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WEASELS, VOLES, AND TREES: INFLUENCE OF MUSTELID SEMIOCHEMICALS ON VOLE POPULATIONS AND FEEDING DAMAGE

Thomas P. Sullivan,[1,3] Druscilla S. Sullivan,[1] Donald G. Reid,[2,4] and Maria C. Leung[2,5]

[1]*Applied Mammal Research Institute, 11010 Mitchell Avenue, R.R. #3, Site 46, Compartment 18, Summerland,*
British Columbia, Canada V0H 1Z0
[2]*Department of Forest Sciences, Faculty of Forestry, University of British Columbia, Vancouver,*
British Columbia, Canada V6T 1Z4

Abstract. The role of predators, particularly small mustelids, in regulating vole (*Microtus* spp.) populations has been the subject of much scientific inquiry over the past several decades. From a management perspective, voles cause economic damage by feeding on seedlings planted on cutover forest land in temperate and boreal zones. Because of the close relationship between small weasels (*Mustela erminea* and *M. nivalis*) and voles, could the indirect effect of weasel scent disrupt vole populations and reduce their damage to forest plantations? This study was designed to test the hypotheses that synthetic weasel odor would: (1) reduce abundance, reproduction, survival, and movement of montane (*Microtus montanus*) and meadow (*M. pennsylvanicus*) vole populations; (2) enhance the activity of small weasels; and (3) reduce feeding damage by voles to tree seedlings. Study areas were located near Summerland and Gavin Lake in south-central British Columbia, Canada. Vole populations were intensively live-trapped on replicate sites from April 1994 to May 1995 during a peak year in abundance. Synthetic weasel odor was continually present on treatment sites from early summer 1994 to spring 1995. Weasel activity was measured by the number of individuals captured in live-traps and by the number of snow tracks on control and treatment sites. Overwinter mortality to planted lodgepole pine (*Pinus contorta*) seedlings from vole feeding was measured on all sites in May 1995.

Mean vole abundance ($n = 4$) was similar between control (32–121 voles/ha) and treatment (37–118 voles/ha) sites. Montane voles declined by 17–36% on treatment sites during early summer when trappability of this species declined dramatically at Summerland. This pattern was not observed for meadow voles at Gavin Lake. Recruitment of new voles was generally similar between control and treatment sites. Weasel odor had no effect on reproduction, in terms of number of successful pregnancies and index of early juvenile survival, or on total survival, movements, or body mass of voles. Activity of small weasels appeared to be higher on treatment than control sites at Gavin Lake. Weasel odor did not reduce mortality of tree seedlings caused by vole feeding.

This study is the first investigation of the population responses of free-living voles to synthetic odor of the short-tailed weasel, a principal predator of *Microtus* spp. Our results demonstrate that by the time voles have reached high densities, it is too late to reduce numbers or curtail feeding damage, regardless of weasel odor-induced antipredatory behavior or enhanced activity of predators. Application of weasel odor during the low phase of the vole population cycle would be a critical test of the hypothesis that small mustelids could lengthen the period of low vole numbers and potentially protect forest plantations from vole damage.

Key words: abundance; feeding damage; forest plantations; Microtus *spp.;* Mustela *spp.; old field; population dynamics; predator–prey; semiochemicals; tree seedlings; voles; weasel odor.*

INTRODUCTION

Populations of some species of voles (*Microtus* spp.) tend to have cyclic fluctuations in abundance every 3–5 years in northern latitudes (Krebs and Myers 1974, Taitt and Krebs 1985, Krebs 1996). In peak years when voles are most abundant, they may feed on deciduous and coniferous seedlings planted on cutover and naturally disturbed lands in temperate and boreal forests (Cayford and Haig 1961, Sartz 1970, Hansson 1985, Bergeron and Jodoin 1989, Sullivan and Martin 1991, Sullivan et al. 1991). Damage primarily occurs during winter months when voles concentrate their feeding on the bark, vascular tissues, and roots of trees. The abundance of vole populations and degree of damage to newly planted trees are usually highest in early-suc-

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[3] E-mail: Sullivan@telus.net

[4] Present address: Ministry of Sustainable Resource Management, P.O. Box 5000, Smithers, British Columbia, Canada V0J 2N0.

[5] Present address: Wild Tracks Ecological Consulting, Smithers, British Columbia, Canada V0J 2N0.

cessional habitats that develop after forest harvesting and in old fields (perennial grasslands) undergoing afforestation (Radvanyi 1980, Bergeron and Jodoin 1989, Ostfeld and Canham 1993, Sullivan et al. 2001). Such habitats are composed of grasses, herbs, and shrubs that provide food and cover for voles. In addition to potentially serious economic loss due to the costs of replanting, there are implications of regeneration delays that may limit the planting of native tree species in certain forest ecosystems.

Much research has been conducted on the regulatory mechanisms that drive vole population cycles (Korpimäki and Krebs 1996, Krebs 1996). The role of predators in regulating rodent populations has been the subject of considerable debate over the past several decades (Pearson 1966, Hansson and Henttonen 1985, Erlinge 1987, Korpimäki et al. 1991). Generalist predators seem to play a role in regulating noncyclic rodent populations (Erlinge et al. 1984, Erlinge 1987), whereas specialist predators may regulate cyclic populations (Henttonen 1987, Hanski et al. 2001). Although enhancement of predators in newly planted forest plantations has been studied, it is unlikely that such measures have a significant effect on vole numbers (Sullivan and Sullivan 1980, Kay et al. 1994, Wolff et al. 1999, Sheffield et al. 2001).

The influence of mustelids on vole populations by direct mortality has received much attention (Erlinge 1983, Oksanen et al. 1985, Korpimäki et al. 1991, Klemola et al. 1997, Korpimäki and Norrdahl 1998). It has also been suggested that indirect effects from the presence of a predator, e.g., weasel, should influence the behavior of its potential prey, e.g., vole (Ydenberg 1987, Lima and Dill 1990, Kats and Dill 1998). Several studies in Europe have concluded that the presence of small mustelids (or their scent) may limit reproductive rates and movements of voles in terms of antipredatory behavior (Ylönen 1989, Jędrzejewski and Jędrzejewska 1990, Jędrzejewski et al. 1993, Korpimäki et al. 1994, Norrdahl and Korpimäki 1998).

Certain predator odors presumably have pheromonal properties providing a means to recognize individuals and breeding or other social status, and to mark territories for other members of that species (Erlinge 1977, Macdonald 1980). Synthetic anal gland secretions of the ferret (*Mustela furo*) and urine of the red fox (*Vulpes vulpes*) act as signaling pheromones that attract conspecifics (Whitten et al. 1980, Clapperton et al. 1988, 1989). However, these odors may also have kairomonal properties by inducing a ‘‘fear’’ response in prey species. If so, such chemical signals (semiochemicals) could be used as area repellents to protect forest plantations from voles, and potentially as attractants for predators of the same species and perhaps additional species.

Avoidance responses by field voles (*Microtus agrestis*) to predator odors, particularly those of the short-tailed weasel (or stoat, also called ermine, *Mustela erminea*) and least weasel (*M. nivalis*), were reported by Gorman (1984) and Stoddart (1976, 1980). These responses appear to be innate and presumably adaptive because they would reduce the chance that an individual vole would suffer predation (Gorman 1984). Short-tailed and least weasels are specialist predators of voles throughout their ranges in north-temperate and boreal latitudes (Hanski et al. 2001). Synthetic compounds from the anal gland secretion of the short-tailed weasel (Crump 1978, 1980) have generated avoidance responses in montane voles (*Microtus montanus*) under experimental field conditions (Sullivan et al. 1988*a*, 1990*a*).

The efficacy of semiochemicals of short-tailed weasels in actually reducing feeding damage by voles to forest and orchard trees has been somewhat mixed. In small-scale (<2-ha) trials, a mixture of synthetic anal gland compounds from this weasel reduced feeding damage to apple (*Malus domestica*) trees during peak populations of montane voles (Sullivan et al. 1988*b*). However, in experiments with coniferous trees, these same weasel compounds reduced overwinter damage by meadow voles (*Microtus pennsylvanicus*) and red-backed voles (*Clethrionomys rufocanus*), but not consistently or to levels acceptable to forest managers (Sullivan et al. 1991, Zimmerling and Zimmerling 1996). These results suggested that perhaps the experimental units were too small and the predator odor effect was too limited in area to affect voles at a population level.

There are several hypotheses concerning the predicted responses of voles to extra weasel odor: predator-induced breeding suppression (PIBS), reductions in movement, and reductions in body mass. The PIBS hypothesis suggests that there is a trade-off between survival and reproduction, whereby there is delayed breeding under high predation risk (Ruxton and Lima 1997, Norrdahl and Korpimäki 2000). This suppression of reproductive activity may be in response to the actual presence of a predator or to its odor. However, there appears to be no direct evidence for breeding suppression of voles exposed to high predation risk, at least for populations in field enclosures (Wolff and Davis-Born 1997, Mappes et al. 1998, Ylönen and Wolff 1999, Jonnson et al. 2000).

Changes in spacing behavior and general activity of voles in response to predators were originally reported in laboratory studies (Jędrzejewski et al. 1993, Ronkainen and Ylönen 1994, Parson and Bondrup-Nielson 1996). In a large-scale predator reduction experiment, Norrdahl and Korpimäki (1998) found that voles moved more when predation risk was low. These authors concluded that voles would respond to their principal predators, small mustelids, by decreasing their mobility to reduce the probability of being preyed upon. Thus, there appears to be a positive linear relationship between mobility and the likelihood of being preyed upon (Nordahl and Korpimäki 1998). In addition, prey typically move less in response to predator odors (Kats and Dill 1998). Equivocal evidence for reduced movements of voles in response to odors has been reported for predator odor studies in field exclosures (Wolff and Davis-Born 1997, Jonnson et al. 2000). Banks et al. (2000) reported a nonlinear (U-shaped) response curve for movements of voles in control and predator-reduction sites. Those animals that moved less, with a corresponding buildup of predator-attracting odorous waste products, were preyed upon to a similar degree as those moving more and increasing the risk of random predator encounters (Banks et al. 2000). This result has implications for the restricted movements of naïve animals introduced into unfamiliar environments (Banks et al. 2002).

In terms of changes in body mass of voles, young animals were particularly lean in the presence of mustelid predators (Norrdahl and Korpimäki 2001). Heavy predation pressures, or perceived predation risk based on mustelid odor, for example, may change the composition of a vole population to one characterized by small (and probably young) individuals.

Several authors have questioned the validity of laboratory studies of vole responses to odor-induced predation risk and their relationships to population dynamics of voles in the field (Korpimäki et al. 1994, Lambin et al. 1995, Ylönen and Wolff 1999). However, subsequent studies (Wolff and Davis-Born 1997, Mappes et al. 1998, Jonnson et al. 2000) have used small ($<$0.25-ha) enclosures with the inherent limitations for movements of voles and mustelid predators into and out of control and treatment sites. Population responses of free-ranging voles to the odor of small weasels have not been measured.

Despite some equivocal and contrary results for responses of vole movements to predator odors and the PIBS hypothesis, respectively, we hypothesized that the presence of a continuous odor of short-tailed weasel would disrupt the population dynamics of voles by reducing reproductive success, survival, and movements during the summer months of a peak year in abundance. This disruption would reduce reproductive success and survival, thereby lowering the abundance of vole populations entering winter months, when tree seedlings are susceptible to feeding damage. A reduction in movement of voles on treatment sites would lower feeding (Norrdahl and Korpimäki 2000) and the encounter rate for seedlings, thereby resulting in less damage to trees.

Thus, this study was designed to test the hypotheses that synthetic odor of the short-tailed weasel would (1) reduce abundance, reproduction, survival, movement, and body mass of montane and meadow vole populations; (2) enhance the activity of short-tailed and least weasels in treatment sites; and (3) reduce feeding damage to planted lodgepole pine (*Pinus contorta*) seedlings by voles in forest plantations.

METHODS

Study areas

This study was conducted at two locations in the south-central interior of British Columbia (B.C.), Canada between April 1994 and May 1995. The Summerland area was located at the Pacific Agri-Food Research Centre in the Okanagan Valley, Summerland, B.C. (49°34′ N; 119°40′ W). This 400-ha area is composed of a mosaic of tree fruit orchards, vineyards, old fields, sagebrush (*Artemisia tridentata*), and Ponderosa pine (*Pinus ponderosa*) habitats. Experimental work was conducted in ''old-field'' habitats that were abandoned ($\geq$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*; see Fig. 1 top). These old-field sites were each 2–3 ha in area within the mosaic and had resident populations of montane voles, the major rodent species with a long history of fluctuating populations and feeding damage to trees (Sullivan et al. 1998). The deer mouse (*Peromyscus maniculatus*), Great Basin pocket mouse (*Perognathus parvus*), western harvest mouse (*Reithrodontomys megalotis*), northwestern chipmunk (*Tamias amoenus*), and long-tailed vole (*Microtus longicaudus*) were also present.

The Gavin Lake area was located in the Alex Fraser Research Forest (University of British Columbia), 75 km northeast of Williams Lake, B.C. (52°29′ N; 121°45′ W) in the sub-boreal spruce (SBS_{dm}) biogeoclimatic zone (Meidinger and Pojar 1991). The general topography is gently rolling to flat at 850–870 m elevation. In mature stands, hybrid Engelmann (*Picea engelmannii*) × white spruce (*Picea glauca*), subalpine fir (*Abies lasiocarpa*), and some Douglas-fir (*Pseudotsuga menziesii*) are mixed with extensive stands of lodgepole pine, which regenerated after wildfires. This study area covered 94 ha and was clear-cut harvested in 1967–1971. The area did not regenerate to coniferous forest; thus in 1991 the willow (*Salix* spp.)–aspen (*Populus tremuloides*) shrub–sapling vegetation was scarified into windrows of debris in preparation for planting of lodgepole pine and spruce seedlings in 1992. This set the area back to an early-successional stage with the vegetation dominated by grasses, herbs, and mosses with some residual willow shrubs and aspen saplings (Fig. 1 bottom). Prominent herb species included yarrow (*Achillea millefolium*), common horsetail (*Equisetum arvense*), heart-leaved arnica (*Arnica cordifolia*), wild strawberry (*Fragaria virginiana*), white-flowered hawkweed (*Hieracium albiflorum*), fringed aster (*Aster ciliolatus*), and northern bedstraw (*Galium boreale*). The debris piles provided ideal cover

FIG. 1. Photographs of the old-field habitat at Summerland (top) and the early-successional forest habitat at Gavin Lake (bottom), south-central British Columbia, Canada.

for meadow voles, which also had a history of fluctuating populations in this general area, at least based on anecdotal reports of periodic feeding damage to trees. The deer mouse, southern red-backed vole (*C. gapperi*), northwestern chipmunk, and shrews (*Sorex* spp.) were also present on these sites.

Experimental design

The study had four replicate sites of each treatment (two replicates of each treatment at each of the Summerland and Gavin Lake study areas). The eight sites (two treatments × four replicates) were selected on the basis of suitable habitat for montane voles (old fields) at Summerland and meadow voles (herb–grass vegetation) at Gavin Lake, and reasonable proximity of sites to one another. The sites were separated by 150–480 m and there were very low levels of movement of voles between sites. Only 21 of 1851 (1.1%) of individual montane voles at Summerland, and 1 of 888 (0.1%) individual meadow voles at Gavin Lake, were captured on more than one site. Thus, with respect to voles, the sites were far enough apart to be statistically independent and represented true replicates (Hurlbert 1984). However, this independence was hard to justify for small weasels because of their greater range of movements.

Small-mammal populations

All animals were live-trapped on 1-ha grids with 49 (7×7) trap stations located at 14.3-m intervals and 1, 2, or 3 Longworth live-traps (Penlon, Abingdon, UK) placed within a 2 m radius of each station. The number of traps at a station was dependent on the number of voles. One grid was located on each of the eight sites. The four grids at Summerland were live-trapped at 3-week (spring, summer, and autumn) and at 4–8 week intervals (winter) from April 1994 to May 1995. The four grids at Gavin Lake were live trapped at 3–4 week (spring, summer, and autumn) and at 3–7 week intervals (winter) from May 1994 to May 1995. Only one pair of control–treatment grids was trapped during the winter (November–March) at Gavin Lake because of difficult access to the study area.

There were four periods in this study: (1) pre-treatment spring (April–May 1994 at Summerland; May–June 1994 at Gavin Lake); (2) treatment summer and autumn (June–October 1994 at Summerland; July–October 1994 at Gavin Lake); (3) treatment winter (November 1994–February 1995); and (4) treatment spring (March–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. We ear-tagged all captured animals with serially numbered tags, noted their breeding condition, weighed them on Pesola spring balances, and recorded their point of capture. The condition of mammaries of the females was used to measure reproductive state (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.

Abundance

Population densities were estimated by the Jolly-Seber (J-S) model (Seber 1982) for reasons indicated by Jolly and Dickson (1983). 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). The J-S estimate was not calculated for the first and last trapping periods; for these sample weeks, a minimum number of animals known to be alive (MNA; Krebs 1966) value was used.

Vole population dynamics

Mass at sexual maturity was used to determine age classes of animals. The percentage of sexually mature animals was used to determine: (1) the mass limitations for juveniles, subadults, and adults, assuming that juveniles were seldom, if ever, sexually mature; (2) that $<50\%$ of the subadults in the upper mass class were mature; and (3) that at least 50% of the adults were sexually mature in the lowest mass class. Voles were classified as juvenile (juvenile and subadult classes pooled) or adult based on body mass (for Summerland, juvenile = 1–26 g, adult $\geq$ 27 g; for Gavin Lake, juvenile = 1–24 g, adult $\geq$ 25 g). Juveniles were considered to be young animals recruited during the study. Recruits were defined as new animals that entered the population through reproduction and immigration.

Reproductive performance was based on the number of successful pregnancies and number of recruits. Estimates of early juvenile survival were derived from the sample of animals captured 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 the number of juvenile animals at week t divided by the number of lactating females caught in week $t - 3$. Mean survival rates (28-day) for the four periods were estimated from the J-S model. Mean body mass of adult and juvenile male and female voles was calculated for pre-treatment, summer, and winter–spring periods. One body mass measurement was made for each individual animal by taking an average value of all mass records for each vole in a given period.

Inter-trap movement of voles between trapping periods was used to analyze mean movements in control and treatment sites during the pre-treatment and summer, winter, and spring treatment periods.

Sampling of weasel activity at Gavin Lake

Short-tailed weasels were captured periodically in live-traps at the Gavin Lake study area. The number of individual weasels captured was recorded for each grid and trapping period. In addition, snow tracks, primarily of short-tailed weasels, but also of least weasels, were counted for five separate snowfalls (within 24 h of the end of a fresh snowfall) between 3 November and 11 December at Gavin Lake. Numbers of tracks crossing the edge of each of the four 1-ha trapping grids were counted for each snowfall, yielding 10 control and 10 treatment samples.

Weasel semiochemicals

Weasel semiochemicals included a 1:1 mixture of 2-propylthietane and 3-propyl-1,2-dithiolane, which were the major compounds identified in the anal gland secretion of the short-tailed weasel and some other mustelid species (Crump 1978, 1980, 1982, Crump and Moors 1985). In terms of generating an avoidance response by voles, the combination of these two major compounds worked as well as the full suite of anal gland compounds (Sullivan et al. 1988*a*). These compounds were encapsulated in 6×0.4 cm polyvinylchloride (PVC) cylinders. These release devices consisted of a 0.5 mm thick sheath and a core plastisol formulated with 2% active ingredient (Phero Tech, Delta, B.C., Canada). Each device weighed ~1.0 g and contained an average of 45.91% 2-propylthietane and 47.27% 3-propyl-1,2-dithiolane with 6.82% as alkyl sulfur impurities. Thus, the simulated anal gland secretion of the short-tailed weasel had a purity of 93.18% and there was, on average, 10.2 mg per release device. Colloidal carbon black was added to the plastisol formulation to help protect the weasel compounds from ultraviolet radiation and other degradation induced by free radicals.

Measurement of the release rates of these compounds under field conditions during summer months indicated that 85.6–91.9% of the compounds were released after 25 days (Phero Tech, D. Wakarchuk, *unpublished data*). In total, 256 wooden (2.5 × 5.0 cm × 30–45 cm in length) stakes were uniformly (16 × 16 matrix) distributed over the area of each treatment grid and a buffer, covering 1.3 ha overall. Based on the release rate data and the goal of providing a continuous odor of short-tailed weasel on the treatment sites, a new weasel odor device was stapled to each stake at 3-wk (summer) to 5-wk (winter) intervals. The experiment commenced on 22 May 1994 at Summerland and on 1 July 1994 at Gavin Lake at an initial application rate of 200 devices/ha. This treatment dose was doubled to 400 devices/ha in October 1994 at both study areas. The treatment was continued throughout the winter of 1994–1995, with the final application on 13 March 1995 at Summerland and on 17 April 1995 at Gavin Lake. The weasel odor devices were not reapplied to the treatment grids at Gavin Lake in December 1994 and January 1995 because of deep snow (up to 60 cm). Application continued in February 1995.

Tree seedlings

One-year-old nursery-raised lodgepole pine (*Pinus contorta*) seedlings were planted in late October and early November 1994 in groups of 10 × 10, one group of 100 seedlings in each corner of each trapping grid on a given treatment site, at the two study areas. The total sample of trees exposed to voles on each grid was 400, which at a planting density every 3 m was ~1100 trees/ha. This density was within the range of typical new plantations of lodgepole pine in the interior of British Columbia, Canada. Lodgepole pine is the coniferous tree species most susceptible to feeding damage by *Microtus* spp. in B.C. (Sullivan et al. 1990*b*).

All 400 seedlings on each treatment site were sampled for overwinter clipping of terminal or lateral shoots and gnawing of terminal shoots in May 1995. Clipping and gnawing of terminal shoots was considered mortality because seedlings rarely, if ever, recover from this damage (Sullivan et al. 1990*b*). Results were categorized as percentage mortality of trees overall and on a per vole basis. The population estimate of voles for October 1994, prior to planting of seedlings and the onset of winter, was used to calculate the percentage of trees eaten per vole.

Statistical analysis

A repeated-measures analysis of variance (RM-ANOVA) was used to determine the effect of weasel odor on mean abundance, mean number of successful pregnancies, mean number of recruits, mean early juvenile survival, mean J-S (Jolly-Seber) 28-day survival, and mean movement over the four (one pre-treatment and three treatment) periods of the study. Mean body mass was analyzed over three periods (one pre-treatment and two treatment periods). For these analyses, a mean estimate of a given parameter for each control and each treatment site and period was calculated. Before performing any analyses, data not conforming to properties of normality and equal variance were subjected to various transformations to best approximate the assumptions required by any ANOVA (Zar 1999). Mauchly's *W* test statistic was used to test for sphericity (independence of data among repeated measures; Littel 1989, Kuehl 1994). For data found to be correlated among periods, the Huynh-Feldt (H-F) correction (Huynh and Feldt 1976) was used to adjust the degrees of freedom of the within-subjects F ratio.

The percentage mortality of tree seedlings due to feeding damage by voles, both overall and per vole, was analyzed with a one-way ANOVA model. The comparison of mortality of trees near a weasel odor device with those trees not near a device used a chi-square 2 × 2 contingency table.

Percentage data were arcsine-transformed prior to analysis. In all analyses, the level of significance was at least $P = 0.05$.

RESULTS

Abundance

Mean numbers of montane and meadow voles were similar ($P > 0.05$) between control and treatment sites, ranging from 31.9 to 121.1 voles/ha in controls and 36.6 to 117.5 voles/ha in treatments (Tables 1 and 3). Changes in abundance throughout the study reflect this pattern for both species (Fig. 2A, B). However, montane voles did decline in abundance during June and July, decreasing in number 17.0–36.2% on the treatment sites while numbers increased on control sites (Fig. 2A). Although abundance of meadow voles declined slightly at this same treatment time, so did that of voles on control sites (Fig. 2B).

The mean rate of change in population size of montane and meadow voles for the three treatment periods was significantly higher in control than treatment sites ($F_{1,4} = 11.72$, $P = 0.03$) and over time ($F_{2,8} = 20.48$, $P < 0.01$). There was also a significant treatment × time interaction ($F_{2,8} = 16.37$, $P < 0.01$; Fig. 3).

Recruitment of new voles was generally similar ($P > 0.05$) between control and treatment sites for mean

TABLE 1. Mean ± 1 SE ($n = 4$; $n = 3$ in winter periods) abundance (Jolly-Seber population estimates) and number of recruits per hectare for montane and meadow voles in control and treatment sites for the four periods of the study in British Columbia, Canada.

Parameter and period	Control	Treatment
Abundance		
Pre-treatment	65.8 ± 13.2	63.4 ± 19.4
Summer 1994	110.0 ± 31.0	105.6 ± 21.1
Winter 1994–1995	121.1 ± 26.0	117.5 ± 32.1
Spring 1995	31.9 ± 4.7	36.6 ± 4.9
Adult recruits		
Pre-treatment	15.7 ± 1.3	22.8 ± 3.7
Summer 1994	13.2 ± 3.3	13.5 ± 3.5
Winter 1994–1995	4.4 ± 1.8	13.0 ± 6.5
Spring 1995	7.0 ± 1.8	10.6 ± 2.0
Juvenile recruits		
Pre-treatment	8.6 ± 2.6	13.3 ± 6.4
Summer 1994	14.8 ± 1.7	14.0 ± 4.1
Winter 1994–1995	20.1 ± 5.8	16.7 ± 4.7
Spring 1995	6.0 ± 1.3	7.3 ± 1.3
Total recruits		
Pre-treatment	24.3 ± 1.3	36.1 ± 10.1
Summer 1994	28.0 ± 4.5	27.5 ± 2.5
Winter 1994–1995	24.5 ± 7.2	29.7 ± 10.7
Spring 1995	13.0 ± 1.6	17.9 ± 2.3

number of adults, juveniles, and totals over the four periods (Tables 1 and 3). There was no difference between males and females, so these data were pooled in the comparisons. There was a significant time effect for adult recruits ($F_{3,12} = 5.55$, $P = 0.03$) and total recruits ($F_{3,12} = 7.20$, $P = 0.01$) as the numbers of new voles appearing on control and treatment sites declined with time (Table 3).

Reproduction and survival

The mean number of successful pregnancies that was recorded for each population of montane and meadow voles was similar between control and treatment sites in pre-treatment and summer periods (Tables 2 and 3). Similarly, the mean index of early juvenile survival of voles also followed this pattern (Tables 2 and 3).

Mean 28-day J-S survival rates were similar between control and treatment sites for female voles (Tables 4 and 7). However, survival of males was significantly ($F_{1,4} = 10.45$, $P = 0.03$) higher in control than treatment sites during the treatment periods. Male survival was 2.3 times higher in control than treatment sites in the spring 1995 period (Table 4). Total survival of voles was similar ($F_{1,4} = 5.10$, $P = 0.09$) in control and treatment sites, but changed significantly ($F_{3,12} = 4.78$, $P = 0.02$) with time (Table 7).

Body mass

Mean body mass of adult montane and meadow voles was similar in control and treatment sites for males and females (Table 5, Figs. 4 and 5). This pattern was also recorded for juvenile voles (Table 5). There were significant time effects, with adults declining in mass and juveniles increasing in mass through the study (Table 7).

Movement

Mean movement of adult voles between trapping periods was similar ($P > 0.05$) in control and treatment sites for males, females, and totals (Tables 6 and 7). There was a significant ($F_{3,12} = 6.88$, $P = 0.01$) response over time as total adult movement increased, particularly in spring. There were insufficient data for analysis of movements by juvenile voles. Although we do not have direct evidence, the low capture rates of montane voles on treatment sites in the summer and fall suggested that these voles were moving less than those on control sites.

Weasel activity

Four individual weasels were recorded on the control sites and seven on the treatment sites in the summer and winter periods at Gavin Lake. No weasels were captured on the Summerland sites.

The number of weasel tracks (both short-tailed and least) crossing the edge of a grid (400-m transect) was significantly ($t = 2.33$, df = 18, $P < 0.05$) higher on treatment (13.9 ± 1.6, mean ± 1 SE) than control (6.1 ± 0.6) sites. This increase in weasel activity on treatment sites was probably related to the odor application. Because of poor snow-tracking conditions (frequent melts and rain) later in the winter, we have data on use of the sites by weasels in November and December 1994 only.

Tree seedlings

Mean mortality of lodgepole pine seedlings on control sites was 18.8%, ranging from 7.0% to 43.0%; mortality on treatment sites was 27.9%, ranging from 22.0% to 33.0%. The mean percentage mortality of trees eaten per vole also followed this pattern, with no significant differences between control and treatment sites for either measurement (Table 8). Because of the very low incidence of feeding damage on the Summerland control vs. treatment sites, an additional analysis compared mortality of seedlings with a nearby (<2 m away) weasel odor device vs. those seedlings without a device nearby (>2 m away) on the two treatment sites. Trees near a weasel odor device had significantly lower mortality (26.0% and 16.0%) than those not near a device (37.0% and 34.0% mortality) on treatment 1 ($\chi^2 = 5.61$, $P = 0.02$) and treatment 2 ($\chi^2 = 17.28$, $P < 0.01$), respectively.

DISCUSSION

Vole populations and weasel odor

Our study is the first comprehensive evaluation of the responses of voles, during the increase and peak phases of a population fluctuation, to synthetic anal gland secretion of short-tailed weasels, a principal

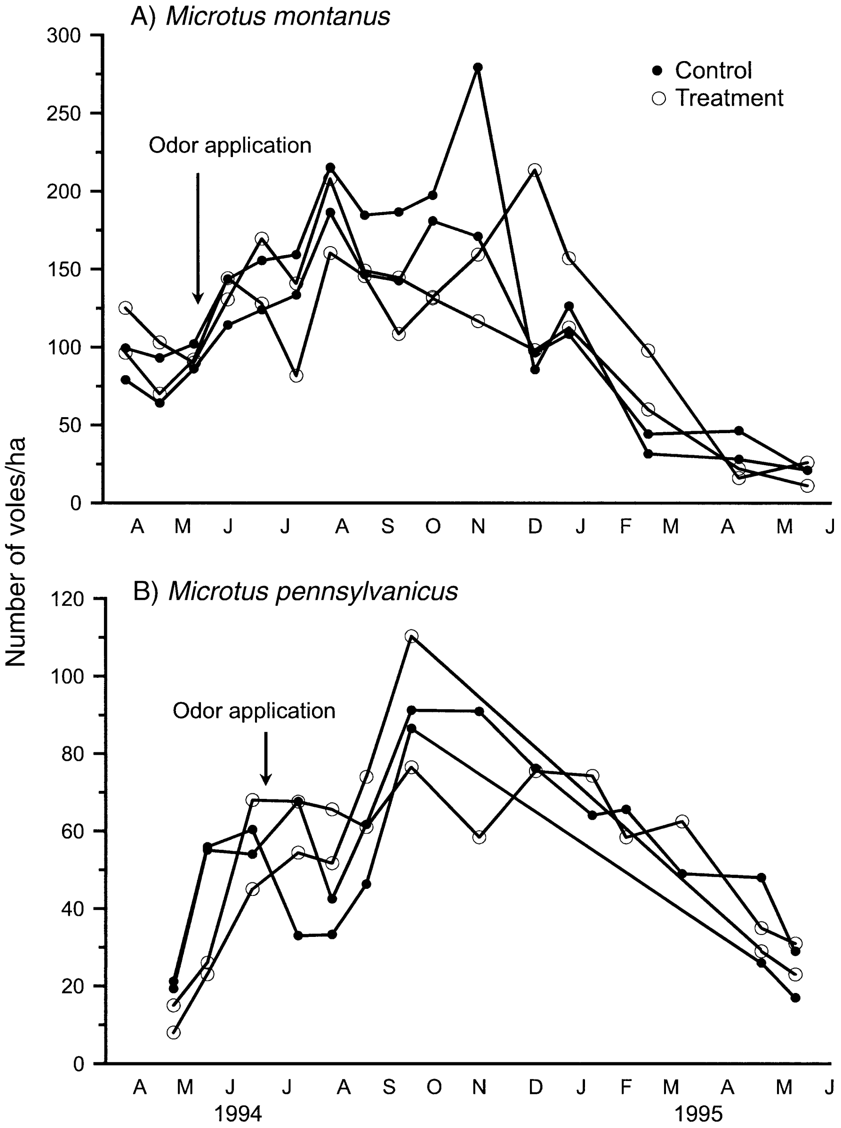

FIG. 2. Abundance (Jolly-Seber population estimates) on control and treatment sites of (A) montane voles at Summerland and (B) meadow voles at Gavin Lake. Weasel odor was applied to treatment sites starting on 22 May 1994 at Summerland and 1 July 1994 at Gavin Lake, and continued to the end of the study. Note different scales on the *y*-axis for panels A and B.

predator of *Microtus* spp. and *Clethrionomys* spp. The background for this study was the antipredatory behavior recorded for voles exposed to the presence (or scent) of small mustelids (Ylönen 1989, Jędrzejewski et al. 1993, Korpimäki et al. 1994, Norrdahl and Korpimäki 1998). As discussed by Korpimäki et al. (1994) and Hanski et al. (2001), fluctuations in vole populations, at least in boreal and subarctic zones, may be driven by small mustelid predators. In addition, the avoidance responses of voles to natural and synthetic anal gland compounds of small weasels in bioassays suggested that these compounds might induce changes in the population dynamics of voles (Stoddart 1976, 1980, Gorman 1984, Sullivan et al. 1988*a*, 1990*a*).

Our first hypothesis that weasel odor would reduce abundance, reproduction, survival, movement, and body mass of vole populations was not supported except for adult male survival. Abundance of montane voles did decline initially (17–36%) in the early treatment summer, but this decrease was short-lived, and was not observed for meadow voles on treatment sites. Although the mean rate of change in population size was significantly lower in treatment than in control sites, this difference appeared mainly in spring 1995 and did not result in a change in abundance of voles in summer 1994. This result was similar to that reported by Klemola et al. (1997), in which the presence of small mustelid predators slowed the population growth of

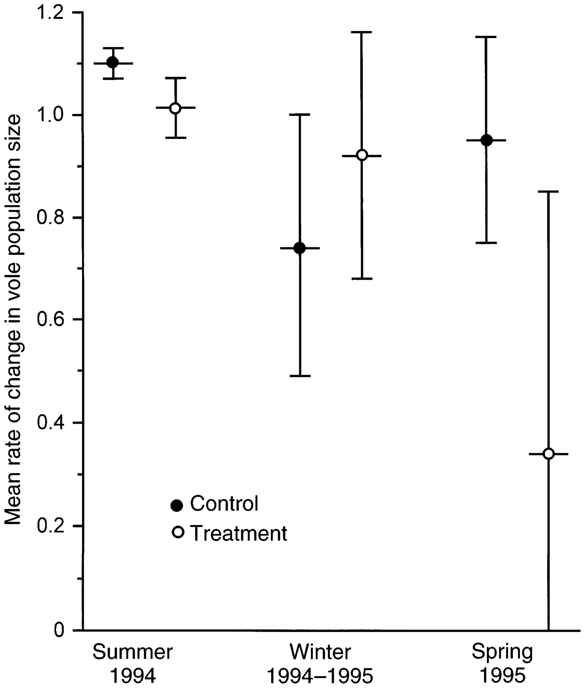

FIG. 3. Mean rate of change ±95% confidence intervals ($n = 4$) in population size of voles per three weeks on control and treatment sites during post-treatment summer 1994, winter 1994–1995, and spring 1995 periods.

Microtus spp. by suppression of breeding in female voles. Our lower rate of population growth on treatment sites was probably related to lower survival of voles on treatment than control sites in spring 1995. In the only other study of vole population responses to this weasel odor, Sullivan et al. (1988*b*) reported that abundance of montane voles did decline temporarily, up to 30% on a single treatment site, in three consecutive winters. The declines were related to significantly lower survival of voles on treatment than on control sites (Sullivan et al. 1988*b*).

TABLE 2. Mean ± 1 SE ($n = 4$) number of successful pregnancies and mean ± 1 SE ($n = 4$) index of early juvenile survival of montane and meadow voles (number of juvenile recruits per successful pregnancy) on replicate control and treatment sites at the two study areas, British Columbia, Canada.

Parameter and period	Control	Treatment
Pregnancies		
Pre-treatment	17.25 ± 3.77	13.00 ± 4.08
Summer 1994	11.32 ± 1.84	9.37 ± 1.16
Juvenile survival		
Pre-treatment	0.54 ± 0.07	0.84 ± 0.18
Summer 1994	1.58 ± 0.17	1.46 ± 0.29

Another prediction of hypothesis 1 was reduced recruitment, because antipredatory behavior (Lima and Dill 1990) might induce dispersing juveniles not to settle. Again, the weasel odor treatment had no effect on mean recruitment of male, female, or either age class of voles. In addition, mean early juvenile survival was similar in control and treatment sites. This result was also recorded by Jędrzejewski and Jędrzejewska (1990) for bank voles *Clethrionomys glareolus* in semi-natural conditions in which juveniles of both sexes and reproducing females maintained their ranges despite the penetration of their home pen by a least weasel. The treatment did not affect reproduction (PIBS, predator-induced breeding suppression) of voles, which was contrary to our prediction, based on results of studies in which small mustelids, or their scent, suppressed reproduction in several species of voles (Henttonen et al. 1987, Ylönen 1989, Korpimäki et al. 1994), but similar to the results of Wolff and Davis-Born (1997), Mappes et al. (1998), and Jonnson et al. (2000). These latter studies, in field enclosures, used the odor of urine and feces from least weasels and mink (*Mustela vison*), whereas we used synthetic major components of the anal gland secretion of the short-tailed weasel.

TABLE 3. Results of repeated-measures ANOVA for Jolly-Seber (J-S) population estimates, numbers of recruits, and reproduction attributes for montane and meadow voles in control and treatment sites.

	Treatment			Time			Time × Treatment		
Parameter	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
J-S population estimates									
Abundance	0.00	1, 4	1.00	17.31†	3, 12	<0.01	0.14†	3, 12	0.83
Adult recruits	0.53	1, 4	0.51	5.55†	3, 12	0.03	0.50†	3, 12	0.62
Juvenile recruits	0.01	1, 4	0.93	3.07†	3, 12	0.08	1.09†	3, 12	0.39
Total recruits	0.52	1, 4	0.51	7.20†	3, 12	0.01	1.54†	3, 12	0.26
Reproduction‡									
Pregnancies	1.59	1, 6	0.25	1.22	1, 6	0.31	0.18	1, 6	0.69
Juvenile survival	0.80	1, 6	0.41	8.89	1, 6	0.02	0.42	1, 6	0.54

† *F* values calculated using an H-F correction factor, which decreased the stated degrees of freedom due to correlation of data among repeated measures (periods).

‡ Due to fewer time periods (two rather than four) for pregnancies and juvenile survival, df = 1, 6 for this analysis.

TABLE 4. Mean ± 1 SE ($n = 4$) 28-day Jolly-Seber survival rates for male, female, and total montane and meadow voles in control and treatment sites for the four periods of the study in British Columbia, Canada.

Sex and period	Control	Treatment
Males		
Pre-treatment	0.64 ± 0.04	0.54 ± 0.06
Summer 1994	0.67 ± 0.05	0.58 ± 0.04
Winter 1994–1995	0.63 ± 0.09	0.67 ± 0.12
Spring 1995	0.72 ± 0.14	0.32 ± 0.07
Females		
Pre-treatment	0.73 ± 0.05	0.69 ± 0.02
Summer 1994	0.74 ± 0.04	0.66 ± 0.02
Winter 1994–1995	0.66 ± 0.06	0.69 ± 0.07
Spring 1995	0.48 ± 0.04	0.36 ± 0.10
Total		
Pre-treatment	0.70 ± 0.04	0.65 ± 0.02
Summer 1994	0.71 ± 0.05	0.64 ± 0.02
Winter 1994–1995	0.65 ± 0.07	0.67 ± 0.09
Spring 1995	0.60 ± 0.06	0.34 ± 0.08

The prediction of reduced mobility of voles in the presence of weasel odor was also not supported. Avoiding predators by reducing mobility may increase the probability of survival (Lima and Dill 1990). This relationship has been demonstrated for several species of voles and small mustelid predators (or their scent) in laboratory, semi-natural, and field experiments (Jędrzejewski and Jędrzejewska 1990, Jędrzejewski et al. 1993, Borowski 1998*a*, Norrdahl and Korpimäki 1998) and for odor of red fox (Dickman and Doncaster 1984, Calder and Gorman 1991, Perrot-Sinal et al. 1999). In particular, these studies have demonstrated that responses are sexually dimorphic, with male voles displaying enhanced behavioral responses to predator odors compared with females (Jędrzejewski and Jędrzejewska 1990, Perrot-Sinal et al. 1999). In addition, the reduction in locomotor activity levels was observed only in reproductive males and not in either breeding females or nonbreeding male or female meadow voles (Perrot-Sinal et al. 1996). It is not clear why breeding males on our treatment sites in summer 1994 did not show reduced movement patterns.

The neutral responses of voles to weasel odor that we observed, in terms of abundance, reproduction, recruitment, female survival, early juvenile survival, and movements, could be related to habitat quality, in terms of both food and cover. Merkens et al. (1991) exposed *Microtus townsendii* to this same weasel odor formulation combined with a lack of cover, or to just one of these factors. When cover was absent, voles preferred to feed away from the area with the weasel odor. However, when cover was present, voles preferred to feed under cover, whether or not the weasel odor was dispensed there. Both of our study areas were located in optimal habitat for montane and meadow voles: old fields and early-successional habitat after forest harvesting (Fig. 1). Thus, our results may not be surprising, particularly with respect to peak populations of both vole species during the study.

An alternative explanation is that voles living in North America may experience less predation from small mustelids than those living in Eurasia (Wolff and Davis-Born 1997). Because small mustelid predation is probably a major factor driving population cycles (Henttonen et al. 1987, Hanski and Henttonen 1996), voles evolved specific behavioral responses to this predation risk (reviewed by Borowski 2002). Although this idea is intriguing, the two major mustelids, short-tailed and least weasels, are both broadly circumpolar in distribution and it seems unlikely that *Microtus* and *Clethrionomys* spp. would not have evolved similar antipredator behavioral responses on both continental land masses.

Activity of mammalian predators

Although the sample sizes were low for individual short-tailed and least weasels captured in live-traps and for tracks in the early winter survey, our results appear to support hypothesis 2, that activity of small weasels would be enhanced in treatment sites. Other examples of synthetic predator odors acting as pheromones to attract conspecifics include anal gland secretion of the ferret (Clapperton et al. 1988, 1989), gray wolf (*Canis lupus*) urine (Raymer et al. 1984), and red fox urine (Whitten et al. 1980). Our study is the first demonstration of the use of synthetic anal gland secretion of the short-tailed weasel to increase the activity of other members of this mustelid species. As discussed by Jędrzejewski et al. (1993), chemical analyses of mustelid anal gland secretions indicated that they contained genus-specific compounds (thietanes and dithiolanes in *Mustela*, benzaldehyde in *Martes*). They also yielded

TABLE 5. Mean ± 1 SE ($n = 4$) body mass (g) for adult and juvenile male and female voles in control and treatment sites for the three periods of the study in British Columbia, Canada.

Age, sex, and period	Control	Treatment
Adult males		
Pre-treatment	36.45 ± 0.66	36.39 ± 1.26
Summer 1994	34.54 ± 0.51	35.32 ± 1.27
Winter–spring 1994–1995	29.65 ± 0.81	31.24 ± 1.54
Adult females		
Pre-treatment	35.19 ± 0.62	35.24 ± 0.73
Summer 1994	34.61 ± 0.65	35.96 ± 0.59
Winter–spring 1994–1995	30.55 ± 0.56	30.71 ± 1.44
Juvenile males		
Pre-treatment	17.46 ± 1.59	18.84 ± 0.68
Summer 1994	21.23 ± 0.51	19.81 ± 0.28
Winter–spring 1994–1995	22.18 ± 0.21	22.47 ± 0.61
Juvenile females		
Pre-treatment	17.86 ± 1.51	19.00 ± 1.00
Summer 1994	21.06 ± 0.40	19.64 ± 0.29
Winter–spring 1994–1995	22.02 ± 0.31	21.37 ± 0.20

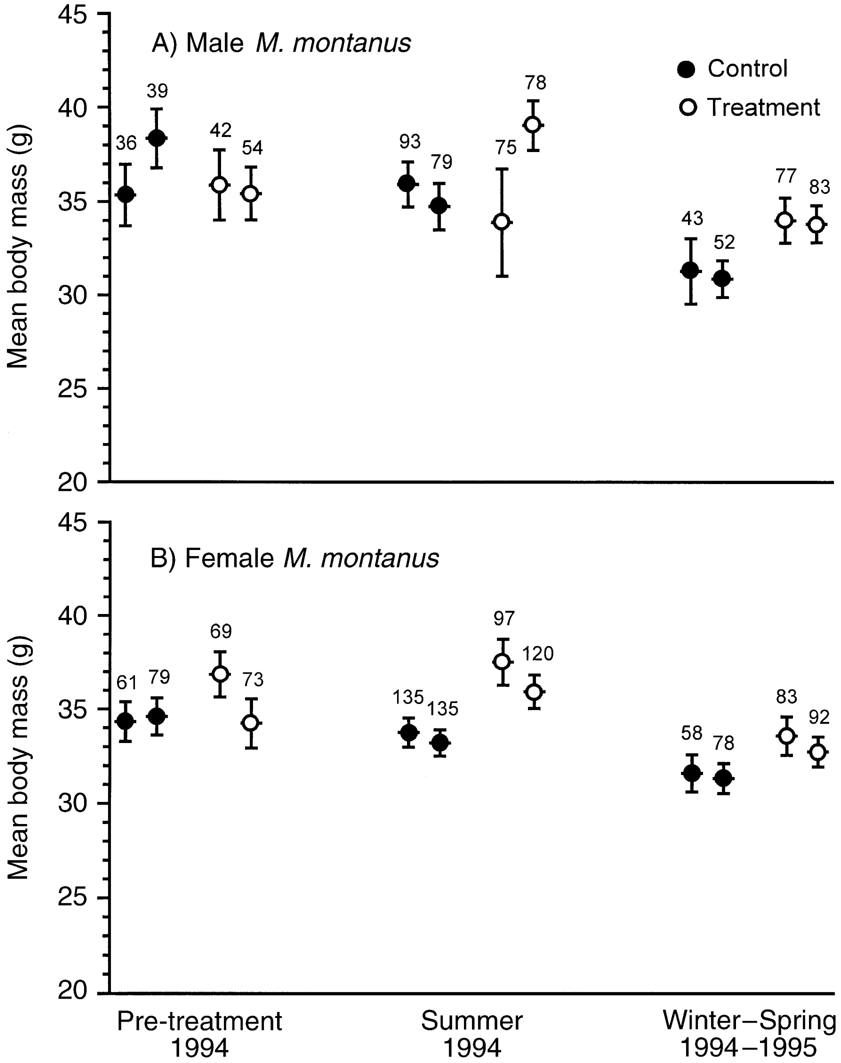

FIG. 4. Mean body mass (g) ± 95% confidence intervals for (A) male and (B) female adult montane voles in control and treatment sites at Summerland for pre-treatment 1994, summer 1994, and winter–spring 1994–1995 periods. Sample size (number of voles) is given above each CI.

species-specific components that differentiated *erminea, putorius,* and *nivalis* within the genus *Mustela* (Brinck et al. 1983, Crump and Moors 1985). Although there are no reports of these mustelid compounds attracting canids or other mammalian carnivores, it is possible that coyotes may have chewed or gnawed the weasel odor devices at Summerland. Coyote scats were common on all four sites throughout the study at Summerland, which had ephemeral and variable snow depths (0–30 cm) in winter. The sites at Gavin Lake had up to 60 cm of snow cover lasting from late October 1994 to early April 1995, with little coyote activity during this time.

Voles may identify predator risk based on recognition of family (e.g., Canidae or Mustelidae), genus, and species-specific components of a given predator odor. It is unlikely that voles would habituate to these odors, because their responses to both natural and synthetic constituents of short-tailed weasels in other studies appeared to be innate (Gorman 1984, Borowski 1998*b*) and relatively long-term (4–5 months; Sullivan et al. 1988*a, b*). Attraction of weasels to treatment sites would presumably reinforce the predation risk for voles and maintain any antipredatory behavior that had developed. The mean home ranges of short-tailed weasels are relatively large, ranging from 10 to 40 ha for males (King 1983) and from 10 to 15 ha for females (Simms 1979). Home ranges of least weasels are 0.6–26 ha for males and 0.2–7 ha for females (Sheffield and King 1994). Thus, the numbers of individual weasels captured in live-traps on our Gavin Lake sites appeared to be high and did not persist through the winter months, possibly because vole numbers were also high in surrounding parts of the 94-ha study area.

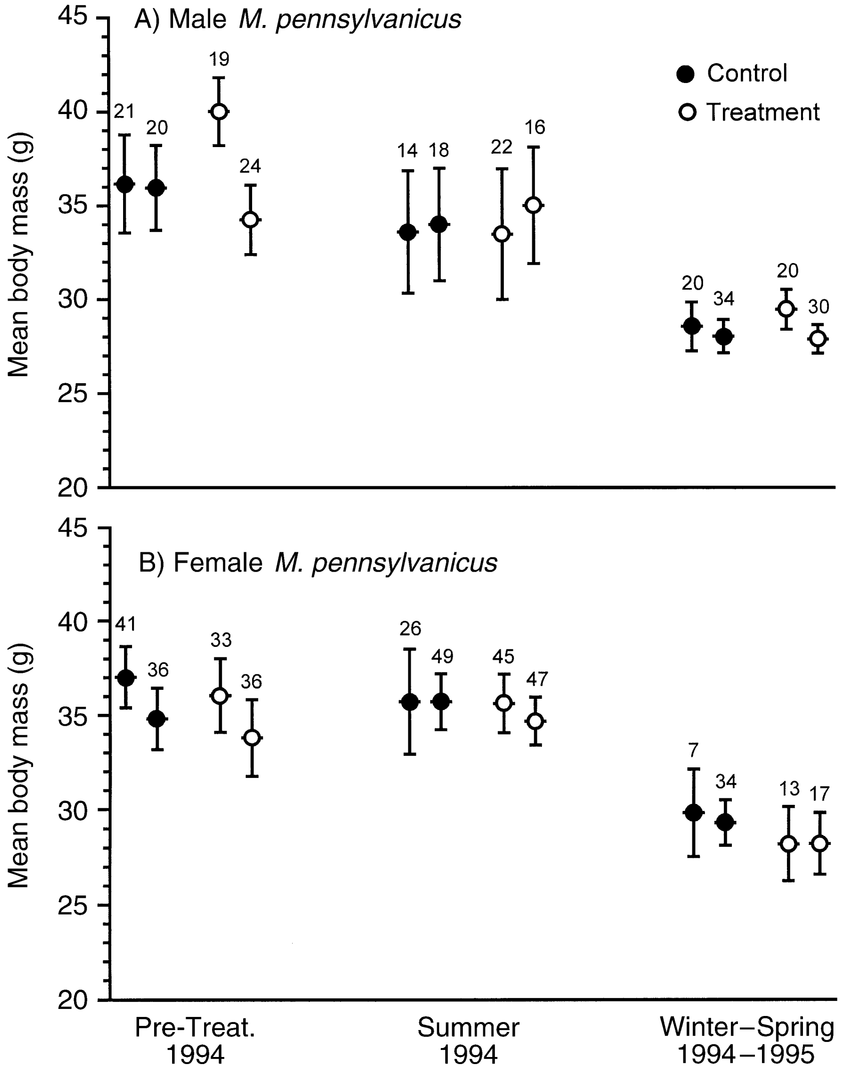

FIG. 5. Mean body mass (g) ± 95% confidence intervals for (A) male and (B) female adult meadow voles in control and treatment sites at Gavin Lake for pre-treatment 1994, summer 1994, and winter–spring 1994–1995 periods. Sample size (number of voles) is given above each CI.

Tree seedlings and voles

Our hypothesis 3, that weasel odor would reduce feeding damage by voles to lodgepole pine seedlings, was not supported. The lack of feeding damage to seedlings on control sites is particularly difficult to explain, because habitat conditions were ideal for *M. montanus* to reach peak abundance, ranging from 171 to 280 voles/ha in November 1994. Old fields providing high levels of cover and food historically have had serious outbreaks of damage to planted coniferous and deciduous trees (Radvanyi 1980, Bergeron and Jodoin 1989, Ostfeld and Canham 1993, Pusenius et al. 2000, Sullivan et al. 2001). The variable incidence of damage to trees on control sites at Gavin Lake may have been related to availability of natural alternative food sources.

The lower level of feeding on trees near weasel odor than on those >2 m from the odor on treatment sites at Summerland suggested that montane voles may have spent less time foraging near the sources of weasel scent. This possible antipredatory behavior reduced the incidence of mortality to an average of 21.0% (near scent) compared with 35.5% (away from scent). These average levels of tree mortality in the presence of weasel odor were still higher than the <10% tree mortality acceptable to forest managers. Similar levels of mortality (mean of 21%, $n = 2$) were recorded for high populations of meadow voles and this same weasel odor formulation in lodgepole pine plantations in northwestern B.C. (Zimmerling and Zimmerling 1996). In another forest plantation study, this weasel odor formulation reduced mortality of Korean pine (*Pinus koraiensis*) seedlings to 45.0% compared with a 66.9% loss on control sites during an overwinter peak in populations of the red-backed vole (*Clethrionomys rufo-*

TABLE 6. Mean ± 1 SE ($n = 4$; $n = 3$ in winter periods) movement (m) of male and female adult voles between trapping periods in control and treatment sites for the four periods of the study.

Sex and period	Control	Treatment
Males		
Pre-treatment	24.4 ± 6.0	20.3 ± 7.4
Summer 1994	13.3 ± 4.0	18.3 ± 2.9
Winter 1994–1995	20.1 ± 1.8	11.2 ± 5.6
Spring 1995	19.4 ± 3.2	17.9 ± 1.9
Females		
Pre-treatment	11.3 ± 3.0	10.8 ± 2.5
Summer 1994	11.0 ± 2.2	13.8 ± 3.1
Winter 1994–1995	8.5 ± 0.7	7.6 ± 1.9
Spring 1995	24.4 ± 12.6	14.6 ± 3.7
Total		
Pre-treatment	15.2 ± 3.6	13.7 ± 3.9
Summer 1994	13.7 ± 4.6	14.5 ± 2.4
Winter 1994–1995	14.3 ± 1.8	10.0 ± 2.7
Spring 1995	23.7 ± 4.4	18.6 ± 1.6

canus) in northeast China (Sullivan et al. 1991). In an agricultural setting, apple tree mortality was 83.3% on a control site and 19.6% on a treatment site with this same weasel odor formulation during a peak winter of montane vole populations (Sullivan et al. 1988*b*).

Experimental design and assumptions

Based on the very low levels of movement of voles between sites, our experimental design had well-interspersed control and treatment sites within each study area at Summerland and Gavin Lake. These sites constituted four true replicates except for some demographic attributes that limited the number of replicates to three in winter 1994–1995 and spring 1995. Combining the replicate populations of montane and meadow voles in our analyses seemed to be reasonable because these two microtines are similar in many habitat affinities and aspects of their population dynamics (Hodgson 1972, Banfield 1974). In addition, both species feed on tree seedlings in forest plantations (Bergeron and Jodoin 1989, Sullivan et al. 2001).

Because of the relatively wide-ranging nature of small weasels and larger mammalian predators (e.g., coyote) that might have been attracted to our weasel odor, it is possible that control sites were not sufficiently separated from treatment sites. Thus, some predators may have been attracted to the general study area in response to the weasel odor, and this may have confounded our results. In addition, weasels may have been present in the landscape at the beginning of the study, and their strong numerical response (reproduction) in light of relatively high food availability probably meant that they were active on all control and treatment sites by August, regardless of the application of any odor. These mustelids probably were already present because the area provided good vole habitat and cover (especially the windrows). The Summerland situation was likely to be different because weasels are very sensitive to their own predation risk, and require abundant cover to avoid being caught by canids and raptors. Their presence, and numerical response, at Summerland would have been much less with so many coyotes (and probably many more raptors) around in an environment with less cover than at the Gavin Lake study area.

Another potential source of bias was the variable release rates of the odor, being relatively higher in summer with warmer ambient temperatures than in the following winter and spring. We did not measure release rates, but assumed that the odor was stronger in summer than in winter months. Similarly, we have assumed that our plastic release devices, with the 1:1 ratio of 2-propylthietane and 3-propyl-1,2-dithiolane, yielded a weasel scent comparable to that given off from the ''neat'' mixture of these two compounds in glass capillary tubes in earlier studies. The higher activity of

TABLE 7. Results of repeated-measures ANOVA for mean ($n = 4$) Jolly-Seber survival estimates, body mass, and movements for montane and meadow voles in control and treatments sites.

	Treatment			Time			Time × Treatment		
Parameter	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
Survival rate									
Males	10.45	1, 4	0.03	0.79	3, 12	0.52	1.90	3, 12	0.18
Females	1.29	1, 4	0.32	13.51	3, 12	<0.01	0.71	3, 12	0.56
Total	5.10	1, 4	0.09	4.87	3, 12	0.02	1.80	3, 12	0.20
Body mass									
Adult males	0.72	1, 6	0.43	17.52	2, 12	<0.01	0.31	2, 12	0.74
Adult females	0.38	1, 6	0.56	29.04†	2, 12	<0.01	0.52†	2, 12	0.58
Juvenile males	0.01	1, 6	0.92	18.89†	2, 12	<0.01	2.16†	2, 12	0.18
Juvenile females	0.19	1, 6	0.68	10.33	2, 12	0.01	1.64	2, 12	0.24
Movement									
Males	0.02	1, 4	0.89	0.37†	3, 12	0.73	1.10†	3, 12	0.38
Females	1.66	1, 4	0.27	3.54†	3, 12	0.10	1.20†	3, 12	0.35
Total	4.05	1, 4	0.11	6.88†	3, 12	0.01	1.25†	3, 12	0.34

† *F* values calculated using an H-F correction factor, which decreased the stated degrees of freedom due to correlation of data among repeated measures (periods).

TABLE 8. Percentage mortality of lodgepole pine seedlings overall and per vole, along with vole density, for each control (C) and treatment (T) site during the overwinter period 1994–1995 at the two study areas.

	Overall seedling mortality (%)				Per-vole seedling mortality (%)				October 1994 vole density (no./ha)			
Study area	C1	C2	T1	T2	C1	C2	T1	T2	C1	C2	T1	T2
Summerland	7.0	11.0	31.5	25.0	0.04	0.06	0.24	0.19	180.9	197.5	131.3	132.2
Gavin Lake	14.0	43.0	22.0	33.0	0.16	0.47	0.29	0.30	86.5	91.2	76.5	110.3
Mean (n = 4)	18.8		27.9		0.18		0.26					

Notes: ANOVA for the mean values indicated no significant differences between control and treatment. For overall seedling mortality, $F_{1,4} = 1.96$, $P = 0.23$; for per vole mortality, $F_{1,4} = 2.69$, $P = 0.18$.

weasels on treatment than control sites at Gavin Lake during November and December 1994 provided some evidence that our devices were indeed mimicking the natural anal gland secretion of short-tailed weasels.

CONCLUSIONS

Contrary to hypothesis 1, synthetic odor of the short-tailed weasel did not reduce abundance, reproduction, survival, movement, or body mass of voles during a peak year for vole numbers. The significant reductions in male survival and rate of change in population size need to be interpreted cautiously because these differences occurred during spring 1995, after vole numbers had declined considerably in the preceding winter. These experimental results from a true field situation provide no support for the PIBS (predator-induced breeding suppression) hypothesis.

There was a suggested increase in the activity of small mustelids on sites treated with weasel odor at Gavin Lake as per the prediction of hypothesis 2. However, it seemed questionable that the odor actually ‘‘attracted’’ weasels because our trapping data showed no change in abundance of voles, owing to direct mortality from predation. Also, because of relatively large home ranges (e.g., up to 40 ha for *M. erminea*), the odor may have resulted in a greater activity of these mustelid predators over the entire Gavin Lake study area. Future studies need to apply weasel odor over large (>10 ha) treatment units that are sufficiently independent for both vole and predator populations.

Hypothesis 3, that feeding damage to planted tree seedlings by voles would be reduced by weasel odor, also was not supported. By the time voles have reached high densities, it is too late to curtail feeding damage, because even relatively low rates of damage can amount to substantial numbers of seedlings killed. A potential way to reduce feeding damage is to maintain voles at low densities during the low and increase phases of the cycle. Weasel odor should be applied prior to and during the early stages of increase. Vole populations probably were already too high at both Summerland and Gavin Lake in early summer 1994. If weasel odor can attract some mammalian predators and generate direct mortality of voles during low population periods, then the low phase of numbers might be prolonged enough to allow sufficient survival (e.g., >90%) of newly planted tree seedlings.

As discussed by Boonstra et al. (1998), the prediction that resident predators, particularly the small mustelids, might deepen declines and extend the length of low periods of vole numbers has been suggested by several authors (Pearson 1966, Fitzgerald 1977, Grödzinski 1977, Korpimäki et al. 1991). Boonstra et al. (1998) suggest that a key experiment to test this hypothesis is to eliminate or reduce predators (e.g., weasels) from areas large enough to affect population dynamics. We also suggest that large-scale application of weasel odor to those areas of high-quality habitat for voles, where reforestation is required, would also provide a test of this critical hypothesis.

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