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Population Dynamics of Deer Mice, *Peromyscus maniculatus,* and Yellow-pine Chipmunks, *Tamias amoenus,* in Old Field and Orchard Habitats

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There are often several rodent species included in the small mammal communities in orchard agro-ecosystems. This study was designed to test the hypothesis that the population levels of Deer Mice (*Peromyscus maniculatus*) and Yellow-pine Chipmunks (*Tamias amoenus*) would be enhanced in old field compared with orchard habitats. Rodent populations were intensively live-trapped in replicate old field and orchard sites over a four-year period at Summerland, British Columbia, Canada. Deer Mouse populations were, on average, significantly higher (2.5 – 3.4 times) in the old field than orchard sites in summer and winter periods. Mean numbers/ha of Deer Mice ranged from 12.1 to 60.4 in old field sites and from 3.3 to 19.9 in orchard sites. Breeding seasons in orchards were significantly longer than those in old field sites, in terms of proportion of reproductive male Deer Mice. Recruitment of new animals and early juvenile survival of Deer Mice were similar in orchard and old field sites. Populations of Yellow-pine Chipmunks ranged in mean abundance/ha from 5.6 – 19.0 in old field sites and from 1.9 – 17.5 on one orchard site, with no difference in mean abundance in 2 of 4 years of the study. Recruitment and mean survival of Yellow-pine Chipmunks also followed this pattern. This study is the first detailed comparison of the population dynamics of these rodent species in old field and orchard habitats. These species should be able to maintain their population levels and help contribute to a diversity of small mammals in this agrarian landscape.

Key Words: Deer Mouse, *Peromyscus maniculatus*, Yellow-pine Chipmunk, *Tamias amoenus*, abundance, demography, old field, orchard, population dynamics, recruitment, reproduction, British Columbia.

Voles of the genus *Microtus* are often the major rodent species in perennial grasslands and agro-ecosystems. In addition to grasses and herbs, these microtines feed on vascular tissues of tree and other crop plants primarily during winter months (Byers 1985; Lewis and O'Brien 1990). Other major rodent species include the Deer Mouse (*Peromyscus maniculatus*) and Yellow-pine Chipmunk (*Tamias amoenus*), which may occur in tree fruit orchards and adjacent habitats in the inland regions of the Pacific Northwest of North America. Neither of these associated species is known to damage orchard trees by their feeding activity as they are granivorous or insectivorous in their feeding habits (Baker 1968; Webster and Jones 1982; Sutton 1992).

Deer Mice or White-footed Mice (*P. leucopus*) commonly occur with *Microtus* in old fields and other perennial grassland habitats (Tamarin 1977; Krebs 1979; Dueser et al. 1981; Sullivan and Krebs 1981; Schweiger et al. 2000; Manson et al. 2001; Pearson et al. 2001) and in orchard agro-ecosystems (Sullivan et al. 1998). Few studies of voles in orchards have reported on the population dynamics of other species in the small mammal community. Sullivan et al. (1998) discussed the population responses of all species to vegetation management in apple (*Malus domestica*) orchards and Sullivan et al. (2000) reported changes in species diversity of these communities in orchards and old fields.

Orchard habitats usually have frequent mowing and vegetation management treatments during summer months, and hence conditions for small mammals are more changeable than in old fields. Thus, this study was designed to test the hypothesis that the population dynamics of Deer Mice and Yellow-pine Chipmunks would be enhanced in old field compared with orchard habitats. To evaluate this hypothesis, we provide a detailed analysis of the population dynamics of these species in the two habitats.

Materials and Methods

Study area and experimental design

This study was conducted at the Pacific Agri-Food Research Centre in the Okanagan Valley, Summerland, British Columbia, Canada. The experimental design consisted of two replicate "old field" and two replicate orchard habitats. The old field habitats were abandoned (≥25 years) hay fields composed of Crested Wheatgrass (*Agropyron cristatum*), Quack Grass (*Agropyron repens*), Downy Brome (*Bromus tectorum*), Diffuse Knapweed (*Centaurea diffusa*), with some minor herbaceous species such as Yellow Salsify (*Tragopogon dubius*), Great Mullein (*Verbascum thapsus*), American Vetch (*Vicia americana*), Prickly Lettuce (*Lactuca serriola*), and Tall Tumble-mustard (*Sisymbrium altissimum*). These old field sites were each 2 to 3 ha in area within a mosaic of sagebrush (*Artemisia tridentata*), Ponderosa Pine (*Pinus ponderosa*) forest, and orchard habitats. These old fields had resident populations of Deer Mice and Yellow-pine Chipmunks. Other species included the Montane Vole (*Microtus montanus*), Great Basin Pocket Mouse (*Perognathus parvus*), Western Harvest Mouse (*Reithrodontomys megalotis)*, and a few Long-tailed Voles (*M. longicaudus*).

The orchards were: (A) a five-year-old apple orchard unit, and (B) a 10-year-old apple orchard combined with a 15-year-old pear (*Pyrus* sp.) orchard as one unit. Both 1.2-ha orchards were located within a 90-ha mosaic of tree fruits and vineyards. Thus, our experimental design had two true replicates of old field sites and two replicates of orchard sites. Each pair of old field and orchard sites was spatially segregated to enhance statistical independence (Hurlbert 1984). A third replicate pair would have strengthened the study but was not possible within the operational setting of the Research Centre.

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 five or six times each summer. Rodenticides were applied 3-4 times each winter in poison-bait feeder stations (Radvanyi 1974) for voles (Mouse Bait II® – zinc phosphide and Ramik Brown® – diphacinone). Rodenticides were not present in the old field sites.

Deer Mouse and Yellow-pine Chipmunk populations

All animals were live-trapped on 1-ha grids with 49 (7 × 7) trap stations located at 14.3-m intervals with one or two Longworth live-traps at each station. One of the old-field grids was an irregular shaped rectangle of 1 ha with the same 49 stations. The four grids (2 orchard and 2 old field) were live-trapped at 3-week (spring, summer, and fall) and at 4- to 6-week (winter) intervals from June 1982 to April 1986.

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 Pesola 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 from 1982 to 1986. We used mass at sexual maturity to infer age classes of animals. Body mass was used as an index of age. 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. Deer Mice (juvenile = 1 – 20 g, adult ≥ 21 g) and Yellow-pine Chipmunks (juvenile = 1 – 44 g, adult ≥ 45 g) were classified as juvenile or adult by body mass. 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 model for reasons indicated by Jolly and Dickson (1983). The Jolly-Seber (J-S) model provides the best estimates of population size for mark and recapture data when trappability values are generally < 70% (Hilborn et al. 1976). However, when population size falls very low and no marked animals are recaptured, the J-S estimate becomes unreliable and impossible to calculate (Krebs et al. 1986). For these sample weeks, a minimum number of animals known to be alive (MNA) (Krebs 1966) value was substituted for a biologically unreasonable J-S estimate.

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). A modified version of this index is number of juvenile animals at week t divided by the number of lactating females caught in week $t - 3$. Mean survival rates (28-day) for summer and winter periods were estimated from the Jolly-Seber model. Mean body mass of combined males and females

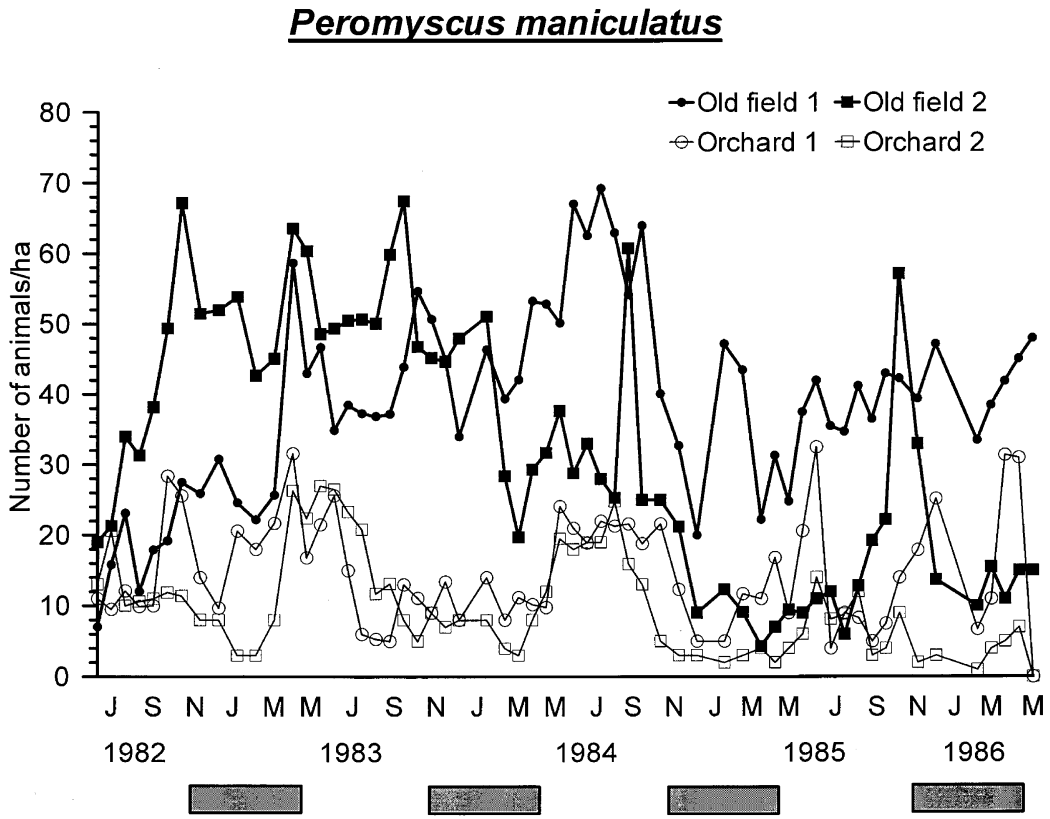

FIGURE 1. Population densities (Jolly-Seber) per ha of Deer Mice in replicate old field and orchard sites during the study. Shaded bars indicate winter periods. Months of year are represented by J = July; S = September; N = November; J January; M = March; M = May.

was used as an index of condition within populations of Deer Mice and Yellow-pine Chipmunks during summer and winter periods.

Statistical analysis

Mean trappability, mean abundance, mean number of recruits, mean Jolly-Seber survival rates, and mean body mass were evaluated by 95% confidence intervals (CI) for Deer Mice and Yellow-pine Chipmunks in old field and orchard sites during summer and winter periods, as per the recommendations of Gerard et al. (1998) and Johnson (1999). Proportion of adult males and adult females breeding was analyzed by a Chi-square 2×2 contingency table (Zar 1984) for each of the four summer periods. These datasets of proportion of animals breeding often include animals captured more than once, and hence they are not completely independent. Thus, the Chi-square analyses provide only an indication of the degree of difference between datasets. In all analyses, the level of significance was $P = 0.05$.

Results

Deer Mouse populations

Totals of 751 and 459 individual Deer Mice were captured on the two old field and two orchard sites, respectively. Mean J-S trappability estimates for Deer Mice ranged from 62.6% to 73.8% in summer and from 46.6% to 76.6% in winter in the old field sites. These estimates in the orchard sites ranged from 48.0% to 81.7% in summer and from 39.0% to 80.8% in winter.

Deer Mouse populations were, on average, generally higher (2.5 – 3.4 times) in the old field than orchard sites in summer and winter periods (Figure 1). There were some exceptions to this pattern in summers 1982 and 1985 and winter 1985-1986 when mean abundance of Deer Mice was similar, at least in one old field—orchard site comparison (Table 1). Numbers of Deer Mice reached annual autumn peaks ranging from 30.8 to 69.3 animals/ha in the old field-1 site and from 57.2 to 67.5 animals/ha in the old field-2 site.

TABLE 1. Mean abundance per ha ± 95% confidence intervals for Deer Mice during summer and winter periods in replicate old field and orchard sites. Sample size (n = number of trapping periods) in parentheses.

		Old field		Orchard	
Period		1	2	1	2
Summer 1982	χ^2	17.5	37.2	15.2	12.6
(7)	95% CI	11.2 – 23.8	21.7 – 52.7	7.7 – 22.7	9.3 – 16.0
Winter 1982-83	χ^2	25.8	49.0	16.8	6.0
(5)	95% CI	21.9 – 29.7	43.0 – 55.1	10.6 – 23.0	2.6 – 9.4
Summer 1983	χ^2	41.9	55.6	15.5	19.9
(9)	95% CI	36.2 – 47.6	50.1 – 61.2	8.3 – 22.8	14.4 – 25.4
Winter 1983-84	χ^2	45.7	39.2	10.6	9.0
(8)	95% CI	39.8 – 51.6	29.5 – 48.8	8.7 – 12.5	2.3 – 15.7
Summer 1984	χ^2	60.4	33.8	19.7	17.7
(8)	95% CI	54.5 – 66.3	24.0 – 43.6	16.1 – 23.3	14.3 – 21.0
Winter 1984-85	χ^2	34.3	13.5	11.1	3.3
(6)	95% CI	22.4 – 46.1	5.1 – 21.8	4.7 – 17.5	2.2 – 4.4
Summer 1985	χ^2	36.3	12.1	12.5	6.9
(9)	95% CI	31.9 – 40.7	7.9 – 16.2	5.4 – 19.6	3.7 – 10.1
Winter 1985-86	χ^2	41.1	22.2	19.6	4.4
(7)	95% CI	36.9 – 45.3	6.2 – 38.2	10.5 – 28.7	1.8 – 7.0

These old field populations also had increased recruitment in early summer (April – May) in some years which was likely related to the decline in breeding activity by mid-summer (see Figure 2).

In terms of mean abundance, Deer Mouse numbers in old field sites ranged from a low of 12.1/ha to a high of 60.4/ha during the four-year study (Table 1). Mean abundance of Deer Mice on the two orchard sites

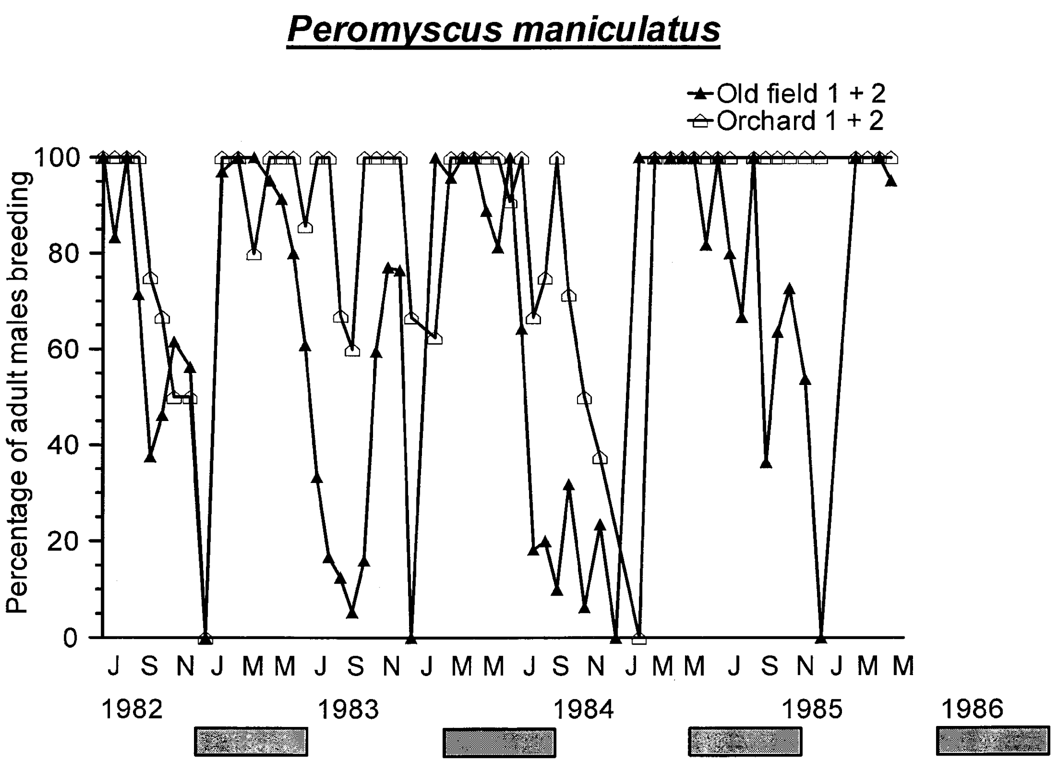

FIGURE 2. Percentage of adult males in reproductive condition for Deer Mice for pooled data in old field and orchard sites during breeding seasons each year. Shaded bars indicate winter periods. Months of year are represented by J = July; S = September; N = November; J = January; M = March; M = May.

ranged from a low density of 3.3/ha to a high of 19.9/ha. Orchard Deer Mice had annual increases in recruitment in early summer with generally higher populations (1.5 times) in summer than winter (Figure 1, Table 1).

Demographic parameters

Adult male Deer Mice commenced breeding in January-February each year and continued up to July in the old field sites and through the summer and autumn months in the orchard sites (Figure 2). This longer breeding season in orchard than old field sites was significantly different in terms of proportion of reproductive males in 3 of 4 years (Table 2). Proportion of breeding female Deer Mice tended to follow this pattern but there was a significant difference between sites in 1984 only (Table 2).

The pattern of recruitment in terms of mean numbers of new Deer Mice was generally similar in old field and orchard sites in both summer and winter periods (Table 3). There was only one period (summer 1985) when an old field – orchard comparison of mean values did not have overlapping 95% CI (Table 3). Thus, productivity within orchard populations of Deer Mice appeared to approach that of old field populations, at least with respect to breeding potential and production of young.

Over the four breeding seasons, early juvenile survival was similar with overall mean values of 3.64 and 2.12 young Deer Mice captured per lactating female in old field and orchard sites, respectively. Mean total survival of Deer Mice was consistently higher in the two old field sites and orchard-1 site than in the orchard-2 site, except in summer 1983 when survival of Deer Mice was significantly lower in the orchard than old field sites (Figure 3).

Mean body mass of Deer Mice was the same or higher in orchard than old field sites during summer and winter periods (Figure 4). Only during winter 1983-1984 did body mass of mice in orchard-2 appear lower than that in the old field sites.

TABLE 2. Proportion of adult male and female Deer Mice in reproductive condition during breeding seasons each year for pooled data in replicate old field and orchard sites and results of Chi-square (χ^2)analysis. Sample size (number of mice) in parentheses. Significant *P* in bold face.

Year	Old field	Orchard	Analysis	
			χ^2	*P*
Males				
1982	0.62 (84)	0.79 (28)	2.60	0.11
1983	0.67 (367)	0.95 (114)	34.87	**<0.01**
1984	0.67 (253)	0.81 (86)	6.58	**0.01**
1985	0.79 (150)	0.97 (39)	7.21	**<0.01**
Females				
1982	0.26 (69)	0.38 (42)	1.77	0.19
1983	0.30 (209)	0.30 (106)	0.00	1.00
1984	0.40 (182)	0.64 (96)	13.82	**<0.01**
1985	0.47 (103)	0.61 (49)	2.84	0.09

TABLE 3. Mean number of recruits ($\bar{x}$) ± 95% confidence intervals for Deer Mice during summer and winter periods in replicate old field and orchard sites. Sample size (*n* = number of trapping periods) in parentheses.

Period		Old field		Orchard	
		1	2	1	2
Summer 1982	$\bar{x}$	5.1	13.1	4.6	5.6
(7)	95% CI	2.6 – 7.7	6.2 – 20.1	1.2 – 8.0	2.2 – 8.9
Winter 1982-1983	$\bar{x}$	4.0	6.6	2.8	2.2
(5)	95% CI	1.7 – 6.3	2.6 – 10.6	0.0 – 5.6	1.2 – 3.2
Summer 1983	$\bar{x}$	6.7	10.0	4.9	5.6
(9)	95% CI	2.0 – 11.3	5.0 – 15.0	2.3 – 7.5	2.2 – 8.9
Winter 1983-1984	$\bar{x}$	5.5	3.5	1.9	3.8
(8)	95% CI	1.5 – 9.5	1.6 – 5.4	0.8 – 2.9	1.9 – 5.6
Summer 1984	$\bar{x}$	9.9	5.5	5.5	5.8
(8)	95% CI	7.3 – 12.4	2.5 – 8.5	2.5 – 8.5	3.2 – 8.3
Winter 1984-1985	$\bar{x}$	3.7	1.5	2.2	0.7
(6)	95% CI	0.6 – 6.7	-0.6 – 3.6	-1.0 – 5.3	0.1 – 1.2
Summer 1985	$\bar{x}$	7.8	3.4	3.9	2.0
(9)	95% CI	4.3 – 11.2	2.1 – 4.8	1.9 – 5.9	1.1 – 2.9
Winter 1985-1986	$\bar{x}$	8.6	3.9	7.0	2.1
(7)	95% CI	1.5 – 15.6	0.5 – 7.3	1.3 – 12.7	0.2 – 4.1

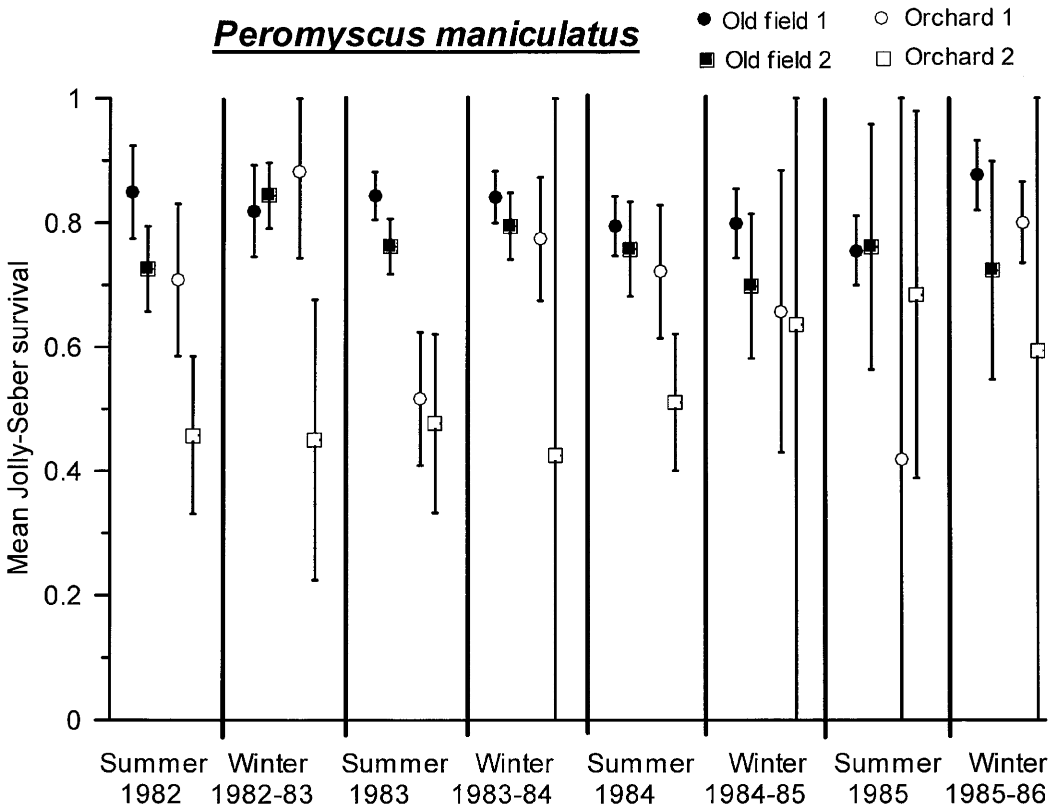

FIGURE 3. Mean Jolly-Seber survival (per 28 days) ± 95% confidence intervals for Deer Mice in replicate old field and orchard sites during summer and winter periods in the study.

Yellow-pine Chipmunk populations

Totals of 137 and 79 individual Yellow-pine Chipmunks were captured in the two old field and two orchard sites, respectively. Only three individual chipmunks were captured in the orchard-2 site during the study. Mean J-S trappability estimates ranged from 30.8% to 63.8% in the old field sites, and from 37.1% to 58.3% in the orchard sites.

Populations of Yellow-pine Chipmunks ranged in mean abundance/ha from 5.6 to 19.0 in old field sites and from 1.9 to 17.5 in the orchard-1 site (Table 4). Mean abundance of Yellow-pine Chipmunks was significantly (non-overlapping 95% confidence intervals) lower in the orchard-1 than old field sites in 1982 and 1985 (Table 4). In terms of population changes over the study, Yellow-pine Chipmunk abundance/ha ranged from 1.0 – 27.0 in old field sites and from 1.0 – 46.3 in the orchard-1 site (Figure 5).

Mean number of Yellow-pine Chipmunk recruits was similar between the old field and orchard-1 sites (Table 4). Mean (± SE) Jolly-Seber survival rates averaged 0.78 ± 0.05 (summer) and 0.96 ± 0.02 (winter) in the old field-1 site and 0.71 ± 0.05 (summer) and 0.91 ± 0.06 (winter) in the orchard-1 site.

Discussion

Deer Mouse and Yellow-pine Chipmunk populations

The pattern of abundance of Deer Mice in our old field sites was somewhat different from that recorded in other old field and perennial grassland studies of *Peromyscus* and *Microtus*. Grant (1972) and Baker (1968) suggested that the Deer Mouse suffers from competition from microtine rodents in perennial grasslands, and is forced to live in woodlands. However, Deer Mouse densities in our studies reached annual peaks ranging from 30.8 to 69.3 animals/ha in the presence of relatively high numbers of Montane Voles (Sullivan et al. 2003). Experimental studies by Grant (1971) and Redfield et al. (1977) concluded that *Microtus* outcompete *Peromyscus* in grassland habitats; however, explanations for this process were not given. Conversely, other studies concluded that competitive interactions among microtine rodents and Deer Mice were unimportant (Gilbert and Krebs 1984; Galindo

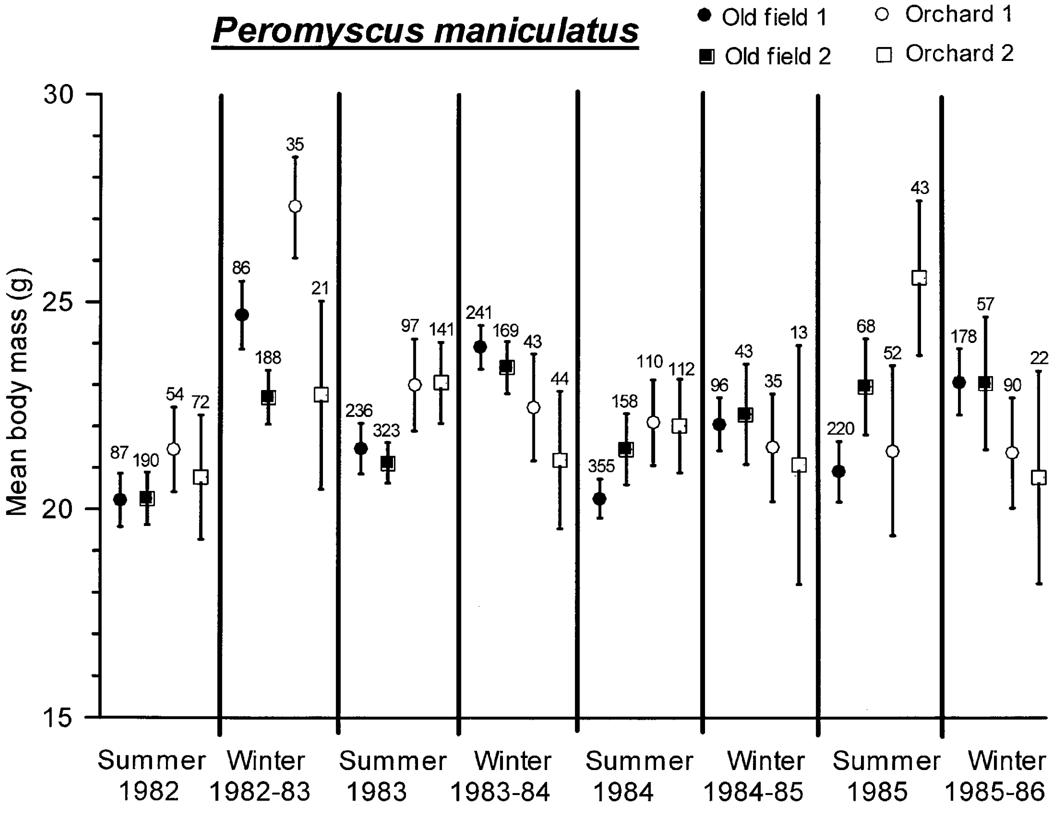

FIGURE 4. Mean body mass (g) ± 95% confidence intervals for Deer Mice in replicate old field and orchard sites during summer and winter periods in the study.

TABLE 4. Mean abundance (x̄) and mean number of recruits per ha (x̄) (± 95% confidence intervals) for Yellow-pine Chipmunks during non-hibernation periods in replicate old field and orchard sites. Sample size (*n* = number of trapping periods) in parentheses.

Attribute and		Old field		Orchard	
period		1	2	1	2
Abundance					
1982	x̄	5.6	7.9	1.9	–
(7)	95% CI	3.6 – 7.7	3.8 – 12.0	0.7 – 3.0	–
1983	x̄	8.1	11.8	9.3	0.1
(13)	95% CI	5.3 – 10.9	9.8 – 13.8	2.2 – 16.4	–
1984	x̄	19.0	8.9	17.5	0.2
(11)	95% CI	15.2 – 22.9	6.2 – 11.6	8.7 – 26.2	–
1985	x̄	14.5	9.8	3.6	–
(10)	95% CI	12.1 – 16.9	6.2 – 13.4	1.9 – 5.4	–
Recruits					
1982	x̄	1.1	2.7	0.6	–
(7)	95% CI	0.5 – 1.8	0.1 – 5.3	-0.2 – 1.3	–
1983	x̄	1.5	1.2	2.3	0.1
(13)	95% CI	0.1 – 3.0	0.0 – 2.4	0.3 – 4.3	–
1984	x̄	2.5	0.7	3.4	0.2
(11)	95% CI	1.2 – 3.9	-0.1 – 1.5	0.6 – 6.1	–
1985	x̄	1.5	2.1	0.4	–
(10)	95% CI	0.7 – 2.3	0.5 – 3.7	-0.3 – 1.1	–

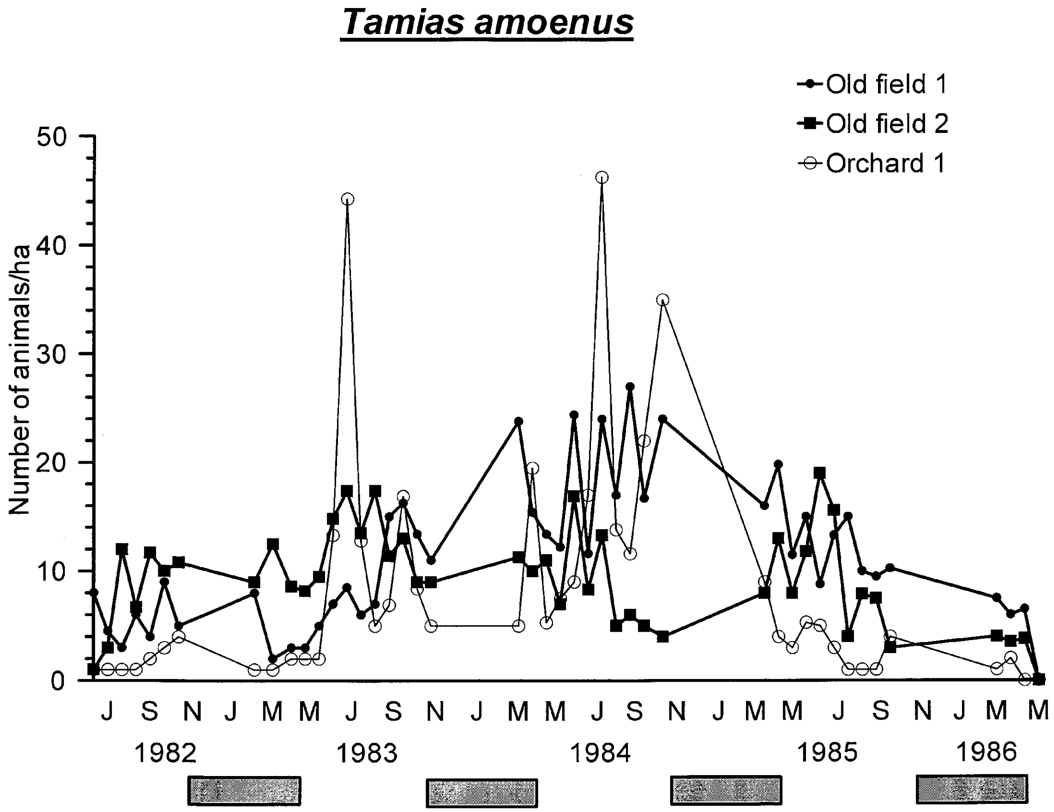

FIGURE 5. Population densities (Jolly-Seber) per ha of Yellow-pine Chipmunks in two old field sites and one orchard site during the study. Shaded bars indicate winter periods. Months of year are represented by J = July; S = September; N = November; J = January; M = March; M = May.

and Krebs 1985). Sullivan and Krebs (1981) reported persistence of Deer Mice with *Microtus* spp. in a grassland habitat. Our densities of Deer Mice were as high as reported in other studies of perennial grassland habitats and orchards (Sullivan and Krebs 1981; Sullivan et al. 1998).

This study is the first detailed investigation of the population dynamics of non-target rodent species in orchards treated with rodenticides for vole control. Populations of Deer Mice in orchard sites showed consistent annual changes in abundance averaging 15.0 animals/ha in summer and 10.1 animals/ha in winter periods. These values were similar to those reported for Montane Voles in these same orchards at 16.5 animals/ha in summer and 21.1 animals/ha in winter (Sullivan et al. 2003). Clearly, Deer Mice seemed productive in the orchard environment, having longer breeding seasons than in the old field sites, and comparable survival of young animals. Winter breeding in Deer Mice has been reported, particularly after substantial mast crops in forests (Wolff 1996) or in supplemental food studies (Taitt 1981). Food resources appeared sufficient to support breeding mice during winter periods and at body masses comparable to old field populations during most periods. These orchards received regular inputs of fertilizer and irrigation, and hence likely produced relatively "rich" habitats in terms of plant production and invertebrate biomass. Mean overall survival of Deer Mice in orchards was poor, in at least one of the sites, relative to old field populations. A lack of vegetative cover may have contributed to greater predation by raptors, weasels (*Mustela* spp.), and Coyotes (*Canis latrans*).

Our orchards were situated in a mosaic of different varieties and age classes of orchards and vineyards with adjacent natural habitats of sagebrush and Ponderosa Pine (*Pinus ponderosa*). As discussed by Sullivan et al. (1998) for their study in this same mosaic, it was possible that our relatively high numbers of Deer Mice (and Yellow-pine Chipmunks) in orchards may have represented transients or animals who lived in nearby sage-pine areas. However, a comprehensive analysis of transient and resident animals suggested strongly that these rodents very likely lived in the actual orchard units (Sullivan et al. 1998). There was no reason to assume that our animal populations behaved differently, and hence our population estimates were considered accurate.

The prediction of the hypothesis that population dynamics of Deer Mice and Yellow-pine Chipmunks would be enhanced in old field compared with orchard habitats is partially accepted. Abundance, recruitment, and overall survival of Deer Mice were higher in old field than orchard sites. However, proportion of breeding animals and length of breeding seasons were greater in the orchard sites. Early juvenile survival and body mass were similar between sites for Deer Mice. Similarly, the general lack of differences in abundance (except in 1982 and 1985) and recruits for Yellow-pine Chipmunks between sites (albeit for one replicate only) also contradicted our prediction.

These rodent species should be able to maintain their population levels in association with *Microtus* in these habitats. Traditional methods of vole control (rodenticides) seem to have had little effect on these two non-target species in the orchard sites. The higher abundance of Deer Mice, and sometimes Yellow-pine Chipmunks, in the old field than orchard sites was more likely a function of habitat quality than exposure to rodenticides. Consequently, Deer Mice and Yellow-pine Chipmunks may assist integrated pest management in orchards because both species persisted in this managed habitat and their consumption of seeds and invertebrates could provide some degree of assistance in reducing weed and insect pests. In addition, as prey species, they may attract a greater number of predators to these sites. A total of six small mammal species was recorded in these orchards, which suggests that these agro-ecosystems and adjacent natural lands help contribute to a diversity of habitats in this agrarian landscape.

Acknowledgments

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