE

Weasels are specialist predators of microtines and are associated with the 3–5-year population cycles in some areas, but not others (Korpimäki & Krebs 1996; Graham & Lambin 2002). In our boreal forest there are two weasel species: the short-tailed weasel (*Mustela erminea* L.) and the least weasel (*M. nivalis* L.), with the former being most common. We used two indices to assess weasel abundance. First, weasels are caught readily in the Longworth live-traps, and thus we documented the frequency of capture over the study. Secondly, we counted the tracks of all weasels each winter (October–April) along a 25-km transect that traversed our study area on days after fresh snowfalls when tracks were distinguishable (O'Donoghue *et al.* 2001b). We made no attempt to distinguish between the tracks of the two species. We calculated annual means and standard errors of these counts using means for the whole winter for each of eight segments of this transect (1.4–4.9 km in length, separated by topographical features), standardized to tracks per 100 km. These counts gave us an index of the numbers of weasels present each winter. From 1986–87 to 1996–97, we counted tracks along 12 194 km of transect. Finally, we assessed habitat use by weasels from snow-tracking data collected while radiocollared lynx and coyote were being followed by trackers (O'Donoghue *et al.* 1998). The number and location of weasel tracks crossing these large carnivore trails were recorded.

SPRUCE SEED PRODUCTION

Spruce trees produce huge numbers of seeds in mast years and these seeds may be an important food source for red-backed voles, red squirrels, chipmunks and passerine birds. We sampled seed production by collecting seeds in buckets 28 cm in diameter and placed at 86 hare-trapping stations on five treatment grids: a control grid, a fertilizer addition grid, a food addition grid, the predator enclosure grid and the predator enclosure + food addition grid. The buckets were set out in late August and collected the following May. The buckets were covered with wire mesh to prevent animal access over winter. Only intact spruce seeds were counted.

STATISTICAL ANALYSIS

We calculated the minimum number of small mammals alive (MNA) for comparison among grids. Because we trapped only three times per trapping session and only twice per year, estimators using Jolly–Seber methods were inappropriate. To assess how efficient our MNA counts were in accurately assessing population size, we examined a population of red-backed voles trapped in a spruce forest in our valley for 7 years [grid S + M, trapped by S. Gilbert (personal communication) from 1983 to 1989, except for 1987] that was trapped at 2–3-week intervals and compared our estimation method (MNA) with robust Jolly–Seber estimates. Two points

can be made from this analysis. First, these voles were highly trappable [mean Jolly estimate of trappability $\text{year}^{-1} = 92.1\% \pm 2.76$ (1 SE), range 81.3–100%] (Krebs & Boonstra 1984)]. Secondly, we correlated the Jolly–Seber estimates to MNA counts and these were highly correlated ($r^2 = 0.99$, $n = 44$), with MNA underestimating the Jolly–Seber estimate by 4% at a population size of five, and by 9% at 20. Thus our MNA counts should closely reflect true population size.

Two sets of analyses were carried out. The first focused on the effect of the treatments on red-backed vole abundance. The second pooled the data from all 12 grids, using them as replicates to assess how the population in the entire valley changed with time and the factors that were related to those changes. To examine whether treatment affected vole population size we used three measures: (1) a density effect ratio comparing the densities on the controls with those on the treatments; (2) a randomization test (described below); and (3) an analysis comparing population growth on the controls and treatments in summer. For the latter, the instantaneous rate of summer population growth per week was calculated per treatment; no rates were calculated for times when zero animals were captured. These data were analysed with a one-way analysis of variance (ANOVA) plus Tukey–Kramer multiple range test using SUPERANOVA (Gagnon *et al.* 1990). For the pooled data set, we also calculated an index of overwintering survival (spring density in year $t + 1$ /late summer density in year t) and the instantaneous rate of population change per week over the reproductive season. We were not able to obtain estimates of overwinter survival based on recovery of tagged animals as few individuals that had been tagged in the previous summer were recaptured in spring. This was a result of movement off the grids over winter and of a grid size too small to include these movements. The index should be reasonably robust, as reproduction ceases at about the same time in all years (mid-August to early September – Gilbert & Krebs 1981; Gilbert *et al.* 1986; Fletcher & Boonstra, personal communication).

Variation in population size among treatments was analysed using a randomization test (Manly 1991). We determined whether a pair of populations differed in size more than would be expected by chance, given a certain background variation in population size. This ‘background variation’ was simulated in the randomization test by using the null hypothesis that there was no difference in population size among treatments. Given this null hypothesis, any variation in population size among treatments was assumed to be random ‘background variation’ within each census period. The randomization test shuffled data points among sampling sites, within each census period, in order to simulate the effect of random variation in population sizes. All statistical tests were pairwise comparisons between treatments, and assessed whether the actual differences in average population size between treatments were larger than the typical random variation among treatments (see Krebs *et al.* 2001a for details of the method). Data are expressed throughout as means \pm 1 SE.

Results

GENERAL OVERVIEW

Over the entire study and on all grids combined we caught 2466 different animals (1813 northern red-backed voles, 412 voles of the genus *Microtus* spp., 66 deer mice (*Peromyscus maniculatus* Wagner), 38 chipmunks (*Tamias minimus* Bachman), 11 heather voles (*Phenacomys intermedius* Merriam) and 126 shrews (*Sorex* spp.) in 22 800 trap nights. Thus, red-backed voles were the most abundant small mammal on these grids, being moderately high in 1987, low from 1988 to spring 1991, growing rapidly over the summer of 1991 to reach high densities in 1992 and moderately high densities in 1993 and 1994, and finally declining to extremely low levels in 1995 (Fig. 1). Population growth occurred in every summer except 1994, when the population remained static. During the years of high snowshoe hare numbers (1988–90) these voles remained low, whereas after the hares declined, these voles increased dramatically.

Only nine short-tailed weasels were caught in live traps over this entire study (two in 1988, five in 1993 and two in 1994). One least weasel was captured (by hand) over the entire study in 1994, and this species appears to be very rare in the Kluane region. From the snow-tracking transect data, numbers of weasels remained low from 1986 to 1991, then increased steadily to a high in 1994–95 and declined again by the winter of 1995–96 (Fig. 2). From the snow-tracking data obtained along the trails of coyotes and lynx, weasels were found mainly in more open habitats. Approximately 39% of their crossings were in habitats with less than 25% overstorey cover, relative to 22% of this habitat available ($\chi^2 = 154.16$, $P < 0.0001$). This was especially true in years when *Microtus* were abundant (1993 and 1994, Boonstra *et al.* 2001); before the winter of 1992–93, weasels used these open habitats as expected.

TREATMENT EFFECTS

There was variation in red-backed vole densities among plots within the same treatment, although the general changes in population abundance over time were correlated. Thus, there was a significant relationship between population changes on control 1 with that on control 2 ($r^2 = 0.56$, $n = 19$, $P = 0.0003$). We obtained an average treatment density within each trapping session and compared treatments by two methods: graphically with a density effect comparison and statistically with the randomization test comparison. The density effect of the treatments at any given time was compared as the ratio of the average effect of the treatment (replicates pooled) to average control densities (Fig. 3). Only the data from 1988 onwards were examined, as the experiments were being set up in 1987. For most treatments there was no consistent positive or negative effect of most of the treatments, with the density ratio being approximately one [i.e. density ratio was 1.30 ± 0.21 (mean \pm SE) for

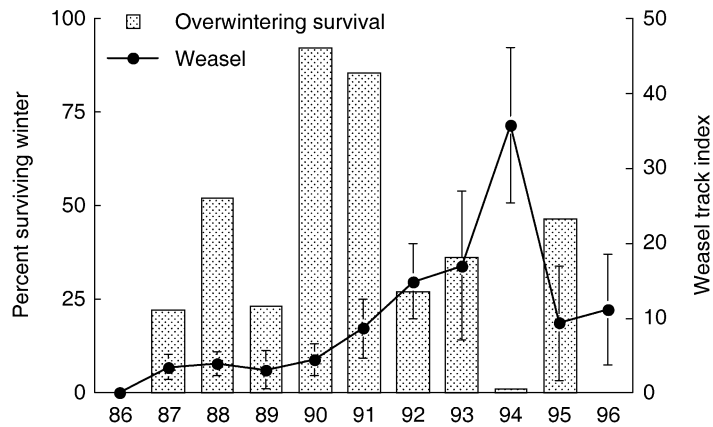


Fig. 2. Overwintering survival of northern red-backed voles relative to an index of weasel abundance. Overwintering survival was calculated as an index = (spring density per ha in year $t + 1$ /late summer density per ha in year t) * 100. The trapping data from all the grids pooled were used to derive these densities. Thus the value presented for 1987 gives the overwintering survival from late summer/autumn 1987 to spring 1988. Abundance of weasel tracks per 100 km (means \pm SE) along a 25-km transect run with snowmobiles during the winters from 1986–87 to 1996–97. Thus the value for 1987 gives the index for the winter for 1987–88. Note that the index is presented for the winters 1986–87 and 1996–97, but the comparable vole overwintering survival estimates are not available for those years.

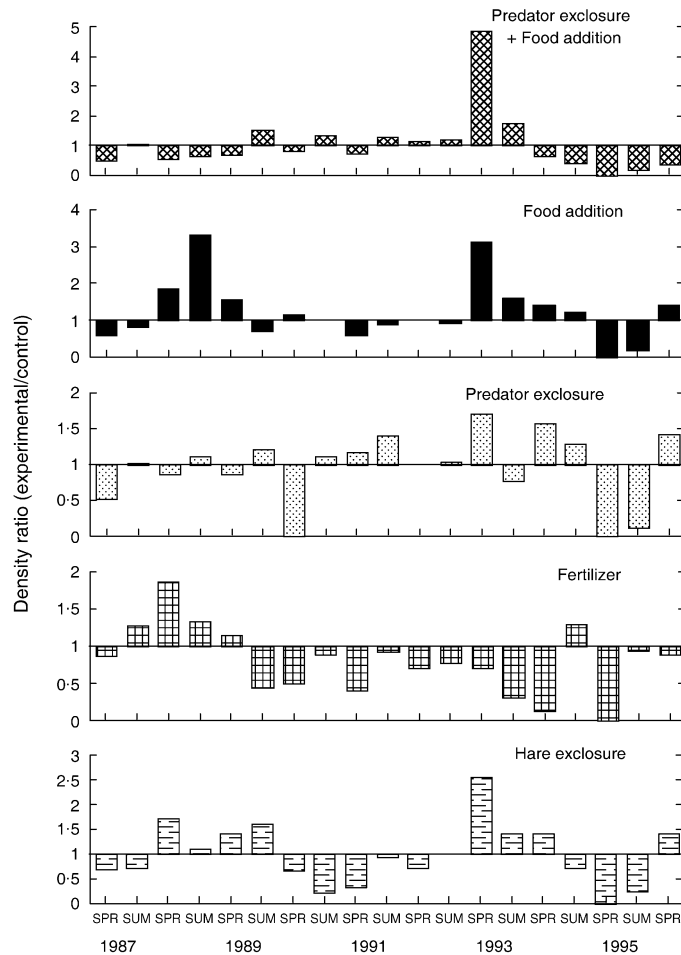


Fig. 3. Ratio of average population densities per trapping session of the northern red-backed vole for the major treatments to average control population densities. Ratios of 1 indicate no difference between treatment and control densities. Values for the food, the fertilizer and the predator exclusion + food were the average of two live-trapping grids.

food addition, 0.98 ± 0.12 for predator exclusion, 1.08 ± 0.26 for predator exclusion + food addition, 1.03 ± 0.16 for hare exclusion and 0.98 ± 0.17 for hare exclusion + fertilization]. In contrast, the predator exclusion + mono

(not shown on Fig. 3) had a density ratio consistently lower than that on the control grids (0.74 ± 0.12), but these lower densities were present from the start of the experiment and thus site-specific effects unrelated to

Table 1. Mean population densities of the northern red-backed vole over the entire study (1988–96) on all treatments. Values for the control, food addition, fertilizer addition, and predator exclusion + food treatments were the average from two live-trapping grids

Grid	Density ha ⁻¹	SE	Range
Control	2.87	0.64	0–10.68
Food addition	3.36	0.66	0–9.79
Predator exclusion	3.01	0.70	0–11.03
Predator exclusion + mono	2.24	0.61	0–11.03
Predator exclusion + food addition	3.41	0.92	0.18–12.99
Fertilizer addition	2.18	0.50	0–8.36
Hare exclusion	2.99	0.70	0–10.68
Hare exclusion + fertilizer	2.64	0.51	0–6.05

the treatment may explain this result. The fertilizer addition grids also had a lower density ratio in the later part of the study, but this effect appeared to be a consequence of the treatment, not of site-specific effects. In the first 3 years of the study (1987–89) the density ratio on the fertilizer addition areas was 1.15 ± 0.19 , but thereafter (1990–96) it declined to 0.66 ± 0.10 . Independent evidence from other long-term fertilization experiments at Kluane and elsewhere indicate that the negative effects on a number of forest herbs and dwarf shrubs take 3 years to become evident (Nams, Folkard & Smith 1993; Strengbom *et al.* 2002; Turkington *et al.* 2002).

Statistical comparison using the randomization analysis resulted in three major conclusions. First, the control treatment was not significantly different from any other treatment except for the predator exclusion + monofilament (Table 1). Secondly, this latter treatment had the lowest average densities per trapping session over the experiment (1988–96) of any treatment, including the other small mammal grid also within the predator exclusion, but not under the monofilament. Thirdly, the fertilizer addition reduced resources needed by these voles, as these grids had lower average densities than the food addition (Table 1) and we interpret this to be a real effect. These conclusions are reinforced by an analysis examining the instantaneous growth rates over summer: there was no treatment effect on summer population growth rate (one-way ANOVA $F_{11,74} = 6.27$, $P = 0.80$).

LARGE-SCALE CHANGES

The northern red-backed vole populations in our region clearly underwent marked fluctuations over this 10-year period (Fig. 1), but except for the negative effect of fertilization, our treatments had no marked effect on population change. All populations fluctuated in relative synchrony (e.g. the correlation between the two control grids is given above; that for the changes in average density on food grids vs. on the predator exclusion + food: $r^2 = 0.76$, $P < 0.0001$). We interpret this to mean that all treatment effects were minimal and that the differences we observed were because of site-specific variation in habitat quality. Thus, using all 12 populations as replicates, we ask the question of what factors limit population density in *C. rutilus*, focusing on survival and population growth and relating these to the supply of a

natural food (spruce seeds), to measures of specialist predators (weasels) and to weather variables. In attempting to tease out these relationships, we will focus the analysis around two questions: first, what determined population growth rate over summer, and secondly, what determined the rate of population decline over winter? We will use both the data from the individual grids to obtain measures of population growth and the overall pooled data set, treating all 12 grids as one large grid. Grid size at low densities was too small, particularly in spring when, out of 118 times, all grids were trapped over the study, no animals were caught during a trapping session 21 times (18%) and including these occasions, < 1 vole ha⁻¹ were caught 42 times (36%). The net result was a great deal of noise in the data for individual trapping grids that the pooled analysis smoothed out. Even with a grid size of 33.72 ha (the sum of all 12 grids), spring densities < 1 ha⁻¹ occurred three times (30%). In late summer this was much less of a problem [i.e. in only 13 of 106 times were densities < 1 ha⁻¹ (12%) and in the pooled data set no values were < 1 ha⁻¹]. In addition, only the pooled data set could be used in some analyses because certain factors such as abundance of weasels from snow-track counts were not collected on individual vole grids, but rather at a much larger scale.

Finally, one density estimate – from spring 1995 – had to be wrong. The highest weasel snow-track index year in the winter of 1994–95 was followed by the capture of only one vole on all 12 grids in spring 1995, with the result that the overwinter survival was calculated to be almost zero. This is clearly an underestimate of actual densities and survival, given that 60 voles were caught on these grids by late summer. The cause of the low capture rate may have been a trapping artefact induced by weasels (Stoddart 1976; Jedrzejewski, Rychlik & Jedrzejewski 1993) (i.e. voles avoided traps previously visited and soiled by weasels). Calculating the relationship between spring densities and late summer densities with 1995 excluded (see below) and assuming that the new regression is approximately correct, we calculate that in spring 1995 there must have been about 0.54 ha⁻¹ (i.e. 18 animals present on the pooled grid). We use this value in the analysis of the pooled data set.

First, to examine if population growth in summer varied over the entire study we carried out a one-way ANOVA on the instantaneous growth rate with year as

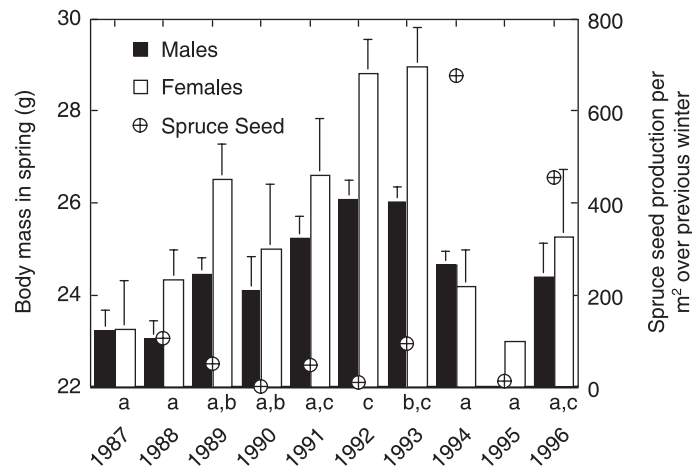


Fig. 4. Variation among years (\pm SE) in the spring body mass (g) of adult northern red-backed voles over all grids pooled and of spruce seed fall. Young of the year (< 16 g) and obviously pregnant females were excluded. Significant differences among years tested by ANOVA and identical superscripts above years indicate means that are not significantly different. Spruce seed fall refers to the number of seeds falling per m^2 during the previous autumn winter (i.e. seed fall on the graph in spring 1991 fell during the winter of 1990–91).

the factor and using the grids as replicates within year. Growth varied significantly among years ($F_{8,77} = 7.30$, $P = 0.0001$), with that in 1994 being the lowest and that in 1991 the highest (ranking the years from the lowest to the highest and with identical superscripts indicating means that were not significantly different: 1994^a, 1990^{ab}, 1987^{ab}, 1988^{ab}, 1995^{abc}, 1992^{bc}, 1993^{bc}, 1989^{bc}, 1991^c). The instantaneous rate of population growth during summer was related inversely to initial spring densities, but the relationship explained only a very small amount of the variation ($r^2 = 0.067$, $n = 86$, $P < 0.02$). This is echoed by the analysis from the pooled data set. Spring density was a good predictor of late summer density and was density dependent (i.e. the slope of a log–log plot was less than 1: \log autumn density = $0.387 + 0.760 \log$ spring density, $r^2 = 0.76$, $n = 9$, $P = 0.002$). The population approximately doubled when spring densities were 1 ha^{-1} and increased only 80% when densities were 5 ha^{-1} . However, late summer density was a marginal predictor of density next spring (\log spring density ($t + 1$) = $-0.203 + 0.634 \log$ autumn density, $r^2 = 0.37$, $n = 9$, $P = 0.08$). Nevertheless, the overall relationship was a positive one, although density dependent, in which higher late summer populations in turn resulted in higher, not lower, populations the next spring.

The analysis of overwinter survival (Fig. 2) provides a slightly different picture. From the pooled data set, overwinter survival was related inversely to late summer densities, but the relationship was not strong ($r^2 = 0.13$, $n = 9$, $P = 0.35$). There are two outlying winters that both have very high overwinter survival ($> 85\%$, Fig. 2): 1990–91 had low late summer densities (1.57 ha^{-1}) and 1991–92 had high late summer densities (5.34 ha^{-1}); their removal marginally improves the relationship ($r^2 = 0.16$, $n = 7$). However, the key point is that good overwinter survival was not dependent on late summer density.

One possible factor accounting for this variable survival was differential predation by weasels. Both spring

densities of voles ($r^2 = 0.09$, $n = 10$, $P = 0.39$) and their overwinter survival ($r^2 = 0.14$, $n = 9$, $P = 0.38$) were negatively, although not significantly, related to the weasel snow-track index from the previous winter (Fig. 2). Thus, while there are winters of poor overwinter survival when weasels are more abundant, there are also winters of poor overwinter survival when weasels are rare (Fig. 2).

Another possible factor accounting for this variable survival is variable food supply from spruce seeds, and we examine this relationship in an assessment of changes in vole body mass. Spring body mass of adults varied over the study (pooled data set, Fig. 4) (two-way ANOVA: sex \times year), with males being significantly smaller than females ($25.03 \text{ g} \pm 0.16$, $n = 330$ vs. $26.76 \text{ g} \pm 0.36$, $n = 221$, respectively; $F_{1,532} = 9.93$, $P < 0.002$) and with voles in some years being much heavier than in others ($F_{9,532} = 9.96$, $P < 0.0001$); there was a marginal interaction effect ($F_{8,532} = 1.82$, $P = 0.07$). Mean male and female spring masses were highly correlated ($r^2 = 0.81$, $n = 9$, $P = 0.0009$). Thus, even though variation in mass owing to reproduction in females is likely (through lactation and undetected pregnancy), the strong covariation in males and females suggests that the variation among years is real. However, to avoid the confounding effects of reproduction on mass in females, we focus only on males in the following analyses. Spring mass was not related to spring population density ($r^2 = 0.04$, $n = 9$). However, the rate of population growth during summer tended to be higher when male spring rates were heavier ($r^2 = 0.41$, $n = 8$, $P = 0.09$) (1995 excluded, as no males were caught in spring). Spring male mass was not related to spruce seed fall during the previous winter ($r^2 = 0.02$, $n = 8$) (Fig. 4). Thus, spring body mass of voles was not related to spruce seed production the previous winter or to spring density.

Higher spruce seed abundance (Fig. 4) did not result in higher overwinter survival (Fig. 2, 1995 corrected for

Table 2. The relationship between the mean snow depth per month during winter from October to March to measures of demographic performance in the northern red-backed vole from the pooled data set of all 12 grids. Population growth was calculated as the instantaneous rate of growth in summer. Number of years in parentheses

	Current year	Next year
Overwintering survival	$r^2 = 0.56$ (9) $P = 0.02$	$r^2 = 0.35$ (9) $P = 0.095$
Spring density ha^{-1}	$r^2 = 0.02$ (10) $P = 0.68$	$r^2 = 0.65$ (9) $P < 0.009$
Male body mass (g) in spring	$r^2 = 0.44$ (9) $P = 0.05$	$r^2 = 0.78$ (8) $P = 0.004$
Population growth/week	$r^2 = 0.55$ (9) $P < 0.03$	$r^2 = 0.09$ (8) $P = 0.48$

low catch; $r^2 = 0.016$, $n = 9$); nor did higher spruce seed abundance overwinter result in higher population growth the following summer. The negative relationship between spruce seed abundance overwinter and the instantaneous rate of population growth the following summer over the pooled data set ($r^2 = 0.54$, $n = 8$, $P = 0.04$) disappeared when the outlier of 1993–94 (high seed production followed by a summer of no growth) was removed ($r^2 = 0.16$, $n = 7$, $P = 0.37$). Thus, spruce seed production was irrelevant to population processes in the northern red-backed vole.

Weather may play a significant in these cold northern forests and aspects of it may explain the above relationships. We examined a number of possible correlations between weather and demography and the only one factor showed a consistent pattern: average snow depth per month on the ground from October to March (mean depth $10.5 \text{ cm} \pm 1.9$, range $3.5\text{--}21.5$, $n = 9$ winters; obtained from the Burwash Landing Climatological Station, 65 km from the Arctic Institute Base – both being on Kluane Lake and thus in the same valley system). Deeper snow was associated with higher overwintering survival to spring, heavier males in spring and a higher population growth rate in the subsequent summer, but had no effect on spring density (Table 2). Snow depth also had delayed effects on vole demography in the following year, improving spring densities and spring body mass, with a tendency to improving overwinter survival the next winter. However, it had no effect on population growth rate in the subsequent summer. The positive impact of snow depth on these demographic indices was not simply the consequence of one winter with exceptional snow depth skewing the relationship. Thus northern red-back population demography was tied intimately to a key aspect of winter weather – the depth of the snowpack.

Discussion

In general, except for a minor fertilizer effect, the experimental treatments had no marked impact on northern red-backed vole populations. There are two possible explanations for this. First, most of our treatments were directed towards snowshoe hares (the dominant herbivore in these forests) and their predators, not towards the other species, and thus the treatments were largely inappropriate for manipulating the abundance of small mammals in this system and for teasing apart

their contribution to it. Although weasels have been regarded as major predators of small mammals in other boreal forest systems (i.e. Fennoscandia), we could not exclude them from our exclosures. Although food addition is known to affect small mammal populations markedly (reviewed in Boutin 1990), we used food that was more appropriate for hares and ground squirrels (Krebs *et al.* 1995; Karels & Boonstra 2000). Thus, we may have had no major effect because we designed the experiments incorrectly from the small mammal standpoint. Secondly, our manipulations should have affected small mammals as well, but did not, because other factors were more important. We think this is the more likely of the two explanations. The responses to the fertilization treatment (which was directed at all members in this ecosystem), the hare exclosures (which were directed specifically at the small mammals) and the other treatments provide insight into the limiting factors influencing this group.

Small mammal populations did not remain constant over time on the main forest grids. On the contrary, both *Clethrionomys* and *Microtus* populations reached two peaks (not simultaneously). Over the 10 years of our study, red-backed vole populations appeared to be related inversely to hare populations (Fig. 1). Was our 10 years window of time long enough to reveal an invariant pattern? The answer is no. However, others have observed striking similarity to the pattern we observed. Gilbert *et al.* (1986) found two *Clethrionomys* peaks, 10 years apart, and both followed hare peaks by about 2 years. They did not find a vole peak just before the hare peak, as we found (also reported in Gilbert & Krebs 1991). Grant (1976) also found peaks in the abundance of *C. gapperi* at 10-year intervals in southern Quebec, but did not have population data on hares. Previous studies in this and adjacent areas on both the northern red-backed vole and the hare allowed us to extend the window of time back another 15 years (17 years for hares). Such combining of data has to be interpreted with caution because of differences among the studies in trapping protocol and of site-specific differences in productivity. However, the general pattern over 25 years is shown and reveals three hare peaks (1971, 1980–81, 1989–90), with each one being followed by a pronounced vole peak 2–3 years later. In addition, minor vole peaks were observed on some sites in 1975 (Krebs & Wingate 1985) and 1987 (Gilbert & Krebs 1991). Figure 5 combines the vole and hare data into one continuous

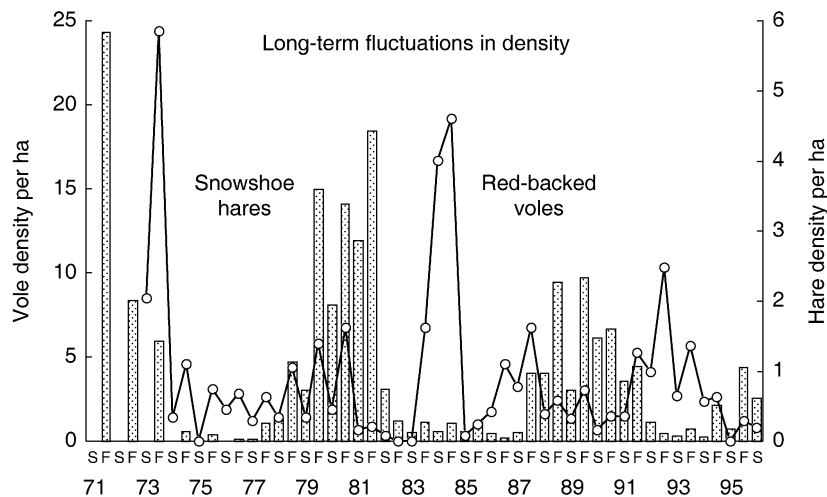


Fig. 5. Long-term fluctuations in the density of northern red-backed voles and snowshoe hares. All data come from the Kluane Lake, Yukon area except that for the 1971–75 hare data, which come from Fairbanks, Alaska. The vole data come from the following sources: 1973–75, Gilbert & Krebs (1981); 1976–86, Gilbert & Krebs (1991); and 1987–96, the present study. The hare data come from the following sources: 1971–75, Keith (1990); 1976–86, Krebs *et al.* (1986) and Boutin *et al.* (1995); and 1987–96, Krebs *et al.* (1995) and the present study.

series and suggests a phase shift between hare and major northern red-back vole peaks of about 2 years. Given this pattern, we evaluate the four hypotheses listed in the introduction.

THE ROLE OF PREDATION

The northern red-backed vole did not respond to the predator removal experiments, whether or not food was added (Fig. 3, Table 1). However our manipulations of predators were limited to the large mammal predators and to a possible reduction of avian predation underneath the monofilament. Diet information indicates that virtually all these predators eat these voles but none specialize on them (Doyle & Smith 2001; O'Donoghue *et al.* 2001a; Rohner, Doyle & Smith 2001). There are three possible reasons for our findings: first, some other compensatory mortality (e.g. socially induced mortality or disease) replaced that normally accounted for by these predators; secondly, weasel predators, which we could not keep out of the enclosures, were the critical predator limiting these voles; or thirdly, predation was neither limiting nor regulating. We discuss the first and second here and the third in later sections. First, compensatory mortality is unlikely given our low densities. Gilbert *et al.* (1986) found that although high density (in peak years) did suppress maturation in juveniles, it did not increase mortality. They concluded that social control of density could not explain population fluctuations.

Secondly, as we found a weak inverse relationship between weasel abundance (Fig. 2) and red-backed vole numbers, we conclude tentatively that weasels had no major impact on our vole populations most of the time. The most common weasel in our area is the short-tailed weasel and, relative to this species in Europe (208–320 g, King 1983), ours are about half as large (45–106 g, Banfield 1974), being more similar in size to large least

weasels in Europe (range 30–60 g for females; 40–100 g for males Güttinger 1995). Thus our short-tailed weasels probably fill an intermediate niche relative to the two European species, and some of the findings of the role of the least weasels in Europe may be relevant to our situation here. We would have liked to correlate the weasel index to actual density estimates, but this would have required radiotracking plus tracking (Jedrzejewski, Jedrzejewski & Szymura 1995). This would have been enormously difficult, given the low densities.

We suggest that in the Kluane area the short-tailed weasel is constrained most of the time by low small mammal densities, particularly in spring. Erlinge (1974) in southern Sweden and Tapper (1979) in England found that least weasels required minimum spring densities of 10 ha⁻¹ and 14 ha⁻¹ field voles (*M. agrestis*), respectively, before they would breed. Our average densities never reached those values (Fig. 1), although on control 1 in spring 1987 (see also data presented in Schweiger & Boutin 1995) and 1991, densities approached them and in 1984 (Fig. 5) they exceeded it on a nearby grid (Gilbert & Krebs 1991). Thus, with low densities prevailing over large areas for extended periods of time, weasels must have a high probability of going extinct locally (Jedrzejewski *et al.* 1995). Extremely low densities would limit the ability of weasels to respond to an increase in vole numbers such as occurred in 1988 (Fig. 1), but when the weasel densities remained low (Fig. 2). In addition, short-tailed weasel populations cannot respond immediately to a vole increase because delayed implantation lags weasel populations about 6–9 months behind that of their prey (King 1983). Finally, there must still be a minimum number of weasels in the area to permit them to have a measurable impact on the prey and we think that for most of the time, vole densities are too low. A prolonged period of higher vole densities may permit weasel numbers to build up. One

such period occurred from 1991 to 1993, when both red-backed voles in the forest (Fig. 1) and *Microtus* in meadows (from 1992 to 1993, Boonstra *et al.* 2001) were high, and this was followed by a high weasel index in the winters of 1993–94 and 1994–95 (Fig. 2). The lowest rate of red-backed vole population growth was observed in summer 1994 (Fig. 1), which is consistent with weasels having a negative impact at that time.

Henttonen (1987) reviewed the evidence in Fennoscandia and proposed that least weasel populations could increase only if high densities of *Microtus* (which are thought to be easier to capture than *Clethrionomys*) were present in meadows and open habitats but that once the weasel population was high, it could then depress both species. If these arguments apply to our area, the *Microtus* in meadows should have been driven to extremely low levels when the weasels peaked in the winter of 1994–95. They were not, but they did decline in 1994 and again in 1995 from their peak in 1993. This evidence is consistent with weasels occasionally having a negative impact on populations of both vole species. However, we suggest that other factors are more likely to explain the dynamics of these two vole species most of the time.

THE ROLE OF FOOD

The northern red-backed vole did not respond to the food addition experiments, whether or not predators were present (Table 1, Fig. 3). Although these voles eat rabbit pellets in the laboratory and there is limited evidence that these voles will eat rabbit pellets in the field, it never resulted in earlier reproduction or higher densities, as it did in snowshoe hares. Relative to boreal forest communities in Fairbanks or Fennoscandia, our forest was unproductive for voles, with densities usually being about 1–3 ha⁻¹ in spring and 2–4 ha⁻¹ in autumn (occasionally reaching maximum densities of 10–20 ha⁻¹) (Figs 1 and 5). Comparable low values were found by Fuller (1985) in the south-western Northwest Territories in *C. rutilus*, with spring densities being < 1 ha⁻¹ and autumn densities being 2–3 ha⁻¹ in most years and 9 ha⁻¹ in peak years. In contrast, the Fairbanks, Alaska, area is more productive, with both West (1982) and Whitney & Feist (1984) reporting northern red-backed voles densities varying from about 5 ha⁻¹ in spring to 40–60 ha⁻¹ in autumn. These estimates are likely to be inflated because of the small size of the grids (0.7 ha) and thus the large edge effect (West 1982). However, neither Alaskan study found any evidence of a 3–5-year cycle, and West (1982) attributed this to chronically poor overwinter survival. In Pallisjärvi, Finland (68° N), Henttonen *et al.* (1987) found densities similar to those in Alaska when combining the numbers of three different species of *Clethrionomys*, with densities typically being two to three times ours (spring densities in peak years being about 10 h⁻¹ and autumn densities 50 ha⁻¹). In northern Sweden, Löfgren (1995) found slightly lower densities. However, in contrast to the North American situation, both these Fennoscandian areas have shown

evidence of the 3–5-year population cycles in the past. The reason for the difference between northern Europe and North America may be related to better overwinter survival in the former and to higher productivity of the ground layer. Jedrzejewski & Jedrzejewski (1996) present evidence to indicate that microtine cycles can occur in ecosystems only where the standing crop of ground vegetation > 4000 kg ha⁻¹, as is found in the boreal forest of northern Europe. In a white spruce forest near Fairbanks (a site likely to be more productive than ours), Grodzinski (1971) calculated that the standing crop of ground vegetation averaged 2250 kg ha⁻¹, of which only 237 kg was herbs and dwarf shrubs and the rest was mosses and lichens. Productivity of the ground layer in Kluane appears even lower than in Alaska and thus our low vole densities are understandable. In contrast, the standing crop of edible birch and willow (the main foods for the cycling snowshoe hare at Kluane) varied between 43 and 168 kg ha⁻¹ during the hare peak to 2200–19 700 kg ha⁻¹ during the hare low (Smith *et al.* 1988). Thus productivity of the ground layer, as opposed to the shrub layer, may be the major reason why cycles are not seen for voles, which rely on the former, but are seen in hares, which rely on the latter.

Populations of small mammals living in deciduous forests with low ground cover in Europe (e.g. Denmark, Poland and the United Kingdom) and eastern North America do not cycle, but do fluctuate, and these are linked directly to years with superabundant production of tree seeds of species (Jensen 1982; Pucek *et al.* 1993; Wolff 1996). However, we found no correlation between spruce seed production and population fluctuations (Fig. 4). Years in which virtually no spruce seeds were produced (1991 and 1992) were followed by springs in which voles were heavy and populations grew to reach high densities. Conversely, the year with maximal seed production (1993) was followed by a spring in which voles were smaller and populations grew poorly. Although the northern red-backed vole eats spruce seeds, these seeds are apparently an incomplete diet, and voles will lose weight if forced to eat only spruce seeds, but not if a supplement of lichens is also given (Dyke 1971; Grodzinski 1971). Thus, the absence of a good spruce seed crop did not prevent high vole densities nor did its presence permit them. Some other food must explain fluctuations in our populations.

The overall pattern of demography suggests that not only must this food permit good population growth in summer; it must also permit good survival overwinter and good survival into the next breeding season. We found that the size of the spring vole population was a good predictor of the size of the autumn population. Gilbert & Krebs (1991) also found this relationship and postulated that the key demographic factor leading to population peaks was high winter survival leading to high spring densities. However, because the size of the autumn population can be increased by up to three times by providing high quality supplementary food in spring and summer (sunflower seeds, but not oats,

Gilbert & Krebs 1981), typical summer food levels must constrain population growth (especially through early juvenile survival before the young are trappable). In addition, Gilbert & Krebs (1981) found that production of higher densities in the autumn did not carry over to the next spring and thus some aspect of winter conditions must also constrain growth. Schweiger & Boutin (1995) tested this idea by adding food during the autumn and winter and produced higher spring densities. However, when they stopped feeding the next spring, these higher spring densities did not result in higher autumn densities. Thus, some aspect of spring or summer food was inadequate to sustain these populations.

A possible candidate is variation in the mushroom crop (both epigeous and hypogeous fungi), but these are available only in summer and early autumn and do not carry through to the next year. Variation in size of crop is dependent on the amount of summer rain (Dyke 1971). *Clethrionomys* spp. eat mushrooms readily and it may be a major summer and early autumn dietary item. Thus, variation in this resource could be expected to affect summer vole populations, but not winter populations. Dyke (1971) found fungi in *C. rutilus* stomachs only in summer and early autumn, not in winter, and concluded that fungi were unimportant thereafter. Merritt & Merritt (1978) found a similar pattern in *C. gapperi* in Colorado. A second candidate is arboreal lichens. These lichens may be a major component of winter diet in *Clethrionomys* spp. West (1982) reported that they made up 12% of the late winter diet of *C. rutilus* in Alaska and Dyke (1971) reporting values of 30–50% in the Northwest Territories (cf. Henttonen, personal communication, found similar values in Finland). However, Merritt & Merritt (1978) found none in *C. gapperi* stomachs from Colorado. Hansson (1999) postulated that the recent declines in intensity and presence of vole cycles in Fennoscandia was related to declines in the overwintering lichen food supply of voles related to landscape level forestry practices. Rapid rotation times in tree-cutting prevented the development of arboreal lichen populations that then reduced vole overwinter food and hence their survival. We think this is an unlikely scenario for *C. rutilus* in northern North America, where forestry is limited, and thus arboreal lichen abundance unlikely to vary much aside from the periodic forest fires. The third candidate is seed produced by dwarf shrubs and herbs, some of which overwinter. Evidence suggests that the critical food permitting good survival in both late summer, winter and into the next growing season is the size of the berry crop produced by dwarf shrubs (Dyke 1971; Grodzinski 1971; West 1982). Thus, what needs to be understood are the factor(s) that cause variation in the size of this crop and its role in supporting overwinter survival of *Clethrionomys*.

THE ROLE OF NUTRIENTS

Bottom-up control of vole populations through nutrients is one possible explanation for population fluctuations.

We suggest that population peaks in the northern red-back vole follow population peaks in snowshoe hares by 2–3 years, because foods required by these voles (particularly seeds and berries produced by herbs and dwarf shrubs) are stimulated by the flush of nutrients released by the decomposition of large quantities of pellets produced by hares at the population peak, particularly those produced during peak winters. Although the nutrients are released primarily in the summer following their winter production (Hik, personal communication), lags are introduced into this system because it takes 2 years to produce a good berry crop (the plants take up the nutrients the first summer producing a bumper crop of berries the next) and a third to obtain peak populations of voles. Stochasticity in weather can affect the exact timing of the seed crop (e.g. severe late frosts in spring may kill the flowers, heavy snowpack overwinter may augment soil moisture needed for seed maturation in summer). If weather conditions permit, high seed abundance in the second autumn results in high overwintering survival of the voles and high spring densities in the third year. The bumper crop of seeds may last long enough into the spring and summer of the third year (especially in years with late snowmelt) to enable the animals to survive until the new vegetation starts growing.

The importance of decaying faeces as stimulators of plant growth through mineral recycling and herbivore population responses have also been postulated for lemmings in the Arctic tundra (Schultz 1969). Outbreaks of forest lepidoptera in northern ecosystems result in large scale defoliation, which then injects pulses of nutrients into these forests (Nilsson 1978; Swank *et al.* 1981). In northern Fennoscandia, Neuvonen (1988) proposed that a nitrogen pulse caused by defoliation of birch forests by a geometrid moth caused an increase in microtine populations. However, definitive evidence on this interaction has yet to be collected.

Evidence for the effect of fertilization on berry production is limited, but appears to depend on the amount of fertilizer used. In Fennoscandia (reviewed in Raatikainen & Niemelä 1994), fertilization generally increases berry production, often with a lag of 1–2 years, but too much fertilizer will decrease berry production as competitors grow more rapidly than the dwarf shrubs (Strengbom *et al.* 2002). In the Arctic tundra, growth of evergreen dwarf shrubs is significantly stimulated by low levels of fertilization (Chapin & Shaver 1985) but higher levels lead to mortality. At the levels of fertilization used in our experiments at Kluane from 1986 to 1995 (Turkington *et al.* 1998, 2002), declines occurred in dwarf shrubs. The decline in vole populations (Table 2, Fig. 3) on the fertilizer plots 2 years after fertilizer addition started is consistent with this interpretation.

An implication of this hypothesis is that if snowshoe hare peaks vary in amplitude, peaks with higher hare densities should result in greater browsing pressure, greater production of hare pellets, increased release of nutrients, greater production of seeds and berries and ultimately in higher red-backed vole densities 2 years

later. Figure 5 suggests that the hare densities in the peak of 1981 may have been twice as high as densities in 1990. Indeed, the mortality rate of tagged twigs of birch and willow tend to corroborate this, as the rate was much higher in the hare peak of 1981 (100% and 57%, respectively, Smith *et al.* 1988) than in the hare peak of 1990 (71–90% and 8–16%, respectively). Figure 5 indicates that vole densities were up to two times higher in 1984 than in 1992. Interestingly, Fig. 5 also indicates that hare densities were about three times higher in 1971 (data from Fairbanks) than in 1992 and vole densities in 1973 were also about three times higher. If the hare peak in Kluane in the early 1970s was also about three times as high as that in 1990, the correlation would be tight. However, given differences in methods of data collection and in higher productivity in Alaska, this latter correlation must be treated with caution. An alternative approach would be to manipulate nutrients experimentally at levels approximating the amounts released in snowshoe hare pellets.

If a hare peak is followed by a red-backed vole peak, preventing the first should prevent the second. Within the hare enclosure (unfertilized) we not only prevented a hare peak, we eliminated hares altogether, and this should have prevented a vole peak within the enclosure. It did not (Table 1, Fig. 3). We were not able to detect any difference between the controls and the hare enclosure. Part of the problem may be one of scale. Relative to the home ranges of these voles, our 4-ha hare enclosure may have been too small. A more intensive monitoring of demography (survival and reproduction) may have permitted us to detect lower indices of demographic performance within the enclosure.

Other boreal forest sites also show irregular *Clethrionomys* fluctuations and some may be associated with the hare cycle. Fuller (1977, 1985) trapped voles in the south-western Northwest Territories from 1961 to 1979. Fuller found peaks in *C. gapperi* in 1961–62, 1974 and 1976, but not at other times. *C. rutilus* was trapped intensively from 1970 to 1979 and peaks similar to those in *C. gapperi* were found in 1974 and 1976. Whitney & Feist (1984) summarized *C. rutilus* data from 1970 to 1981 (the data after 1972 were collected intermittently and those for 1977–78 was missing) for live-trapping grids near Fairbanks and found increasing populations in 1971, peak populations in 1972, and low populations at all other times. For the same general area, West (1982) live-trapped voles from 1972 to 1976, and found peak populations in 1976. Mihok *et al.* (1985) snap-trapped *C. gapperi* in the springs from 1969 to 1981 in spruce forests in southern Manitoba and found high vole populations only from 1978 to 1980. Thus, there seems to be some evidence of peaks in *Clethrionomys* being 10 or more years apart, but the link to the snowshoe hare cycle is less clear in these areas than for our area, where we have good trapping data on both species. Because our site is more arid than most boreal forest sites and thus productivity is less, it may be more sensitive to fluctuations in nutrients and moisture than other sites (Carrier & Krebs 2002).

THE ROLE OF WEATHER

Variation in winter weather may explain the pattern characteristic of North American red-backed vole demography in the boreal forest. It may operate directly through changes in overwinter survival or indirectly through changes in moisture available for the next growing season. Fuller (1969) focused on what happened at the start and end of winter, postulating that more severe winters, particularly those with unfavourable autumn periods before stabilization of snow cover and those with unfavourable spring periods with delayed snowmelt and accumulation of melt water, should cause poor survival and depress *Clethrionomys* populations. However, he rejected this hypothesis (Fuller 1977), concluding that a population's ability to withstand the stresses of winter varied over time and that some unknown property (possibly related to food) was responsible for better survival in years when winter conditions were more severe. Interestingly, a deterioration in the stability of winter weather, operating through more frequent thaws, shorter periods of protective snow cover and ice formation at ground level may be associated with an attenuation of the cycles characteristic of Fennoscandia (Hörnfeldt *et al.* 2005).

West (1982) argued that winter survival in Alaska was largely contingent on the size of the autumn berry crop, but that the benefits of a large overwintering berry crop could be eliminated by an early spring with rapid melt-off, which would cause the rapid disappearance of remaining berries due to decomposition, foraging birds and insects; the result would be vole populations that would decline rapidly in spring. A late spring snowmelt would delay this loss and bridge the period until other foods became available. The spring of 1992 appears to be an example of this in our study. In that year, approximately twice as much snow fell in April and May as normal and snowmelt was delayed for almost 3 weeks (until the end of May) (Hubbs & Boonstra 1997). In contrast, 1992 stood out as one of the best years of our study for *Clethrionomys*, and populations reached high spring densities (Fig. 1), females were at their heaviest (Fig. 4) and the population had a high growth rate that summer. Dyke (1971) experienced a similar set of environmental conditions but, interestingly, these conditions benefited only *C. rutilus*, not *C. gapperi* or *P. maniculatus*, both of which declined. Thus, spring conditions may accentuate the amplitude of a vole peak and prolong it if a bountiful berry crop occurred the previous summer; the critical point is which winter factor may cause variation in the berry crop.

Our evidence indicates that the depth of winter snowpack is key (a factor that Fuller did not explore). Deeper snowpack has direct benefits through higher overwinter survival and heavier spring body weights in the following spring (Table 2). Simple positive benefits in terms of reduced energy demand is the probable explanation. However, the longer-term benefits (higher summer growth, higher spring populations in the

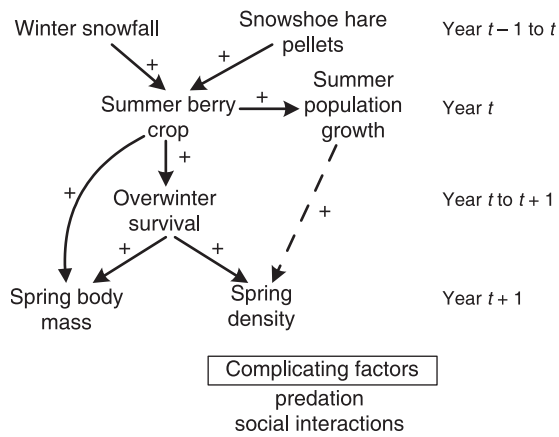


Fig. 6. Proposed model for population fluctuations in *Clethrionomys rutilus* from the boreal forest region of Canada and Alaska.

subsequent year, heavier animals in the subsequent year and a tendency to higher overwinter survival in the following winter (Table 2) all indicate a carryover, beneficial effect. The most obvious link is that deeper snows immediately provide higher moisture in spring that directly benefits the dwarf berry-producing shrubs as they flower and set seed. In bilberries (*V. myrtillus* L.), a dwarf berry-producing shrub in Fennoscandia, the number of berries produced is commonly much lower than the number of flower shoots produced (Flower-Ellis 1971). Thus, in our area, high spring moisture from overwintering snowmelt may permit more of these flowers to develop in to berries.

A UNIFYING HYPOTHESIS

We propose that two factors independently, both operating through the size of the dwarf berry crop, interact to drive population changes of red-backed voles in the boreal forest in the Kluane area (Fig. 6). First, the primary 10-year cycle in snowshoe hares results in a secondary cycle in northern red-backed voles. The latter occurs with a time lag as the decay of large quantities of faeces produced at the hare peak fertilizes plants whose seeds are eaten by the voles. Secondly, heavy winter snowfalls induce good berry crop independent of the hare cycle. This causal sequence diagrammed in Fig. 6 leads to a series of questions for further investigation, as follows.

1. How does the size of the principal foods of the northern red-backed vole, particularly the berry crop, vary over time, and is this variation related to winter weather and nutrient release following snowshoe hare peaks?
2. Is the impact of predation in the Kluane small rodent community as minimal as we have suggested? Because *Microtus* voles are heavily eaten by all predators, perhaps predation limits populations of these voles.
3. Given that the northern red-backed vole has well-developed territoriality and social control of female reproductive rates, what role does social regulation play in the population changes observed in this species in the boreal forest?

Acknowledgements

We thank all the ecologists who have worked on the Kluane Boreal Forest Ecosystem Project for their contributions in collecting these data, particularly the chief technicians during the project: V. Nams, S. Schweiger, M. O'Donoghue, and J. McDowell; and W. Hochachka for carrying out the randomization tests. This research was supported by the Natural Sciences and Engineering Research Council of Canada through a Collaborative Special Grant (to C. J. K and the Kluane Team) and Discovery Grants to R. B. and C. J. K. The Arctic Institute of North America provided facilities at Kluane Lake and we thank Andy Williams for his assistance. This is contribution No. 179 from the Kluane Boreal Forest Ecosystem project.

References

Banfield, A.W.F. (1974) *The Mammals of Canada*. National Museum of Canada, University of Toronto Press, Toronto.

Boonstra, R., Krebs, C.J., Gilbert, S. & Schweiger, S. (2001) Voles and mice. *Ecosystem Dynamics of the Boreal Forest: the Kluane Project* (eds C.J. Krebs, S. Boutin & R. Boonstra), pp. 216–239. Oxford University Press, Oxford.

Boutin, S. (1990) Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Canadian Journal of Zoology*, **68**, 203–220.

Boutin, S. *et al.* (1995) Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos*, **74**, 69–80.

Boutin, S., Krebs, C.J., Nams, V.O., Sinclair, A.R.E., Boonstra, R., O'Donoghue, M. & Doyle, C. (2001) Experimental design and practical problems of implementation. *Ecosystem Dynamics of the Boreal Forest: the Kluane Project* (eds C.J. Krebs, S. Boutin & R. Boonstra), pp. 49–66. Oxford University Press, New York.

Byrom, A.E. (1997) *Population ecology of arctic ground squirrels in the boreal forest during the decline and low phases of a snowshoe hare cycle*. PhD Thesis, University of British Columbia, Vancouver.

Carpenter, S.R., Chisholm, S.W., Krebs, C.J., Schindler, D.W. & Wright, R.F. (1995) Ecosystem experiments. *Science*, **269**, 324–327.

Carrier, P. & Krebs, C.J. (2002) Trophic effects of rainfall on *Clethrionomys rutilus* voles: an experimental test in a xeric boreal forest in the Yukon Territory. *Canadian Journal of Zoology*, **80**, 821–829.

Chapin, F.S. III & Shaver, G.R. (1985) Individualistic growth responses of tundra plant species to environmental manipulations in the field. *Ecology*, **66**, 564–576.

Cheveau, M., Drapeau, P., Imbeau, L. & Bergeron, Y. (2004) Owl winter irruptions as an indicator of small population cycles in the boreal forest of eastern North America. *Oikos*, **107**, 190–198.

Doyle, F.I. & Smith, J.N.M. (2001) Raptors and scavengers. *Ecosystem Dynamics of the Boreal Forest: the Kluane Project* (eds C.J. Krebs, S. Boutin & R. Boonstra), pp. 378–404. Oxford University Press, Oxford.

Dyke, G.R. (1971) *Food and cover of fluctuating populations of northern cricetids*. PhD Thesis, University of Alberta, Edmonton.

Erlinge, S. (1974) Distribution, territoriality and numbers of the weasel *Mustela nivalis* in relation to prey abundance. *Oikos*, **25**, 308–314.

Erlinge, S., Göransson, G., Högstedt, G., Jansson, G., Liberg, O., Loman, J., Nilsson, I., von Schantz, T. & Sylvén, M. (1984)

- Can vertebrate predators regulate their prey? *American Naturalist*, **123**, 125–133.
- Flower-Ellis, J.G.K. (1971) Age structure and dynamics in stands of bilberry (*Vaccinium myrtillus* L.). Research note no. 9. Department of Forest Ecology and Forest Soils, Royal College of Forestry, Stockholm.
- 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.
- Fuller, W.A. (1977) Demography of a subarctic population of *Clethrionomys gapperi*: numbers and survival. *Canadian Journal of Zoology*, **55**, 42–51.
- Fuller, W.A. (1985) Demography of *Clethrionomys gapperi*, parapatric *C. rutilus*, and sympatric *Peromyscus maniculatus* in northern Canada. *Annales Zoologici Fennici*, **22**, 229–241.
- Gagnon, J., Roth, J., Finzer, B., Hofmann, R., Haycock, K., Simpson, J. & Feldman, D. (1990) *Super ANOVA – Accessible General Linear Modelling*. Abacus Concepts, Inc., Berkeley, CA, USA.
- Gilbert, B.S. & Krebs, C.J. (1981) Effects of extra food of *Peromyscus* and *Clethrionomys* populations in the southern Yukon. *Oecologia*, **51**, 326–331.
- Gilbert, B.S. & Krebs, C.J. (1991) Population dynamics of *Clethrionomys* and *Peromyscus* in southwestern Yukon, 1973–89. *Holarctic Ecology*, **14**, 250–259.
- Gilbert, B.S., Krebs, C.J., Talarcio, D. & Cichowski, D.B. (1986) Do *Clethrionomys rutilus* females suppress maturation of juvenile females? *Journal of Animal Ecology*, **55**, 543–552.
- Graham, I.M. & Lambin, X. (2002) The impact of weasel predation on cyclic field-vole survival: the specialist predator hypothesis contradicted. *Journal of Animal Ecology*, **71**, 946–956.
- Grant, P.R. (1976) An 11-year study of small mammals populations at Mont St. Hilaire, Quebec. *Canadian Journal of Zoology*, **54**, 2156–2173.
- Grodzinski, W. (1971) Energy flow through populations of small mammals in the Alaskan taiga forest. *Acta Theriologica*, **16**, 231–275.
- Güttinger, R. (1995) *Mustela nivalis* L., 1766. *Saugetiere der Schweiz* (ed. J. Hausser), pp. 383–388. Birkhäuser-Verlag, Basel, Switzerland.
- Hanski, I., Hansson, L. & Henttonen, H. (1991) Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology*, **60**, 353–367.
- Hansson, L. (1999) Intraspecific variation in dynamics: small rodents between food and predation in changing landscapes. *Oikos*, **86**, 159–169.
- Hansson, L. & Henttonen, H. (1985) Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia*, **67**, 394–402.
- Henttonen, H. (1987) The impact of spacing behavior in microtine rodents on the dynamics of least weasels *Mustela nivalis* – a hypothesis. *Oikos*, **50**, 366–370.
- Henttonen, H. (2000) Long-term dynamics of the bank vole *Clethrionomys glareolus* at Pallasjärvi, northern Finnish taiga. *Polish Journal of Ecology*, **48** (Suppl.), 87–96.
- Henttonen, H., Oksanen, T., Jortikka, A. & Haukialmi, V. (1987) How much do weasels shape microtine cycles in the northern Fennoscandian taiga? *Oikos*, **50**, 353–365.
- Hörnfeldt, B., Hipkiss, T. & Eklund, U. (2005) Fading out of vole and predator cycles? *Proceedings of the Royal Society London, Series B*, **272**, 2045–2049.
- Hubbs, A.H. & Boonstra, R. (1997) Population limitation in Arctic ground squirrels: effects of food and predation. *Journal of Animal Ecology*, **66**, 527–541.
- Jedrzejewski, W. & Jedrzejewski, B. (1996) Rodent cycles in relation to biomass and productivity of ground vegetation and predation in the Palearctic. *Acta Theriologica*, **41**, 1–34.
- Jedrzejewski, W., Jedrzejewski, B. & Szymura, L. (1995) Weasel population response, home range, and predation on rodents in a deciduous forest in Poland. *Ecology*, **76**, 179–195.
- Jedrzejewski, W., Rychlik, L. & Jedrzejewski, B. (1993) Responses of bank voles to odours of seven species of predators: experimental data and their relevance to natural predator–vole relationships. *Oikos*, **68**, 251–257.
- Jensen, T.S. (1982) Seed production and outbreaks of non-cyclic rodent populations in deciduous forests. *Oecologia*, **54**, 184–192.
- Kalela, O. (1962) On the fluctuations in the numbers of arctic and boreal small rodents as a problem of production biology. *Annales Academiae Scientiarum Fennicae Series A*, **IV**, 1–38.
- Karels, T.J. & Boonstra, R. (2000) Concurrent density dependence and independence in populations of arctic ground squirrels. *Nature*, **408**, 460–463.
- Keith, L.B. (1990) Dynamics of snowshoe hare populations. *Current Mammalogy*, **2**, 119–195.
- King, C.M. (1983) *Mustela erminea*. *Mammalian Species*, **195**, 1–8.
- Korpimäki, E. & Krebs, C.J. (1996) Predation and population cycles of small mammals. A reassessment of the predation hypothesis. *Bioscience*, **46**, 754–764.
- Korpimäki, E., Norrdahl, K., Klemola, T., Pettersen, T. & Stenseth, N.C. (2002) Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. *Proceedings of the Royal Society London, Series B*, **269**, 991–997.
- Koshkina, T.V. & Korotkov, Y.S. (1975) Regulative adaptations in populations of the red vole (*Clethrionomys rutilus*) under optimum conditions of its range. *Fauna and Ecology of Rodents*, **12**, 5–61 [in Russian, translated by W. A. Fuller, University of Alberta].
- Krebs, C.J. (2002) Beyond population regulation and limitation. *Wildlife Research*, **29**, 1–10.
- Krebs, C.J. & Boonstra, R. (1984) Trappability estimates for mark–recapture data. *Canadian Journal of Zoology*, **62**, 2440–2444.
- Krebs, C.J., Boutin, S. & Boonstra, R. (2001a) *Ecosystem Dynamics of the Boreal Forest: the Kluane Project*. Oxford University Press, Oxford.
- Krebs, C.J., Gilbert, B.S., Boutin, S., Sinclair, A.R.E. & 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.
- Krebs, C.J., Boutin, S., Boonstra, R., Sinclair, A.R.E., Smith, J.N.M., Dale, M.R.T., Martin, K. & Turkington, R. (1995) Impact of food and predation on the snowshoe hare cycle. *Science*, **269**, 1112–1115.
- Krebs, C.J., Dale, M.R.T., Nams, V.O., Sinclair, A.R.E. & O'Donoghue, M. (2001b) Shrubs. *Ecosystem Dynamics of the Boreal Forest: the Kluane Project* (eds C.J. Krebs, S. Boutin & R. Boonstra), pp. 92–115. Oxford University Press, Oxford.
- Krebs, C.J. & Wingate, I. (1985) Population fluctuations in the small mammals of the Kluane Region, Yukon Territory. *Canadian Field-Naturalist*, **99**, 51–61.
- Löfgren, O. (1995) Spatial organization of cyclic *Clethrionomys* females: occupancy of all available space at peak densities? *Oikos*, **72**, 29–35.
- Manly, B.F.J. (1991) *Randomization and Monte Carlo Methods in Biology*. Chapman & Hall, London.
- Martell, A.M. & Fuller, W.A. (1979) Comparative demography of *Clethrionomys rutilus* in taiga and tundra in the low Arctic. *Canadian Journal of Zoology*, **57**, 2106–2120.
- Merritt, J.F. & Merritt, J.M. (1978) Population ecology and energy relationships of *Clethrionomys gapperi* in a Colorado subalpine forest. *Journal of Mammalogy*, **59**, 576–598.

- Mihok, S., Schartz, B. & Iverson, S.L. (1985) Ecology of the red-backed voles (*Clethrionomys gapperi*) in a gradient of gamma radiation. *Annales Zoologici Fennici*, **22**, 257–271.
- Nams, V.O., Folkard, N.F.G. & Smith, J.N.M. (1993) Effects of nitrogen fertilization on several woody and nonwood boreal forest species. *Canadian Journal of Botany*, **71**, 93–97.
- Neuvonen, S. (1988) Interactions between geometrid and microtine cycles in northern Fennoscandia. *Oikos*, **51**, 393–397.
- Nilsson, I. (1978) The influence of *Dasychira pudibunda* (Lepidoptera) on plant nutrient transports and tree growth in a beech *Fagus sylvatica* forest in southern Sweden. *Oikos*, **30**, 133–148.
- O'Donoghue, M., Boutin, S., Murray, D.L., Krebs, C.J., Hofer, E.J., Breitenmoser, U., Breitenmoser-Würsten, Zuleta, G., Doyle, C. & Nams, V.D. (2001a) Coyotes and lynx. *Ecosystem Dynamics of the Boreal Forest: the Kluane Project* (eds C.J. Krebs, S. Boutin & R. Boonstra), pp. 276–323. Oxford University Press, Oxford.
- O'Donoghue, M., Boutin, S., Hofer, E.J. & Boonstra, R. (2001b) Other mammalian predators. *Ecosystem Dynamics of the Boreal Forest: the Kluane Project* (eds C.J. Krebs, S. Boutin & R. Boonstra), pp. 325–336. Oxford University Press, Oxford.
- O'Donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L. & Hofer, E.J. (1998) Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology*, **79**, 1193–1208.
- Oksanen, L. (2001) Logic of experiments in ecology: is pseudoreplication a pseudoissue? *Oikos*, **94**, 27–38.
- Pucek, Z., Jedrzejewski, W., Jedrzejewska, B. & Pucek, M. (1993) Rodent population dynamics in a primeval deciduous forest (Bialowieza National Park) in relation to climate, seed crop and predation. *Acta Theriologica*, **38**, 199–232.
- Raatikainen, M. & Niemelä, M. (1994) The effect of fertilization on the yield of wild forest berries. *Biology Research Reports (University of Jyväskylä)*, **38**, 123–129.
- Rohner, C., Doyle, F.I. & Smith, J.N.M. (2001) Great horned owls. *Ecosystem Dynamics of the Boreal Forest: the Kluane Project* (eds C.J. Krebs, S. Boutin & R. Boonstra), pp. 340–376. Oxford University Press, Oxford.
- Rohner, C. & Krebs, C.J. (1998) Response of great horned owls to experimental 'hot spots' of snowshoe hare density. *Auk*, **115**, 694–705.
- Schindler, D.W. (1998) Replication versus realism: the need for ecosystem-scale experiments. *Ecosystems*, **1**, 323–334.
- Schultz, A.M. (1969) A study of an ecosystem: the arctic tundra. *The Ecosystem Concept in Natural Resource Management* (ed. G.M. van Dyne), pp. 77–93. Academic Press, New York, USA.
- Schweiger, S. & Boutin, S. (1995) The effects of winter food addition on the population dynamics of *Clethrionomys rutilus*. *Canadian Journal of Zoology*, **73**, 419–426.
- Sinclair, A.R.E. (1989) Population regulation in animals. *Ecological Concepts* (ed. J.M. Cherrrett), pp. 197–241. Blackwell Scientific Publications, Oxford.
- Smith, J.N.M., Krebs, C.J., Sinclair, A.R.E. & Boonstra, R. (1988) Population biology of snowshoe hares. II. Interactions with winter food plants. *Journal of Animal Ecology*, **57**, 269–286.
- Stoddart, M. (1976) Effect of the odour of weasels (*Mustela nivalis* L.) on trapped samples of their prey. *Oecologia*, **22**, 439–441.
- Strengbom, J., Nordin, A., Näsholm, T. & Ericson, L. (2002) Parasitic fungus mediates change in nitrogen-exposed boreal forest vegetation. *Journal of Ecology*, **90**, 61–67.
- Swank, W.T., Waide, J.B., Crossley, D.A. Jr & Todd, R. (1981) Insect defoliation enhances nitrate export from forest ecosystems. *Oecologia*, **51**, 297–299.
- Tapper, S. (1979) The effects of fluctuating vole numbers (*Microtus agrestis*) on a population of weasels (*Mustela nivalis*) on farmland. *Journal of Animal Ecology*, **48**, 603–618.
- Turkington, R., John, E., Watson, S. & Seccombe-Hett, P. (2002) The effects of fertilization and herbivory on the herbaceous vegetation of the boreal forest in north-western Canada: a 10-year study. *Journal of Ecology*, **90**, 325–337.
- Turkington, R., Krebs, C.J., John, R.E., Dale, M., Nams, V., Boonstra, R., Boutin, S., Martin, K., Sinclair, A.R.E. & Smith, J.N.M. (1998) The effects of NPK fertilization for nine years on the vegetation of the boreal forest in north-western Canada. *Journal of Vegetation Science*, **9**, 333–346.
- West, S.D. (1982) Dynamics of colonization and abundance in central Alaskan populations of the northern red-backed vole, *Clethrionomys rutilus*. *Journal of Mammalogy*, **63**, 128–143.
- Whitney, P. & Feist, D. (1984) Abundance and survival of *Clethrionomys rutilus* in relation to snow cover in a forested habitat near College, Alaska. *Special Publication of the Carnegie Museum of Natural History*, **10**, 113–120.
- Wolff, J.O. (1996) Population fluctuations of mast-eating rodents are correlated with production of acorns. *Journal of Mammalogy*, **77**, 850–856.

Received 3 January 2006; accepted 6 July 2006