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Influence of diversionary foods on vole (*Microtus montanus* and *Microtus longicaudus*) populations and feeding damage to coniferous tree seedlings☆

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Abstract

This study was designed to test the hypotheses that diversionary food would: (1) reduce feeding by voles (*Microtus* spp.) to lodgepole pine (*Pinus contorta*) seedlings; and (2) provide a food source without increasing vole populations. Two experiments (A and B) were conducted with montane voles (*M. montanus*) in old field habitats at Summerland, British Columbia, Canada from 1996 to 1998. A third experiment (C) was conducted with long-tailed voles (*M. longicaudus*), meadow voles (*M. pennsylvanicus*), and southern red-backed voles (*Clethrionomys gapperi*) in young lodgepole pine plantations in forested areas in 1998–1999. Diversionary food was prepared in the form of "logs" composed of alfalfa pellets, wood pellets, or bark mulch mixed with wax and sunflower oil. Vole populations were intensively live-trapped on control and treatment sites. Mean percentage of seedlings eaten per vole was significantly reduced with bark mulch logs during a peak damage period in old field habitat. Alfalfa logs also tended to reduce seedling damage but only for the first month after placement. None of the diversionary foods tested had any effect on mean abundance of vole populations. In forest plantations, seedlings on control sites suffered mortality from vole feeding at levels 2.6–2.8 times higher than those on alfalfa and bark mulch sites. This difference was not statistically significant ($P = 0.09$) but very likely was biologically significant in terms of seedling protection. This result was achieved with *Microtus* spp. on clearcut sites, but not on patch cut sites where red-backed voles were the most abundant microtine. The concept of seedling protection with these diversionary foods appears sound, but additional research is warranted.

Keywords: Alfalfa; Bark mulch; *Clethrionomys gapperi*; Diversionary food; Feeding damage; Forest plantations; Lodgepole pine; *Microtus* spp.; Tree seedlings; Voles

1. Introduction

Prompt regeneration of cutover forest land is essential to renewal and sustainability of forest resources. Planting of nursery-grown seedlings is the major method of reforestation across temperate coniferous forests of North America and many parts of Europe and Asia. Strategies range from uniform planting of seedlings on those units harvested by clearcutting to spot planting of smaller patch cut and selection cut units.

Voles of the genus *Microtus* are considered one of the major mammalian pests in coniferous and deciduous tree plantations in North America (Cayford and Haig, 1961; Sartz, 1970; Buckner, 1972; Radvanyi, 1980; Sullivan and Martin, 1991), Europe (Myllymäki, 1977; Hansson, 1985a), and Asia (Shu, 1985; Sullivan et al., 1991). Although the diet of voles consists primarily of grasses, sedges, and forbs (Batzli, 1985; Ostfeld, 1985; Bergeron and Jodoin, 1989), these rodents will feed on tree seedlings and saplings, particularly during winter months. Voles may feed on bark, vascular tissues, and sometimes roots of trees. This damage may result in direct mortality from girdling and clipping of tree stems or reduced growth of surviving trees which have sub-lethal injuries. In terms of conservation and sustainability of temperate forests, this feeding damage may limit regeneration of appropriate tree species in certain forest ecosystems.

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Because conifer species have bark protein levels that can barely satisfy the minimum requirements for voles when they have to detoxify phenolic compounds, seedlings may be merely subsistence food items that voles ingest during overwinter periods (Lindroth and Batzli, 1984; Bucyanayandi et al., 1990). Conifers contain both positive (protein, nonstructural carbohydrates) and negative (phenols, terpenes) nutritional components that herbivores ingest when feeding on bark tissue (Bucyanayandi et al., 1990). High protein content in diets appears to reduce or eliminate the negative digestion-disrupting effects of phenolic compounds (Lindroth and Batzli, 1984). This process may help explain why voles show strong preferences for herbaceous species of plants with high protein/total phenols ratios (Bergeron and Jodoin, 1987; Bucyanayandi and Bergeron, 1990).

In addition, voles on clearcut forest land in Sweden appear to seek sodium and perhaps calcium, particularly in cyclic fluctuating populations during peak winters (Hansson, 1990). Bark is high in sodium content (Likens and Borman, 1970), and hence voles may seek both energy and minerals in their bark consumption during winter food shortages (Hansson, 1991).

Provision of diversionary food is a method of habitat modification designed to temporarily satisfy part, or a majority, of the food requirements of a problem species in a localized area (Howard, 1967; Sullivan, 1979). In laboratory studies, Hansson (1971) reported that voles (*M. agrestis*) did not girdle tree stems if green vegetation and small twigs supplemented a diet of laboratory food pellets. In subsequent studies, voles preferred various oil- and sugar-impregnated sticks (Hansson, 1973), and meadow (*M. pennsylvanicus*) and montane (*M. montanus*) voles preferred sticks impregnated with soybean oil compared with sucrose and sorbitol (Sullivan and Sullivan, 1988). Preliminary evidence from small-scale trials in young apple (*Malus domestica*) orchards suggested that a combination of bark mulch, soybean oil, and wax reduced feeding damage by voles to apple trees (Sullivan and Sullivan, 1988). These studies suggested that certain foods, which are more palatable than tree bark and of similar or lower nutritive value than natural foods, may have potential for reducing tree damage by voles.

If coniferous tree seedlings are subsistence overwinter food for voles, then it may be possible to provide an artificial diversionary food that is more palatable to voles than tree bark and vascular tissues, but not necessarily nutritious enough to maintain or increase population size. However, several studies have documented the positive influence of supplemental food on vole population dynamics (Cole and Batzli, 1978; Taitt and Krebs, 1981; Boutin, 1990). Thus, this study was designed to test the hypotheses that diversionary food would (1) reduce feeding damage by voles to lodgepole pine seedlings; and (2) provide a food source without increasing vole populations.

2. Materials and methods

2.1. Study areas

Two experiments (A and B) were conducted in the Okanagan Valley at the Pacific Agri-Food Research Centre, Summerland, British Columbia, Canada. Experiments A and B were located in “old field” habitats which were abandoned ($\geqslant$ 25 years) hay fields composed of crested wheatgrass (*Agropyron cristatum*), quack grass (*Agropyron repens*), downy brome (*Bromus tectorum*), diffuse knapweed (*Centaurea diffusa*), with some minor herbaceous species such as yellow salsify (*Tragopogon dubius*), great mullein (*Verbascum thapsus*), American vetch (*Vicia americana*), prickly lettuce (*Lactuca serriola*), and tall tumble-mustard (*Sisymbrium altissimum*). These old field treatment units were each 2–3 ha in area within a mosaic of sagebrush (*Artemisia tridentata*), Ponderosa pine (*Pinus ponderosa*) forest, and orchard habitats. These old fields had resident populations of montane voles which was the major rodent species with a long history of fluctuating populations and feeding damage to trees (Sullivan et al., 1998b). The deer mouse (*Peromyscus maniculatus*), Great Basin pocket mouse (*Perognathus parvus*), western harvest mouse (*Reithrodontomys megalotis*), northwestern chipmunk (*Tamias amoenus*), and long-tailed vole (*M. longicaudus*) were also present in variable numbers. Experiment A had six experimental units (3 treatments $\times$ 2 replicates of each treatment) and Experiment B had 12 experimental units (4 treatments $\times$ 3 replicates of each treatment).

Experiment C was conducted in young lodgepole pine (*Pinus contorta*) plantations located in the bald range 25 km west of Summerland in south-central British Columbia, Canada (49°40′N; 119°53′W). This area is within the upper Interior Douglas-fir (IDF_{dk}) and Montane Spruce (MS_{dm}) biogeoclimatic zones (Meidinger and Pojar, 1991). Topography ranges from hilly to rolling hills at 1300–1520 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* $\times$ *P. 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).

Candidate sites were chosen from patch cut (IDF) and clearcut (MS) units that were harvested in 1996. Prior to harvesting, all stands were composed of a mixture of lodgepole pine with variable amounts of Douglas-fir, spruce, and subalpine fir. Average ages of lodgepole pine ranged from 82 to 120 years and for Douglas-fir ranged from 120 to 228 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. The area of nine patch cuts (each with one plantation site) averaged 0.93 ha (range 0.41–2.12 ha). The area of three clearcuts (each with three independent plantation sites) averaged 12.9 ha (range 10.2–15.7 ha).

2.2. Experimental design

In our design a "site" represented an experimental unit. Each of the three experiments had a randomized block design. Replicate sites were selected on the basis of proximity, similar habitat, and reasonable grouping into respective blocks based on location. Treatments were assigned randomly to sites within blocks and sites were spatially segregated to enhance statistical independence (Hurlbert, 1984). The patch cuts and clearcuts, with their respective plantation sites, were the size of typical forestry operations. Plantation sites within each of the three clearcut units were spatially segregated such that they represented true replicates (Hurlbert, 1984).

2.3. Diversionary foods

Diversionary food was prepared in the form of "logs" composed of alfalfa pellets (15% protein, 27% fiber, and 10% moisture), wood pellets (compressed sawdust), or Douglas-fir bark mulch mixed with wax and sunflower oil. The melted wax/oil mixture was poured into 250-ml paper cups containing the solid food. After the wax/oil mix had solidified in the food cups, the "logs" were transported to the field. Sunflower oil was chosen to enhance the attractiveness of the food to voles. Sunflower oil contains 51–68% linoleic acid (Noller, 1966), a fatty acid reported by Hansson (1973) to be a highly attractive pure oil compound to voles. The pellets acted as a source of protein and fibre and the bark simulated the bark and tissues of plantation trees. The wax acted as a cohesive, water-proof matrix. To optimize cost vs. vole attractiveness, three concentrations of sunflower oil (20, 40, and 60%) were tested in the alfalfa and wood logs of Experiment A.

2.4. Vole populations

Montane vole populations were live-trapped on 0.5-ha checkerboard grids with Longworth live-traps. Trap stations were located every 7.15 m with one live-trap per station in 10×10 or 7×14 configurations with one grid per treatment site in Experiments A and B. Grids were live-trapped at 4-week intervals (6- to 10-week intervals in winter — November–March) from May 1996 to May 1997 in Experiment A and from September 1997 to April 1998 in Experiment B.

Long-tailed voles, meadow voles, and southern red-backed voles (*Clethrionomys gapperi*) were live-trapped on 1.0-ha checkerboard grids with Longworth live-traps on the control sites of Experiment C. 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 1998, and from May to October 1999. Snow conditions limited access to grids during the overwinter period of 1998–1999.

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 serial numbered tags, breeding condition noted, weighed on Pesola spring balances, and the point of capture was recorded.

Population densities were estimated by the Jolly–Seber model (Seber, 1982) for reasons indicated by Jolly and Dickson (1983). The Jolly–Seber (J–S) model provides the best estimates of population size for mark and recapture data when trappability values are generally $< 70\%$ (Hilborn et al., 1976). However, when population size falls very low and no marked animals are recaptured, the J–S estimate becomes unreliable and impossible to calculate (Krebs et al., 1986). For these sample weeks, a minimum number of animals known to be alive (MNA) (Krebs, 1966) value was substituted for a biologically unreasonable J–S estimate.

2.5. Experiment A

This experiment was designed to answer: (1) what is the optimum concentration of sunflower oil in logs to enhance feeding by voles on the diversionary food?, (2) will trees with logs survive better than those without logs?, and (3) does diversionary food affect vole population density?

In Experiment A, 400 1-year-old containerized lodgepole pine seedlings were planted at 3-m spacing in a 20×20 configuration on the vole grid on each of the six treatment sites on October 31–November 1, 1996. This planting pattern was equivalent to a density of 1100 trees/ha. These trees served as test material for the evaluation of diversionary foods. Lodgepole pine is the most susceptible coniferous tree species to feeding damage by *Microtus* spp. in the interior of BC (Sullivan et al., 1990). Diversionary food logs were placed in the field at a density of two logs/tree when the tree seedlings were planted. Logs were placed around (but not obstructing access by voles) every second tree. Each of the four diversionary food plantations was divided systematically into thirds with each third receiving logs with one of three concentrations of sunflower oil, and hence this design constituted pseudoreplication (Hurlbert, 1984). The two control sites had no logs.

The overwinter consumption of diversionary food by voles and damage to tree seedlings was measured on April 11–15, 1997. Log consumption was estimated in 25% increments ($1 = 1$–25%, $2 = 26$–50%, $3 = 51$–75%, $4 = 76$–100%) and tallied for all logs of each of the three concentrations of oil. All 400 seedlings were sampled for clipping of terminal or lateral shoots and gnawing of terminal shoots. Clipping and gnawing of terminal shoots were considered mortality since seedlings rarely, if ever, recover from this damage. Damage was recorded separately for trees with logs, and those without logs.

2.6. Experiment B

This experiment was designed to answer: (1) will uniform distribution of logs (i.e. not systematically placed near trees) improve efficacy over results achieved in Experiment A?, (2) will an initial application of diversionary food, prior to snowfall, have the potential to reduce feeding damage to seedlings by voles throughout an overwinter period?, and (3) do any of these diversionary foods affect vole population density?

In Experiment B, 400 (20×20) containerized lodgepole pine seedlings were planted on November 10, 1997 on the 0.5-ha grid on each of the 12 treatment sites. Diversionary food logs included a mixture of wax and sunflower oil (40% concentration) with alfalfa pellets, bark mulch, or sunflower seeds. Logs were distributed uniformly with eight logs placed in each $7.15\,\text{m} \times 7.15\,\text{m}$ square of each checkerboard trapping grid. Four logs were placed in each of the outside $7.15\,\text{m} \times 3.58\,\text{m}$ squares around the perimeter of each grid. A total of 800 logs was placed on each grid on a given treatment site. The three control sites had no logs. One log was to be sampled of the four or eight in each square and was marked by a metal flag. Every fourth seedling ($n = 100$) was marked by a metal flag and sampled for feeding damage by voles.

Consumption of logs and damage to seedlings was measured, in an identical manner to Experiment A, at five times during the overwinter period: November 28–30 and December 31, 1997; January 28, March 1, and April 12, 1998.

2.7. Experiment C

This experiment tested alfalfa pellet and bark mulch logs (identical formulation to Experiment B) in reducing feeding damage to seedlings by voles in a forested environment through the winter of 1998–1999. In Experiment C, 100 (10×10) containerized lodgepole pine seedlings were planted on each of the nine sites on the patch cuts and 400 (20×20) pine seedlings were planted on each of the nine sites on the clearcuts on October 26–30, 1998. Immediately after planting of seedlings, logs were distributed uniformly over the sites in an identical manner to Experiment B. Totals of 150 and 600 alfalfa logs were placed on each of three patch cut and three clearcut sites, respectively. Totals of 100 and 400 bark mulch logs were also placed on each of three patch cut and three clearcut sites, respectively. The three patch cut and three clearcut control sites had no logs. Sample logs and trees on the clearcut sites were marked in an identical manner to Experiment B. All logs and 50 trees were sampled on each of the patch cut sites. Consumption of logs and damage to tree seedlings was measured, in an identical manner to experiments A and B, on May 20–21, 1999.

2.8. Statistical analysis

A randomized block 2-way analysis of variance (ANOVA)— Model III (Zar, 1984) with fixed effects of factors oil concentration and presence of logs with factor blocks as a random effect, compared percentage of seedlings eaten by voles among treatments in Experiment A. This same ANOVA, with fixed effects of factors site treatment and time with factor blocks as a random effect, was used to compare mean abundance of voles among treatments.

A randomized block ANOVA— Model III with fixed effect of factor site treatment with factor blocks as a random effect, was used to test for differences in percentage of tree seedlings eaten overall and per vole and consumption of diversionary food among treatments. Percentage data were arcsine-transformed prior to analysis. 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. Experiment A

The mean percentage of trees eaten by voles during the 1996–1997 winter was similar ($F_{2,2} = 1.35$; $P = 0.43$) among control (35.6%), alfalfa (57.1%), and wood (30.7%) treatments. Feeding damage was similar for trees with logs and for those without logs for alfalfa ($F_{1,6} = 2.14$; $P = 0.19$) and wood ($F_{1,6} = 0.22$; $P = 0.65$). Feeding damage to trees was also similar across concentrations of sunflower oil for both alfalfa ($F_{2,6} = 0.88$; $P = 0.46$) and wood ($F_{2,6} = 0.02$; $P = 0.98$) (Table 1).

Consumption of the diversionary foods indicated that the 20% concentration of sunflower oil was not sufficient to attract voles to the food source (Table 2). There was a significant ($F_{2,2} = 23.38$; $P = 0.04$) difference

Table 1
Mean ($n = 2$) ± SE percentage of lodgepole pine seedlings eaten by montane voles, at three concentrations of sunflower oil, for trees with and without logs in Experiment A

				Analysis					
	Concentration of sunflower oil			Conc. oil		Logs		Conc. × Logs	
Divers. food	20%	40%	60%	$F_{2,6}$	P	$F_{1,6}$	P	$F_{2,6}$	P
Alfalfa pellets				0.88	0.46	2.14	0.19	0.08	0.93
With logs	51.8 ± 3.4	73.4 ± 0.4	73.0 ± 7.3						
Without logs	40.3 ± 21.9	49.2 ± 22.8	55.3 ± 17.5						
Wood pellets				0.02	0.98	0.22	0.65	0.14	0.87
With logs	34.1 ± 14.4	34.5 ± 10.3	28.6 ± 1.3						
Without logs	28.8 ± 1.5	27.3 ± 1.9	30.9 ± 10.0						

Table 2
Mean ($n = 2$) ± SE percentage of diversionary food logs eaten by montane voles, at three concentrations of sunflower oil, in Experiment A. Within rows, mean values followed by different letters are significantly different according to Duncan's multiple range test

	Concentration of sunflower oil			Analysis	
Diversionary food	20%	40%	60%	$F_{2,2}$	P
Alfalfa pellets	58.9 ± 20.1	89.8 ± 4.5	97.3 ± 0.7	3.64	0.22
Wood pellets	27.5[a] ± 6.2	69.2[b] ± 7.1	75.5[b] ± 14.3	23.38	0.04

among oil concentrations for the wood but not alfalfa food ($F_{2,2} = 3.64$; $P = 0.22$), with higher levels of feeding on the 40 and 60% concentrations than the 20% concentration. Diversionary food had no effect on mean abundance of vole populations, either among treatments ($F_{2,2} = 0.03$; $P = 0.97$) or over time ($F_{1,2} = 0.17$; $P = 0.72$) (Fig. 1).

In summary, a concentration of at least 40% sunflower oil is required to enhance feeding on logs by voles. Feeding damage was similar for trees with logs and for those without logs. These diversionary foods had no effect on vole population density.

3.2. Experiment B

Tree seedling mortality from voles began in November 1997 with the majority of feeding completed by early January 1998 (Fig. 2). Some additional feeding continued through to April 1998. Based on the mean percentage of seedlings eaten, regardless of vole abundance, there were no significant differences among the treatments during the December ($F_{3,6} = 1.12$; $P = 0.41$), January ($F_{3,6} = 0.93$; $P = 0.48$), February ($F_{3,6} = 0.75$; $P = 0.56$), March ($F_{3,6} = 0.64$; $P = 0.62$), or April ($F_{3,6} = 0.48$; $P = 0.71$) sampling periods.

Despite this lack of significant differences, the bark mulch treatment appeared to provide some degree of protection for trees based on percentage of seedlings

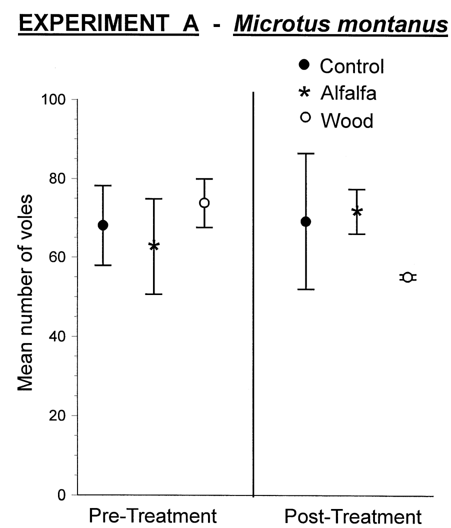

Fig. 1. Mean ($n = 2$) ± 1 SE population densities of montane voles per 0.5 ha on control, alfalfa pellet, and wood pellet sites during Experiment A in 1996–1997.

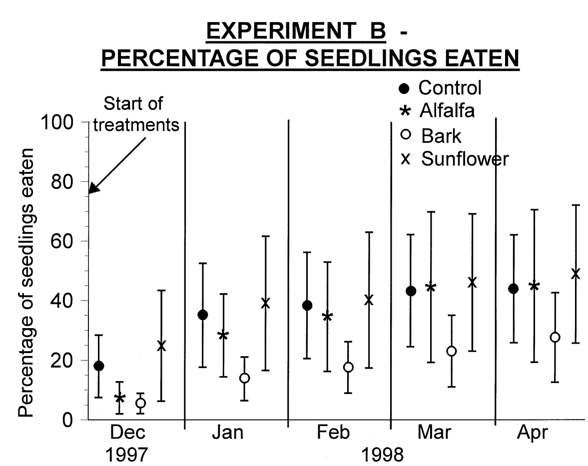

Fig. 2. Mean ($n = 3$) ± 1 SE cumulative percentage of lodgepole pine seedlings eaten by montane voles on control, alfalfa, bark mulch, and sunflower seed sites during Experiment B in 1997–1998.

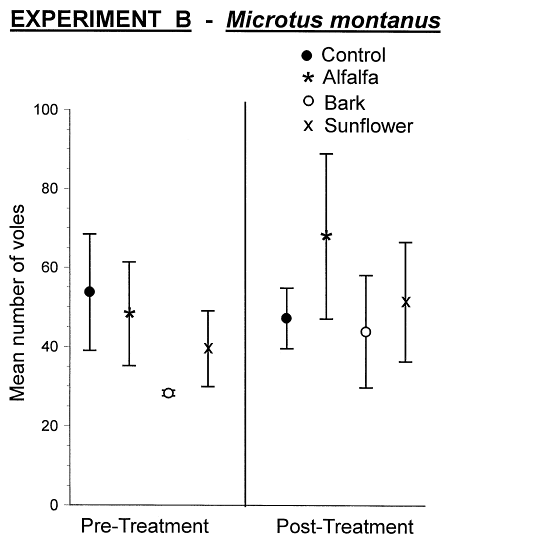

Fig. 3. Mean ($n = 3$) $\pm$ 1 SE population densities of montane voles per 0.5 ha on control, alfalfa pellet, bark mulch, and sunflower seed sites during Experiment B in 1997–1998.

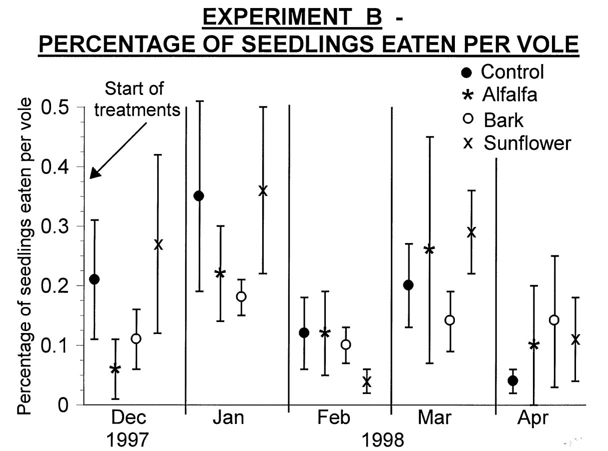

Fig. 4. Mean ($n = 3$) $\pm$ 1 SE percentage of lodgepole pine seedlings eaten per vole on control, alfalfa pellet, bark mulch, and sunflower seed sites during Experiment B in 1997–1998.

eaten (Fig. 2). There was a considerably lower abundance of voles on the treatment sites of replicate 1 (mean = 29.9/0.5 ha) than on the other two replicates (means = 55.5 and 60.6/0.5 ha) (Fig. 3). This low density of voles resulted in minor feeding (< 12%) on tree seedlings on sites in this replicate throughout the winter. Thus, a more realistic analysis of the effects of these diversionary foods on seedling damage was to evaluate the percentage of seedlings eaten per vole at each of the overwinter sampling periods. In addition, because of the lack of feeding pressure on sites in replicate 1, analysis of percentage of seedlings eaten per vole was conducted on replicates 2 and 3 with higher numbers of voles and feeding, as well as on all three replicates.

Based on two replicates, diversionary foods significantly ($F_{3,3} = 10.00$; $P = 0.05$) reduced feeding on trees per vole during the peak damage period in January, but not December ($F_{3,3} = 2.08$; $P = 0.28$). However, mean percentage of seedlings eaten per vole was 0.09% for bark mulch, 0.10% for alfalfa, 0.40% for sunflower, and 0.33% for the control during this December sampling period. For the significant difference in January, the lowest mean feeding per vole was bark mulch (0.16%); followed by alfalfa (0.30%) and sunflower (0.30%) and the control (0.40%) which were all similar (DMRT; $P = 0.05$). There were no significant differences among treatments for the February ($F_{3,3} = 0.56$; $P = 0.68$), March ($F_{3,3} = 0.00$; $P = 1.00$), or April ($F_{3,3} = 3.00$; $P = 0.20$) sampling periods. Based on three replicates, there were no significant differences among treatments at any of the sampling periods (Fig. 4).

In terms of mean number of voles pre- and post-treatment, diversionary food had no effect as a treatment ($F_{3,6} = 2.80$; $P = 0.13$) or over time ($F_{1,2} = 1.03$; $P = 0.42$). However, vole populations on the alfalfa sites were, on average, 1.5 times higher in mean abundance than on the controls in the first post-treatment sampling period (Fig. 3). Mean numbers of voles were at comparable levels in late January and early April.

Cumulative consumption of diversionary foods by voles was significantly different among treatments for the December ($F_{2,4} = 15.73$; $P = 0.02$), January ($F_{2,4} = 15.80$; $P = 0.02$), February ($F_{2,4} = 19.59$; $P = 0.01$), and April ($F_{2,4} = 14.10$; $P = 0.02$) sampling periods (Fig. 5). In the first two periods, consumption of the sunflower seed logs was significantly (DMRT; $P = 0.05$) greater than that of the alfalfa or bark mulch, which were both consumed at similar rates. This pattern continued in the third period, but the bark mulch was consumed significantly (DMRT; $P = 0.05$) less than both the alfalfa and sunflower seed. At the final sampling period, alfalfa and sunflower seed had been consumed at a similar level which was significantly (DMRT; $P = 0.05$) higher than that of the bark mulch (Fig. 5). Approximately 35% of the alfalfa and 69% of the bark mulch logs remained, whereas only 8.2% of the sunflower was left. Both alfalfa and bark mulch logs appeared to have the potential to last an entire winter under snow.

In summary, a uniform distribution of logs appeared to improve efficacy but only during a 1-month period. Alfalfa and bark mulch logs lasted throughout an overwinter period. Diversionary foods had no effect on population density of voles.

3.3. Experiment C

The mean percentage of lodgepole pine seedlings eaten by meadow voles, long-tailed voles, and red-backed voles was significantly different among treatments in the patch cut sites ($F_{2,4} = 38.34$; $P < 0.01$) but not in the clearcut sites ($F_{2,4} = 4.59$; $P = 0.09$) (Table 3). The highest loss of

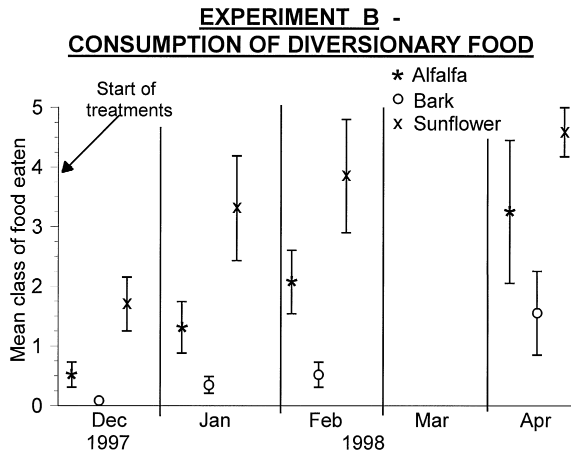

Fig. 5. Mean ($n = 3$) ± 1 SE cumulative consumption of diversionary food, based on classes (1 = 1–20%; 2 = 21–40%; 3 = 41–60%; 4 = 61–80%; 5 = 81–100%), on alfalfa pellet, bark mulch, and sunflower seed sites during Experiment B in 1997–1998.

seedlings was in the alfalfa treatment (35.0%) with no difference between control and bark mulch on the patch cut sites (DMRT; $P = 0.05$). The alfalfa logs were completely consumed on all three replicates and this occurred at some time during the 1998–1999 winter, and prior to the evaluation of seedling survival conducted in May 1999. Thus, it is possible that seedlings were not protected by the alfalfa diversionary food for some part of the overwinter period on the patch cut sites. Approximately 25% of bark mulch logs remained on the patch cut sites in the spring.

Although not statistically significant, control seedlings on the clearcut sites suffered mortality from vole feeding at levels of 2.6–2.8 times higher than those on the alfalfa and bark mulch treatments (Table 3). Again, the alfalfa logs were completely consumed at some time during the overwinter period, and about 25% of the bark mulch logs were also remaining on the clearcut sites.

Combined mean (± SE) numbers of meadow voles, long-tailed voles and red-backed voles on the patch cut control sites were 11.4 ± 3.1 animals/ha in summer 1998, prior to the overwinter experiment and 7.4 ± 4.4 animals in summer 1999, after the experiment. Red-backed voles comprised an average of 78.3 and 80.9% of the vole populations in 1998 and 1999, respectively. Overall mean numbers of voles were similar ($F_{1,4} = 0.57$; $P = 0.49$) between years. Combined mean numbers of meadow voles and long-tailed voles on the clearcut control sites were 20.7 ± 2.3 animals/ha in summer 1998, prior to the overwinter experiment, and 7.3 ± 2.5 animals/ha in summer 1999, after the experiment. Overall mean numbers of these voles were significantly ($F_{1,4} = 15.78$, $P = 0.02$) different between years.

4. Discussion

4.1. Tree damage

We conclude from our experimental results that diversionary foods, in the form of alfalfa pellet logs and bark mulch logs, may have the potential to significantly reduce feeding damage by voles to tree seedlings during overwinter periods. Thus, hypothesis (1) appears to be supported, at least by the results from Experiment B during the peak feeding period in the winter of 1997–1998 and from the clearcut sites in Experiment C. However, this conclusion is tentative and the concept requires further testing and analysis.

Although diversionary food formulations in Experiment A were ineffective at reducing damage, it was clear that at least a 40% concentration of sunflower oil was required to optimize feeding by voles on the diversionary food logs. A more rigorous evaluation of these oil concentrations should have included true replicates (i.e. separate grids) rather than pseudoreplicates (Hurlbert, 1984). The importance of various oils to voles of the genus *Microtus* was reported by Hansson (1973) and Sullivan and Sullivan (1988). The wax–oil matrix appeared to provide a highly palatable food for voles and was essentially water-proof for field application. Location of logs adjacent to trees seemed to attract voles

Table 3
Mean ($n = 3$) ± SE percentage of lodgepole pine seedlings eaten and diversionary food consumed by meadow, long-tailed, and red-backed voles on patch cut and clearcut sites in Experiment C. Within a site, mean values followed by different letters are significantly different according to Duncan's multiple range test

Site	Treatment				
	Control	Alfalfa pellets	Bark mulch	$F_{2,4}$	P
Patch cuts					
Seedlings	11.5a ± 2.4	35.0b ± 5.6	11.6a ± 4.5	38.34	< 0.01
Diversionary food	—	100.0 ± 0.0	74.7 ± 15.3		
Clearcuts					
Seedlings	34.7a ± 12.7	12.3b ± 6.6	13.2b ± 8.1	4.59	0.09
Diversionary food	—	100.0 ± 0.0	74.8 ± 25.2		

to trees, even though statistical comparisons were not significant for either alfalfa or wood pellets in Experiment A. However, for the alfalfa logs, damage to trees with logs was 1.3–1.5 times higher than for trees without logs (Table 1), which may have biological significance. Regardless, from a practical reforestation perspective, the degree of damage to trees was unacceptably high in all treatments. Although difficult to generalize, seedling losses to voles of 10–15% could be tolerated if there was a single damage event during the first few years after plantation establishment (Sullivan et al., 1990).

Substitution of Douglas-fir bark mulch for the compressed sawdust wood pellets improved palatability to voles and provided a waterproof food source in Experiment B. The wood pellets did not weather well in Experiment A as moisture resulted in collapse of the pellets and wax/oil matrix. The uniform distribution of logs improved efficacy, at least during the major feeding period by voles in the winter of 1997–1998. The bark mulch formulation lowered damage based on percentage of seedlings eaten per vole during January in Experiment B. Although this analysis used just 2 of 3 replicate blocks, the results were encouraging because this experiment was conducted under very severe conditions in prime habitat for peak populations of voles. Numbers of voles reached up to 244 voles/ha on some sites. This level of abundance was considerably higher than the number recorded on our clearcut sites (up to 49 voles/ha) in Experiment C, which was typical (up to 100 animals/ha) for *Microtus* spp. in forested environments (Sullivan and Krebs, 1981; Van Horne, 1982; Anthony and Morrison, 1985; Taitt and Krebs, 1985; Sullivan et al., 1998a).

In addition, vole preference for lodgepole pine seedings was similar to other mammal pest-forest plantation interactions worldwide, where pines are generally the most susceptible species to feeding damage (Hansson, 1985a; Sullivan et al., 1991). Planted stock are preferred by these rodents, which may reflect the fertilization regime in nursery production whereby seedlings become highly palatable and nutritious for herbivores such as voles (Sullivan and Martin, 1991). Thus, these first two experiments were conducted in rigorous conditions to test the various treatment alternatives. Proportions of both the alfalfa and bark mulch logs lasted through the winter of Experiment B despite the very high feeding pressure.

4.2. Vole populations

The diversionary foods tested in Experiments A and B did not affect vole abundance, thereby providing support for hypothesis (2) that we could provide an alternative food source without increasing vole populations. Alfalfa and bark mulch logs were applied to sites where intensive sampling of vole populations was conducted both before and after treatments. Thus, if these formulations were to increase vole abundance by stimulating reproduction or enhancing overwinter survival, this pattern was not evident from our data. This result is similar to those recorded in other diversionary food studies with small mammals (Sullivan and Sullivan, 1982, 1988; Sullivan and Klenner, 1993; Hines, 1997).

Populations of *Microtus* in supplemental food studies do respond positively with increases in abundance (Cole and Batzli, 1978; Taitt and Krebs, 1981; Desy and Thompson, 1983). If reasonably nutritious foods are supplied, numbers of *Microtus* have increased 2–5 times on fed compared with control areas and this is a common response among small mammals (Boutin, 1990). Therefore, our diversionary foods appear not sufficiently nutritious to increase vole numbers.

4.3. Diversionary foods and forest plantations

If coniferous tree seedlings are subsistence overwinter food for voles, and our foods are more palatable than tree bark and vascular tissues, then these foods clearly have potential to reduce damage to plantation trees. A critical test of this prediction was conducted in Experiment C during a winter of peak populations of meadow voles and long-tailed voles. Although there was a higher level of tree damage with alfalfa logs at the patch cut sites, much of this damage may have occurred after the supply of logs was exhausted. A similar result may have occurred on the alfalfa clearcut sites where some seedlings may have been eaten after the diversionary food was gone. On average, about 75% of the bark mulch logs were eaten. Thus, the amounts of this food (400 logs/0.5 ha) were likely adequate to feed voles at densities up to 50/ha throughout a 6-month winter period. The amount of alfalfa logs (600/0.5 ha) may need to be increased to provide protection for seedlings over the entire winter.

The lack of a positive response in the patch cut sites may be related to the red-backed vole which dominated the vole community. This species feeds primarily on herbs, fungi, and lichens as well as some seeds and berries (Martell, 1981; Hansson, 1985b). Feeding damage to seedlings by this species appears likely based on abundance of animals and loss of trees on a given site (Sullivan and Sullivan, 2000). Our diversionary food formulations may not have been suited to the feeding preferences of southern red-backed voles. However, this approach did seem to work reasonably well in reducing feeding damage to Scotch pine (*P. sylvestris*) trees by red-backed voles (*C. rufocanus*) in northeast China (Sullivan et al., 1991).

4.4. Management implications

Our results suggest that diversionary foods, formulated as alfalfa pellets and bark mulch in a wax–oil matrix, may have the potential to reduce feeding damage to newly planted lodgepole pine seedlings by voles. In particular, the proportion of damaged trees was 2.6–2.8 times higher (but not statistically significant) on control than food-treated sites on clearcuts with resident populations of *Microtus pennsylvanicus* and *Microtus longicaudus*. This combination of *Microtus* populations and plantation establishment on early successional sites after harvesting is the most common scenario for outbreaks of feeding damage to seedlings in temperate and boreal forests. Clearcuts, or clearcuts with reserves, continue to be the major method of forest harvesting in temperate and boreal coniferous forests.

Although additional work is required to make this technique operationally viable in terms of both manual and aerial application, the concept of seedling protection with diversionary food appears sound. The cost of replanting or spot planting those sites with tree loss, due to vole feeding, will have to be compared with the cost of applying a commercially available diversionary food, such as tested in our study. Further work in this direction is planned for the near future.

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References

Anthony, R.G., Morrison, M.L., 1985. Influence of glyphosate herbicide on small mammal populations in western Oregon. Northwest Sci. 59, 159–168.

Batzli, G.O., 1985. Nutrition. In: Tamarin, R.H. (Ed.), Biology of New World Microtus, Spec. Publ. No. 8. American Society of Mammal., Boston, MA, pp. 779–811.

Bergeron, J.M., Jodoin, L., 1987. Defining "high quality" food resources of herbivores: the case for meadow voles (*Microtus pennsylvanicus*). Oecologia 71, 510–517.

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

Boutin, S., 1990. Experimental addition of food to terrestrial vertebrates: patterns, problems and the future. Can. J. Zool. 68, 203–220.

Buckner, C.H., 1972. The strategy for controlling rodent damage to pines in the Canadian midwest. In: Marsh, R.E. (Ed.), Proceedings of the Fifth Vertebrate Pest Conference, pp. 242–253. Fresno, California, March 1972. University of California, Davis.

Bucyanayandi, J.D., Bergeron, J.M., 1990. Effects of food quality on feeding patterns of meadow voles (*Microtus pennsylvanicus*) along a community gradient. J. Mammal. 71, 390–396.

Bucyanayandi, J., Bergeron, J., Menard, J., 1990. Preferences of meadow voles (*Microtus pennsylvanicus*) for conifer seedlings: chemical components and nutritional quality of bark of damaged and undamaged trees. J. Chem. Ecol. 16, 2569–2579.

Cayford, J.H., Haig, R.A., 1961. Mouse damage to forest plantations in Southeastern Manitoba. J. For. 59, 124–125.

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

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.

Hansson, L., 1971. Habitat, food, and population dynamics of the field vole, *Microtus agrestis*, in south Sweden. Viltrevy 8, 267–378.

Hansson, L., 1973. Fatty substances as attractants for *Microtus agrestis* and other small rodents. Oikos 24, 417–421.

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

Hansson, L., 1985b. Clethrionomys food: generic, specific and regional characteristics. Ann. Zool. Fenn. 22, 315–318.

Hansson, L., 1990. Mineral selection in microtine populations. Oikos 59, 213–224.

Hansson, L., 1991. Bark consumption by voles in relation to mineral contents. J. Chem. Ecol. 17, 735–743.

Hilborn, R., Redfield, J.A., Krebs, C.J., 1976. On the reliability of mark and recapture census of voles. Can. J. Zool. 54, 1019–1024.

Hines, R., 1997. Rodent damage control in no-till corn and soybean production. In: Armstrong, E.B. (Ed.), Proceedings of the East. Wildl. Damage Management Conference, Vol. 7, pp. 195–201.

Howard, W.E., 1967. Biological control of vertebrates. Proc. Vertebr. Pest Conf. 3, 137–157.

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.

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

Krebs, C.J., Gilbert, B.S., Boutin, S., Sinclair, A.R.E., Smith, J.N.M., 1986. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon, 1976–1984. J. Anim. Ecol. 55, 963–982.

Likens, G.E., Borman, E.H., 1970. Chemical Analysis of Plant Tissues from the Hubbard Brook Ecosystem in New Hampshire. Yale University School of Forestry, Bull. No. 79, 25 pp.

Lindroth, R.L., Batzli, G.O., 1984. Plant phenolics as chemical defenses: effects of natural phenolics on survival and growth of prairie voles (*Microtus ochrogaster*). J. Chem. Ecol. 10, 229–244.

Martell, A.M., 1981. Food habits of southern red-backed voles (*Clethrionomys gapperi*) in northern Ontario. Can. Field-Nat. 95, 325–328.

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

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

Noller, C.R., 1966. Textbook of Organic Chemistry. W.B. Saunders Co., Philadelphia, PA. 760 pp.

Ostfeld, R.S., 1985. Limiting resources and territoriality in microtine rodents. Amer. Nat. 126, 1–15.

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

Sartz, R.S., 1970. Mouse damage to young plantations in south-western Wisconsin. J. For. 66, 88–89.

Seber, G.A.F., 1982. The Estimation of Animal Abundance and Related Parameters, 2nd Edition. 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. Sinica 5, 263–267.

Sullivan, T.P., 1979. The use of alternative foods to reduce conifer seed predation by the deer mouse (*Peromyscus maniculatus*). J. Appl. Ecol. 16, 475–495.

Sullivan, T.P., Harestad, A.S., Wikeem, B.M., 1990. Control of mammal damage. In: Lavender, D.P., Parish, R.P., 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, pp. 302–318.

Sullivan, T.P., Klenner, W., 1993. Influence of diversionary food on red squirrel populations and damage to crop trees in young lodgepole pine forest. Ecol. Applica. 3, 708–718.

Sullivan, T.P., Krebs, C.J., 1981. *Microtus* population biology: demography of *M. oregoni* in southwestern British Columbia. Can. J. Zool. 59, 2092–2102.

Sullivan, T.P., Martin, W.L., 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., Nowotny, C., Lautenschlager, R.A., Wagner, R.G., 1998a. Silvicultural use of herbicide in sub-boreal spruce forest: implications for small mammal population dynamics. J. Wildl. Manage. 62, 1196–1206.

Sullivan, T.P., Sullivan, D.S., 1982. The use of alternative foods to reduce lodgepole pine seed predation by small mammals. J. Appl. Ecol. 19, 33–45.

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., 2000. Influence of variable retention harvests on forest ecosystems: II. Vole (*Microtus spp. and Clethrionomys gapperi*) population dynamics and forest regeneration. J. Appl. Ecol., submitted for publication.

Sullivan, T.P., Sullivan, D.S., Hogue, E.J., Lautenschlager, R.A., Wagner, R.G., 1998b. Population dynamics of small mammals in relation to vegetation management in orchard agroecosystems: compensatory responses in abundance and biomass. Crop Prot. 17, 1–11.

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.

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 Mammal., Boston, MA, pp. 567–620.

Van Horne, B., 1982. Demography of the long-tail vole *Microtus longicaudus* in seral stages of coastal coniferous forest, southeast Alaska. Can. J. Zool. 60, 1690–1709.

Zar, J.H., 1984. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, NJ, USA.