

Influence of a granivorous diversionary food on population dynamics of montane voles (*Microtus montanus*), deer mice (*Peromyscus maniculatus*), and western harvest mice (*Reithrodontomys megalotis*)

Thomas P. Sullivan*, Druscilla S. Sullivan

Applied Mammal Research Institute, RR#3, Site 46, Comp.18, 11010 Mitchell Avenue, Summerland, BC, Canada V0H 1Z0

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Abstract

Feeding damage to forest and agricultural crops by voles of the genera *Microtus* and *Clethrionomys* occurs periodically in temperate and boreal ecosystems. Application of diversionary food is an alternative management practice that does not rely on a reduction in the target population. This study tested two hypotheses that a granivorous diversionary food, sunflower seeds, would (1) reduce feeding damage to tree seedlings by montane voles (*Microtus montanus*) without enhancing abundance or other population attributes and (2) enhance population dynamics of non-target deer mice (*Peromyscus maniculatus*) and western harvest mice (*Reithrodontomys megalotis*) in old field habitats at Summerland, British Columbia, Canada in 1993–1995. Small mammal populations were intensively live-trapped on replicate control and food sites pre- and post-treatment in two (A and B) experiments (food application rates of 68.1 and 113.5 kg/ha). Mean abundance and recruitment of voles/ha were similar between control and treatment sites. Mean abundance and recruitment of deer mice was higher on treatment than control sites in Experiment B but not in A. Mean abundance and recruitment of western harvest mice was similar between control and treatment sites. Overall survival (28-day), early juvenile survival, and body mass showed no patterns for any of the species when comparing control and treatment sites. This granivorous diversionary food did not reduce feeding damage by voles to lodgepole pine (*Pinus contorta*) seedlings. The supply of sunflower seed was likely insufficient to divert voles from feeding on trees through the overwinter (5–6 months) period. The predicted increase in numbers of deer mice and western harvest mice appeared only as brief pulses of animals, and hence may not have increased the intensity of competition with voles.

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1. Introduction

The problem of feeding damage to forest and agricultural crops by herbivorous small mammals has a long history in temperate and boreal ecosystems of North America and Eurasia (Moore, 1940; Myllymäki, 1977; Byers, 1984; Getz, 1985; Conover, 2002). In forestry, voles of the genera *Microtus* and *Clethrionomys* are considered the major mammalian species affecting coniferous and deciduous tree plantations in North America (Sartz, 1970; Radvanyi, 1980; Bergeron and

Jodoin, 1989; Sullivan et al., 1990), Europe (Hansson, 1985, 1991), and Asia (Shu, 1985; Sullivan et al., 1991). Populations of some species of voles tend to have cyclic fluctuations in abundance in northern latitudes (Krebs and Myers, 1974; Taitt and Krebs, 1985; Korpimäki and Krebs, 1996; Boonstra et al., 1998). It is primarily during overwinter periods when high populations of these microtines feed on plantation trees. Voles feed on bark, vascular tissues (phloem and cambium), and sometimes roots of trees. Direct mortality may result from girdling and clipping of tree stems.

Abundance of *Microtus* populations and degree of damage is usually highest in early successional habitats that develop after forest harvesting by clearcutting (Hansson, 1989, 1991; Sullivan and Sullivan, 2001;

*Corresponding author. Tel.: +1-250-494-7160;
fax: +1-250-494-7260.

E-mail address: Sullivan@telus.net (T.P. Sullivan).

Sullivan et al., 2001) and in old fields (perennial grasslands) undergoing afforestation (Radvanyi, 1980; Bergeron and Jodoin, 1989; Ostfeld and Canham, 1993; Ostfeld et al., 1997). Grasses, herbs, and shrubs in these habitats provide food and cover for voles (Batzli, 1985; Ostfeld, 1985). Deer mice (*Peromyscus maniculatus*) and western harvest mice (*Reithrodontomys megalotis*) commonly occur with *Microtus* spp. in old field habitats (Krebs, 1979; Dueser et al., 1981; Sullivan and Krebs, 1981; Webster and Jones, 1982; Schweiger et al., 2000; Manson et al., 2001; Pearson et al., 2001). Neither of these species damages trees because their feeding activities are granivorous and insectivorous (Baker, 1968; Whitaker and Mumford, 1972; Webster and Jones, 1982).

Application of diversionary food is an alternative management practice that has shown promise in alleviating damage to forest and agricultural crops by montane (*M. montanus*) and long-tailed (*M. longicaudus*) voles without the detrimental side effects of toxicants that are used to reduce the target pest population (Sullivan and Sullivan, 1988; Sullivan et al., 2001). These diversionary food studies used “bark mulch logs” to provide an overwinter food source for voles that would be more palatable than apple trees (*Malus domestica*) or planted lodgepole pine (*Pinus contorta*) seedlings, but of a similar or lower nutritive value than natural foods. The objective was to provide an artificial diversionary food that would be more palatable than tree bark and vascular tissues but not be nutritious enough to maintain or increase population size of voles.

Another source of diversionary food is sunflower seeds (*Helianthus annuus*) which are readily eaten by most species of rodents. Provision of sunflower seeds has reduced conifer seed predation by the deer mouse and bark stripping by red squirrels (*Tamiasciurus hudsonicus*) (Sullivan and Sullivan, 1982; Sullivan and Klenner, 1993). However, several studies using sunflower seeds and other grains as supplemental foods have recorded positive effects on abundance and related demographic attributes of vole populations (Cole and Batzli, 1978; Taitt and Krebs, 1981; Boutin, 1990). Thus, what would be the response of montane vole populations in old field habitat to provision of sunflower seeds as a diversionary food? A secondary question concerns what effect this food will have on deer mice and western harvest mice and their potential interaction with montane voles?

This study was designed to test the hypotheses that provision of sunflower seeds would (1) reduce feeding damage to lodgepole pine seedlings by montane voles without enhancing abundance or other population attributes and (2) enhance the population dynamics of deer mice and western harvest mice in this small mammal community.

2. Methods

2.1. Study area

This study was conducted at the Pacific Agri-Food Research Center in the Okanagan Valley, Summerland, BC, Canada (49°34'N: 119°40'W). Four “old field” habitats were abandoned (≥ 25 years) hay fields composed of crested wheatgrass (*Agropyron cristatum*), quack grass (*A. 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 sites were each 2–3 ha in area within a 400-ha mosaic of sagebrush (*Artemisia tridentata*), ponderosa pine (*Pinus ponderosa*) forest, vineyards, and tree fruit orchard habitats. These old fields had resident populations of montane voles which were the major rodent species with a long history of fluctuating populations and feeding damage to trees. The deer mouse and western harvest mouse were two other common species. The Great Basin pocket mouse (*Perognathus parvus*), northwestern chipmunk (*Tamias amoenus*), and long-tailed vole (*M. longicaudus*) were also present in variable numbers.

2.2. Experimental design

Four sites were chosen for study. Two experiments (A and B) were conducted using these sites, with Experiment B following the year after Experiment A. Each experiment followed the same design and applied two treatments, a control and diversionary food. Two sites were randomly assigned to each treatment in Experiment A. The sites receiving treatment and control in Experiment A were reversed for Experiment B. Each of the four sites was observed for two time periods, prior to treatment and post-treatment. Thus, the experimental design follows a two-factor repeated measures data structure where period is the repeated factor. All sites were relatively interspersed, being 150–335 m apart, and hence were considered statistically independent and represented true replicates (Hurlbert, 1984).

2.3. Small mammal populations

All animals were live-trapped on 1-ha grids with 49–50 (7×7) or (5×10) trap stations located at 14.3-m intervals with 1 or 2 Longworth live-traps at each station. One grid was located on each of the four sites. In Experiment A, the grids were live-trapped at 3-week intervals from May to October 1993 and at 3- to 4-week intervals from November 1993 to April 1994. In Experiment B, the grids were live-trapped at 3-week

intervals from May to October 1994 and at 3- to 8-week intervals from November 1994 to April 1995. There were two periods in Experiment A: pre-treatment (May–November 1993) and post-treatment (December 1993–April 1994); and two periods in Experiment B: pre-treatment (May–November 1994) and post-treatment (December 1994–May 1995).

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, and breeding condition noted. They were weighed on Pesola spring balances, and the point of capture was recorded. The duration of the breeding season was noted by palpation of male testes and the condition of mammarys of the females (Krebs et al., 1969). A pregnancy was considered successful if a female was lactating during the period following the estimated time of birth of a litter. Animals were released on the grids immediately after processing.

2.4. Population dynamics

Demographic attributes were measured for populations of montane voles, deer mice, and western harvest mice on all sites. Trappability was estimated by the Jolly calculation (Krebs and Boonstra, 1984). Population densities were estimated by the Jolly–Seber (J–S) model (Seber, 1982). The J–S model provides the best estimate of population size for mark and recapture data when trappability values are generally <70% (Hilborn et al., 1976). This model has a considerably lower negative bias than minimum number of animals known to be alive (MNA) (Krebs, 1966) under conditions of unequal trappability (Jolly and Dickson, 1983). The MNA value was used for the first and last trapping periods when the J–S estimate was not calculated. Recruits were defined as new animals that entered the population through reproduction and immigration.

The proportion of female animals in breeding condition was derived from the sample of animal captures in each trapping session and then summed for each period. Early juvenile survival is an index relating recruitment of young into the trappable population to the number of lactating females (Krebs, 1966). A modified version of this index is number of juvenile animals at week t divided by the number of lactating females caught in week $t-3$. Mean survival rates (28-day) were estimated from the J–S model. Mean body mass of male and female animals for each of the three main species was used as an index of condition within these populations.

Mass at sexual maturity was used to determine age classes of animals. The percentage of sexually mature animals was used to determine the mass limitations for

juveniles, subadults, and adults assuming that juveniles were seldom, if ever, sexually mature; that <50% of the subadults in the upper mass class were mature; and that at least 50% of the adults were sexually mature in the lowest mass class. Animals were classified as “young” (includes juvenile and subadult classes pooled) or “adult” by body mass: montane voles; young 1–26 g, adult ≥ 27 g; deer mice; young 1–20 g, adults ≥ 21 g; western harvest mice; young 1–10 g, adults ≥ 11 g.

2.5. Diversionary food

In Experiment A, diversionary food in the form of sunflower seeds were manually spread at a rate of 68.1 kg per ha on each of the two 1.3-ha treatment (1.0 ha live-trapping grid and 0.3 ha buffer) sites on November 13, 1993, and again on February 20, 1994. Ten 1.0-m² quadrats were randomly located on each treatment site to provide a measure of seed predation. The locations of 15–25 sunflower seeds per quadrat were marked with wooden toothpicks, placed approximately 0.5 cm from each seed. These quadrats were sampled at each trapping period to measure seed survival in the post-treatment period. Remains of eaten sunflower seeds or disappearance of the seed was recorded as predation by seed-eating rodents. The rate of seed loss was a measure of predation rate, but seed remains could not be identified to a rodent species.

In Experiment B, sunflower seeds were spread manually at a rate of 113.5 kg per ha on each of the two 1.3-ha treatment sites on November 16, 1994, and again on January 16, 1995. Thus, there was 1.67 times as much diversionary food available to the rodent community in Experiment B than in A and this difference corresponded to the relatively higher numbers of montane voles in 1994–1995 than in 1993–1994. Ten quadrats to measure seed predation were set up in an identical manner as in Experiment A for each of the two seed application events in Experiment B.

2.6. Tree seedlings

Lodgepole pine seedlings (one-year old nursery raised) were planted in four groups of 100 (10 × 10) trees, one group in each corner of each trapping grid, for a total of 400 seedlings per control or treatment site. Trees were planted on November 11–12, 1993 (Experiment A) and on November 18–23, 1994 (Experiment B) at a density of 1100 per ha which was within the density range of new plantations of pine in the interior of British Columbia.

One hundred sample trees were randomly chosen from the 400 planted seedlings on each control and treatment site. These trees were sampled for overwinter clipping of terminal or lateral shoots and gnawing of terminal shoots in April 1994 (Experiment A) and April

1995 (Experiment B). These types of feeding damage to terminal shoots were considered mortality since seedlings rarely, if ever, recover. Incidence of damage was categorized as percentage mortality of trees overall and on a per vole basis. This latter calculation was based on the population estimate of voles for November each year, prior to the start of each experiment.

2.7. Statistical analysis

A repeated measures analysis of variance (RM-ANOVA) was used to determine, for each experiment, the effect of diversionary food on mean abundance, mean number of recruits, mean index of early juvenile survival, mean 28-day J–S survival, and mean body mass for each species between control and treatment sites. Mauchly's W -test statistic was used to test for sphericity (independence of data among repeated measures) (Littel, 1989; Kuehl, 1994). There were no autocorrelations detected in these data sets. Mean Jolly trappability was evaluated by 95% confidence intervals (CI) for animals in control and treatment sites. The mean percentage mortality of tree seedlings from feeding damage by voles, both overall and per vole, were analyzed with a one-way ANOVA model. Arcsine transformations were performed to fit proportional data to a normal distribution (Zar, 1999). In all analyses, the level of significance was at least $P = 0.05$.

3. Results

3.1. Abundance and recruitment

Totals of individual animals captured in this study were 2142 montane voles, 1289 deer mice, and 347 western harvest mice. Mean trappability (susceptibility to capture) of montane voles ranged from 48.8% to 81.6% in the two experiments with no differences (overlapping 95% CI) between controls and treatments. Mean trappability for deer mice ranged from 33.3% to 75.3% with no differences between controls and treatments. Estimates of mean trappability for western harvest mice were highly variable ranging from a low of 20.0% to a high of 100.0% and wide confidence intervals in several cases.

Mean abundance of voles was similar between control and treatment sites in both experiments, with mean numbers/ha ranging from 12.9 to 91.2 in Experiment A and from 70.8 to 161.6 in Experiment B (Table 1). Mean recruitment of voles was significantly ($F_{1,2} = 21.65$; $P = 0.04$) higher in treatment than control sites in Experiment A but there was no difference between these sites in Experiment B (Table 2). The interaction term in Experiment A was not significant which indicates that the difference in mean number of vole recruits was likely related to pre-treatment population conditions rather than to the diversionary food treatment.

Table 1

Mean ($n = 2$) $\pm$ SE abundance per ha of small mammal species for control and treatment sites in each of Experiments A and B and results of RM-ANOVA

Species and period	Control	Treatment	Overall analysis					
			Treatment		Time		Treatment $\times$ time	
			$F_{1,2}$	P	$F_{1,2}$	P	$F_{1,2}$	P
<i>Experiment A</i>								
<i>Microtus montanus</i>			4.23	0.18	11.35	0.08	1.43	0.35
Pre-T	12.9 $\pm$ 8.3	39.6 $\pm$ 11.3						
Post-T	61.6 $\pm$ 1.1	91.2 $\pm$ 9.4						
<i>Peromyscus maniculatus</i>			0.35	0.61	18.52	0.05	2.45	0.26
Pre-T	28.1 $\pm$ 21.0	8.0 $\pm$ 2.3						
Post-T	45.5 $\pm$ 16.0	45.6 $\pm$ 9.7						
<i>Reithrodontomys megalotis</i>			0.70	0.49	192.42	< 0.01	14.18	0.06
Pre-T	4.4 $\pm$ 4.1	10.0 $\pm$ 0.9						
Post-T	29.2 $\pm$ 23.5	32.0 $\pm$ 8.0						
<i>Experiment B</i>								
<i>Microtus montanus</i>			4.96	0.16	9.78	0.09	9.42	0.09
Pre-T	161.6 $\pm$ 18.9	75.3 $\pm$ 3.7						
Post-T	70.8 $\pm$ 3.0	77.1 $\pm$ 19.6						
<i>Peromyscus maniculatus</i>			65.93	0.02	1.20	0.39	1.60	0.33
Pre-T	51.7 $\pm$ 2.0	64.8 $\pm$ 2.3						
Post-T	51.3 $\pm$ 6.2	80.1 $\pm$ 3.6						
<i>Reithrodontomys megalotis</i>			0.55	0.54	0.95	0.43	0.88	0.45
Pre-T	3.4 $\pm$ 1.6	4.7 $\pm$ 1.8						
Post-T	3.3 $\pm$ 1.3	8.2 $\pm$ 5.3						

Pre-T = pre-treatment; Post-T = post-treatment.

Table 2

Mean ($n = 2$) $\pm$ SE recruitment per ha of small mammal species for control and treatment sites in each of Experiments A and B and results of RM-ANOVA

Species and period	Control	Treatment	Overall analysis					
			Treatment		Time		Treatment $\times$ time	
			$F_{1,2}$	P	$F_{1,2}$	P	$F_{1,2}$	P
<i>Experiment A</i>								
<i>Microtus montanus</i>			21.65	0.04	2.64	0.25	0.22	0.69
Pre-T	6.2 $\pm$ 2.8	13.2 $\pm$ 3.3						
Post-T	16.2 $\pm$ 6.5	22.1 $\pm$ 0.1						
<i>Peromyscus maniculatus</i>			0.03	0.89	14.92	0.06	4.05	0.18
Pre-T	7.5 $\pm$ 3.9	4.2 $\pm$ 0.6						
Post-T	9.3 $\pm$ 2.0	12.5 $\pm$ 2.9						
<i>Reithrodontomys megalotis</i>			0.18	0.71	9.94	0.09	11.09	0.08
Pre-T	2.2 $\pm$ 1.9	3.8 $\pm$ 0.6						
Post-T	5.6 $\pm$ 4.0	3.7 $\pm$ 0.4						
<i>Experiment B</i>								
<i>Microtus montanus</i>			4.64	0.16	15.56	0.06	0.99	0.42
Pre-T	42.0 $\pm$ 0.9	23.4 $\pm$ 0.7						
Post-T	17.9 $\pm$ 3.6	14.5 $\pm$ 4.3						
<i>Peromyscus maniculatus</i>			396.48	<0.01	3.80	0.19	13.21	0.07
Pre-T	12.8 $\pm$ 2.2	17.5 $\pm$ 2.3						
Post-T	4.5 $\pm$ 0.8	23.8 $\pm$ 0.8						
<i>Reithrodontomys megalotis</i>			0.19	0.71	0.24	0.67	1.42	0.36
Pre-T	2.1 $\pm$ 1.1	2.0 $\pm$ 0.6						
Post-T	1.6 $\pm$ 0.4	2.9 $\pm$ 1.4						

Pre-T = pre-treatment; Post-T = post-treatment.

Mean abundance of deer mice was similar between control and treatment sites in Experiment A, but with numbers increasing significantly ($F_{1,2} = 18.52$; $P = 0.05$) with time; mean numbers/ha ranged from 8.0 to 45.6/ha (Fig. 1a, Table 1). However, in Experiment B, mean abundance of deer mice was significantly ($F_{1,2} = 65.93$; $P = 0.02$) higher on treatment than control sites with mean numbers ranging from 51.3 to 80.1 animals/ha (Fig. 1a, Table 1). Mean recruitment of deer mice was similar on control and treatment sites in Experiment A, but was significantly ($F_{1,2} = 396.48$; $P < 0.01$) higher on treatment than control sites in Experiment B (Table 2). Mean recruitment of new deer mice increased from 17.5 to 23.8/ha on treatment sites while declining from 12.8 to 4.5/ha on control sites in Experiment B. Comparing post- to pre-treatment periods in Experiment A, there was, on average, 2.96 times as many new deer mice appearing on sites with sunflower seeds than on those (1.23 times) with no diversionary food (Table 2).

Mean abundance of western harvest mice was similar between control and treatment sites during both experiments, with mean numbers/ha ranging from 4.4 to 32.0 in Experiment A and from 3.3 to 8.2 in Experiment B (Fig. 1b, Table 1). Mean recruitment of harvest mice also followed this pattern, ranging overall from 1.6 to 5.6 mice per ha (Table 2).

3.2. Survival

Mean index of early juvenile survival was similar between control and treatment sites for each of the three small mammal species (Table 3). These indices were generally higher in the pre- than post-treatment periods since the majority of breeding occurred during summer and fall months.

Mean J–S survival of montane voles was similar between control and treatment sites, ranging from 0.72 to 0.78 in Experiment A and from 0.57 to 0.80 in Experiment B (Table 4). Deer mice exhibited a similar pattern as voles, with mean survival ranging from 0.69 to 0.80 in both experiments (Table 4). Mean survival of the western harvest mouse was also similar, and highly variable between control and treatment sites, ranging from 0.56 to 0.87 in Experiment A and from 0.40 to 0.74 in Experiment B (Table 4).

3.3. Body mass

Mean ($\pm$ SE) body mass of male and female montane voles was generally similar between control and treatment sites, except for a significantly ($F_{1,2} = 906.47$; $P < 0.01$) higher mean mass of females voles in treatment ($\bar{x} = 32.6 \pm 0.6$ g) than control ($\bar{x} = 24.3 \pm 0.6$ g) sites in Experiment B. A similar pattern of no consistent

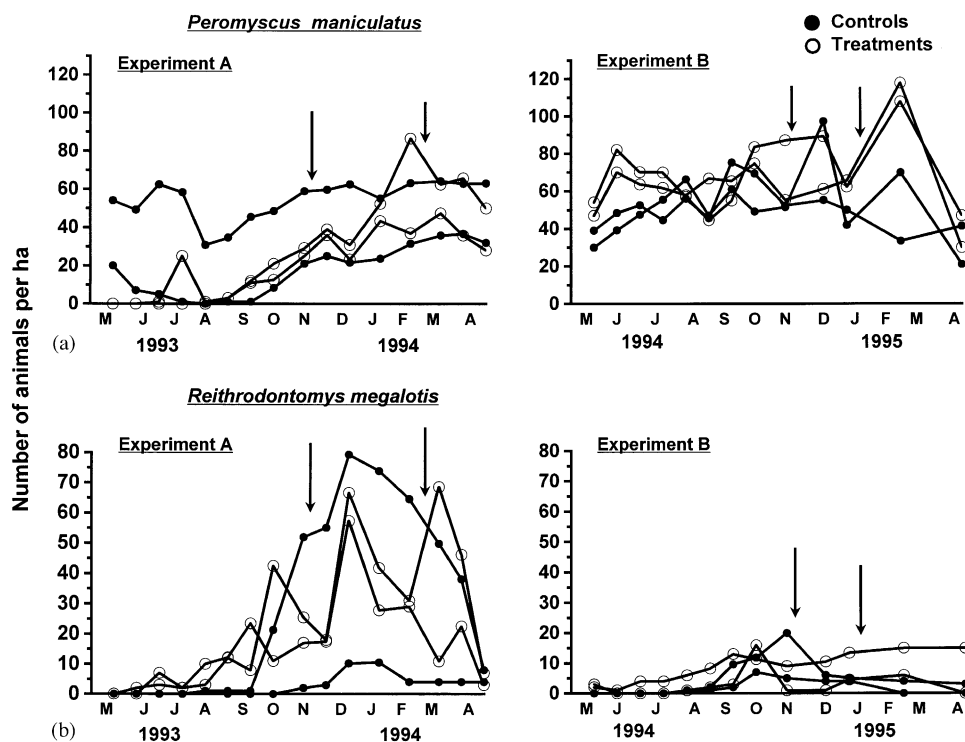


Fig. 1. Population density (Jolly-Seber) per ha of (a) *Peromyscus maniculatus* and (b) *Reithrodontomys megalotis* in the replicate control and treatment sites for each of Experiments A and B. Seed applications indicated by vertical arrows.

Table 3

Mean ($n = 2$) $\pm$ SE index of early juvenile survival per ha of small mammal species for control and treatment sites in each of Experiments A and B and results of RM-ANOVA

Species and period	Control	Treatment	Overall analysis					
			Treatment		Time		Treatment $\times$ time	
			$F_{1,2}$	P	$F_{1,2}$	P	$F_{1,2}$	P
<i>Experiment A</i>								
<i>Microtus montanus</i>			1.56	0.34	42.88	0.02	8.13	0.10
Pre-T	5.75 $\pm$ 1.25	2.28 $\pm$ 1.11						
Post-T	0.62 $\pm$ 0.12	0.81 $\pm$ 0.12						
<i>Peromyscus maniculatus</i>			46.34	0.02	9.43	0.09	12.03	0.07
Pre-T	1.13 $\pm$ 0.07	18.88 $\pm$ 9.13						
Post-T	1.34 $\pm$ 0.16	1.75 $\pm$ 0.25						
<i>Reithrodontomys megalotis</i>			6.71	0.12	1.25	0.38	0.56	0.53
Pre-T	0	2.85 $\pm$ 0.30						
Post-T	1.91 $\pm$ 1.91	3.66 $\pm$ 1.10						
<i>Experiment B</i>								
<i>Microtus montanus</i>			9.67	0.09	60.85	0.02	11.14	0.08
Pre-T	1.07 $\pm$ 0.10	1.14 $\pm$ 0.04						
Post-T	0	0.65 $\pm$ 0.21						
<i>Peromyscus maniculatus</i>			56.67	0.02	0.23	0.68	0.01	0.94
Pre-T	5.75 $\pm$ 1.75	2.67 $\pm$ 0.11						
Post-T	6.25 $\pm$ 0.75	2.92 $\pm$ 0.14						
<i>Reithrodontomys megalotis</i>			0.06	0.83	4.93	0.16	0.06	0.83
Pre-T	9.00 $\pm$ 9.00	4.75 $\pm$ 1.25						
Post-T	0	0						

Pre-T = pre-treatment; Post-T = post-treatment.

Table 4

Mean ($n = 2$) $\pm$ SE Jolly–Seber 28-day survival per ha of small mammal species for control and treatment sites in each of Experiments A and B and results of RM-ANOVA

Species and period	Control	Treatment	Overall analysis					
			Treatment		Time		Treatment $\times$ time	
			$F_{1,2}$	P	$F_{1,2}$	P	$F_{1,2}$	P
<i>Experiment A</i>								
<i>Microtus montanus</i>			3.42	0.21	0.42	0.58	0.00	0.99
Pre-T	0.72 $\pm$ 0.06	0.74 $\pm$ 0.01						
Post-T	0.74 $\pm$ 0.04	0.78 $\pm$ 0.03						
<i>Peromyscus maniculatus</i>			1.86	0.31	0.86	0.45	0.20	0.70
Pre-T	0.78 $\pm$ 0.01	0.69 $\pm$ 0.08						
Post-T	0.80 $\pm$ 0.04	0.76 $\pm$ 0.01						
<i>Reithrodontomys megalotis</i>			0.00	0.96	2.45	0.26	0.10	0.78
Pre-T	0.59 $\pm$ 0.30	0.56 $\pm$ 0.11						
Post-T	0.83 $\pm$ 0.05	0.87 $\pm$ 0.07						
<i>Experiment B</i>								
<i>Microtus montanus</i>			0.05	0.84	259.00	<0.01	252.23	<0.01
Pre-T	0.68 $\pm$ 0.02	0.80 $\pm$ 0.04						
Post-T	0.68 $\pm$ 0.04	0.57 $\pm$ 0.04						
<i>Peromyscus maniculatus</i>			0.08	0.81	1.76	0.32	0.19	0.70
Pre-T	0.79 $\pm$ 0.02	0.80 $\pm$ 0.05						
Post-T	0.73 $\pm$ 0.09	0.69 $\pm$ 0.01						
<i>Reithrodontomys megalotis</i>			9.40	0.09	2.04	0.29	0.22	0.69
Pre-T	0.40 $\pm$ 0.02	0.59 $\pm$ 0.01						
Post-T	0.49 $\pm$ 0.14	0.74 $\pm$ 0.07						

Pre-T = pre-treatment; Post-T = post-treatment.

differences in mean body mass between control and treatment sites was recorded for deer mice and western harvest mice in both experiments.

3.4. Diversionary food and tree seedlings

Sunflower seed was readily consumed on treatment sites in both experiments, with re-application needed by mid-February 1994 in Experiment A and by mid-January 1995 in Experiment B (Table 5). Sunflower seed was essentially exhausted by April in both years.

Mean ($\pm$ SE) overwinter consumption (%) of lodgepole pine seedlings by voles, in both experiments combined, was significantly ($F_{1,5} = 13.40$; $P = 0.01$) higher on treatment (33.7 ± 4.2) than control (12.5 ± 3.7) sites. This pattern was also recorded for a significantly ($F_{1,5} = 6.33$; $P = 0.05$) higher mean percentage of trees eaten per vole on treatment than control sites.

4. Discussion

This study is the first evaluation of the influence of a granivorous diversionary food on vole populations and feeding damage to tree seedlings. Although our vole populations did not increase on treatment sites in response to sunflower seed, populations of *Microtus* in

supplemented food studies have responded positively with increases in abundance (Cole and Batzli, 1978; Taitt and Krebs, 1981; Desy and Thompson, 1983). Numbers of *Microtus* may increase 2–5 times on food-supplemented compared with control sites, particularly if a reasonably nutritious food source is used (Boutin, 1990). This response pattern is likely crucial to rodent-feeding damage problems since many small mammal populations in temperate regions appear to be food limited (Boutin, 1990).

Sunflower seeds are a highly nutritious food (Mrosovsky, 1966), comparable to the energy content of tree seeds of several coniferous species (Smith, 1968), and voles will readily eat them as do the seed-eating deer mouse and western harvest mouse. The lack of increase in abundance and related demographic parameters of voles is perhaps not surprising since seed was applied only twice during each of the two overwinter experiments. This level of food provision falls considerably short of that in many supplemental food studies where food is often available to the target animal ad libitum and sometimes for several years (Boutin, 1990). The period of feeding damage by voles to tree seedlings in temperate zone forests is primarily from October to April, a 5–6 month interval during which a diversionary food must presumably be in constant supply. It seems unlikely that we met this requirement in our study. In addition, populations of deer mice and western harvest

Table 5

Percentage survival of sunflower seeds on treatment sites in Experiments A and B. Each treatment site had 10 1-m² quadrats with 15–25 marked seeds to assess seed survival

Sample date	Experiment A		Sample date	Experiment B	
	Treatment-1	Treatment-2		Treatment-1	Treatment-2
Nov. 12, 1993	100.0	100.0	Nov. 16, 1994	100.0	100.0
Dec. 3, 1993	85.3	67.3	Dec. 17, 1994	42.8	30.6
Dec. 21, 1993	50.7	51.3	Jan. 4, 1995	13.9	Snow
Jan. 22, 1994	28.7	36.7	Jan. 16, 1995	10.5	18.3
Feb. 19, 1994	0.7	11.3			
Seed re-applied			Seed re-applied		
Feb. 20, 1994	100.0	100.0	Jan. 16, 1995	100.0	100.0
Mar. 20, 1994	26.0	41.3	Feb. 8, 1995	46.7	0.0
Apr. 4, 1994	13.3	6.0	Mar. 13, 1995	6.8	0.0
Apr. 24, 1994	2.7	2.7	Apr. 24, 1995	0.0	0.0

mice made up 46.9% of the small mammal community on treatment sites, at least in terms of numbers of individual animals.

In other studies using sunflower seeds as a diversionary food, red squirrel and deer mouse populations either changed little or increased in abundance only temporarily on food-supplemented areas (Sullivan and Sullivan, 1982; Sullivan and Klenner, 1993). In both these cases, feeding damage was significantly reduced in the presence of diversionary food. However, the damage period was 8–10 weeks for red squirrels (vascular tissues of lodgepole pine) and 4–6 weeks for deer mice (conifer seed) during spring. Thus, if the damage period is relatively short and predictable, a “pulse” of highly nutritious food such as sunflower seeds may effectively reduce feeding damage. If long periods of feeding are required to divert animals away from the crop to be protected, either the target population may increase substantially or the food supply may be temporarily exhausted.

The higher mortality of tree seedlings on the diversionary food sites was somewhat surprising. However, the supply of sunflower seeds may have been rapidly depleted in at least some localized patches on the treatment sites. This depletion of a diversionary food potentially leading to higher seedling mortality was also recorded by Sullivan et al. (2001). Thus, a prediction of hypothesis (1) that sunflower seeds would reduce feeding damage by voles to tree seedlings is not supported by our results. However, the associated prediction that sunflower seeds would not enhance abundance or other population attributes of voles appears to be partially supported, except for higher mean body mass of female voles on treatment sites in Experiment B, at least for this level and period of provision of a granivorous diversionary food.

Although mean abundance of deer mice in Experiment A and western harvest mice in both experiments

did not change in response to diversionary food, there were some temporary increases in numbers for both species immediately following seed application (Figs. 1a and b). These “pulses” of animals were reflected in the higher recruitment of new deer mice on treatment sites. The highly variable numbers of western harvest mice was similar to that reported for this species in a long-term study in Arizona (Skupski, 1995). Associated demographic attributes did not change in any clear way in response to diversionary food for either of these nontarget species. Thus, except for the brief “pulses” of animals, the prediction of hypothesis (2), that diversionary food would enhance the population dynamics of these two species, was not supported.

It was likely that the period of food addition was too brief to cause a persistent change in abundance for these nontarget species. Other longer-term food supplementation studies with deer mice have documented substantial increases in density as a result of food addition (Fordham, 1971; Gilbert and Krebs, 1981; Taitt, 1981). Similarly, early maturity and increased growth of individual animals has also been a common response to supplemental food (Bendell, 1959; Cole and Batzli, 1978; Hansen and Batzli, 1978; Taitt, 1981).

Sullivan and Klenner (1993) reported temporary increases in abundance of northwestern chipmunks (*Tamias amoenus*) and Columbian ground squirrels (*Spermophilus columbianus*) in response to sunflower seeds used as a diversionary food for red squirrels. Those ephemeral population increases and the “pulses” recorded in our study may have several implications for the use of diversionary food as a management tool. First, such increases may increase competitive interactions between voles and nontarget species. Both the western harvest mouse (Heske et al., 1984) and the deer mouse (Grant, 1972; Redfield et al., 1977) compete with *Microtus* in old field habitats, with the potential to at least partially inhibit the productivity of vole

populations. Competition between deer mice and western harvest mice is less likely since these species appear to utilize somewhat different microhabitats (Kaufman et al., 1988). Secondly, the overall abundance of small mammal species in diversionary food sites may enhance predator populations, possibly shifting predation onto the target population of voles.

Our study had two true replicates (Hurlbert, 1984) of control and treatment sites in each of two experiments conducted in successive years. Because the control and treatment sites were interchanged between Experiments A and B, there was the possibility that a latent effect of the diversionary food treatment might have influenced the control populations in Experiment B. However, the sunflower seeds in Experiment A were completely exhausted by late April 1994 which suggested that carry-over effects into the subsequent summer were unlikely on those sites. There were several species of seed-eating birds such as the dark-eyed junco (*Junco oreganus*) and black-capped chickadee (*Parus atricapillus*) that occurred in our general study area. Although these birds were not observed feeding on sunflower seeds during sampling times, their potential consumption of at least some seeds cannot be ruled out.

The higher level of mortality to seedlings on treatment than control sites was likely an artifact of a very low incidence of feeding pressure. The high-density (up to 280 voles/ha) populations on control sites in Experiment B ate only 7.0% and 11.0% of seedlings. This inexplicable result seemed clearly out of place since voles at such densities have consumed up to 73% of tree seedlings in these old field sites in other years (Sullivan et al., 2001). A potential remedy for this variability is additional replicates, but this was not possible in our study.

The granivorous diversionary food did not reduce feeding damage by voles to lodgepole pine seedlings. We were able to apply sunflower seeds to treatment sites prior to snow cover in the late fall (November) and again in mid-winter (January or February) because of ephemeral snow conditions in the general study area. However, if a diversionary food targeting vole populations is to be successful in areas with winter snow cover, enough food to last the winter must be in place prior to the first snowfall. There may not have been a consistent supply of seeds throughout each of the two winters of our experiments to deter voles from feeding on seedlings. In addition, the predicted increase in numbers of deer mice and western harvest mice appeared as brief pulses of animals on treatment sites, and hence may not have increased the intensity of competition with voles. As discussed by Sullivan et al. (2001), a durable and sufficient diversionary food that is effective throughout the overwinter damage period, and does not increase abundance or alter other demographic attributes of voles, would be ideal.

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References

- Baker, R.H., 1968. Habitats and distribution. In: Tamarin, R.H. (Ed.), Special Publication No. 8. American Society of Mammalogists, Boston, MA, pp. 621–646.
- Batzli, G.O., 1985. Nutrition. In: Tamarin, R.H. (Ed.), Biology of New World *Microtus*. Special Publication Number 8. American Society of Mammalogists, Boston, MA, pp. 779–811.
- Bendell, J.F., 1959. Food as a control of a population of white-footed mice. *Peromyscus leucopus noveboracensis* (Fischer). Can. J. Zool. 37, 173–209.
- 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. Hort. 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.
- Dueser, R.D., Wilson, M.L., Rose, R.K., 1981. Attributes of dispersing meadow voles in open-grid populations. Acta Theriol. 26, 139–162.
- Fordham, R.A., 1971. Field populations of deer mice with supplemental food. Ecology 52, 138–146.
- Getz, L.L., 1985. Habitats. In: Tamarin, R.H. (Ed.), Special Publication Number 8. American Society of Mammalogists, Boston, MA, pp. 286–309.
- Gilbert, B.S., Krebs, C.J., 1981. Effects of extra food on *Peromyscus* and *Clethrionomys* populations in the southern Yukon. Oecologia 51, 326–331.
- Grant, P.R., 1972. Interspecific competition among rodents. Ann. Rev. Ecol. System. 3, 79–106.
- 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 small rodents. Holarctic Ecol. 12, 345–350.
- Hansson, L., 1991. Bark consumption by voles in relation to mineral contents. J. Chem. Ecol. 17, 735–743.
- Hansen, L.P., Batzli, G.O., 1978. The influence of food availability on the white-footed mouse: populations in isolated woodlots. Can. J. Zool. 56, 2530–2541.

- Heske, E.J., Ostfeld, R.S., Lidicker Jr., W.Z., 1984. Competitive interactions between *Microtus californicus* and *Reithrodontomys megalotis* during two peaks of *Microtus* abundance. *J. Mammal.* 65, 271–280.
- 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.
- 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.
- Kaufman, G.A., Kaufman, D.W., Finck, E.J., 1988. Influence of fire and topography on habitat selection by *Peromyscus maniculatus* and *Reithrodontomys megalotis* in ungrazed tallgrass prairie. *J. Mammal.* 69, 342–352.
- 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., 1979. Dispersal, spacing behaviour, and genetics in relation to population fluctuations in the vole *Microtus townsendii*. *Fortschr. Zool.* 25, 61–77.
- Krebs, C.J., Boonstra, R., 1984. Trappability estimates for mark-recapture data. *Can. J. Zool.* 62, 2440–2444.
- 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.
- Kuehl, R.C., 1994. *Statistical Principles of Research Design and Analysis*. Duxbury Press, Belmont, CA.
- Littel, R.C., 1989. Statistical analysis of experiments with repeated measures. *Hortscience* 24, 36–40.
- Manson, R.H., Ostfeld, R.S., Canham, C.D., 2001. Long-term effects of rodent herbivores on tree invasion dynamics along forest-field edges. *Ecology* 82, 3320–3329.
- Moore, A.W., 1940. Wild animal damage to seed and seedlings on cutover Douglas fir lands of Oregon and Washington. USDA Technical Bulletin Number 706.
- Mrosovsky, N., 1966. Acceleration of annual hibernating cycle to six weeks in captive dormice. *Can. J. Zool.* 44, 903–911.
- 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., 1985. Limiting resources and territoriality in microtine rodents. *Am. Nat.* 126, 1–15.
- 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.
- Pearson, D.E., Ortega, Y.K., McKelvey, K.S., Ruggiero, L.F., 2001. Small mammal communities and habitat selection in northern Rocky Mountain bunchgrass: implications for exotic plant invasions. *Northwest Sci.* 75, 107–117.
- Radvanyi, A., 1980. Control of small mammal damage in the Alberta oil sands reclamation and afforestation program. *For. Sci.* 26, 687–702.
- Redfield, J.A., Krebs, C.J., Taitt, M.J., 1977. Competition between *Peromyscus maniculatus* and *Microtus townsendii* in grasslands of coastal British Columbia. *J. Anim. Ecol.* 46, 607–616.
- Sartz, R.A., 1970. Mouse damage to young plantations in southwestern Wisconsin. *J. For.* 66, 88–89.
- Schweiger, E.W., Diffendorfer, J.E., Holt, R.D., Pierotti, R., Gaines, M.S., 2000. The interaction of habitat fragmentation, plant, and small mammal succession in an old field. *Ecol. Monogr.* 70, 383–400.
- 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. Sin.* 5, 263–267.
- Skupski, M.P., 1995. Population ecology of the western harvest mouse, *Reithrodontomys megalotis*: a long-term perspective. *J. Mammal.* 76, 358–367.
- Smith, C.C., 1968. The adaptive nature of social organization in the genus of tree squirrels, *Tamiasciurus*. *Ecol. Monogr.* 38, 31–63.
- 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. Appl.* 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., 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., 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., 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., 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.
- 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., 1981. The effect of extra food on small rodent populations. I. Deer mice (*Peromyscus maniculatus*). *J. Anim. Ecol.* 50, 111–124.
- 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 Number 8. Amer. Soc. Mammal., Boston, MA, pp. 567–620.
- Webster, W.D., Jones Jr., J.K., 1982. *Reithrodontomys megalotis*. Mammalian Species, Number 167. American Society of Mammalogists, Provo, UT, USA.
- Whitaker, J.O., Mumford, R.E., 1972. Ecological studies on *Reithrodontomys megalotis* in Indiana. *J. Mammal.* 53, 850–860.
- Zar, J.H., 1999. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ, USA.