

Thomas P. Sullivan^{1,2}, Druscilla S. Sullivan, Applied Mammal Research Institute, 11010 Mitchell Avenue, R.R. #3, Site 46, Comp. 18, Summerland, British Columbia, Canada V0H 1Z0, and

Eugene J. Hogue, Pacific Agri-Food Research Centre, Agriculture and Agri-Food Canada, 4200 Highway 97, Summerland, British Columbia, Canada V1X 7S3

Demography of Montane Voles in Old Field and Orchard Habitats in Southern British Columbia

Abstract

Voles occupy perennial grasslands and agricultural areas in many parts of North America. This study was designed to provide a detailed analysis of the population dynamics of montane voles in old field and orchard habitats. Vole populations were intensively live-trapped in replicate old field and orchard sites over a 4-yr period at Summerland, British Columbia. Populations of montane voles reached peak densities of 186 and 144 voles/ha in old field sites before declining to numbers averaging <60 voles/ha. Orchard populations of montane voles also followed this pattern but at consistently lower numbers than old field sites. This difference in abundance ranged from 2.3-3.6 times during the peak year to 23.8-116.3 times in the decline year, at which time montane voles had declined to a mean number of 0.3-2.4 voles/ha in orchard sites. Length of breeding seasons, proportion of reproductive voles, and mean number of recruits were generally similar in old field and orchard sites. Overall mean survival of voles tended to decline through time in orchard sites, averaging 0.47 compared with old field survival of 0.76. Mean body mass of voles was consistently higher in old field than orchard sites. Montane vole populations in orchards seemed to be linked to source area dynamics of populations in old fields.

Introduction

Populations of voles (*Microtus* spp.) fluctuate in abundance every 2 to 5 yr in North America (Krebs and Myers 1974, Taitt and Krebs 1985). These rodent species prefer perennial grassland habitats that provide both cover and food sources such as grasses, sedges, and forbs (Reich 1981, Getz 1985). Multi-annual population fluctuations appear to require a minimum level of vegetative cover to generate increases in abundance of voles (Birney et al. 1976).

The montane vole (*M. montanus*) is distributed throughout the central cordilleran region of western North America (Banfield 1974). This species appears to prefer arid short grassland in high elevation alpine meadows in the southern part of its range, but it occurs at lower elevations and in valley bottoms towards the northern extent of its range (Banfield 1974). The montane vole is similar to the meadow vole (*M. pennsylvanicus*) in many of its habits with some limited evidence reported for both multi-annual and annual cycles of abundance (Negus et al. 1986, Pinter 1986, 1988). Based on the review of Taitt and Krebs (1985), the montane vole is the least stud-

ied microtine of all the major vole species in North America.

Montane voles and meadow voles are the most common microtine species affecting tree fruit production in western North America (Godfrey 1986, Sullivan and Hogue 1987, Askham 1988). The meadow vole and pine vole (*M. pinetorum*) cause similar damage to orchards in the eastern part of the continent (Byers 1984). Apple (*Malus domestica*) trees are particularly susceptible to feeding damage during winter periods when voles feed on bark, vascular tissues, and roots. This damage may lead to direct mortality from girdling or reduced growth and yield from sub-lethal feeding (Pearson and Forshey 1978).

There is a dearth of intensive population studies of voles in orchard habitats. Previous work reported that fine-textured soils limited the distribution of pine voles (Fisher and Anthony 1978), invasion of voles from nearby fields caused a rapid increase in vole populations (Horsfall 1964), and voles responded negatively to herbicide-induced weed control in orchard agro-ecosystems (Sullivan et al. 1998, 2000, Merwin et al. 1999). Thus, this study was designed to determine the abundance and population fluctuations of montane voles in old field and orchard ecosystems, with respect to variability between habitats, seasons, years, and the interactions of these factors.

¹ Author to whom correspondence should be addressed. E-mail: sullivan@telus.net

² Summerland Research Station Publication no. 2207.

Methods

Study Area and Experimental Design

This study was conducted from 1982-1986 at the Pacific Agri-Food Research Centre in the Okanagan Valley, Summerland, British Columbia. The experimental design consisted of two old field and two orchard habitats. The old field habitats were abandoned (≥ 25 yr) hay fields composed of crested wheatgrass (*Agropyron cristatum*), quack grass (*Agropyron repens*), downy brome (*Bromus tectorum*), diffuse knapweed (*Centaurea diffusa*), with some minor forbs such as yellow salsify (*Tragopogon dubius*), great mullein (*Verbascum thapsus*), American vetch (*Vicia americana*), prickly lettuce (*Lactuca serriola*), and tall tumble-mustard (*Sisymbrium altissimum*). Both old field sites were each 2 to 3 ha within a mosaic of sagebrush (*Artemisia tridentata*), ponderosa pine (*Pinus ponderosa*) forest, and orchard habitats. These old fields had resident populations of montane voles and a few long-tailed voles (*M. longicaudus*). Other species included the deer mouse (*Peromyscus maniculatus*), northwestern chipmunk (*Tamias amoenus*), Great Basin pocket mouse (*Perognathus parvus*), and western harvest mouse (*Reithrodontomys megalotis*).

The two orchards were: (1) a 5-yr-old apple orchard unit and (2) a 10-yr-old apple orchard combined with a 15-yr-old pear (*Pyrus* sp.) orchard as one unit. Both 1.2-ha orchards were located within a 90-ha mosaic of fruit trees and vineyards. Our experimental design had two replicate blocks, each consisting of one old field site and one orchard site. Each pair of old field and orchard sites was spatially segregated to enhance statistical independence (Hurlbert 1984). Common grass species on the orchard sites included orchard grass (*Dactylis glomerata*), quack grass, bluegrass (*Poa* spp.), smooth brome (*Bromus inermis*), and crested wheatgrass. These orchards were mowed 5-6 times each summer. Montane voles were the major microtine species with deer mice and northwestern chipmunks also present. Rodenticides were applied 3-4 times each winter in poison-bait feeder stations.

Vole Populations

All voles were live-trapped on 1-ha grids with 49 (7 x 7) trap stations located at 14.3-m intervals with 1-2 Longworth live-traps at each station. When

capture success exceeded 80% of the 49 traps on a grid, an additional trap was added at each station to prevent trap saturation. One of the old-field grids was an irregular shaped rectangle of 1 ha with 49 stations. The two orchard and two old field grids were live-trapped at 3-wk (spring, summer, and fall) and at 4-6-wk (winter) intervals from June 1982 to April 1986. Trapping effort was the same for all four grids throughout the study.

Traps were baited with whole oats, peanut butter, and carrot; coarse brown cotton was supplied as bedding. Traps were set on day-1, checked on the morning and afternoon of day-2 and morning of day-3, and then locked open between trapping periods. All animals captured were ear-tagged with serially numbered tags, breeding condition noted, weighed on spring balances, and point of capture recorded. The duration of the breeding season was noted by palpation of male testes and the condition of mammaries 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.

Seasons were defined as summer (April to September) and winter (October to March) periods. Thus, there were four summer and four winter periods. We used age at sexual maturity to determine age classes of voles. Body weight was used as an index of age. The percentage of sexually mature animals was used to determine the weight limitations for juveniles, subadults, and adults assuming that juveniles were seldom, if ever, sexually mature; that $< 50\%$ of the subadults in the upper weight class were mature; and that $\geq 50\%$ of the adults were sexually mature in the lowest weight class. Voles were classified as juvenile (includes juvenile and subadult classes pooled) or adult by body weight (juvenile = 1 - 26 g, adult ≥ 27 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. All handling of animals was in accordance with the principles of the Animal Care Committee, University of British Columbia.

Demographic Parameters

Population densities were estimated by the Jolly-Seber (J-S) model (Seber 1982) for reasons in-

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

Measurements of recruitment, number of lactating females, and early juvenile survival were derived from the sample of animals captured in each trapping session and then summed for summer periods. Early juvenile survival is an index relating recruitment of young into the trappable population to the number of lactating females (Krebs 1966). We used a modified version of this index, which was 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 voles in summer and winter periods were estimated from the J-S model. Mean body mass of combined males and females was used as an index of condition within populations of voles during summer and winter periods.

Statistical Analysis

Our design was a 2x2x4 randomized complete block factorial Model I analysis of variance (ANOVA) (Zar 1999). We had three factors: A was habitat with 2 levels (old field and orchard); B was season with 2 levels (summer and winter); and C was year with 4 levels (1982-83, 1983-84, 1984-85, 1985-86). This analysis was conducted to test differences in mean abundance, mean number of recruits, mean J-S survival, and mean early juvenile survival of voles between old field and orchard sites. For the analyses, a single estimate of the given parameter for each habitat, season, and year was derived to test for differences between the two treatments.

Proportion of adult males and adult females breeding was analyzed by a χ^2 2 x 2 contingency table (Zar 1999) for each of the four summer periods. These datasets of proportion of animals breeding often include voles captured more than once, and hence they are not completely independent. Thus, the χ^2 analyses provide only an indication of the degree of difference between

datasets. Mean J-S survival rates and mean body mass were presented with 95% confidence intervals (CI) to provide a range of measurements for summer and winter periods.

In all analyses, the level of significance was $P = 0.05$.

Results

Abundance

We captured 1,877 individual montane voles in two old field and 712 voles in two orchard sites. Mean J-S trappability (susceptibility to capture) estimates ranged from 61.4% to 78.1% (summer) and from 65.0% to 78.7% (winter) in the old field sites. These estimates ranged from 47.0% to 88.9% (summer) and from 28.6% to 85.7% (winter) in the orchard sites.

Old field abundance increased during summer 1982 and winter 1982-83 reaching peak densities of 186 and 144 voles/ha in late fall-early winter 1983 (Figure 1). Montane vole populations in the orchard sites also tended to follow this pattern, but at significantly lower mean numbers than in old field sites ($P < 0.01$) (Table 1). This difference ranged from 1.5-2.9 times in summer 1982 to 23.8-116.3 times in winter 1985-86, by which time montane voles had declined to low numbers (0.3 to 2.4 voles/ha on average) in the orchard sites (Figure 1, Table 1). Numbers in the old field sites declined over winter 1983-84 before peaking again in 1984 at densities of 156 and 146 voles/ha. Vole populations then declined during 1985 and 1986 to numbers averaging < 60 voles/ha (Table 1). The season x year interaction was significant ($P = 0.04$), thereby indicating that the pattern of higher abundance during winter than summer periods was not maintained through time on the orchard sites. No other sources of variance were significant.

Reproduction and Recruitment

The breeding season for montane voles, based on reproductive condition of adult males, began in February each year and continued until at least October. This pattern was the same in both old field and orchard sites. The proportion of adult females with successful pregnancies ranged from 0.30 to 0.58 in the old field sites and from 0.24 to 0.55 in the orchard sites (Table 2). A significantly greater proportion of adult female voles was

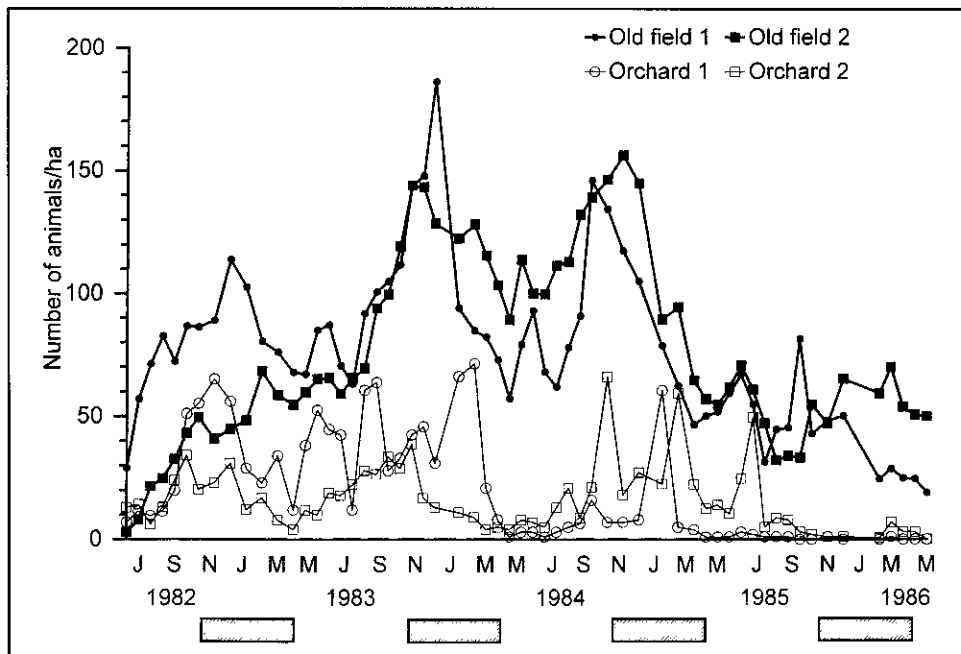


Figure 1. Population densities (Jolly-Seber) per ha of montane voles in replicate old field and orchard sites during the study. Shaded bars indicate winter periods.

TABLE 1. Mean (\pm SE) abundance per ha for montane voles during summer and winter periods in replicate old field and orchard sites. Sample size (n = number of trapping periods) in parentheses.

Period		Replicate 1		Replicate 2	
		Old field	Orchard	Old field	Orchard
Summer 1982	(7)	69.2 \pm 7.8	23.6 \pm 7.8	26.0 \pm 6.5	17.8 \pm 3.5
Winter 1982-83	(5)	92.4 \pm 7.0	41.4 \pm 8.1	52.1 \pm 5.0	18.2 \pm 4.1
Summer 1983	(9)	82.0 \pm 5.2	39.3 \pm 6.3	70.3 \pm 5.2	19.3 \pm 3.2
Winter 1983-84	(8)	115.5 \pm 14.1	39.8 \pm 7.6	125.7 \pm 4.8	15.8 \pm 4.3
Summer 1984	(8)	84.3 \pm 9.9	4.8 \pm 1.7	112.4 \pm 5.9	11.0 \pm 2.4
Winter 1984-85	(6)	90.8 \pm 13.8	15.3 \pm 9.1	116.1 \pm 15.5	35.9 \pm 8.6
Summer 1985	(9)	54.0 \pm 4.8	1.2 \pm 0.3	50.1 \pm 4.7	15.1 \pm 4.8
Winter 1985-86	(7)	34.9 \pm 4.4	0.3 \pm 0.2	57.2 \pm 3.1	2.4 \pm 0.9

lactating in the orchard than old field sites in 1984 ($P < 0.01$), with no significant differences between sites in the other years.

Mean number of new voles was not significantly different, between old field and orchard sites, during summer and winter seasons, and over time (Table 3). There were no significant interactions for any of the factors.

Survival and Body Mass

Mean J-S survival was not significantly different between orchard and old-field sites during sum-

mer and winter seasons and over time (Figure 2). The habitat \times year interaction approached significance ($P = 0.06$) and this pattern was clearly outlined in the declining survival of voles in orchard sites from 1982 to 1984 (Figure 2). Mean survival of voles was 0.73 ± 0.02 in summer and 0.78 ± 0.02 in winter in old field sites compared with 0.46 ± 0.05 in summer and 0.47 ± 0.05 in winter in orchard sites. An index of early juvenile survival was similar in orchard and old field sites (Table 4). There were no other significant interactions for any of the factors relating to these survival parameters.

TABLE 2. Proportion of adult male (scrotal testes) and female (successful pregnancies) montane voles in reproductive condition during breeding seasons each year for pooled data in replicate old field and orchard sites. Sample size (number of voles) in parentheses. The only significant difference, by χ^2 , was for females in 1984.

Year	Old field	Orchard
Males		
1982	0.94 (154)	0.90 (61)
1983	0.92 (416)	0.96 (134)
1984	0.92 (525)	0.94 (48)
1985	0.92 (349)	0.98 (40)
Females		
1982	0.30 (251)	0.24 (100)
1983	0.34 (1005)	0.33 (193)
1984	0.31 (969)	0.47 (68)
1985	0.58 (521)	0.55 (47)

Mean body mass of montane voles appeared to be higher in old field than orchard sites in most seasons (Figure 3). Old field populations of voles generally had lower mean body masses in winter than summer periods.

Discussion

Patterns of Abundance

Our study covered a 4-yr period during an increase, peak, and decline in the cyclic fluctuation of the montane vole, and it is the first detailed comparison of vole population dynamics in old field and orchard habitats. Abundance of voles in the two old field sites ranged from a mean overwinter value in 1982 of 72.3 animals/ha to 120.6 in 1983 and 103.5 in 1984, before declining to 46.1 in 1985.

TABLE 3. Mean (\pm SE) number of recruits per ha for montane voles during summer and winter periods in replicate old field and orchard sites. Sample size (n = number of trapping periods) in parentheses.

Period	Replicate 1		Replicate 2	
	Old field	Orchard	Old field	Orchard
Summer 1982	(7) 20.4 \pm 2.8	8.6 \pm 1.9	10.6 \pm 1.7	8.1 \pm 2.0
Winter 1982-83	(5) 20.0 \pm 5.4	9.2 \pm 1.4	12.0 \pm 2.4	7.4 \pm 2.8
Summer 1983	(9) 17.4 \pm 3.3	9.9 \pm 1.4	16.1 \pm 2.1	8.0 \pm 1.3
Winter 1983-84	(8) 22.4 \pm 4.5	10.5 \pm 2.1	18.4 \pm 3.4	7.3 \pm 1.8
Summer 1984	(8) 19.1 \pm 3.8	2.8 \pm 1.4	21.0 \pm 3.3	6.6 \pm 1.4
Winter 1984-85	(6) 18.5 \pm 5.4	4.7 \pm 1.3	17.5 \pm 4.8	8.7 \pm 1.1
Summer 1985	(9) 10.9 \pm 2.3	0.7 \pm 0.3	8.3 \pm 1.5	4.1 \pm 1.6
Winter 1985-86	(7) 8.4 \pm 1.4	0.3 \pm 0.2	11.7 \pm 2.3	1.3 \pm 1.0

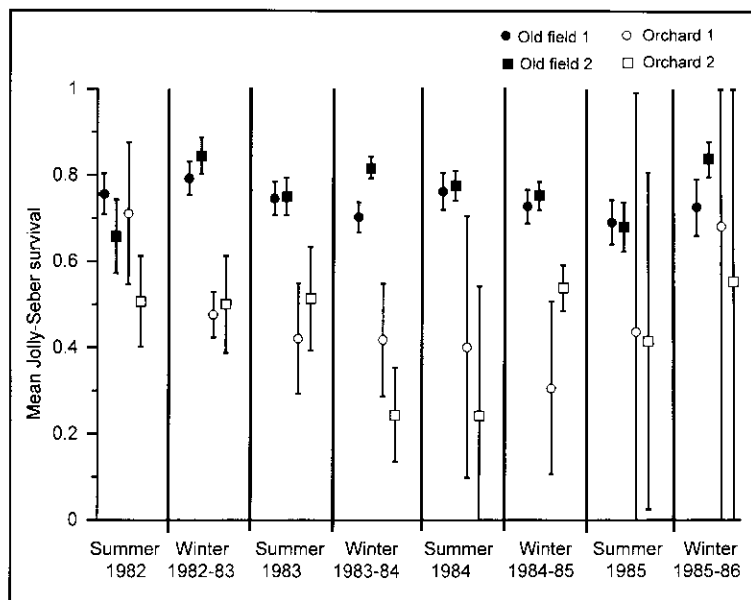


Figure 2. Mean Jolly-Seber survival (per 28 days) \pm 95% confidence intervals for montane voles in replicate old field and orchard sites during summer and winter periods in the study.

TABLE 4. Index of early juvenile survival of montane voles (number of juvenile recruits per lactating female) during breeding seasons each year in replicate old field and orchard sites. Sample size (number of lactating females) in parentheses.

Year	Replicate 1		Replicate 2	
	Old field	Orchard	Old field	Orchard
1982	2.09 (55)	4.33 (9)	2.24 (21)	2.93 (15)
1983	0.81 (175)	1.45 (44)	0.60 (164)	2.85 (20)
1984	0.83 (149)	4.33 (9)	0.79 (155)	2.09 (23)
1985	0.41 (198)	2.75 (4)	0.71 (102)	1.59 (22)

Maximum and minimum densities per ha were 186 and 19, which was similar to the range reported for meadow voles by Taitt and Krebs (1985). Conversely, orchard populations had similar mean winter numbers ranging from 29.8 voles/ha in 1982 to 27.8 in 1983 and 25.6 in 1984, before declining to 1.4 in 1985. Thus, montane voles in these

orchards appeared to have an annual cycle of abundance with low spring densities and relatively higher numbers in autumn, although the habitat x season interaction was not significant. Old field populations had a multi-annual population fluctuation overlying annual changes in abundance (Figure 1). This dichotomy of population dynamics fits the patterns described for voles for which the amplitude of numerical change is < 5-fold for annual fluctuations and usually >10-fold for multi-annual cycles (Taitt and Krebs 1985).

In the only long-term (19-yr) study, montane vole populations appeared to fluctuate every 3-4 yr at high elevation meadows in Wyoming (Pinter 1986, 1988). This pattern of population fluctuation was similar to the closely related meadow vole (Krebs and Myers 1974, Taitt and Krebs 1985). The temporal heterogeneity inherent in montane habitats for populations of montane voles was also reported by Negus et al. (1977). Negus et al. (1986), however, studied a noncycling population of montane voles over 8 yr in a low elevation salt marsh habitat in Utah.

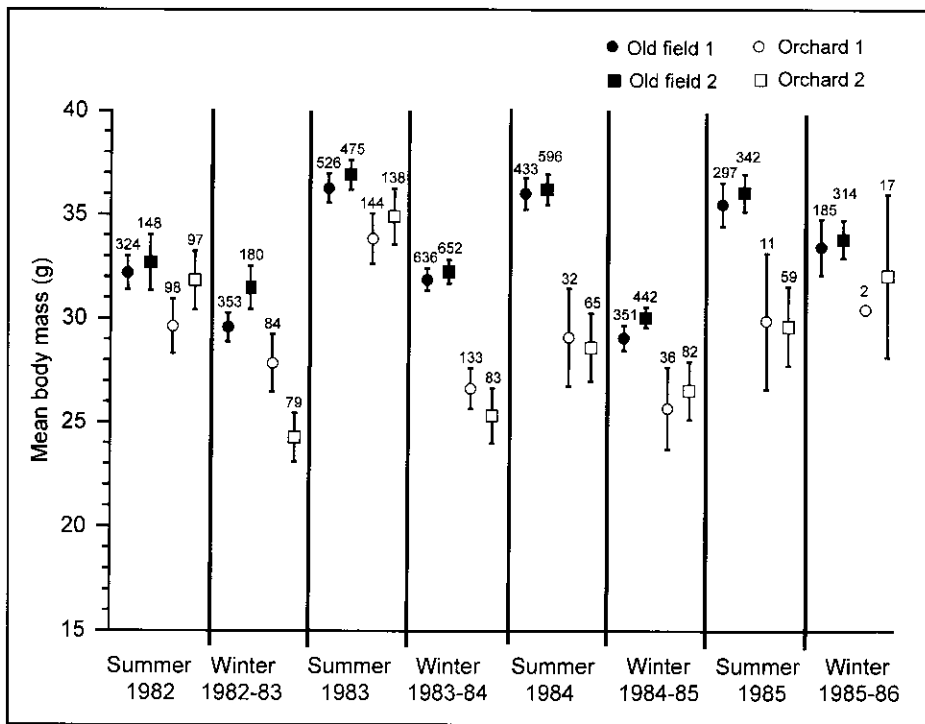


Figure 3. Mean body mass (g) ± 95% confidence intervals for montane voles in replicate old field and orchard sites during summer and winter periods in the study.

Despite the differences in habitat, length of breeding seasons and proportion of reproductive animals were similar in orchard and old field sites. Winter breeding (Jannett 1984) and a long breeding season prior to a peak population of voles are classic characteristics of cyclic behavior and seem to have occurred in these populations. Larger body size at the peak than in other phases of the cycle is another characteristic and may have occurred in the old field sites during summer 1983, winter 1983-84, and summer 1984 (Figure 3). However, mean body mass measurements in summer 1985 and winter 1985-86 did not fit this pattern.

Orchard Populations

This study is the first intensive mark-recapture analysis of vole populations in orchard agro-ecosystems. Relative population levels of voles have traditionally been monitored by activity measures such as fresh sign or an apple indexing method recording tooth-marks (Byers 1984, 1985). Most vole species require a minimum level of vegetative cover to increase in numbers during multiannual population fluctuations (Birney et al. 1976). Natural grasslands or old fields are the preferred habitats of most *Microtus* spp. (Getz 1985). Thus, it is not surprising that our orchard sites had significantly lower abundance of voles than the old field sites (Table 1). Our orchard sites were mowed, and herbicide was applied to tree rows for weed management, on a regular basis during summer periods. The influence of these cultural practices in reducing vole populations has been reported by Byers and Young (1978), Godfrey (1986), Sullivan and Hogue (1987), and Merwin et al. (1999). Orchard habitats appear to provide a predictable environment for montane voles and thus may explain the relatively consistent, albeit low, abundance patterns over the 4 yr.

We were not able to measure the effect of rodenticides on vole populations as no untreated orchard sites were available for comparison. However, based on the patterns of abundance in the two habitats, orchard population changes may have been influenced more by natural factors than by rodenticides. Merwin et al. (1999) reported that anticoagulant rodenticides did not adequately control meadow voles in apple orchards in New York. Despite the variability in efficacy, rodenticides continue to be the major method used to reduce vole populations in orchards (Byers 1985, Merwin et al. 1999).

The relationship between vole populations in old field or source area habitats and orchards is likely a source-sink whereby lands adjoining an orchard may contribute to population recovery and maintenance through immigrating animals (Horsfall 1964). Clearly, there were substantial populations in our old field sites and during increase periods (e.g. autumn 1983 and 1984), dispersal of voles was high, as documented experimentally by Myers and Krebs (1971) and Krebs et al. (1976). During these periods of high dispersal in autumn and early winter attempts at population reduction are essentially futile owing to the surplus of animals available to colonize depopulated areas (Sullivan 1986). This surplus of animals was particularly dramatic in the outbreaks of montane voles in the western U.S. in 1906-1908 and in 1957-1958 when this microtine caused widespread damage to agricultural crops (Getz 1985).

Orchard populations of montane voles appear to be linked to source area dynamics of populations in old field habitats. Mean abundance of voles/ha ranged from 26.0-125.7 in old field sites and from 0.3-41.4 in orchard sites. Mean recruits/ha also followed this pattern (Table 5). Length of breeding seasons and proportion of reproductive voles were generally similar in old field and orchard sites, but overall survival and mean body mass were consistently higher in old field than

TABLE 5. Summary of the population dynamics of montane voles in old field and orchard habitats over a 4-year period.

Parameter and period	Old field	Orchard
Mean abundance per ha (range)		
Summer	26.0 - 112.4	1.2 - 39.3
Winter	34.9 - 125.7	0.3 - 41.4
Mean recruits per ha (range)		
Summer	8.3 - 21.0	0.7 - 9.9
Winter	8.4 - 22.4	0.3 - 10.5
Reproduction (proportion) (n=4)		
Males	0.93	0.95
Females	0.38	0.40
Early juvenile survival (n=8)	1.06	2.79
Total survival (n=8)		
Summer	0.73	0.46
Winter	0.78	0.47
Mean body mass (n=8)		
Summer	35.3	31.0
Winter	31.5	27.4

orchard sites (Table 5). Traditional methods of vole control (rodenticides) have little effect on vole numbers during peak years as voles from adjacent habitats readily move into orchards. Our study suggests that other methods of vole control (habitat alteration) may be more effective at limiting vole-caused damage.

Literature Cited

- Askham, L. R. 1988. A two year study of the physical and economic impact of voles (*Microtus montanus*) on mixed maturity apple (*Malus* spp.) orchards in the Pacific Northwestern United States. Pages 151-155 *In* A.C. Crabb and R.E. Marsh (editors), Proceedings of the 13th Vertebrate Pest Conference. University of California, Davis, California.
- Banfield, A. W. F. 1974. The Mammals of Canada. University of Toronto Press, Toronto, Ontario.
- Birney, E. C., W. E. Grant, and D. D. Baird. 1976. Importance of vegetative cover to cycles of *Microtus* populations. *Ecology* 57:1043-1051.
- Byers, R. E. 1984. Control and management of vertebrate pests in deciduous orchards of the eastern United States. *Horticultural Reviews* 6:253-285.
- Byers, R. E. 1985. Management and control. Pages 621-646 *In* R. H. Tamarin (editor), *Biology of New World Microtus*. Special Publication Number 8. American Society of Mammalogists, Boston, Massachusetts.
- Byers, R. E., and R. S. Young. 1978. Effect of orchard culture on pine vole activity. *Journal of the American Society for Horticultural Science* 103:625-626.
- Fisher, A. R., and R. G. Anthony. 1978. The effect of soil texture on distribution of pine voles in Pennsylvania orchards. *American Midland Naturalist* 104:39-46.
- Getz, L. L. 1985. Habitats. Pages 286-309 *In* R. H. Tamarin (editor), *Biology of New World Microtus*. Special Publication Number 8. American Society of Mammalogists, Boston, Massachusetts.
- Godfrey, M. E. R. 1986. Cultural practices affecting montane voles in Washington apple orchards. *In* C. G. J. Richards, and T. Y. Ku (editors), *Control of Mammal Pests*. Supplement Number 1 to *Tropical Pest Management* 32: 127-138.
- Hilborn, R., J. A. Redfield, and C. J. Krebs. 1976. On the reliability of enumeration for mark and recapture census of voles. *Canadian Journal of Zoology* 54:1019-1024.
- Horsfall, F., Jr. 1964. Pine mouse invasion and reinfestation of orchards subsequent to removal of adjacent woody plant cover or the use of ground sprays. *Proceedings of the American Society for Horticultural Science* 85:161-171.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187-211.
- Jannett, F. J., Jr. 1984. Reproduction of the montane vole, *Microtus montanus*, in subnivean populations. Pages 215-224 *In* J. F. Merritt, (editor), *Winter Ecology of Small Mammals*. Carnegie Museum of Natural History Special Publication Number 10.
- Jolly, G. M., and J. M. Dickson. 1983. The problem of unequal catchability in mark-recapture estimation of small mammal populations. *Canadian Journal of Zoology* 61:922-927.
- Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs* 36:239-273.
- Krebs, C. J., B. S. Gilbert, S. Boutin, A. R. E. Sinclair, and J. N. M. Smith. 1986. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon. *Journal of Animal Ecology* 55:963-982.
- Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. *Ecology* 50:587-607.
- Krebs, C. J. and J. H. Myers. 1974. Population cycles in small mammals. *Advances in Ecological Research* 8:267-399.
- Krebs, C. J., I. Wingate, J. LeDuc, J. A. Redfield, M. Taitt, and R. Hilborn. 1976. *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii*. *Canadian Journal of Zoology* 54:79-95.
- Merwin, I. A., J. A. Ray, and P. D. Curtis. 1999. Orchard groundcover management systems affect meadow vole populations and damage to apple trees. *Horticultural Science* 34:271-274.
- Myers, J. H., and C. J. Krebs. 1971. Genetic, behavioral, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. *Ecological Monographs* 41:53-78.
- Negus, N. C., P. J. Berger, and J. B. Forslund. 1977. Reproductive strategy of *Microtus montanus*. *Journal of Mammalogy* 58:347-353.
- Negus, N. C., P. J. Berger, and B. W. Brown. 1986. Microtine population dynamics in a predictable environment. *Canadian Journal of Zoology* 64:785-792.
- Pearson, K., and C. G. Forshey. 1978. Effects of pine vole damage on tree vigor and fruit yield in New York orchards. *Horticultural Science* 13:56-57.
- Pinter, A. J. 1986. Population dynamics and litter size of the montane vole, *Microtus montanus*. *Canadian Journal of Zoology* 64:1487-1490.
- Pinter, A. J. 1988. Multiannual fluctuations in precipitation and population dynamics of the montane vole, *Microtus montanus*. *Canadian Journal of Zoology* 66:2128-2132.

Acknowledgements

We thank the Research Branch of Agriculture Canada and the Applied Mammal Research Institute for financial support; the study area and facilities provided by the Summerland Research Station; and field assistants W. Kaiser, J. Gareau, B. Jones, J. Krebs, and C. Robinson.

- Reich, L. M. 1981. *Microtus pennsylvanicus*. Mammalian Species 159:1-8.
- Seber, G. A. F. 1982. The Estimation of Animal Abundance and Related Parameters, 2nd Edition. Charles Griffin, London, UK.
- Sullivan, T. P. 1986. Understanding the resiliency of small mammals to population reduction: poison or population dynamics? C. G. J. Richards and T.Y. Ku (editors). In Control of Mammal Pests. Supplement Number 1 to Tropical Pest Management 32:69-82.
- Sullivan, T. P., and E. J. Hogue. 1987. Influence of orchard floor management on vole and pocket gopher populations and damage in apple orchards. Journal of the American Society for Horticultural Science 112:972-977.
- Sullivan, T. P., D. S., Sullivan, and E. J. Hogue. 2000. Impact of orchard vegetation management on small mammal population dynamics and species diversity. Pages 398-403. In T. P. Salmon and A. C. Crabb (editors), Proceedings of the 19th Vertebrate Pest Conference, University of California, Davis, California.
- Sullivan, T. P., D. S., Sullivan, E. J., Hogue, R. A., Lautenschlager, and R. G. Wagner. 1998. Population dynamics of small mammals in relation to vegetation management in orchard agroecosystems: compensatory responses in abundance and biomass. Crop Protection 17:1-11.
- Tait, M. J., and C. J. Krebs. 1985. Population dynamics and cycles. Pages 567-620 In R. H. Tamarin (editor), Biology of New World *Microtus*. Special Publication Number 8. American Society of Mammalogists, Boston, Massachusetts.
- Zar, J. H. 1999. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

Received 30 October 2002

Accepted for publication 29 May 2003