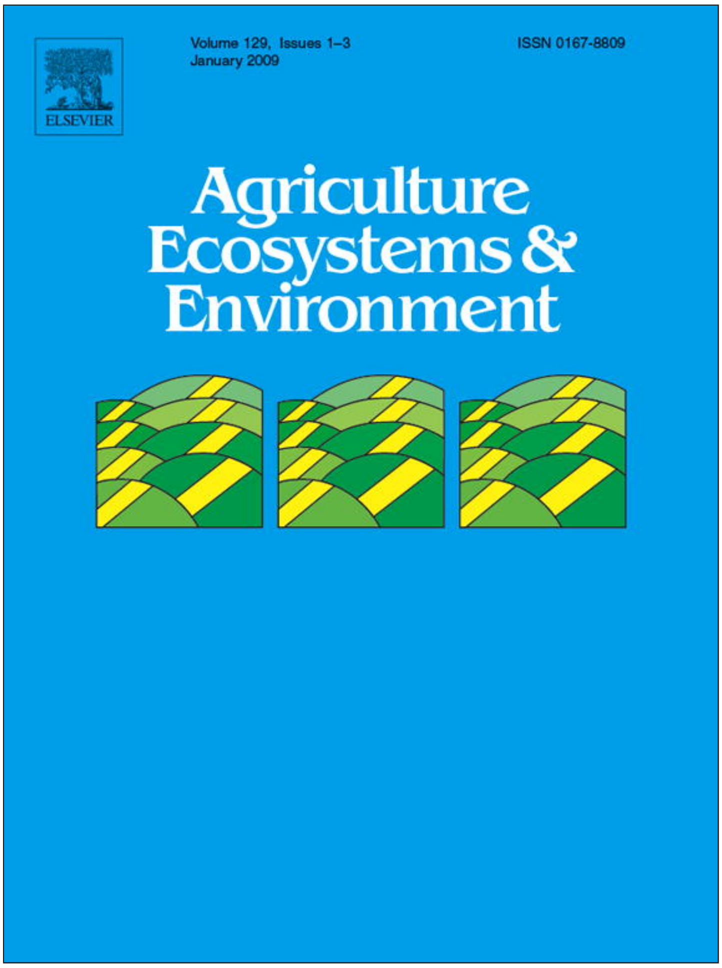

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Are linear habitats in agrarian landscapes source areas of beneficial or pest rodents?

Thomas P. Sullivan[a,b,*], Druscilla S. Sullivan[a]

[a] *Applied Mammal Research Institute, 11010 Mitchell Avenue, Summerland, BC, Canada V0H 1Z8*
[b] *Agroecology Program, Faculty of Land and Food Systems, 2357 Main Mall, University of British Columbia, Vancouver, BC, Canada V6T 1Z4*

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ABSTRACT

This study tested the hypotheses that populations of the montane vole *Microtus montanus* (a potential pest species) and deer mouse *Peromyscus maniculatus* (a potential beneficial species) in linear habitats will be (i) positively related to the type of vegetation (abundance and diversity of vascular plants) within and adjacent to those habitats; and (ii) correlated with population changes and productivity (reproductive performance, recruitment, and survival) in nearby apple (*Malus domestica*) orchards. Population dynamics of *M. montanus* and *P. maniculatus* were measured by intensive live-trapping from 2003 to 2006 in replicated hedgerows, riparian strips, and nearby orchards, in southern British Columbia, Canada. Hedgerows were borders between orchards, orchards and old fields, as well as orchards and natural forest. Contrary to hypothesis (i), *M. montanus* and *P. maniculatus* populations were not positively related to vegetation type within linear habitats and their adjacent crop and non-crop areas. Mean abundance and diversity of vegetation attributes were similar among linear habitats. Hypothesis (ii) was not supported for *M. montanus* populations in linear habitats since they did not correlate with population changes in nearby apple orchards, during a peak year in abundance. Populations of *P. maniculatus* were similar in abundance and other demographic variables among the linear habitats and apple orchards, and hence hypothesis (ii) was supported for this species.

1. Introduction

A major conservation objective of non-crop areas is to provide habitat for a variety of small mammal species and their predators including birds of prey (Tattersall et al., 2000; Butet and Leroux, 2001). Non-crop linear habitats include hedgerows, field margins, riparian zones along streams, and other field boundary delineations such as ditches and roadsides (Marshall et al., 2002; Tattersall et al., 2002). Terrestrial small mammals are common inhabitants of these areas (Butet and Leroux, 2001) and distribute beneficial mycorrhizal fungi and seeds for tree regeneration in woodlands and along hedgerows, and consume invertebrates, plants, and their seeds (Buckner, 1966; Golley et al., 1975). However, species of *Microtus* and *Clethrionomys* may become pests by feeding on crops such as alfalfa (*Medicago sativa* L.), cereals, and orchard trees (Byers, 1984; Wood, 1994; Jacob, 2003).

Populations of some species of voles tend to have cyclic fluctuations in abundance in northern latitudes with a peak every 3–5 years and these periods may be interspersed with annual fluctuations in abundance (Krebs and Myers, 1974; Taitt and Krebs, 1985). Montane voles (*Microtus montanus* Peale) and meadow voles (*M. pennsylvanicus* Ord.) are the most common microtine species affecting tree fruit production in western North America (Sullivan and Hogue, 1987). A second major species associated with these orchard agroecosystems is the deer mouse (*Peromyscus maniculatus* Wagner), a rodent with generalist dietary and habitat requirements (Banfield, 1974; Sullivan et al., 2004). Recent reports suggest that *P. maniculatus* may be valuable consumers of weed seeds, and hence directly beneficial to crop production (Westerman et al., 2005).

Thus, this study was designed to test the hypotheses that populations of *M. montanus* and *P. maniculatus* in linear habitats (hedgerows and riparian strips) will be (i) positively related to the type of vegetation (abundance and diversity of vascular plants) within the linear habitats and their adjacent crop and non-crop areas; and (ii) correlated with population changes and productivity (reproductive performance, recruitment, and survival) in nearby apple orchards.

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[*] Corresponding author at: Applied Mammal Research Institute, 11010 Mitchell Avenue, Summerland, BC, Canada V0H 1Z8. Tel.: +1 604 822 6873; fax: +1 604 822 2184.
E-mail address: tom.sullivan@ubc.ca (T.P. Sullivan).

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2. Materials and methods

This study was located in Prairie Valley, Summerland, British Columbia (BC), Canada (49°34′N; 119°40′W). Our linear habitat 'hedgerows' were borders between (i) adjacent orchards, (ii) orchards and old fields, and (iii) orchards and natural ponderosa pine (*Pinus ponderosa* Dougl.) forest; as well as (iv) 'riparian strips'. Vegetation along hedgerows was composed primarily of shrubs and some herbs. Hedgerows were usually up to 2 m wide and at least 100 m in length. The riparian habitats were located along a 3-km long year-round flowing stream which bisected Prairie Valley.

Apple orchards were 6- to 7-year-old Royal Gala cultivars in spacings of 0.5–1 m × 3–4 m and 10–30-year-old McIntosh and Red Delicious cultivars at spacings of 3–4 m × 5 m. Common herbaceous species in apple orchards included orchard grass (*Dactylis glomerata* L.), annual blue-grass (*Poa annua* L.), mountain brome (*Bromus marginatus* Nees ex Steud.), common dandelion (*Taraxacum officinale* Weber), white clover (*Trifolium repens* L.), and perennial ryegrass (*Lolium perenne* L.). These orchards were mowed in alleys and sprayed 3–4 times per growing season with Roundup® herbicide for weed control along tree rows. Orchard sites were each 4–7 ha in area.

Old fields were abandoned hay fields or orchards (with trees removed) composed of crested wheatgrass (*Agropyron cristatum* L.), quack grass (*Agropyron repens* L.), downy brome (*Bromus tectorum* L.), diffuse knapweed (*Centaurea diffusa* Lam.), and some minor herbaceous species such as yellow salsify (*Tragopogon dubius* Scop.). These sites were each 2–3 ha in area.

The natural forest habitats were composed of ponderosa pine as the major tree species with understory herbs such as arrow-leaved balsamroot (*Balsamorhiza sagittata* Nels & Macbr.), bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith), diffuse knapweed, downy brome, and sporadic shrubs such as big sagebrush (*Artemisia tridentata* Nutt.) and rabbitbrush (*Chrysothamnus nauseosus* (Pall.) Britt.).

The study had a completely randomized design with three replicate sites of each of the four types of linear habitats and the apple orchards. The 15 sites (five habitat types × three replicates) were selected on the basis of availability of intact hedgerows with nearby riparian strips and apple orchards. Orchard sites were the size of typical farming operations in the Okanagan Valley of BC. All sites were far enough apart (0.12–1.00 km) to be statistically independent.

2.1. Vegetation

Two 25 m transects, consisting of five 5 m × 5 m plots were systematically located along each linear habitat following the method of Stickney (1980). Each plot contained three sizes of nested sub-plots: a 5 m × 5 m plot for sampling trees, a 3 m × 3 m sub-plot for sampling shrubs; and a 1 m × 1 m sub-plot for sampling herbs. A visual estimate of percentage cover of the ground was made for each species height class combination within the appropriate nested sub-plot. These data were then used to calculate a crown volume index (m^3/0.01 ha) for each plant species. The product of percentage cover and representative height gives the volume of a cylindroid which represents the space occupied by the plant in the community. Crown volume index values were then averaged by species for each plot size and converted to a 0.01-ha base to produce the values given for each species and layer (herbs, shrubs, and trees). Sampling was done in June–July 2003. Species richness, species diversity, and structural diversity were calculated for these data.

2.2. Vole and deer mouse populations

Vole and deer mouse populations were sampled at 4-week (summer) and 4–6-week (winter) intervals from April 2003 to March 2006. One trapping grid (1 ha), with 49 (7 × 7) trap stations at 14.3 m intervals, and one Longworth live-trap at each station were located in each of two orchard sites, with a third orchard site that had an irregular-shaped 1 ha grid. Each hedgerow and riparian strip had seven trap stations at 14.3 m intervals with four Longworth live-traps at each station. Additional traps were added to stations when required to sample high numbers of animals. Traps were supplied with whole oats and carrot, with cotton as bedding. Traps were set on the afternoon of day 1, checked on the morning and afternoon of day 2 and morning of day 3, and then locked open between trapping sessions.

All voles and deer mice captured were ear-tagged with individually numbered tags, and released at point of capture (Krebs et al., 1969). Seasons were defined as summer (April–September) and winter (October–March) periods. Thus, there were three summer and three winter periods that had at least five trapping sessions. We used mass at sexual maturity to infer age classes of animals. The percentage of sexually mature animals was used to determine the mass limitations for juveniles and adults assuming that juveniles were seldom, if ever, sexually mature, and that at least 50% of the adults were sexually mature in their lowest mass class. *M. montanus* (juvenile = 1–26 g, adult ≥ 27 g) and *P. maniculatus* (juvenile = 1–20 g, adult ≥ 21 g) were classified as juvenile or adult by body mass. All handling of animals was in accordance with the principles of the Animal Care Committee, University of British Columbia.

Trappability and population density were measured to compare the abundance of *M. montanus* and *P. maniculatus* in the different habitats. Population densities were estimated by the Jolly-Seber (J–S) model (Seber, 1982) with small sample size corrections (Krebs, 1991). Measurements of recruitment, number of successful pregnancies, and early juvenile survival were derived from the sample of animals captured in each trapping session and then summed for summer periods. A pregnancy was considered successful if the female was lactating during the period following the estimated time of birth of a litter. Early juvenile survival was an index relating recruitment of young into the trappable population to the number of lactating females. A modified version of this index was the number of juvenile animals at week t divided by the number of lactating females caught in week $t - 4$. Mean survival rates per 28 days for summer and winter periods were estimated from the J–S model.

2.3. Statistical analyses

A one-way analysis of variance (ANOVA) (Zar, 1999) was used to determine the effect of linear habitat type on mean crown volume index, mean species richness and diversity, and mean structural diversity of the herb, shrub, and tree layers. A repeated-measures (RM) ANOVA was conducted to test for differences among linear habitats for the demographic variables of mean abundance, mean number of recruits, mean number of successful pregnancies, mean early juvenile survival, and mean J–S survival for populations of *M. montanus* and *P. maniculatus*. Data not conforming to properties of normality and equal variance were subjected to various transformations to best approximate the assumptions required by an 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 datasets that were correlated among years, the Huynh–Feldt (H–F) correction (Huynh and Feldt, 1976) was used to adjust the degrees of freedom of the within-subjects *F*-ratio.

A simple linear regression analysis was used to investigate the relationship between mean abundance of *M. montanus* and *P. maniculatus* and the habitat variables of abundance, species diversity, and structural diversity of vegetation. We also calculated overall mean abundance with 95% confidence intervals (CI) for each species. Duncan's multiple range test (DMRT) was used to compare mean values. In all analyses, the level of significance was at least $P = 0.05$.

3. Results

Mean crown volume index of herbs (range of 12.3–21.4 m^3/0.01 ha) ($F_{3,8} = 0.29$; $P = 0.83$) and shrubs ($F_{3,8} = 3.01$; $P = 0.10$) were statistically similar among sites. However, it may be biologically significant that the abundance of shrubs in the orchard-old field hedgerows (169.1 m^3/0.01 ha) and riparian (222.6 m^3/0.01 ha) habitats were 4.1–5.4 times higher than in the orchard–forest hedgerow (41.6 m^3/0.01 ha). Mean crown volume index of trees also followed this pattern of similarity ($F_{3,8} = 0.78$; $P = 0.54$) among habitats. Again, it should be noted that the orchard-old field hedgerows and riparian habitats had seemingly greater amounts (averaging 3.0–3.4 times) of tree volume than the other two types of hedgerows.

A total of 67 species of herbs, 22 species of shrubs, and 12 species of trees was sampled in this study. Mean species richness and diversity of herb, shrub, and tree layers were all similar ($P > 0.05$) among sites. Mean total species richness of plants was similar ($F_{3,8} = 0.41$; $P = 0.75$) among sites, as was mean total species diversity ($F_{3,8} = 0.67$; $P = 0.60$). Mean structural diversity of herb, shrub, and tree layers were all similar ($P > 0.05$) among sites; mean total structural diversity also followed this pattern ($F_{3,8} = 1.88$; $P = 0.21$).

A total of 37 trapping periods was conducted from April 2003 to March 2006. The total number of individual *M. montanus* captured was 987 and of *P. maniculatus* was 1937. Estimates of trappability tended to be variable among species, with overall mean values ranging from 34.3% to 91.2% for *M. montanus* and 44.5% to 83.9% for *P. maniculatus*.

Population changes of *M. montanus* in the four types of linear habitats exhibited seasonal patterns of abundance with lower numbers (<5 voles/line) in spring followed by higher numbers (5–10 voles/line) in the fall-winter each year (Fig. 1A). Mean abundance of *M. montanus* was similar ($F_{3,7} = 0.21$; $P = 0.89$) among linear habitats, but did change significantly ($F_{5,35} = 4.82$; $P < 0.01$) over time with numbers at 10–15/line in summer 2005 (Fig. 1A). Peak numbers of voles was reached in August 2005 in all linear habitats (range of 12.0–25.4 voles/line) and nearby apple orchards (12.3 voles/ha). The overall mean estimates of abundance showed overlapping 95% CIs for all four linear habitats; but mean (±95% CI) abundance of voles was significantly higher (non-overlapping 95% CIs) in the orchard-old field (6.5 ± 3.3) and orchard-pine (6.5 ± 2.6) linear habitats than in the orchards (1.5 ± 0.7).

Population changes of *P. maniculatus* were markedly seasonal with dramatic increases in numbers each fall-winter after relatively low numbers in the summer months in the four linear habitats (Fig. 1B). The riparian strips had 1.9–2.7 times as many *P. maniculatus*, on average, as the three hedgerow habitats, but mean abundance/line was similar ($F_{3,7} = 1.48$; $P = 0.30$) among habitats. Overall mean (±95% CI) abundance was significantly higher (non-overlapping 95% CIs) in the riparian strips (19.8 ± 4.3) than other linear habitats (range of means 7.3–10.6). Orchard populations of *P. maniculatus* were similar to those of the linear habitats except for the orchard-pine which had a lower overall mean abundance.

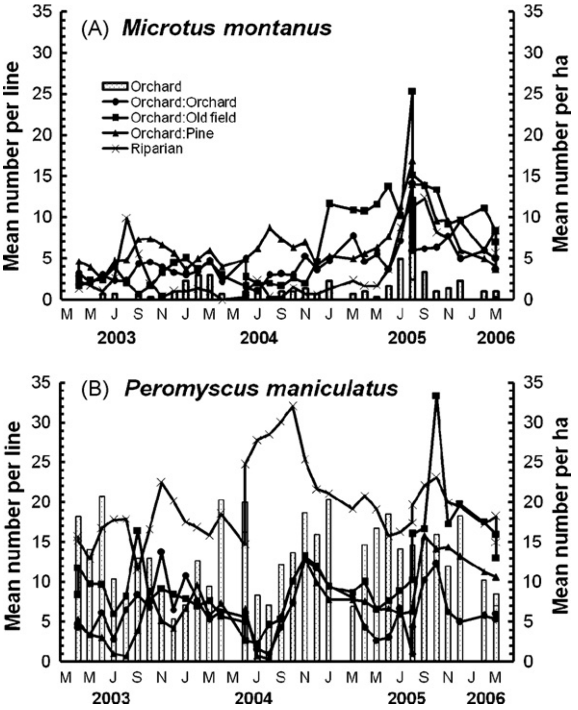

Fig. 1. Population changes in mean number of animals per line from 2003 to 2006 for (A) *M. montanus* and (B) *P. maniculatus* in the four linear habitats and mean number per ha in apple orchards (histograms) at Summerland, BC, Canada.

Reproductive performance was measured by number of successful pregnancies and for *M. montanus* was similar ($F_{3,7} = 0.31$; $P = 0.82$) among linear habitats, but increased significantly ($F_{2,14} = 6.55$; $P = 0.01$) with time. Overall mean values ranged from 4.1 to 11.7 for the linear habitats which were 1.7–4.8 times higher than that recorded for the orchard (mean = 2.4) population of voles. Mean number of juvenile vole recruits was also similar ($F_{3,8} = 0.40$; $P = 0.76$) among linear habitats, and increased significantly ($F_{2,16} = 10.44$; $P < 0.01$) with time. A pattern of fewer juvenile recruits in the orchard (mean = 5.89) populations of *M. montanus* than for those populations in the linear habitats (range of 5.89–16.67) followed that of the successful pregnancies. However, a mean index of early juvenile survival was similar ($F_{3,3} = 1.35$; $P = 0.41$) among linear habitats and 1.5–2.2 times higher than the orchard (mean = 0.88) populations of *M. montanus*.

Mean number of successful pregnancies for *P. maniculatus* was similar ($F_{3,7} = 1.01$; $P = 0.44$) among linear habitats with overall mean values ranging from 5.1 to 11.3. This measure of reproductive performance also increased significantly ($F_{5,35} = 7.92$; $P < 0.01$) with time. Mean number of pregnancies was 19.0 for the orchard population of deer mice which was 1.7–3.7 times higher than in the linear habitats. Mean number of juvenile recruits of *P. maniculatus* was also similar ($F_{3,8} = 3.06$; $P = 0.09$) among linear habitats, but with the riparian strips having 1.6–2.9 times as many new juvenile deer mice as the hedgerow habitats. Mean early juvenile survival of *P. maniculatus* was similar ($F_{3,5} = 2.55$; $P = 0.17$) among linear habitats ranging from 3.10 to 6.51. These values were 1.3–2.6 times higher than the early juvenile survival recorded in the orchard (2.48) population of *P. maniculatus*.

Mean number of total recruits was similar among linear habitats for both *M. montanus* ($F_{3,7} = 0.15$; $P = 0.93$) and *P. maniculatus* ($F_{3,7} = 0.81$; $P = 0.53$), with a significant ($P < 0.01$) increase with time. Overall mean vole recruits was 5.8 in the orchard population which was substantially lower (1.5–2.7 times) than in the linear habitats. This pattern was not evident for *P. maniculatus* where both the riparian and orchard (overall mean of 29.0) populations had twice as many new deer mice as the hedgerow habitats.

Mean estimates of J–S survival for both species were similar ($P > 0.05$) among linear habitats. Overall mean values were similar for populations within these linear habitats, and for both species, mean survival in orchards was consistently lower than in the linear habitats.

Linear regression analysis indicated that there was a weak ($P = 0.08$) positive relationship between overall mean abundance of *M. montanus* and total structural diversity of vegetation. However, there were no other relationships between mean abundance of either rodent species and any parameter representing the abundance and diversity of vegetation along linear habitats.

4. Discussion

There were no significant relationships between the abundance and diversity of vascular plants along linear habitats and mean abundance of either rodent species, other than a weak correlation between mean abundance of *M. montanus* and structural diversity of vegetation. Thus, hypothesis (i), that *M. montanus* and *P. maniculatus* populations will be positively related to vegetation type within linear habitats and their adjacent crop and non-crop areas, was not supported. However, the lack of differences in vegetation attributes among these four types of linear habitats suggested that concentration of non-crop vegetation into linear configurations, whether of hedgerow or riparian structure, provided essential habitat for the specialist *M. montanus*, but not necessarily for the generalist *P. maniculatus* within an agrarian landscape. This pattern was similar to the species' preferences and apparent lack of difference in small mammal abundance and diversity between linear and non-linear habitats in non-crop set-aside reported by Tattersall et al. (2002).

The significant increase in vole abundance with time was likely a reflection of a multi-annual 3–5 year population cycle for *M. montanus* with a high year in 2005 (Taitt and Krebs, 1985). It is usually in the winter of the peak year in abundance that voles feed on perennial crops such as apple trees (Byers, 1984). Thus, this population peak tested rigorously hypothesis (ii), that vole and deer mouse populations in linear habitats will be correlated with population changes and productivity in nearby apple orchards. However, it was clear from Fig. 1A that population changes within linear habitats did not correlate substantially with vole abundance within nearby orchards, and hence hypothesis (ii) was rejected, at least for *M. montanus* during this particular peak population. Similarly, demographic attributes of reproductive performance, recruitment, and survival of *M. montanus* populations in apple orchards were lower or similar to those in the linear habitats. The highest density recorded for *M. montanus* in orchards was 12.3 voles/ha in August 2005, with considerably fewer (<5/ha) occurring there in the subsequent fall and winter. The mean summer 2005 abundance was 3.7 voles/ha in the orchards. This pattern contrasted dramatically with a mean abundance of up to 41 voles/ha in orchards during peak populations reported by Sullivan et al. (2003), but was similar to mean numbers of <1/ha recorded in Sullivan and Sullivan (2006).

Orchard agroecosystems with effective vegetation management on the orchard floor render habitats unattractive to voles (Sullivan and Hogue, 1987). Conversely, organic orchards without "clean" culture and the consequent "enhanced" food and cover may actually encourage vole numbers (Brown, 1999). Thus, the combined effects of poor habitat in our well-maintained orchards, and preferred habitat for resident populations of *M. montanus* in our linear habitats, precluded a pest problem. Similar results were also reported for *M. arvalis* in wildflower strips (Briner et al., 2005) and abandoned alfalfa fields (Heroldová et al., 2005).

Populations of *P. maniculatus* were similar in abundance and other demographic variables among the linear habitats and apple orchards, and hence hypothesis (ii) was supported. Although *P. maniculatus* had generally similar population parameters in orchards and linear habitats, the low index of early juvenile survival in orchards suggested a "population sink" (Pulliam, 1988).

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