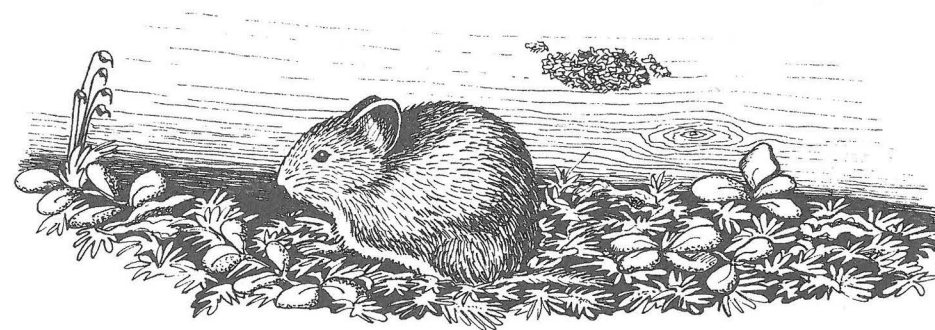

Voles and Mice

RUDY BOONSTRA, CHARLES J. KREBS, SCOTT GILBERT,
& SABINE SCHWEIGER



Small mammals are a ubiquitous, but less obvious, component of the herbivore community in the boreal forest. Small mammals are defined as those <100 g and generally represent <4% of the herbivore biomass in the Kluane Lake ecosystem. Across the boreal forest of North America, there are three main genera of cricetids. There are two species of the genus *Clethrionomys*, with the northern red-backed vole (*C. rutilus*) occupying the forests approximately north of 60° latitude (Martell and Fuller 1979, West 1982, Gilbert and Krebs 1991) and the southern red-backed vole (*C. gapperi*), occupying the rest (Grant 1976, Fuller 1985, Vickery et al. 1989). The deer mouse, *Peromyscus maniculatus*, is present throughout most of the boreal forest region (though in the Kluane area it is nearing the northern limit of its range). The *Microtus* voles (in order of decreasing abundance: the meadow vole, *M. pennsylvanicus*; the root vole, *M. oeconomus*; the singing vole, *M. miurus*; and the long-tailed vole, *M. longicaudus*) all occupy primarily grassy regions within the forest (meadows, marshes, and forest openings). In addition, the Kluane area has a rich diversity of rarer species (Krebs and Wingate 1976, 1985).

10.1 Natural History and Food Web Links

In this chapter we focus primarily on the northern red-backed vole and on the *Microtus* voles. We do not discuss the deer mouse, as it has been rare over the last 10 years, though formerly it made up about half of the small mammals captured (Krebs and Wingate 1985, Gilbert and Krebs 1991). For both groups of microtines, the breeding season typically lasts from May to the end of August or mid-September. Both have typical litter sizes of five or six. *Clethrionomys* females can produce 28 young per season, while *Microtus* females can produce 19–23 young per season. However, more realistic rates of increase are half or less than this (i.e., sevenfold for *Clethrionomys*; four- to sixfold for *Microtus*; Krebs and Wingate 1985).

The northern red-backed vole eats a wide variety of foods (documented in studies from Fairbanks, Alaska: Grodzinski 1971, West 1982; and from Great Slave Lake, Northwest Territories: Dyke 1971). It prefers to eat seeds (particularly of *Arctostaphylos* spp., *Vaccinium* spp., *Geocaulon lividum*, spruce seeds, but also *Empetrum nigrum*), leaves of some trees and shrubs (especially trembling aspen in spring but also a modest amount of *Shepherdia*, *Vaccinium*, and *Empetrum*), leaves of a number of herbs (particularly *Equisetum pratense* in spring, but also *Geocaulon* and *Cornus*), lichens (especially during winter: *Alectoria jubata*, *Usnea* spp., *Cladonia* spp., *Parmelia* spp., and *Peltigera aptosa*), fungi (especially *Laccinum scaber*, *Russula* spp., *Clavaria* spp., *Hygrocybe punicea*, and *Hydrellium* spp.) and occasionally mosses. It will also readily eat arthropods. Because of its consumption of both epigeous and hypogeous fungi (Maser et al. 1978), it may play a significant ecosystem role in the boreal forest by dispersing spores of decomposer and ectomycorrhizal fungi (Johnson 1996, Pastor et al. 1996), particularly after fires (West 1982).

Members of the genus *Microtus* are primarily herbivorous, eating both dicotyledon and monocotyledon leaves, stems, and roots, with the proportion varying depending on season and site (Batzli 1985, Bergeron and Jodoin 1989). Seeds generally make up a small proportion of the diet (particularly in root voles; Grodzinski 1971), and arthropods are generally insignificant in the diet (Tast 1974). In Alaska, root voles also consume leaves of *Salix*, *Shepherdia*, *Vaccinium*, and *Viburnum*, as well as the herbs *Equisetum*, *Linnaea*,

Cornus, and *Mertensia* (Grodzinski 1971). Fungi, lichens, and mosses may be eaten, but appear to be minor components of the diet (Grodzinski 1971, Maser et al. 1978, Pastor et al. 1996). Finally, virtually all predators eat *Microtus* spp. and *Clethrionomys*, and thus small rodents may play a significant ecosystem role in influencing the dynamics of the predators.

10.2 Community Interactions and Factors Affecting Population Dynamics

Two major peaks in *Clethrionomys* have occurred in the last 20 years, one in 1973 and one in 1984, and with additional modest vole peaks in 1975 and 1987 (Krebs and Wingate 1985, Gilbert et al. 1986, Gilbert and Krebs 1991, Boutin et al. 1995). Both major peaks coincided with the late decline or low phase of the snowshoe hare cycle. Four possible explanations can be proposed for this inverse relationship: competition, predation, stochastic processes, and nutrient release. First, red-backed voles may be acting as a buffer prey, such that when hares are abundant, so are their predators, which 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 and Henttonen 1985). In northern Fennoscandia, numbers of small mammal species show 3- to 4-year cycles, and predators have been implicated in causing population declines (Henttonen et al. 1987, Hanski et al. 1991, Korpimäki and Norrdahl 1991). Second, competition for food between hares and red-backed voles during the peak summers of hare abundance may seriously depress food supply for the latter. Third, 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 and Fuller 1979, Whitney and Feist 1984). In northern Europe, *C. glareolus* outbreaks followed years with a superabundant production of seeds from deciduous trees, and these mast years were directly related to weather patterns (Jensen 1982, Pucek et al. 1993). Fourth, a nutrient release hypothesis proposes that high hare densities at the peak cause high production of hare pellets, which then fertilize the forest. Plants critical to the diet of small mammals, particularly seed-bearing forbs, capture nutrients from the decay of these pellets. Forbs 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 by Pieper [1964] and Schultz [1969]). With the large-scale experiments discussed in chapter 4, we were able to examine each of these hypotheses.

Though densities of meadow and root voles vary from one year to the next in the Kluane area, there is no clear evidence of a 3- to 4-year cycle in *Microtus* voles. However, Whitney (1976) found evidence of a 3-year cycle in root voles in Fairbanks, Alaska. Because *Microtus* species occur primarily in grassland habitat (which makes up about 7% of the valley; see chapter 2) and our experiments were directed principally at the boreal forest, we did not expect any major response from these voles to most of our manipulations. The fertilization experiment, however, was the exception because the boreal forest is nutrient limited (Chapin and Shaver 1985, Bonan and Shugart 1989), and grass growth was stimulated by fertilization (chapter 5, Nams et al. 1993, John and Turkington 1995, Turk-

ington et al. 1998). We thus predicted that *Microtus* species should benefit from this manipulation and that the effects would be particularly pronounced on grassland meadows which occurred throughout the study area. In addition, in Fennoscandia, *Microtus* has been postulated to be more vulnerable to predation than *Clethrionomys* (Hansson 1987, Henttonen et al. 1987), and if this relationship holds for the boreal forest in North America, we predicted that dynamics of *Clethrionomys* should be closely tied to that of *Microtus*.

10.3 Methods

10.3.1 Small Mammal Trapping

We trapped small mammals from 1987 to 1996. Additional information on the small mammals for this area covers the period from 1973 to 1989 (Krebs and Wingate 1976, Gilbert and Krebs 1991). We set up 12 trapping grids to assess the responses of small mammals to the experimental manipulations. Each grid covered 2.81 ha (including a buffer strip around the perimeter) and had 100 trap points spaced 15.24 m apart and arranged in a 10×10 pattern. Traps were placed at every other trap point for a total of 50 traps. 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, herb, and grass layers. We had two replicate small mammal grids for the treatments. In 1989, we set up three additional grids to cover meadow habitats (grass and shrub) that were present in the valley but which we were not trapping. Each covered 1.49 ha and had 49 trap points in a 7×7 pattern.

Trapping sessions were carried out twice per year, with the first occurring in mid- to late May just after snow melt to assess overwinter survival and the second occurring in mid- to late August to assess summer production. Longworth livetraps were left permanently on the grids at all times and covered with protective boards to protect the traps against sun and rain. All grids on the study area were trapped within 2 weeks of each other. One week before trapping, we prebaited all traps with oats. During a trapping session, traps were set in the evening of the first day and checked three times: by 0900 h the next morning, by 2000 h the next evening, and by 0900 h the second morning, when all traps were locked open. Traps were baited with oats and a slice of apple; cotton stuffing was provided for warmth. When first caught, animals were ear tagged; tag number, species, location, weight, sex, and sexual condition (males, scrotal or not; females, vagina perforate or not, lactating or not, and pregnant or not) were recorded, and the animals were immediately released (CD-ROM frame 29). Because *Microtus* species were difficult to tell apart, especially the female root voles from the female meadow voles, we pooled them into a single *Microtus* category.

Before giving the results, two caveats must be born in mind, which may have affected the quality of the data. First, in the trapping sessions of 1987 and spring 1988, traps on many of the grids were disturbed by arctic ground squirrels and red squirrels. By the summer of 1988 we eliminated this problem by putting each trap inside a protective wire mesh cage. Second, an outfitter allowed his horses to range freely on the study area from 1987 to the spring 1990. The horses were found almost exclusively on fertilizer 1.

10.3.2 Data 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 the Jolly-Seber method or the CAPTURE program (White et al. 1982, Menkens and Anderson 1988) were inappropriate. For each trapping grid we calculated the finite rate of summer population growth standardized to a 4-month period; no rates were calculated for times when zero animals were captured. These data were analyzed with a one-way ANOVA plus Tukey-Kramer multiple range test using SuperANOVA (Gagnon et al. 1990). For the overall northern red-backed vole data set, we calculated an index of overwintering survival as spring density in year $t + 1$ /late summer density in year t . We were not able to get estimates of overwinter survival based on recovery of tagged animals because few were recaptured in spring that had been tagged in summer. Variation in population size among treatments was statistically analyzed using a randomization test (e.g., Manly 1991).

10.3.3 Robustness of Data

To assess the efficiency of our trapping technique in accurately assessing the small mammal populations, 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 from 1983 to 1989, except for 1987). This population was trapped in most years at 2- to 3-week intervals, and we used it to compare our estimation method (MNA) with a robust estimation method (Jolly-Seber). Two points can be made from this analysis. First, these voles were highly trappable (mean Jolly estimate of trappability/year = $92.1\% \pm 2.76$ (SE), range 81.3–100%; Krebs and Boonstra 1984). Second, the Jolly estimate and MNA were highly correlated ($r^2 = .99$, $n = 44$), with MNA underestimating the Jolly estimate by 4% at a population size of 5 and by 9% at 20. Thus, our trapping method should accurately reflect demographic parameters.

10.4 Impacts of the Manipulations

Over the entire study and on all areas combined, we caught 2780 different animals (1813 northern red-backed voles, 732 voles of the genus *Microtus*, 66 deer mice, 38 chipmunks, 11 heather voles, and 126 shrews) in 24,650 trap nights. In addition, 9 short-tailed weasels (*Mustela erminea*) were caught in live traps (2 in 1988, 5 in 1993, and 2 in 1994). To assess general population changes over the study area, the data were divided into the major species and pooled for all the grids we trapped continuously from 1987–1996. Red-backed voles were generally the most abundant small mammal in the valley. Their population density was moderately high in 1987, low from 1988 to spring 1991, growing rapidly over the summer of 1991, at high densities in 1992, moderately high densities in 1993 and 1994, and finally declining to extremely low levels in 1995 (figure 10.1). During the years of high snowshoe hare numbers (1988–1990), the northern red-backed voles remained low, whereas after the hares declined, these voles increased dramatically in density. Spring densities of these two species were inversely correlated ($r = -.76$, $N = 9$, $p = .02$).

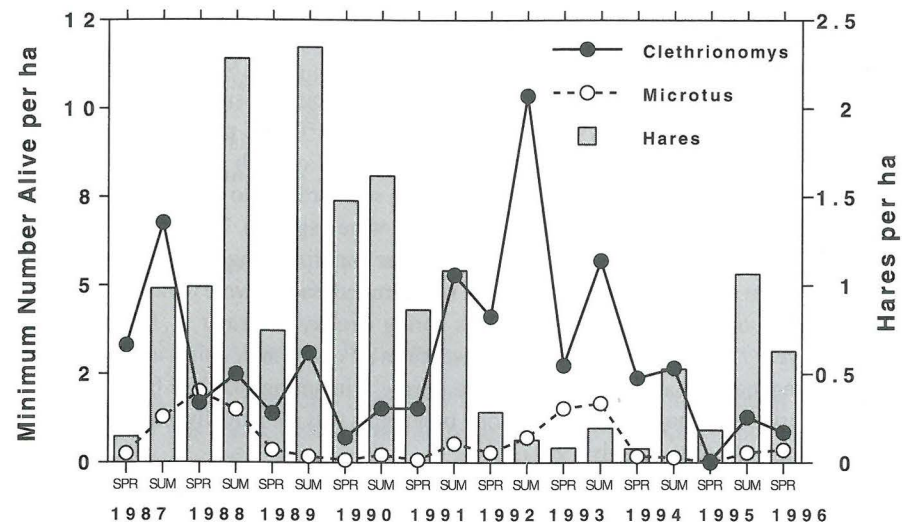


Figure 10.1 Population changes in small mammals at Kluane. All live-trapping grids were pooled. For the small mammal estimates (scale on the left y axis), only those forest grids trapped from the start of the study were included. Changes in snowshoe hare density on control grids were plotted for comparison.

Microtus voles were found at high densities in 1988 and 1993 but at low densities in all other years on the main trapping grids (figure 10.1). There was no relationship between *Microtus* density and either *Clethrionomys* density ($r = .32$) or snowshoe hare density ($r = .01$). *Microtus* density was unrelated to our index of weasel abundance (vole density in spring vs. weasel abundance the previous winter [$r = .37$] or vole density in autumn vs. weasel abundance the next winter [$r = .03$]). Both chipmunks and deermice made up minor parts of the small mammal community, being consistently low throughout the study.

Shrews (*Sorex cinereus* and *S. vagrans*) were only periodically abundant and almost never were caught in spring (only 4% shrews were caught then). The year of peak shrew abundance, 1995, may have been associated with an outbreak of spruce bark beetle, whose effects were becoming particularly pronounced at that time. Shrews were patchily distributed on the grids. In the sample in which all the grids were pooled, there was no obvious correlation between shrews and any of the other species (e.g., shrews vs. late-summer density of *Clethrionomys*, $r = .41$; shrews vs. late-summer density of hares, $r = .14$).

10.4.1 Northern Red-Backed Vole

Treatment Effects Variation in red-backed vole densities among plots within the same treatment was great, but 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 ($r = .74$, $N = 19$, $p = .0003$). 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 a randomization test compar-

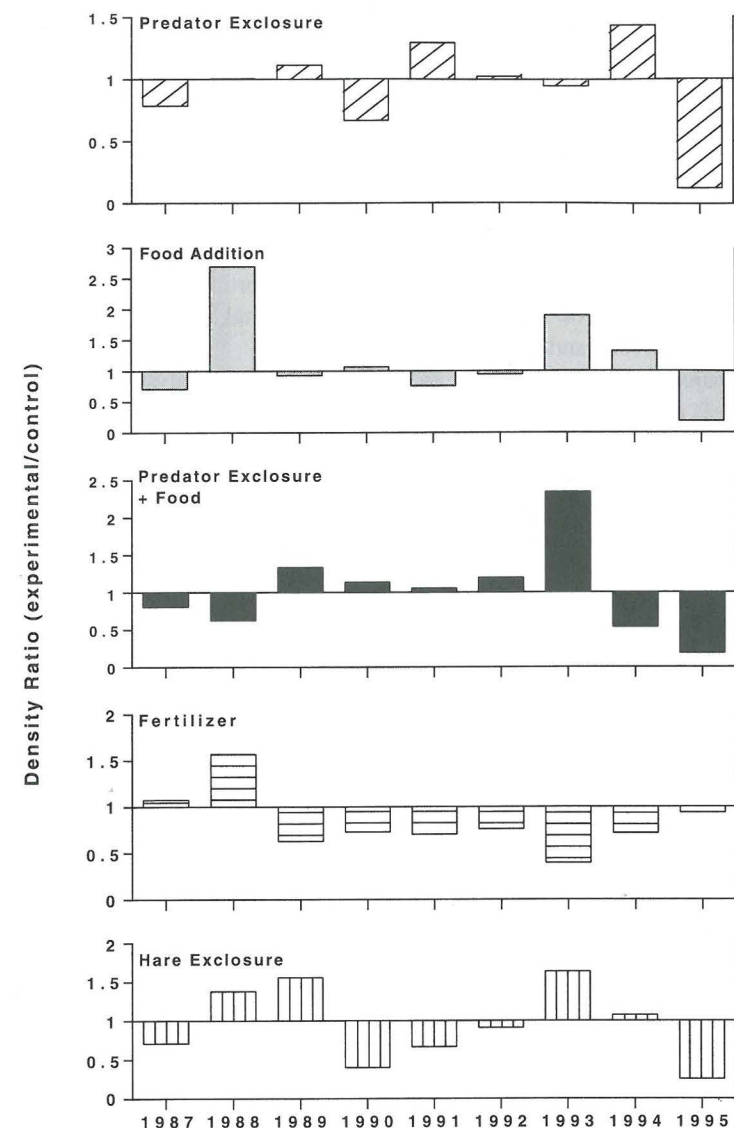


Figure 10.2 Ratio of the average population densities per year of *Clethrionomys rutilus* for the major treatments to the average control population densities at the same time. If there is no treatment effect, we expect a ratio of 1.0.

ison. The density effect of the treatments was compared as the ratio of the average effect of the treatment (replicates pooled) to average control densities (figure 10.2). Initially only the data from 1988 onward were examined, as the experiments were being set up in 1987. For most treatments there appeared to be no consistent effect, with the density ratio being approximately 1 (i.e., averaged density ratio was 1.3 for food addition, 1.0 for predator

closure, 1.1 for predator closure + food addition, 1.0 for hare closure, and 1.0 for hare closure + fertilization). In contrast, the predator closure + monofilament had consistently lower average densities (0.7), but those lower densities were present from the start of the experiment, and thus site-specific effects may explain these effects. The fertilizer density ratio averaged 0.78 from 1988 onward and 0.66 from 1990 onward. Fertilization actually reduced vole numbers. From 1987 to 1988, populations on the fertilized grids were either similar or higher than those on control grids, and thus it is unlikely that there were initial site-specific peculiarities limiting numbers. Independent evidence from other long-term experiments at Kluane on the effects of fertilizer indicates that the negative effects on a number of forest herbs and dwarf shrubs take 3 years to become evident (Nams et al. 1993; John and Turkington 1995).

Three major conclusions result from the randomization analysis. First, the control treatment was not significantly different from any other treatment except for the predator closure + monofilament. Second, this latter grid had the lowest average densities per trapping session over the 10-year period (mean \pm SE, 2.21 ± 0.55) of any treatment (e.g., controls 3.27 ± 0.64), including the other small mammal grid also within the predator enclosure, but not under the monofilament (3.28 ± 0.67). We do not know why this occurred. Third, the fertilizer treatment (2.74 ± 0.60) had lower average densities than the food treatment (3.53 ± 0.61 ; figure 10.2), and we interpret this to be a real effect. In the first summer (1987), average densities of red-backed voles were higher on the fertilizer treatments than on the food treatments, but thereafter they were almost always lower. This result could be caused by a slight positive effect of food addition on red-backed vole populations, a negative effect of fertilization on critical plant foods, or both. Because of changes in the vegetation with fertilization (chapter 5), we believe that a negative effect of fertilization on certain herbs was probably the cause of these patterns in density.

Large-Scale Effects In no case did the treatments prevent large fluctuations in numbers over time, and all numbers fluctuated in relative synchrony (e.g., correlation for control grids given above; changes in average density on fertilizer vs. food grids: $r = .62$, $p = .004$). We interpret this to mean that the treatment effects, for the most part, were not dramatic and that many of the differences we observed were due to site-specific variation in vegetation or in site-quality factors. To examine which factors may have caused the large-scale fluctuations in numbers (figure 10.1) and to remove the noise caused by site-specific differences among grids, we pooled the entire data set and treated our 12 trapping grids as one large grid. In attempting to tease out the relationships, we focus the analysis around two questions: what determined population growth in summer, and what determined the rate of population decline over winter?

Initial spring density was a good predictor of late-summer density ($r = .88$, $N = 9$), but late-summer density did not predict densities the next spring ($r = -.26$). Spring densities and overwinter survival were unrelated either to the track index of weasel (see 14.5) abundance ($r = .30$ and $r = -.16$, respectively) or to the average production of spruce seeds (see 7.1.3) in our valley ($r = .03$ and $r = .04$, respectively). Overwinter survival was positively related to the finite growth rate the next summer ($r = .75$). Thus, conditions that produced good overwintering survival appear to carry over into the next summer, resulting in higher densities in late summer.

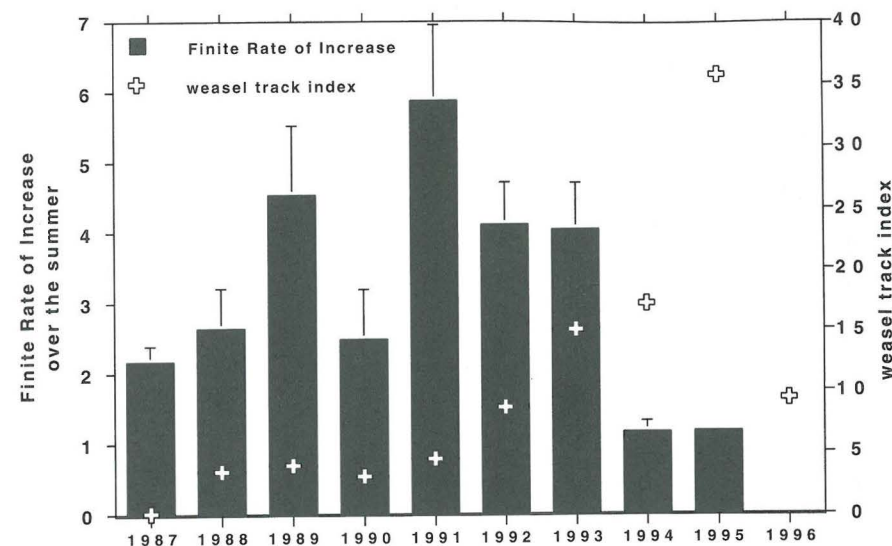


Figure 10.3 Variation among years (\pm SE) in the finite rate of population growth of *Clethrionomys rutilus* over the summer (May–August) and an index of weasel winter abundance (number of weasel tracks per 100 km of snow machine traveled). The weasel index as plotted refers to the previous winter (i.e., index for 1991 refers the winter of 1990–1991). Average finite rates of growth were calculated for each grid separately (only those with non-zero captures in spring and late summer were included). All grids but 1 had zero spring captures in 1995 and there were no late summer trapping in 1996. The year 1991 differed significantly from 1994, 1987, and 1988.

There were pronounced differences in summer population growth among years ($F = 3.86$, $df = 8, 77$, $p = .0007$), with 1991 having the highest rate and 1994 the lowest (figure 10.3). Summer population growth bore no relationship to spruce seed fall the previous autumn ($r = -.20$) or to snowshoe hare spring abundance ($r = -.26$). Weasel abundance the previous winter was unrelated to growth the next summer ($r = -.47$, $p = .20$).

Spring body mass varied significantly over the study (figure 10.4; two-way ANOVA, sex \times year), with males being significantly smaller than females (mean \pm SE, $24.77 \text{ g} \pm 0.20$, $N = 315$ vs. $26.62 \text{ g} \pm 0.38$, $N = 214$, respectively; $F = 7.75$, $df = 1, 510$, $p = .006$). In some years animals were much heavier than in other years ($F = 7.66$, $df = 9, 510$, $p < .0001$). There was no interaction between sex and year ($p = .16$). Male and female spring mass were correlated ($r = .87$, $p < .001$) and thus reflected the same processes. Body mass of females in spring did not predict the rate of population growth (figure 10.4; $r = .38$). Female mass bore no relationship to the index of weasel abundance the previous winter ($r = .04$). Thus, patterns of population growth and body mass were unrelated to levels of one possible winter food (spruce seeds) and to the abundance of a specialist small mammal predator.

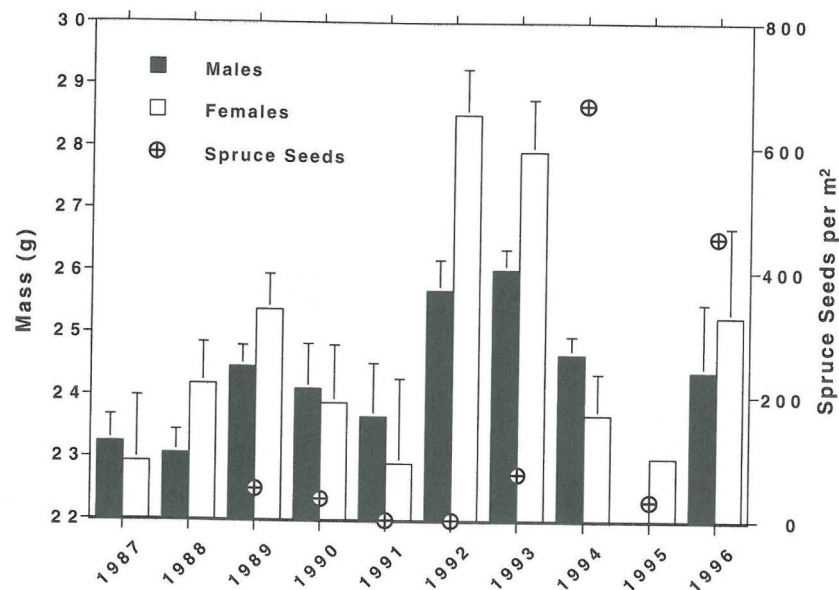


Figure 10.4 Variation (+ SE) in the spring body mass of *Clethrionomys rutilus* and spruce seed fall, 1990–1996. Spruce seed production refers to the previous winter (e.g., numbers for 1991 refer to the winter of 1990–1991). Obviously pregnant females were excluded from the averages.

10.4.2 *Microtus* Voles

Of 776 individual *Microtus* voles captured over the study, 37% (286) were caught on the two grassland meadow grids over an 8-year period (1989–1996 = 17.9/grid/year), and the rest were caught on the other 13 grids (about 3.9/grid/year). Because capture on these latter grids was sporadic and bore no relation to the treatments, our primary focus is on the meadow grids (figure 10.5). Though *Microtus* populations on the shrub meadow grid were correlated with those on the unfertilized meadow grid ($r = .72, p = .002$), average densities were much lower on the former (1.52 ± 0.50 per ha) than on the latter (6.41 ± 1.10), and so we ignore the shrub meadow grid in the following analysis. We ask three questions. First, were changes in the grassland meadow correlated? We would expect this if they were responding to some major environmental variable, even if fertilizer caused an overall increase on the fertilized meadow. Second, were changes in *Microtus* populations in the grassland meadow correlated with changes in forest *Clethrionomys* populations? It has been argued that predators such as weasels find it easier to capture *Microtus* than *Clethrionomys*. Thus, if predators were causing *Clethrionomys* populations to crash or remain low, *Microtus* populations should also crash or remain low simultaneously. The meadows were small and interspersed throughout the spruce forest. Third, as the soils of the boreal forest are nutrient limited, did fertilization stimulate grass growth in meadows and in more open forests, causing *Microtus* populations to increase? We address these questions in turn.

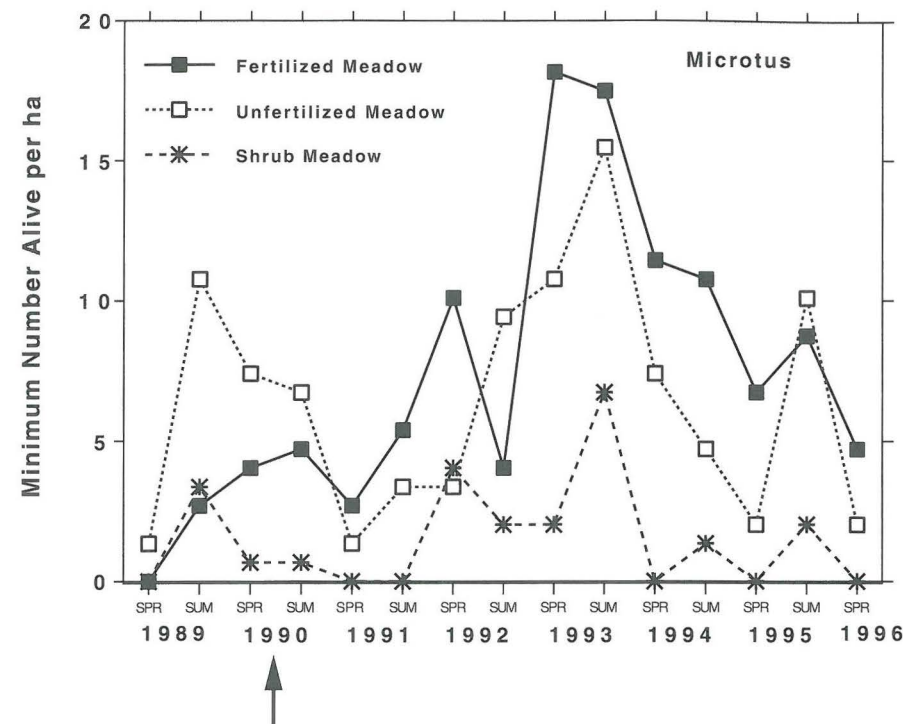


Figure 10.5 Population changes in *Microtus* spp. on the meadow grids over the study. Horses were selectively grazing the fertilized meadow until the summer of 1990 when they were removed, as indicated by the arrow.

We examined only the data collected from 1991 onward because the horses had major effects on the vegetation before that time. *Microtus* populations in the two grassland meadows were correlated ($r = .71, N = 11, p = .01$). We thus pooled these data and compared it with the pooled *Clethrionomys* sample from the two control grids (population changes on these were also correlated; see above). There was no correlation between changes in these two species, either when we examined only the spring periods ($r = .15$) or when we included both periods per year ($r = .14$). Thus, the species of small mammals living in the grasslands were not fluctuating in synchrony with those living in the forest. Neither was there any correlation between the weasel track index and either the pooled *Microtus* meadow spring populations (1991–1996, $r = .10$) or the unfertilized *Microtus* spring populations (1989–1996, $r = .37$). Thus, even when overwintering weasel indices reached their second highest level (1994–1995; figure 10.3), spring *Microtus* numbers in meadows remained moderately high (figure 10.5).

Finally, fertilization appeared to have positive effects on the growth of *Microtus* populations in grassland (figure 10.5). From 1991 to 1996, densities averaged 9.2 ± 1.6 per ha on fertilized grassland meadow versus 6.4 ± 1.4 on the unfertilized meadow ($p = .01$; a modest 44% increase). In addition, a comparison of the changes in densities on the for-

est fertilizer 1 and nearby control 2 grids (two grids that were the most similar in vegetation; figure 10.5), indicated that *Microtus* numbers were similar on both grids in the first 3 years (1987–1989: fertilizer 1, 1.1 ± 0.4 vs. control 2, 1.2 ± 0.5). Thereafter, *Microtus* populations on the fertilizer 1 grid were virtually always higher than on control 2 (1990–1996: fertilizer 1, 2.2 ± 0.8 vs. control 2, 1.0 ± 0.5). In contrast, the *Clethrionomys* populations showed the opposite pattern. Thus, we conclude that fertilization had a modest positive effect on *Microtus* numbers.

10.5 What Limits Mice and Vole Populations at Kluane?

In general, except for a minor fertilizer effect, the treatments had no marked impact on any of the small mammal species in our study area. There are two possible explanations for this. First, most of our treatments were directed toward the principal actors in the boreal forest, the snowshoe hares and their predators. Thus, the treatments were largely inappropriate for manipulating the abundance of the small mammals in this system and for teasing apart their contribution to it. Though weasels have been regarded as major predators of small mammals in other boreal forest systems (e.g., Fennoscandia), we could not exclude them from our exclosures. Though 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. Thus, our manipulations may have had no major effect because we designed the experiments incorrectly from the small mammal viewpoint. Second, our manipulations should have affected small mammals as well, but did not because other factors were more important. The responses to the fertilization treatment (which was directed at all players in this system), the hare exclosures (which were directed specifically at the small mammals), and the other treatments give insight into the 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, *Clethrionomys* populations appeared to be inversely related to hare populations (figure 10.1). Was our 10-year 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 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 did (also reported in Gilbert and Krebs, 1991). Grant (1976) 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). Combined data have to be interpreted with caution because of differences among the studies in trapping protocol and because of site-specific differences in productivity. However, the general pattern over 25 years is shown and reveals three hare peaks (1971, 1980–1981, 1989–1990), with each one being followed by a pronounced vole peak 2–3 years later. In addition, minor vole peaks were observed at some sites in 1975 (by Krebs and Wingate 1985, and Gilbert and Krebs 1991, but not by Gilbert et al. 1986; figure 10.4) and in 1987 (Gilbert and Krebs 1991). Combining the vole data into one continuous series (1973–1975 from Gilbert et al. 1986; 1976–1986 from Gilbert and Krebs, 1991; 1987–1996, our data) and correlating it to a similar series in hare

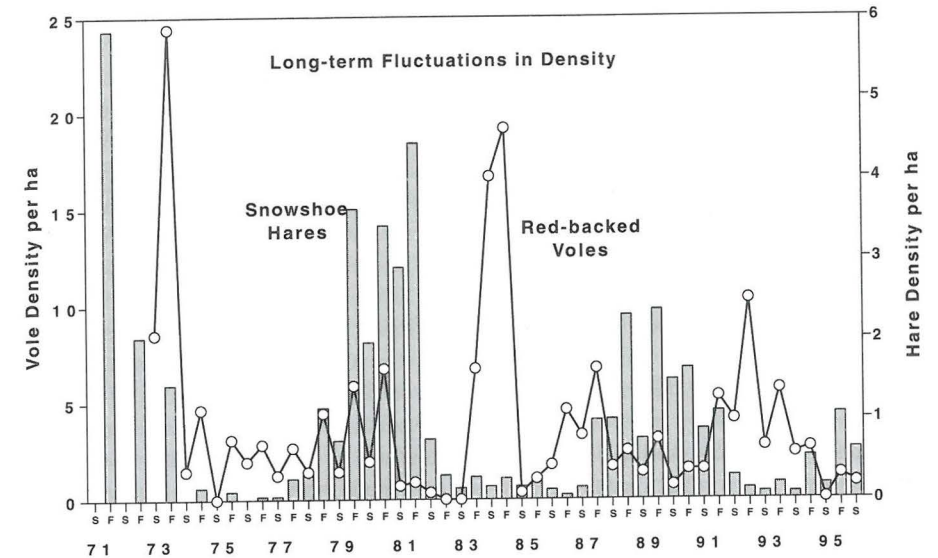


Figure 10.6 Long-term fluctuations in the density of northern red-backed voles and snowshoe hares. All data come from the Kluane Lake, Yukon, area except for the 1971–1975 hare data, which come from Fairbanks, Alaska. The vole data come from the following sources: 1973–1975, Gilbert and Krebs (1981); 1976–1986, Gilbert and Krebs (1991); 1987–1996, present study. The hare data come from the following sources: 1971–1975, Keith (1990); 1976–1986, Krebs et al. (1986) and Boutin et al. (1995); 1987–1996, Krebs et al. (1995) and present study.

data (see figure 10.6) indicated no correlation between vole and hare densities either in spring ($r = .23$, $N = 19$, $p = .34$) or in autumn ($r = .19$, $N = 20$, $p = .43$; $r = .08$, $N = 23$, $p = .72$ if the Alaska hare data are included; see also Boutin et al. 1995). This suggests that hares and northern red-backed voles do not compete directly for resources. However, a phase shift is suggested between hare and major *Clethrionomys* peaks of about 2 years (between autumn hare densities and autumn *Clethrionomys* densities 1 year later, $r = .08$, $N = 23$, $p = 0.72$, and 2 years later is $r = .37$, $N = 23$, $p = .09$). Below we argue that the coupling between hare and vole peaks is real and propose a plausible mechanism that does not preclude secondary vole peaks occurring at other times.

10.5.1 Northern Red-Backed Vole

Role of Predation The northern red-backed vole did not respond to the predator removal experiments, whether or not food was added (figure 10.2). However, our manipulations of predators was limited to the large mammal predators and to a possible reduction of avian predation underneath the monofilament. Diet information indicates that virtually all predators eat this vole, but none specialize on it. There are three possible reasons for our findings. First, some other compensatory mortality (e.g., socially induced mortality or disease) replaced mortality normally accounted for by these predators. Sec-

ond, weasel predators, which we could not keep out of the exclosures, were the critical predator component limiting these voles. Or, third, predation was neither limiting nor regulating. We discuss the first and second explanations here and the third in later sections.

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. Because we found no relationship between weasel abundance and *Clethrionomys* numbers, we conclude that weasels had no major impact on our vole populations (figure 10.3). The most common weasel in our area is the short-tailed weasel. Compared to this weasel 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. Our conclusion of no impact is relatively weak. We would have liked to correlate the weasel index to actual density estimates, but this would have required radio collaring plus tracking (Jedrzejewski et al. 1995), and because the larger carnivores were deemed more significant, this is where we put our resources.

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 increase. One such period occurred from 1991 to 1993 when both *Clethrionomys* in the forest (figure 10.1) and *Microtus* in meadows (1992–1993; figure 10.5) were high and this was followed by a high weasel index in the winters of 1993–1994 and 1994–1995 (figure 10.3; see also chapter 16). The lowest rate of *Clethrionomys* population growth was observed in the summers of 1994 and 1995 (figure 10.3), which is consistent with weasels continuing to exert a negative impact then. The *Clethrionomys* data for 1995 present a problem. In spring 1995, only 1 *Clethrionomys* was caught on 12 grids, whereas in late summer 1995, 60 were caught. Vole numbers cannot increase at this rate, and we suggest that the low numbers in spring 1995 were a trapping artifact induced by trap avoidance related to high weasel abundance in the winter of 1994–1995 (Stoddart 1976, Jedrzejewski et al. 1993).

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. 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 1994–1995. This was not observed (figure 10.5), but *Microtus* 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 both populations of both species. However, we suggest that other factors (probably overwintering food supplies) are more likely to explain the dynamics of these two species most of the time.

Role of Food The northern red-backed vole did not respond to the food addition experiments, whether or not predators were present (figure 10.2). Though we have limited evidence that these voles will occasionally eat rabbit chow (unpublished data), food ad-

dition never resulted in earlier reproduction or higher densities as it did in hares (chapter 8) and ground squirrels (chapter 9). Relative to boreal forest communities in Fairbanks or Fennoscandia, our forest was unproductive for voles, with densities usually being about 1–3/ha in spring and 2–4/ha in autumn (occasionally reaching maximum densities of 10–20/ha; figures 10.1, 10.6). Comparable low values were found by Fuller (1985) in the southwestern Northwest Territories in *C. rutilus*, with spring densities being <1/ha and autumn densities being 2–3/ha in most years and 9/ha in peak years; parapatric populations of *C. gapperi* were slightly higher. In contrast, the Fairbanks, Alaska, area appears more productive; both West (1982) and Whitney and Feist (1984) reported *C. rutilus* densities varying from about 5/ha in spring to 40–60/ha in autumn. However, neither study found evidence of a 3- to 4-year cycle. West (1982) attributed this to chronically poor overwintering 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 2–3 times ours (spring densities in peak years being about 10/ha and autumn densities 50/ha). In northern Sweden, Lofgrén (1995) found slightly lower densities. However, in contrast to the North American situation, both these Fennoscandian areas have shown evidence of the 3–4 year population cycles. The reason for this difference between northern Europe and North America may be related to better overwintering survival and to higher productivity of the ground layer in Europe.

Jedrzejewski and Jedrzejewska (1996) presented evidence indicating that these microtine cycles can only occur in ecosystems where the standing crop of ground vegetation is >4000 kg/ha, 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, 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 from 43–168 kg/ha during the hare peak to 2200–19,700 kg/ha 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 that cycles are not seen for voles that rely on the ground layer, but are seen in hares that rely on the shrub layer.

Populations of small mammals living in forests of Europe and eastern North America with low ground cover do not cycle, but do fluctuate, and these are directly linked to years with superabundant production of tree seeds (Jensen 1982, Pucek et al. 1993, Wolff 1996). However, we found no correlation between spruce seed production and population fluctuations in *Clethrionomys* (figures 10.1, 10.4). 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. Though the northern red-backed vole eats spruce seeds, these apparently are an incomplete diet, and voles will lose weight if forced to only eat spruce seeds, but not if a supplement of lichens is also available (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 food supply permit good population growth in summer, it must also permit good survival overwinter and good survival into the next breeding season. Both we and Gilbert and Krebs (1991) found that the size of the vole population in the spring was a good predictor of the size of the autumn population. Gilbert and Krebs (1991) thus 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 and Krebs 1981), typical summer food levels must constrain population growth (especially through survival of juveniles). In addition, Gilbert and 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 and Boutin (1995) tested this idea by adding food during the autumn and winter and observed 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.

The mushroom crop (both epigeous and hypogeous fungi) may be a critical component of the diet, but mushrooms are available only in summer and early autumn and do not carry through to the next year. The size of the mushroom crop depends on the amount of summer rain (Dyke 1971). *Clethrionomys* spp. readily eat mushrooms, and they may be a major summer and early autumn dietary item. Variation in this resource could be expected to affect summer vole populations. However, 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 and Merritt (1978) found a similar pattern in *C. gapperi* in Colorado.

Another potentially critical food item is seed produced by dwarf shrubs and herbs, some of which overwinter (*Arctostaphylos uva-ursi*, *Vaccinium* spp., *Rosa* spp., *Juniperus* spp.). 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). What needs to be understood are the factors that cause variation in the size of this crop and the crop's role in supporting overwinter survival of *Clethrionomys*.

Role of Stochastic Events Stochastic events, primarily variation in weather from one year to the next, may affect small mammal populations. In general, variation in winter weather does not explain variation in densities. Fuller (1977, 1985) postulated that more severe winters, particularly those with unfavorable autumns before stabilization of snow cover and those with unfavorable springs with delayed snow melt and accumulation of melt water, should cause poor survival and depress *Clethrionomys* populations. However, he rejected this hypothesis and concluded 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. 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. The early spring and rapid melt would cause remaining berries to disappear due to foraging birds and insects and decomposition.

The result would be vole populations that would decline rapidly in spring. A late spring snow melt 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 that year, approximately twice as much snow fell in April and May as normal, and snowmelt was delayed almost 3 weeks (until the end of May) (Hubbs and Boonstra 1997). These conditions were detrimental for arctic ground squirrel populations, which declined markedly that spring. In contrast, 1992 stood out as one of the best years of our study for *Clethrionomys*: populations reached their highest spring densities (figure 10.1), females were their heaviest (figure 10.4), and the population had a high growth rate that summer (figure 10.3). Dyke (1971) experienced a similar set of environmental conditions, but interestingly, it only benefitted *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.

Does the size of the berry crop vary from year to year, and, if so, what is the cause? Virtually no effort has been made to measure the size of the berry crop over a long time and correlate it with environmental variables. Dyke (1971) found extreme variation from one year to the next in overwintering berry crops in the Northwest Territories. *Arctostaphylos uva-ursi* varied from 72.4 berries/m² in 1966 to 0.6 in 1967 and to 0.5 in 1968 in jackpine–juniper stands; *Vaccinium vitis-idea* at the same time varied from 13.3 berries/m², 1.4, and 5.6, respectively, in jackpine–juniper stands and 51.4 berries/m², 5.9, and 0.6, respectively, in black spruce. High seed production in the autumn of 1966 was associated with high *C. rutilus* density throughout the next summer (1967); conversely, low seed abundance in 1967 was associated with low density in 1968. Dyke attributed this variation to an early, warm growing season in 1965 and 1966 and a delayed, cool, and wet season in 1967 and 1968. West (1982) found modest variation in the berry crop over 3 years in Fairbanks (29.0–63.7 berries/m²), but this variation had no effect on vole density the next year.

Kalela (1962) proposed that microtine density fluctuations were coupled to variation in plant production caused by variation in weather. Tast and Kalela (1971) fine-tuned this hypothesis, proposing that favorable climatic conditions in northern latitudes, particularly warm temperatures, over several years were needed to create a synchronous pulse of seed and vegetative production, after which plants had low production as they rebuilt their energy levels. Microtine populations were proposed to track these years of good and bad production, resulting in cycles. However, tests of this hypothesis have been equivocal or contradictory (Laine and Henttonen 1983, Järvinen 1987, Oksanen and Ericson 1987), and the evidence argues in favor of microtine grazing being the cause, not the consequence, of the variation in vegetation performance.

We attempted to relate vole density in spring to a variety of environmental variables in the growing seasons 1 and 2 years before (i.e., average temperatures and precipitation in each of the months May to August and summed combinations of these). Only one variable was significant: the precipitation in July in one year was positively correlated to spring vole densities the next ($r^2 = .28$, $N = 20$, $p = .02$). Thus, in our area, which is a relatively dry boreal forest site (see chapter 2), moisture during the height of the growing season, not temperature, may partly limit productivity. Given suitable conditions several years in a row, productivity could remain high (e.g., 1992–1994) and result in an extended period of high numbers. However, much of the variation remains unexplained, and below

we propose a hypothesis that includes a critical variable, nutrients, not included in the various weather hypotheses.

Role of Nutrients We propose that the above evidence is consistent with the following hypothesis: population peaks in *Clethrionomys* follow population peaks in hares by 2–3 years. 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. Though the nutrients are released primarily in the summer after their winter production (D. S. Hik personal communication), lags are introduced into this system because it takes 2 years to produce a good berry crop. This delay is due to the development of flower primordia in the first summer and then berries in the next summer. The high berry production stimulates population growth of voles in the third year. Stochasticity in weather can affect the exact timing of the seed crop (e.g., severe late frosts in spring may kill the flowers, or drought in summer may prevent adequate seed maturation). 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 pellets as stimulators of plant growth through mineral recycling and herbivore population responses have also been postulated for lemmings in the arctic tundra by Pieper (1964) and by Schultz (1969). Outbreaks of forest lepidoptera in northern ecosystems result in large-scale defoliation, which then inject 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 cause 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 it appears to depend on the amount of fertilizer used. In Fennoscandia (reviewed in Raatikainen and 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. In the arctic tundra, growth of evergreen dwarf shrubs is significantly stimulated by low levels of fertilization (Chapin and Shaver 1985, Henry et al. 1986), but higher levels lead to mortality. At the levels of fertilization used in our long-term experiments at Kluane (John and Turkington 1995, Turkington et al. 1998), declines occurred in dwarf shrubs. The decline in *Clethrionomys* populations (figure 10.2) on the fertilizer 1 grid 2 years after fertilizer addition started is consistent with this interpretation.

Are the amounts of nutrients released from hare pellets significant to stimulate plant growth? From a study to predict snowshoe hare densities based on hare pellet counts (Krebs et al. 1987), we were able to estimate how many pellets were produced at peak densities. In the autumn of 1980, we estimate that peak hare densities of 3.4/ha produced 71.2 pellets/m² and in the autumn of 1989, peak hare densities of 2.34/ha produced 46.0 pellets/m². Low levels of nutrients likely to come from these large numbers of decaying pellets may be sufficient to stimulate berry and seed production. Shrub biomass reaches its highest level at the peak (1990) and in the next 2 years (figures 6.2, 6.5), particularly

in willow, but possibly also in birch (see Turkington et al. 1998). In addition, high levels of browsing by hares on birch and willow in peak years may make them less competitive relative to the dwarf shrubs and may increase the amount of illumination reaching the dwarf shrubs. Dwarf shrubs may then be able to sequester larger amounts of nutrients than they would when the taller shrubs are growing vigorously. In addition, we know from our fertilizer experiment that plants immediately incorporate the nutrients when they are added artificially. Our evidence indicates that the shrub growth is responding dramatically at and just after the peak, and this is consistent with the argument that there has been a stimulation of growth resulting from release of nutrients from hare pellets.

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 *Clethrionomys* densities 2 years later. Figure 10.6 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. The mortality rate was much higher in the hare peak of 1981 (100% and 57%, respectively, of twigs of the two shrub species that were clipped 0–100 cm above the ground; Smith et al. 1988) than in the hare peak of 1990 (71–90% and 8–16%). Figure 10.6 indicates that vole densities were up to two times higher in 1984 than in 1992. Interestingly, figure 10.6 also indicates that hare densities were about three times higher in 1971 (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 given higher productivity in Alaska (chapter 2), this correlation must be treated with caution. An alternative approach would be to examine the size of the vole peaks within treatments that increased hare densities (through food addition, exclusion of predators, or both). We predict that this should result in high production of hare pellets, the subsequent release of a large amount of fertilizer, and the production of a large berry crop. However, all of these treatments were confounded by increased summer foraging on herbs and dwarf shrubs due to high hare and ground squirrel densities (chapters 8 and 9), and we saw no effect on vole densities.

If a hare peak is followed by a *Clethrionomys* 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 *Clethrionomys* peak within the enclosure. It did not (figure 10.2). 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 was too small. 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, though the nature of the hare cycle is unknown for these areas. Fuller (1977, 1985) trapped voles in the southwestern Northwest Territories from 1961 to 1979 and found peaks in *C. gapperi* in 1961–1962, 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 and Feist (1984) summarized

C. rutilus data from 1970 to 1981 (the data after 1972 were collected intermittently and were missing for 1977–1978) 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 lower, it may be more sensitive to fluctuations in nutrients than other sites.

We propose that for the boreal forest in the Kluane area, the primary 10-year cycle in snowshoe hares results in a secondary cycle in northern red-backed voles (cf. Angelstam et al. 1985). This occurs through a fertilization effect on the plants eaten by voles as a consequence of the production and decay of large quantities of hare pellets produced during the hare peak. Other vole peaks can occur independent of the hare cycle, but we suggest that these are more related to stochastic weather events which cause variation in size of the berry crop of the dwarf shrubs and mushroom production.

10.5.2 *Microtus Species*

All our major experiments, except for fertilization, had no effect on *Microtus* populations, and this is understandable given that these voles primarily eat grass and our experiments were directed at boreal forest sites. On the forest grids, *Microtus* populations reached higher numbers (mean of about 2/ha) twice, both after *Clethrionomys* peaks (figure 10.1). We do not know why this occurred. From the standpoint of the dynamics of the vertebrate predators in the boreal forest, populations of *Microtus* in meadows, marshes, forest clearings, and stream margins may be particularly significant, especially during decline and low phases of the hare cycle. Diet information (see chapters 13–18) indicates that all predators consume *Microtus*, and some (especially coyotes) appear to preferentially hunt for them during hare declines. *Microtus* voles even feature prominently in the diet of great horned owls and boreal owls, both species that are regarded as typical forest predators (chapter 16). Thus, the importance of *Microtus* to sustaining the predators in the boreal forest ecosystem during hare declines and lows may not be proportional to their numerical abundance.

Fertilization stimulated grass growth (Nams et al. 1993, John and Turkington 1995, Turkington et al. 1998) and *Microtus* populations in meadows responded with a modest population increase (44%; figure 10.5). Passerine birds also showed a modest increase (46%) in response to fertilization (Folkard and Smith 1995; see chapter 12). Our results argue that growth of vegetation in these meadows is also severely constrained by low nutrient abundance characteristic of the boreal forest. It is possible that predators cued into these hot spots of higher vole density, and, if we had been able to remove predators, the differences would have been even more marked than we observed. In summary, only two groups of vertebrates responded to fertilization of this nutrient limited ecosystem: the microtine herbivores and the passerine insectivores.

10.6 Summary

There are some unanswered questions that remain. How does the size of the principal foods of the northern red-backed vole, particularly the berry crop, vary over time, and what are the causes for this? Does nutrient release following snowshoe hare peaks play any role in this variation? As all predators heavily eat *Microtus* voles, what is the role of predation in limiting the population size of this group?

We propose that the key variable limiting northern red-backed vole populations in the boreal forest of North America is overwintering survival and that this is a function of overwintering food, not predation. Evidence from other research indicates that the key food necessary for good overwintering survival is overwintering berries from dwarf shrubs, not white spruce seeds, and that this may vary as a function of weather. We propose that production of overwintering berry crop is usually low because primary productivity in the shrub layer in North American boreal forests is concentrated in the tall shrubs, not in the dwarf shrubs, as it is in Fennoscandia. Because of this, vole densities are usually low (1–3/ha), though occasionally they increase dramatically. Most of the major factors we manipulated with our large-scale treatments (large mammalian predators, snowshoe hares, and food in the form of rabbit chow) did not affect northern red-backed voles. Large-scale fertilization had a slight negative effect on these vole populations, probably acting through a reduction in dwarf shrubs (and hence the food produced by them) caused by competition from grasses that were stimulated by fertilizer. Specialist weasel predators are irrelevant as limiting factors most of the time because vole densities usually do not reach densities high enough to sustain weasel populations, and the other boreal forest predators do not focus on these voles. However, if the red-backed vole population were to increase over a series of years, this may permit weasel populations to increase and then depress these voles in the winter. Our long-term trapping data, in which red-backed vole peaks always follow hare peaks by 2–3 years, suggest that periodic fertilization pulses produced by large quantities of hare pellets at hare peaks stimulates dwarf shrub berry crops and produces high overwintering survival and good summer reproduction of voles.

We propose that one of the key factors limiting *Microtus* populations in the meadows of the boreal forest is the low productivity of the grasslands. Both grassland productivity and *Microtus* population density can be increased by fertilization. Predation by both specialist and nonspecialist predators following the hare decline may also periodically depress *Microtus* in meadows. The impact of weasels on these voles is uncertain because the patchiness of meadows within the forest and their small size could make it difficult for weasels to use *Microtus* efficiently.

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