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Vole-feeding damage and forest plantation protection: Large-scale application of diversionary food to reduce damage to newly planted trees

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Abstract

Forest and agricultural crops periodically experience feeding damage from herbivorous rodents such as voles of the genera *Microtus* and *Clethrionomys*. This problem has a long history, which needs a management solution that is both economically and ecologically viable. This study tested the hypothesis that large-scale (6–16 ha) application of diversionary food would reduce vole-feeding damage to newly planted trees. Four overwinter Experiments (A, B, C, and D) were conducted with long-tailed vole (*Microtus longicaudus*) populations in new forest plantations of lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), and interior spruce (*Picea glauca* × *Picea engelmannii*) near Golden, British Columbia, Canada, from 2003 to 2007. Diversionary food "pucks" were composed of Douglas-fir bark mulch and alfalfa (*Medicago sylvatica*) pellets/meal mixed with canola (*Brassica rapa*) oil and wax. Mean percentage ($\pm$SE) survival of trees was similar ($P = 0.18$) between control (72.6 ± 11.8) and food (86.2 ± 8.7) sites in Experiment A. Experiment B had intensive feeding by voles and near exhaustion of the food supply in three of five replicates, with no statistical difference ($P = 0.11$) between control and treatment sites. This pattern continued in Experiment C with total tree survival appearing highest ($P = 0.06$) in the intermediate puck density. Mean ($\pm$SE) percentage survival of total trees was significantly ($P = 0.05$) higher in food (85.0 ± 6.3) than control (62.5 ± 14.3) sites in Experiment D. Despite these variable results, in those experimental units with substantial feeding pressure by voles and a sufficient overwinter supply of diversionary food, tree survival was 20–25% higher in food than control sites. If food can help maintain sufficient trees on a site and it is required for only one or two winters, diversionary feeding may be an economical and ecological solution to this significant reforestation problem.

Keywords: Alfalfa; Coniferous tree seedlings; Diversionary food; Feeding damage; Food pucks; Forest plantations; *Microtus* spp.; Populations; Voles

1. Introduction

Voles of the genera *Microtus* and *Clethrionomys* are considered to be major mammalian pests in coniferous and deciduous tree plantations in North America and Eurasia (Myllymäki, 1977; Byers, 1984; Hansson, 1985; Shu, 1985; Sullivan et al., 1990). The diet of voles consists primarily of grasses, sedges, forbs, and sometimes seeds. However, these rodents will feed on tree seedlings and saplings, particularly during winter months of peak years in abundance. Some species of voles tend to have cyclic population fluctuations in northern latitudes with a peak in abundance every 3–5 years (Krebs and Myers, 1974; Korpimäki and Krebs, 1996; Boonstra et al., 1998). These cyclic periods may occasionally be interspersed with annual fluctuations in abundance (Taitt and Krebs, 1985).

Voles may feed on bark, vascular tissues (cambium and phloem tissues), and roots of trees, depending on their food limitations during winter. Girdling and clipping of tree stems is the main cause of direct mortality from vole feeding. Reduced growth of surviving trees results from sub-lethal feeding injuries (Sullivan et al., 1990). Planted trees, with their nursery fertilization regime and enhanced

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palatability and nutrition, are nearly always preferred by voles over wildlings arising from natural regeneration (Sullivan and Martin, 1991). Feeding damage may limit regeneration of appropriate tree species in certain forest ecosystems, and hence may impact conservation of natural forests. In addition, this damage increases the cost to reforest these stands in time for "free growing status", decreases net productive forested area, and results in loss of mean annual growth increment. Feeding damage appears to be associated with high populations of voles in early successional habitats that develop after harvesting by clearcutting (Hansson, 1989; Sullivan and Sullivan, 2001). Old fields (abandoned farmland) that are being afforested are also prime habitats for voles and subsequent damage to planted trees (Radvanyi, 1980; Bergeron and Jodoin, 1989; Ostfeld and Canham, 1993; Ostfeld et al., 1997).

There are three species of *Microtus*: the long-tailed vole (*M. longicaudus*), the meadow vole (*M. pennsylvanicus*), and the montane vole (*M. montanus*) that are implicated as major consumers of tree seedlings in western North America. A fourth species, the heather vole (*Phenacomys intermedius*), is also present in these small mammal communities but occurs at low abundance (<5 animals/ha). In addition, populations of the southern red-backed vole (*Clethrionomys gapperi*) occur primarily in mature stands of timber but may spill over into recently cut areas for 1–2 years after harvest (Merritt, 1981; Kirkland, 1990).

This damage problem has a long history which begs the question: is there a management solution, near at hand, that is both economically and ecologically viable? Considering the several species of pest voles and other rodent members of most coniferous forest ecosystems, a method that is least disruptive to these animal communities is highly desired (Conover, 2002). Application of diversionary food is an alternative management practice that has shown promise in alleviating damage to forest and agricultural crops by montane and long-tailed voles without the detrimental direct and indirect (non-target) side effects of rodenticides that are used to reduce the target pest population (Sullivan and Sullivan, 1988; Sullivan et al., 2001). A similar response was reported for protection of Scotch pine (*Pinus sylvestris*) trees from feeding by red-backed voles (*Clethrionomys rufocanus*) by use of diversionary food in northeast China (Sullivan et al., 1991). These three studies provided an artificial diversionary food that was presumably more palatable than tree bark and vascular tissues, but of low nutrient content to avoid population increases of voles. Diversionary food ("logs" or "pucks") composed of wax and sunflower oil mixed with bark mulch or alfalfa pellets reduced damage to lodgepole pine (*Pinus contorta*) trees by voles, but not to a statistically significant level (Sullivan et al., 2001). A granivorous diversionary food composed of sunflower seed, designed to attract seed-eating deer mice (*Peromyscus maniculatus*) and western harvest mice (*Reithrodontomys megalotis*), was not effective in reducing vole damage to tree seedlings (Sullivan and Sullivan, 2004). Vole populations did not increase in response to these food additions in either study (Sullivan et al., 2001; Sullivan and Sullivan, 2004).

In these experiments with diversionary foods, and many other ecological field studies (Hurlbert, 1984), the scale of application or treatment unit has been quite small (usually $\leqslant 1$ ha). Operational-scale ("real-world") results may be different from those recorded in small-scale experiments (Walters and Holling, 1990). In particular, small-scale provision of food, whether in supplemental or diversionary food studies, may result in "aggregation responses" by target animals, thereby distorting the actual population parameters of interest (Boutin, 1990). Thus, this study was designed to (1) test the hypothesis that large-scale (6–16 ha treatment units) application of diversionary food to new forest plantations would reduce overwinter-feeding damage by voles and (2) determine the optimum density of diversionary food "pucks" to be distributed in plantations.

2. Materials and methods

2.1. Study areas

Four experiments were conducted in consecutive winters: A (2003–2004), B (2004–2005), C (2005–2006), and D (2006–2007); and located in several study areas at Glenogle Creek and Roth Creek, 25 km east of Golden, British Columbia (BC), Canada (51°18′N; 116°45′W). These areas were within the Interior Douglas-fir (IDF_{dm}), Montane Spruce (MS_{dk}), and Interior Cedar-Hemlock (ICH_{mk}) biogeoclimatic zones (Meidinger and Pojar, 1991). Topography ranged from hilly to very steep terrain at 1125–1540 m elevation.

The upper IDF and MS have a cool, continental climate with cold winters and moderately short, warm summers. The average temperature is below 0 °C for 2–5 months, and above 10 °C for 2–5 months, with mean annual precipitation ranging from 30 to 90 cm. Open to closed mature forests of Douglas-fir (*Pseudotsuga menziesii*) cover much of the IDF zone, with even-aged post-fire lodgepole pine stands at higher elevations. The MS landscape has extensive young and maturing seral stages of lodgepole pine, which have regenerated after wildfire. Hybrid interior spruce (*Picea glauca* × *Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are the dominant shade-tolerant climax trees. Douglas-fir is an important seral species in zonal ecosystems and is a climax species on warm south-facing slopes in the driest ecosystems. Trembling aspen (*Populus tremuloides*) is a common seral species and black cottonwood (*Populus trichocarpa*) occurs on some moist sites (Meidinger and Pojar, 1991).

The ICH has an interior, continental climate with cool wet winters and warm dry summers. Mean annual temperature ranges from 2 to 8.7 °C. The temperature averages below 0 °C for 2–5 months, and above 10 °C for 3–5 months of the year. Mean annual precipitation is 500–1200 mm, 25–50% of which falls as snow. Upland coniferous forests dominate the ICH landscape and comprise the highest diversity of tree species of any zone in BC. Western red cedar and western hemlock dominate mature climax forests, with white spruce, Engelmann spruce, their hybrids, and subalpine fir common in these stands (Meidinger and Pojar, 1991).

Candidate sites were chosen from clearcut units, with some retention of residual Douglas-fir in patches and reserves, that were harvested from 2001 to 2005. Much of the cut was salvage harvesting of lodgepole pine from stands of mountain pine beetle (*Dendroctonus ponderosae*)-killed trees. Prior to harvesting, all stands were composed of a mixture of lodgepole pine with variable amounts of Douglas-fir, western red cedar, spruce, and subalpine fir. Average ages of lodgepole pine ranged from 80 to 120 years and for Douglas-fir ranged from 120 to 220 years. Average tree heights ranged from 10.5 to 19.5 m for lodgepole pine and from 16.7 to 27.5 m for Douglas-fir.

2.2. Experimental design

A "site" represented an experimental unit. Each of the four experiments had a randomized block design with paired control and treatment (food) sites. Replicate sites were selected on the basis of operational scale, reasonable proximity to one another and grouping into respective blocks based on location, and availability of sites that were 1–3 years post-harvest with substantial vole populations (e.g., >30 voles/ha). Treatments were assigned randomly to sites within blocks, and sites were spatially segregated to enhance statistical independence (Hurlbert, 1984). The clearcuts, with their respective plantation sites, were the size of typical forestry operations (Table 1).

2.3. Diversionary food treatments

Diversionary food "mouse pucks" for Experiments A, B, C, and D were prepared during the period May–September of 2003, 2004, 2005, and 2006, respectively, at the Applied Mammal Research Institute manufacturing facility. Diversionary food was prepared in the form of "pucks" composed of alfalfa (*Medicago sylvatica*) pellets (15% protein, 27% fiber, and 10% moisture), fine-grain Douglas-fir bark mulch mixed with wax and canola (rapeseed (*Brassica rapa*)) oil. The melted mixture was poured into 50-ml urethane molds and allowed to harden on cooling. After the wax/oil mix had solidified, "pucks" were placed in waxed 20 kg capacity boxes and transported to the field. Canola oil was used to enhance the attractiveness of the food to voles (Sullivan et al., 2001). The alfalfa pellets/meal acted as a source of protein and fibre, while the bark mulch simulated the bark and tissues of plantation trees. The wax acted as a cohesive, water-proofing matrix.

Diversionary food treatments were established in October each year on those selected sites with substantial vole populations. Diversionary food "mouse pucks" were applied manually to new plantations at a given density per hectare (Table 1). The locations of 100 sample pucks per site were marked by staked flags to determine overwinter consumption by voles on each site. Puck consumption was estimated in 25% increment classes (1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–99%, 5 = 100%) and tallied for all pucks in a given treatment.

Trees were planted at a consistent density (~1400/ha) among replicates and their locations were marked by species-specific colored flags to sample for evidence of

Table 1
Description of treatments, results of ANOVA, and mean (±SE) percentage survival of total trees in control and treatment sites for Experiments A, B, C, and D

Exp	Rep	Size of units (ha)		Tree species		Diversionary food		% Survival of total trees		Analysis	
		Control	Treatment	Control	Treatment	Density/ha	kg/ha	Control	Treatment		
A	1	6.0	7.0	Pl	Pl	1200	80	72.6±11.8	86.2±8.7	$F_{1,3}$	P
	2	9.5	9.5	Pl	Pl	1200	80			3.02	0.18
	3	8.0	8.0	Pl	Pl	1200	80				
	4	7.0	7.0	Pl	Pl	1200	80				
B	1	8.0	8.0	Pl	Pl	1750	100	38.2±7.1	50.1±8.4	$F_{1,4}$	P
	2	8.0	8.0	Pl	Pl	1750	100			4.11	0.11
	3	8.0	8.0	Pl	Pl	1750	100				
	4	8.0	8.0	Pl	Pl	1750	100				
	5	8.0	8.0	Pl	Pl	1750	100				
C	1	15.0	15.0	Df	Df, Sp	1050, 1750, 2800	60, 100, 160	63.0±7.9	71.9±3.6	$F_{1,2}$	P
	2	15.0	15.0	Pl, Df, Sp	Pl, Df, Sp	1050, 1750, 2800	60, 100, 160			1.22	0.39
	3	15.0	15.0	Pl, Df, Sp	Pl, Sp	1050, 1750, 2800	60, 100, 160				
D	1	16.0	16.0	Pl, Df, Sp	Df, Sp	1750	100	62.5±14.3	85.0±6.3	$F_{1,2}$	P
	2	16.0	16.0	Pl, Df, Sp	Pl, Df, Sp	1750	100			18.67	0.05
	3	16.0	16.0	Pl, Df, Sp	Pl, Df, Sp	1750	100				

Exp = experiment; Rep = replicate; Pl = lodgepole pine; Df = Douglas-fir; Sp = Spruce.

feeding damage during the overwinter period. One hundred sample seedlings (lodgepole pine, Douglas-fir, or interior spruce) were chosen randomly on each site. Clipping of terminal and lateral shoots, as well as gnawing on stems, was recorded for each sample seedling in the spring (May) of each year. Removal of the terminal shoot was considered as mortality unless another vigorous lateral shoot was available to replace it. Girdling and removal of $\geqslant 50\%$ of stem bark and vascular tissues was also considered as seedling mortality. Lodgepole pine followed by Douglas-fir are the most susceptible coniferous tree species to feeding damage by *Microtus* spp. in the interior of BC (Sullivan et al., 1990). All seedlings on control and food sites were newly planted in the spring, prior to each of Experiments A, B, and C. Seedlings in Experiment D had been planted the previous year, and hence were a year older, and at densities of 900–1000/ha.

2.4. *Sequence of experiments*

Experiments A and B were designed to test diversionary food as a means to reduce feeding damage by voles over relatively larger (6–16 ha) plantation units than previously tested ($\leqslant 1$ ha). Details of site areas are listed in Table 1. Two replicates in Experiment A had relatively little feeding ($\leqslant 20\%$ mortality) to trees by voles. Therefore, this treatment was repeated in Experiment B at a higher density of both pucks (1750/ha) and voles than in Experiment A.

Experiment C was designed to determine the optimum density of pucks to be used to protect tree seedlings. Thus, three densities of pucks per ha: 1050, 1750, and 2800 were each tested in 5 ha sub-units within each 15 ha food-treatment site. Experiment D used a slightly revised formulation of diversionary food: alfalfa meal (ground-up pellets) was used instead of pellets. This reformulation yielded a more homogeneous puck that did not break apart under wet conditions in the field. The amounts of alfalfa in this new formulation, as well as the protein and fibre content, were identical to those of the pellet formulation.

2.5. *Vole populations*

To provide a general indication of vole abundance across our experimental sites, we sampled rodent populations on three replicate sites starting immediately after clearcut harvesting (winter 2003–2004) and continuing through 2006. Populations of long-tailed voles were sampled on 1.0-ha checkerboard grids with Longworth live-traps on three newly clearcut sites. Meadow voles, southern red-backed voles, and heather voles were also present but at low numbers. Trap stations were located every 14.3 m with one live-trap per station in a 7×7 configuration. These grids were live-trapped at 4-week intervals from May to October 2004, 2005, and 2006. Snow conditions limited access to grids during overwinter periods.

On all grids, traps were baited with whole oats and carrot; coarse brown cotton was supplied as bedding. Traps were set on day 1, checked on the morning and afternoon of day 2 and morning of day 3, and then locked open between trapping periods. All animals captured were ear-tagged with serially numbered tags, breeding condition noted, weighed on Pesola spring balances, and the point of capture was recorded (Krebs et al., 1969). Population densities were estimated by the Jolly–Seber stochastic model (Seber, 1982) for reasons indicated by Jolly and Dickson (1983). A minimum number of animals known to be alive (Krebs, 1966) value was substituted for the first and last sample weeks when the Jolly–Seber estimate could not be calculated.

2.6. *Statistical analysis*

A randomized block analysis of variance (ANOVA) Model III, with factor site treatment as a fixed effect and factor block as a random effect, was used to test for differences in percentage of trees surviving vole damage between control and diversionary food treatments in all four overwinter Experiments: A, B, C, and D. This same analysis was also used in Experiment C to compare overall tree survival. Additional analyses in this experiment had factors tree species and puck density as fixed effects. Similarly, in Experiment D, tree species was a fixed effect.

An overall comparison of tree survival between control and diversionary food sites, during the four winters, used this same ANOVA design with 15 replicates. Mean summer (May–October) abundance of long-tailed voles $\pm 95\%$ confidence intervals (CIs) was calculated for the three sample grids for each of the three post-harvest years 2004–2006. Proportional data were arcsine-transformed prior to analysis (Zar, 1999). Duncan's multiple range test (DMRT) was used to compare mean values. In all analyses, the level of significance was at least $P = 0.05$.

3. Results

3.1. *Vole populations and tree plantations*

The major rodent species inhabiting our study areas was the long-tailed vole. Populations of this microtine colonized newly clearcut sites and increased in mean summer abundance/ha from 3.5 in 2004 to 15.3 in 2005 to 33.0 in 2006 (Fig. 1), during the 3 years post-harvest. Mean ($n = 3$) densities per ha of long-tailed voles in October, prior to the overwinter experiments, were 8.6 (2004), 27.1 (2005), and 45.7 (2006). Thus, in general, our study areas had reasonably high numbers of voles to provide feeding pressure on experimental sites during the four overwinter experiments.

3.2. *Experiments A and B*

In three of four locations (replicates 1, 2, and 4), with substantial feeding damage by voles, the presence of diversionary food reduced damage to trees in Experiment A (Fig. 2). However, the overall effect of food on mean (±SE) survival of trees was statistically similar ($F_{1,3} = 3.02$; $P = 0.18$) between control (72.6±11.8) and food (86.2±8.7) sites (Table 1). Since replicate 3 had negligible feeding damage to trees by voles, an analysis of just three replicates also was not statistically significant ($F_{1,2} = 9.52$; $P = 0.09$), but may have been biologically and economically meaningful.

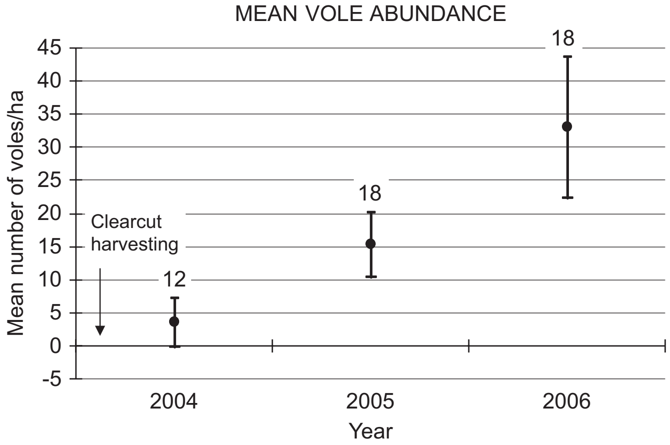

Fig. 1. Mean (±95% CI) summer abundance per hectare of the long-tailed vole in the first 3 years post-harvest (2004–2006). Sample size (3 grids × number of trapping periods) is given above the upper confidence interval for each year.

In Experiment B, seedlings appeared to survive better with food than without, but only in those cases where the food was not exhausted (Fig. 3). ANOVA results ($n = 5$ replicates) were not formally significant ($F_{1,4} = 4.11$; $P = 0.11$), but there appeared to be biological significance, particularly if we examine the effect of (a) the potential impact of the food supply being exhausted (note replicates 1 and 4 in Fig. 3) and (b) the relationship of successional age to number of voles (note replicate 5 in Fig. 3). Factor (a) helped direct the design of Experiment C, which evaluated different densities of mouse pucks (including both lower and higher amounts of diversionary food). Mean (±SE) percentage survival of trees in Experiment B was 38.1±7.1 on control sites and 50.1±8.4 on treatment sites (Table 1).

3.3. *Experiment C*

In Experiment C, there was no statistical difference ($F_{1,2} = 1.22$; $P = 0.39$) between control and food sites in survival of total trees (lodgepole pine, Douglas-fir, and spruce species) (Table 1) nor ($P > 0.05$) for any of the individual species. However, mean survival of Douglas-fir in two food sites, where this species was planted, was 59.8% (59.5% and 60.0%) compared with a mean value of 30.3% (18.7%, 61.1%, and 11.1%) in the three control sites. Mean survival of lodgepole pine + Douglas-fir combined and spruce were similar in control and food sites (Fig. 4), but it was unclear as to why so few pine seedlings were eaten by voles during this winter. Some of this

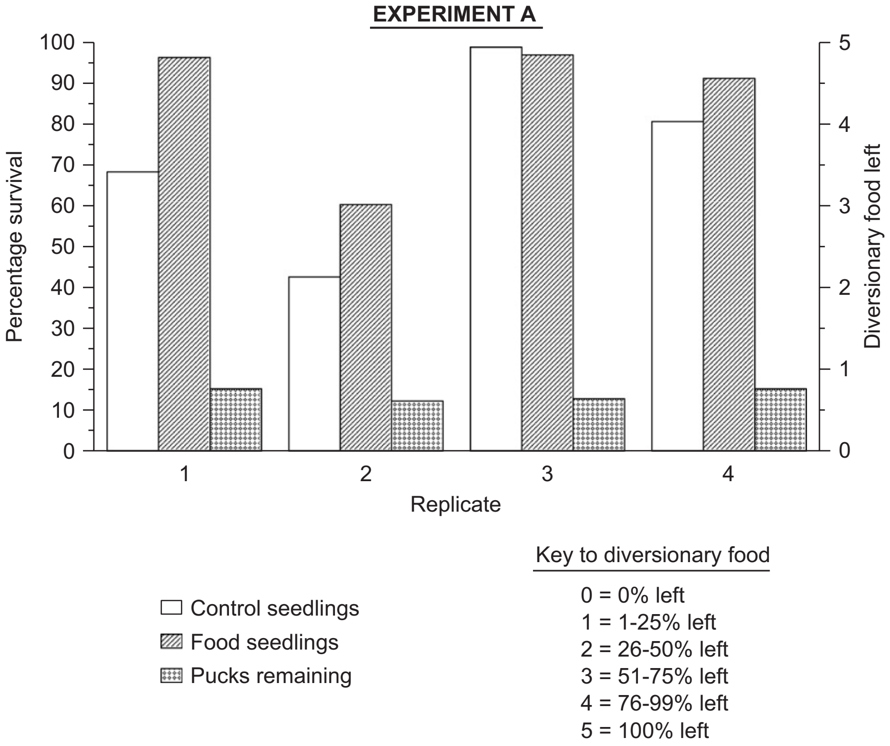

Fig. 2. Mean percentage survival of lodgepole pine seedlings for the four replicates of control (no food) and treatment (diversionary food) sites in Experiment A, 2003–2004 winter period. Amount of diversionary food pucks remaining is given per 25% increment classes.

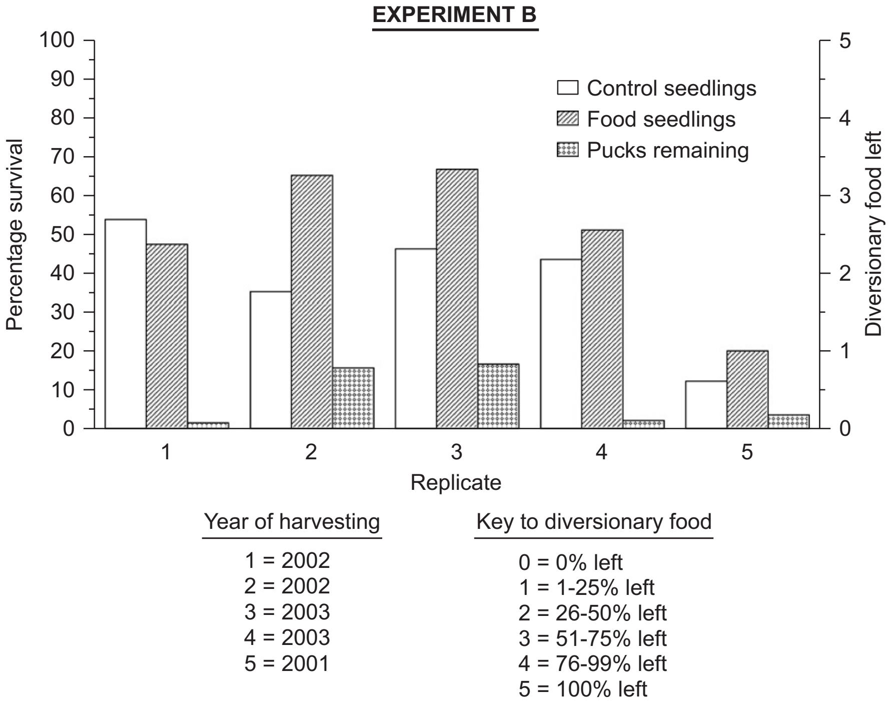

Fig. 3. Mean percentage survival of lodgepole pine seedlings for the five replicates of control (no food) and treatment (diversionary food) sites in Experiment B, 2004–2005 winter period. Amount of diversionary food pucks remaining is given per 25% increment classes.

variability in feeding damage may have been related to tree species preferences by voles, as well as the relative densities of pucks on each food site. Pine and fir seedlings were combined in this analysis because several sites had only two of the three species planted, as required by ecological conditions.

The major objective of Experiment C was to compare the three densities of pucks to determine an optimum application rate for this diversionary food treatment. Tree survival for both pine/fir and spruce appeared to be highest in the intermediate density of 1750 pucks/ha (Fig. 5). Statistical analysis of this trend did not show a significant difference among puck densities for either the pine/fir ($F_{2,4} = 4.42$; $P = 0.10$) or spruce ($F_{2,4} = 4.17$; $P = 0.11$) species. However, this comparison approached significance ($F_{2,4} = 5.95$; $P = 0.06$) for total trees. Thus, voles tended to eat more trees at the lower (1050 pucks/ha) and upper (2800 pucks/ha) densities of food than at the intermediate amount (Fig. 5). In terms of food remaining at the completion of Experiment C in May 2006, there was a significant ($F_{2,4} = 6.58$; $P = 0.05$) difference among puck densities, with more (DMRT; $P = 0.05$) food left on the high- than low-density treatment (Fig. 5).

3.4. Experiment D

Experiment D incorporated a revised formulation with the diversionary food having alfalfa meal rather than pellets. Mean (±SE) percentage survival of total trees was significantly ($F_{1,2} = 18.67$; $P = 0.05$) higher in the food (85.0±6.3) than control (62.5±14.3) sites (Table 1). Mean survival of the individual tree species followed a similar pattern, with Douglas-fir approaching significance ($F_{1,2} = 12.34$; $P = 0.07$) and spruce trees surviving significantly ($F_{1,2} = 34.45$; $P = 0.03$) better in food than control sites (Fig. 6). Lodgepole pine trees also appeared to survive better in food than control sites in replicates 2 and 3 where comparisons were possible (Fig. 6). Comparable amounts of diversionary food were left at the completion of this experiment in May 2007.

3.5. Overall results

An overall analysis of the four experiments yielded 15 replicates. Mean (±SE) percentage survival of combined lodgepole pine and Douglas-fir was significantly ($F_{1,14} = 9.48$; $P < 0.01$) higher in the food (70.4±5.8) than control (55.6±6.5) sites. This pattern was also recorded for mean (±SE) percentage survival of total trees of all three species: a significant ($F_{1,14} = 17.18$; $P < 0.01$) difference between food (71.0±5.5) and control (57.2±5.9) sites.

4. Discussion

4.1. Diversionary food results

Our study is the first evaluation of large-scale (6–16 ha treatment sites) application of a diversionary food to protect forest plantations from feeding damage by voles. Results in Experiments A, B, and C were not statistically significant when comparing survival of trees between control and food sites. However, results from Experiment

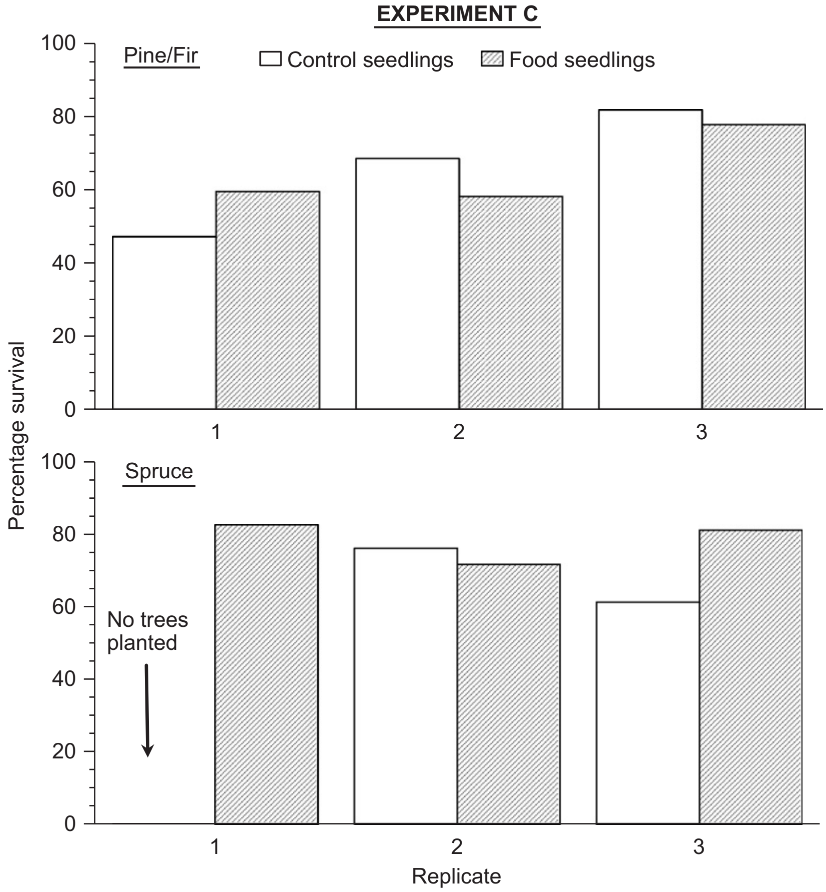

Fig. 4. Mean percentage survival of combined lodgepole pine + Douglas-fir and interior spruce seedlings for the three replicates of control (no food) and treatment (diversionary food) sites in Experiment C, 2005–2006 winter period.

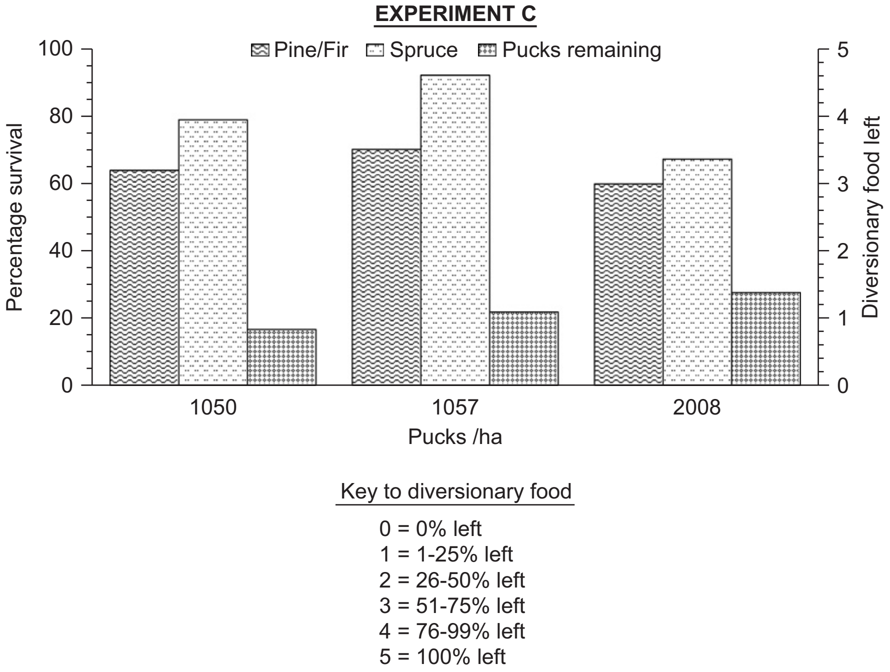

Fig. 5. Mean percentage survival of combined lodgepole pine + Douglas-fir and interior spruce seedlings on sites with the three food puck densities in Experiment C, 2005–2006 winter period. Amount of diversionary food pucks remaining is given per 25% increment classes.

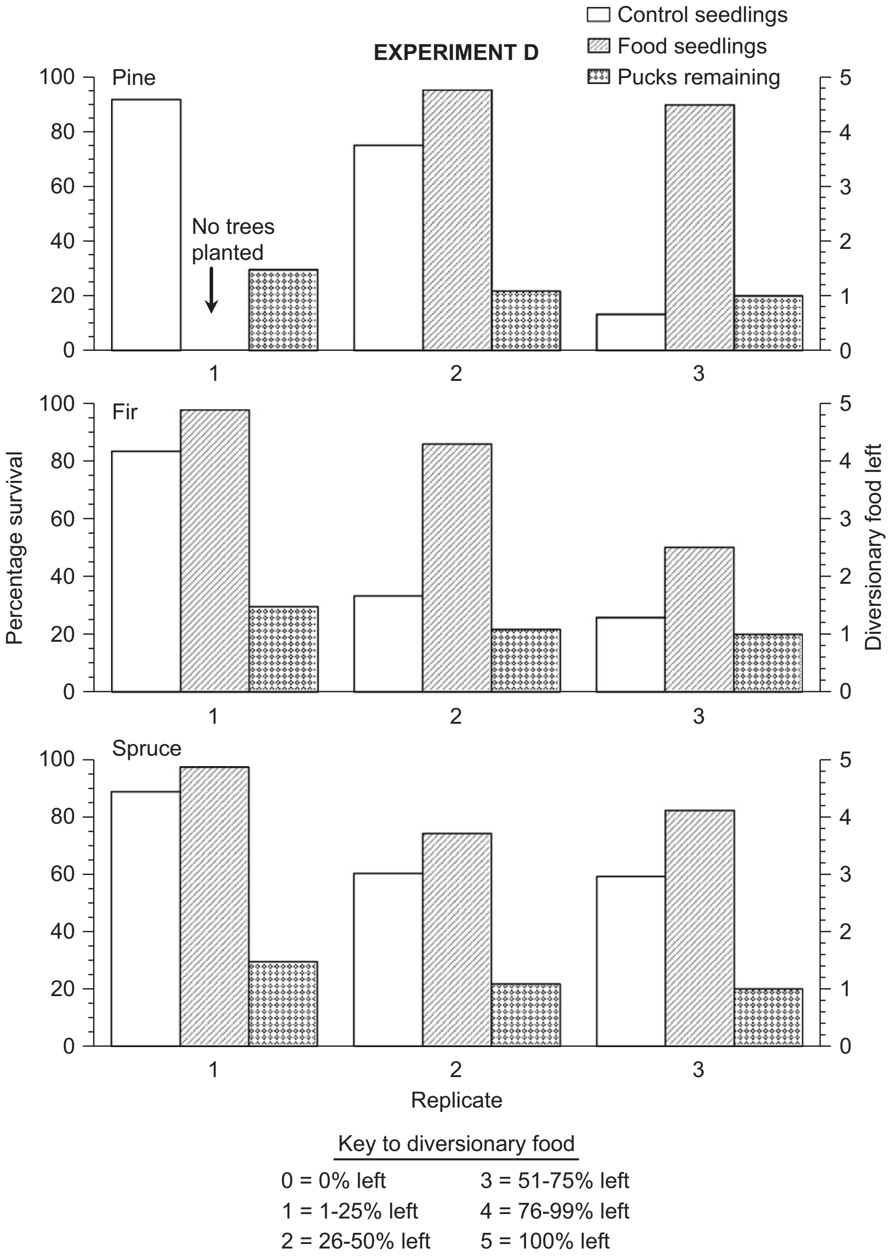

Fig. 6. Mean percentage survival of lodgepole pine, Douglas-fir, and interior spruce seedlings for the three replicates of control (no food) and treatment (diversionary food) sites in Experiment D, 2006–2007 winter period. Amount of diversionary food pucks remaining is given per 25% increment classes.

D, and overall, did show a significant effect of the food pucks in protecting plantation trees. These variable results were similar to those reported by Sullivan et al. (2001) for much smaller ($\leqslant$1.0 ha) treatment units and a similarly formulated diversionary food. Much of this variability seems to relate to a lack of uniformly substantial feeding pressure over all sites by voles. Variability in feeding pressure is usually related to abundance of voles (Sullivan and Sullivan, 2007). Thus, it was possible that a principal predator such as the short-tailed weasel (*Mustela erminea*) may have reduced vole populations and consequent feeding damage to trees, at least on a localized basis. Similarly, variability in snow accumulation among sites, during the respective winters, may have affected vole abundance and activity. However, we do not have data to evaluate either of these potential factors.

Experiment A had two replicates (3 and 4) with little feeding damage (see Fig. 2). Mean survival of control and food seedlings in the two replicates with substantial feeding pressure (1 and 2) was 55.5% and 78.3%, respectively, a 22.8% increase in tree survival with food present. Less than 25% of the diversionary food was left in this experiment. In Experiment B, which had the most feeding pressure by voles of all the experiments, the food pucks were essentially exhausted in three of five replicates. Unfortunately, because of overwinter snow cover, we do not know when the pucks were exhausted nor the chronology of tree consumption by voles. In those replicates with food remaining (2 and 3) (see Fig. 3), mean survival of control and food seedlings was 40.7% and 66.0%, respectively, a 25.3% increase in tree survival with food present.

The non-significant results in Experiment C may have been related to the three densities of food pucks on each of the three replicate food sites. This particular design may have constituted pseudoreplication (Hurlbert, 1984), but could not be avoided with the dual objectives to test the food puck density question and concurrent comparison of control and food sites. The pattern of more trees eaten by voles at the low- and high-density than medium-density applications may have contributed to this result. Another potential source of ambiguity was the lack of feeding on lodgepole pine seedlings on control sites; this tree species, over all other conifers, is most preferred by voles (Sullivan et al., 1990; Sullivan and Martin, 1991).

The significant results from Experiment D with an increase of 22.5% tree survival on food than control sites may have been related to the revised formulation with alfalfa meal, thereby making the pucks more palatable for voles owing to their durability throughout the winter season. Alternatively, these results may have been related to the seedlings in this experiment being 1 year older than in the other experiments. However, this factor was the same for both control and food sites and did not seem to affect the degree of feeding by voles. The remaining food pucks (25–37%) in Experiment D suggested that medium density (1750 pucks/ha) may be an optimum application rate.

4.2. *Vole populations*

Ideally, vole populations should have been monitored on each of our control and food sites. However, that was not logistically possible and so we relied upon the population changes recorded during the first 3 years after forest harvesting (Fig. 1). These data generally represented relative vole numbers on the respective experimental sites, since all plantation sites used were $\leqslant 3$ years post-harvest age. The increase in vole numbers from 2004 to 2006 was not related to the diversionary food treatments as the population-monitoring sites were at least 5 km from the food sites. In addition, all control-food replicates in a given experiment were the same age and history. It is perhaps not surprising that the only 3-year post-harvest pair of control-food sites was replicate 5 in Experiment B, which had the highest degree of damage (and probably vole abundance) recorded.

Our study area was unique in that the long-tailed vole populations did not show dramatic 3–4-year fluctuations in abundance as reported elsewhere (Sullivan and Sullivan, 2001). This consistently high abundance of voles allowed us to conduct the sequence of annual overwinter food bioassays.

The influence of diversionary food on vole populations has been a major concern. However, as discussed by Sullivan et al. (2001) and Sullivan and Sullivan (2004), our formulation has not promoted an increase in vole abundance. Several studies have reported a positive response in vole numbers with provision of supplemental food (Cole and Batzli, 1978; Taitt and Krebs, 1981; Desy and Thompson, 1983; Boutin, 1990). The key factor in these responses seems to be nutrition, whereby numbers of *Microtus* may increase 2–5 times on food-supplemented compared with control sites (Boutin, 1990). Our diversionary food formulation attempted to simulate the bark and vascular tissues of coniferous seedlings, thereby providing a food source of relatively low nutrition. Thus, an increase in vole numbers in response to our food pucks seemed quite unlikely and was not measured in this study.

4.3. *Management implications*

Loss of seedlings to voles in new plantations has been a particularly troublesome issue for forest regeneration in temperate and boreal ecological zones. Although the outbreak of damage is site-specific and often associated with high populations of voles, a solution to the problem, which does not rely on a reduction in the target population, seems illusive. Our diversionary food appears to offer a solution that can increase tree survival by up to 20–25% over that for unprotected trees. Thus, our hypothesis that large-scale application of diversionary food to new forest plantations would reduce overwinter-feeding damage by voles may be supported. Although several experimental results were not statistically significant, this difference in tree survival between control and food units, at a real-world scale, likely has management significance for decision-making in reforestation (Walters and Holling, 1990; Ellison, 1996). However, this incremental improvement in tree survival needs to be evaluated based on (1) the need to re-plant a site because tree loss is still unacceptably high (e.g., <700 surviving trees/ha), (2) cost of the diversionary food, and (3) how many years of protection are required before the vole-damage problem subsides.

Most new plantations in the interior of BC are planted at 1400–1600 trees/ha. Thus, some mortality of trees from voles and other agents can be tolerated before the need to re-plant a site is necessary. Both numbers of trees lost and their spatial distribution in a plantation are important factors. Variable feeding pressure by voles may be dependent on population fluctuations, successional change in vegetation since harvesting, as well as site-specific factors related to moisture, coarse woody debris, and proximity to source populations. It is important to note that the majority of tree damage from voles occurs in the first winter after planting when the seedlings still have residual fertilization effects from nursery production. Damage can still be high in the second and subsequent winters, depending on vole populations, but tends to be minor by 4–5 years post-planting. An analysis of this damage pattern is currently underway (Sullivan and Sullivan, 2007).

In general, the financial cost to re-plant a site (e.g., ~$700/ha) tends to be the same as the original planting effort. If provision of diversionary food (e.g., ~$250–300/ha) can maintain sufficient trees on a site, without the need to re-plant, and this protection is required only for the first winter, or even two, then it may be a cost-effective and ecological solution to this problem.

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References

Bergeron, J.M., Jodoin, L., 1989. Plant composition in relation to vole damage in conifer tree plantations. For. Chron. 65, 206–209.

Boonstra, R., Krebs, C.J., Stenseth, N.C., 1998. Population cycles in small mammals: the problem of explaining the low phase. Ecology 79, 1479–1488.

Boutin, S., 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future. Can. J. Zool. 68, 203–220.

Byers, R.E., 1984. Control and management of vertebrate pests in deciduous orchards of the eastern United States. Hortic. Rev. 6, 253–285.

Cole, F.R., Batzli, G.O., 1978. Influence of supplemental feeding on a vole population. J. Mammal. 59, 809–819.

Conover, M., 2002. Resolving Human–Wildlife Conflicts. The Science of Wildlife Damage Management. Lewis Publishers. CRC Press Company, Boca Raton, FL.

Desy, E.A., Thompson, C.F., 1983. Effects of supplemental food on a *Microtus pennsylvanicus* population in central Illinois. J. Anim. Ecol. 52, 127–140.

Ellison, A.M., 1996. An introduction to Bayesian inference for ecological research and environmental decision-making. Ecol. Appl. 6, 1036–1046.

Hansson, L., 1985. Damage by wildlife, especially small rodents, to North American *Pinus contorta* provenances introduced into Sweden. Can. J. For. Res. 15, 1167–1171.

Hansson, L., 1989. Landscape and habitat dependence in cyclic and semi-cyclic rodents. Holarctic Ecol. 12, 345–350.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.

Jolly, G.M., Dickson, J.M., 1983. The problem of unequal catchability in mark-recapture estimation of small mammal populations. Can. J. Zool. 61, 922–927.

Kirkland Jr., G.L., 1990. Patterns of initial small mammal community change after clearcutting of temperate North American forests. Oikos 59, 313–320.

Korpimäki, E., Krebs, C.J., 1996. Predation and population cycles of small mammals. Bioscience 46, 754–764.

Krebs, C.J., 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecol. Monogr. 36, 239–273.

Krebs, C.J., Myers, J.H., 1974. Population cycles in small mammals. Adv. Ecol. Res. 8, 267–399.

Krebs, C.J., Keller, B.L., Tamarin, R.H., 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology 50, 587–607.

Meidinger, D., Pojar, J., 1991. Ecosystems of British Columbia, Research Branch, Ministry of Forests, Victoria, British Columbia Special Report Series No. 6.

Merritt, J.F., 1981. *Clethrionomys gapperi*. Mamm. Species 146, 1–9.

Myllymäki, A., 1977. Outbreaks and damage by the field vole, *Microtus agrestis* (L.), since World War II in Europe. EPPO Bull. 7, 177–208.

Ostfeld, R.S., Canham, C.D., 1993. Effects of meadow vole population density on tree seedling survival in old fields. Ecology 74, 1792–1801.

Ostfeld, R.S., Manson, R.H., Canham, C.D., 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. Ecology 78, 1531–1542.

Radvanyi, A., 1980. Control of small mammal damage in the Alberta oil sands reclamation and afforestation program. For. Sci. 26, 687–702.

Seber, G.A.F., 1982. The Estimation of Animal Abundance and Related Parameters, second ed. Charles Griffin, London, UK.

Shu, F., 1985. On the number of large-toothed red-backed voles (*Clethrionomys rufocanus*) on different slopes and its meaning in rodent pest prevention for young forests. Acta Theriol. Sin. 5, 263–267.

Sullivan, T.P., Martin, W., 1991. Influence of site factors on incidence of vole and lemming feeding damage to forest plantations. West. J. Appl. For. 6, 64–67.

Sullivan, T.P., Sullivan, D.S., 1988. Influence of alternative foods on vole populations and damage in apple orchards. Wildl. Soc. Bull. 16, 170–175.

Sullivan, T.P., Sullivan, D.S., 2001. Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. J. Appl. Ecol. 38, 1234–1252.

Sullivan, T.P., Sullivan, D.S., 2004. Influence of a granivorous diversionary food on population dynamics of montane voles (*Microtus montanus*), deer mice (*Peromyscus maniculatus*), and western harvest mice (*Reithrodontomys megalotis*). Crop Prot. 23, 191–200.

Sullivan, T.P., Sullivan, D.S., 2007. Vole feeding damage and forest plantation protection: susceptibility of new plantations to damage, in preparation.

Sullivan, T.P., Harestad, A.S., Wikeem, B.M., 1990. Control of mammal damage. In: Lavender, D.P., Parish, R., Johnson, C.M., Montgomery, G., Vyse, A., Willis, R.A., Winston, D. (Eds.), Regenerating British Columbia's forests. University of British Columbia Press, Vancouver, BC, Canada, pp. 302–318.

Sullivan, T.P., Zhen-hao, J., Heli, L., Shou-cai, W., 1991. Control of vole populations in young pine plantations in northeast China. For. Chron. 89, 43–47.

Sullivan, T.P., Sullivan, D.S., Hogue, E.J., 2001. Influence of diversionary foods on vole (*Microtus montanus* and *Microtus longicaudus*) populations and feeding damage to coniferous tree seedlings. Crop Prot. 20, 103–112.

Taitt, M.J., Krebs, C.J., 1981. The effect of extra food on small rodent populations. II. Voles (*Microtus townsendii*). J. Anim. Ecol. 50, 125–137.

Taitt, M.J., Krebs, C.J., 1985. Population dynamics and cycles. In: Tamarin, R.H. (Ed.), Biology of New World *Microtus*, Special Publication No. 8. American Society of Mammalogists, Boston, MA, pp. 567–620.

Walters, C.J., Holling, C.S., 1990. Large-scale management experiments and learning by doing. Ecology 71, 2060–2068.

Zar, J.H., 1999. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, NJ, USA.