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Relative Abundance and Habitat Associations of Small Mammals in Chamberlain Basin, Central Idaho

Abstract

We sampled small mammal populations and measured habitat structure in forested and non-forested habitats in the wilderness of central Idaho over a 5-year period using pit and snap traps. Although results from pit and snap trapping differed for northern pocket gophers (*Thomomys talpoides*), capture rates for the two methods were similar across habitats for the other common species. Southern red-backed voles (*Clethrionomys gapperi*) and shrews (*Sorex vagrans* and *S. cinereus*) were the most common species captured. Spruce-fir forest exceeded other habitats in the abundance of small mammals while all sites had low species richness ($s = 4-7$). Habitat associations of the common small mammals (southern red-backed voles, shrews, deer mice (*Peromyscus maniculatus*), and yellow-pine chipmunks (*Tamias amoenus*)) differed, based on both broad patterns and microhabitat gradients. Our data corroborate the results of other investigations by demonstrating the relatively low abundance of small mammals in subalpine habitats of the Rocky Mountains. Furthermore the differences in small mammal communities among forest types suggests a mosaic pattern of small mammal communities in the Rockies which results from the patchy nature of forests in this region.

Introduction

Small mammal populations play important roles in subalpine ecosystems. Patterns of succession and species composition of forests may be altered through seed consumption patterns of mice, voles, and chipmunks (e.g. Abbott 1961, Sullivan 1979, Halvorson 1982, Vander Wall 1992). Similarly, dispersion patterns of hypogeous mycorrhizal fungi occurs, in part, from the dispersal of spores by squirrels and voles which feed on the below-ground fruiting bodies (Fogel and Trappe 1978, Maser *et al.* 1978, Urc and Maser 1982). The success of young conifers may depend on whether they successfully form a symbiotic relationship with mycorrhizal fungi (Marks and Kozlowski 1973, cited by Maser *et al.* 1978). In addition to their interaction with primary producers and decomposers, small mammals are essential prey for several subalpine carnivores including boreal owls (*Aegolius funereus*) (Hayward *et al.* 1993), great gray owls (*Strix nebulosa*) (Bull *et al.* 1989), and American marten (*Martes americana*) (Clark *et al.* 1987). Furthermore, small mammals themselves prey upon insects and may influence these taxa (e.g. Johnson 1964, Martell and Macaulay 1981, Merritt 1981).

Despite the important functions of small mammals in subalpine and montane ecosystems, current knowledge does not provide a sound understanding of small mammal distribution and abundance among subalpine habitats in the northern Rocky Mountains. Existing literature provides a limited geographic base and is derived primarily from short-term (1 or 2 year) studies. Two studies have examined small mammal communities in subalpine forests in Wyoming. Raphael (1988) described the abundance and habitat associations of small mammals in subalpine forest based on 3 years of intensive live trapping over 2 watersheds. Brown (1967), during 2 summers, sampled 127 sites in the Medicine Bow mountains including many sites within the subalpine. Over a 3-year span, Millar *et al.* (1985) sampled 102 subalpine sites in Alberta. Williams (1955) examined small mammal communities in montane habitats in Colorado. Several studies have compared small mammal abundance in harvested and unharvested sites in the Rockies (e.g. Campbell and Clark 1980, Halvorson 1982, Medin 1986, Scrivner and Smith 1984, Ramirez and Hornocker 1981).

We collected data on the relative abundance and habitat associations of small mammals in the wilderness of central Idaho. These data complement those of earlier studies by furthering the basis for inferring patterns of species distribution

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and determining the extent to which patterns are similar among geographic locales. Few studies have examined small mammals from subalpine fir (*Abies lasiocarpa*) forests in Idaho. Furthermore, our study examined a landscape which had not experienced catastrophic disturbance (i.e. stand replacement events) in at least 100 years. The forest stands we sampled were mature and older forest in a landscape where older forest predominates.

Study Area

We examined habitat use by small mammals in the mountains of central Idaho in the northern portion of the 956,515-ha Frank Church, River of No Return Wilderness (RNRW). The study area lay within a ~15,000 ha portion of Chamberlain Basin which extends from 1,580 to 2,194 m elevation on a high, dissected plateau. The entire area is mountainous but lacks steep jagged peaks; few slopes exceed 50%.

Chamberlain Basin lies in the *Abies* life zone and conifer forest covers over 95% of the area (Hayward *et al.* 1993). Lodgepole pine (*Pinus contorta*) dominated the forest, especially in cold-air drainages where monospecific stands of this species covered areas exceeding 300 ha. Lodgepole pine stands generally exceeded 120 years old and some stands included 2 or more age classes of pines. South facing slopes below 1,825 m supported open forest of 60-130 cm diameter-at-breast-height (dbh) ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). Limited ring counts suggest that these stands exceeded 250 years since the last stand replacement disturbance. Large woody debris was present on these sites but not abundant. We refer to these forests as mixed-conifer. On cooler aspects up to 2,000 m, Douglas-fir dominated unless fire had produced a lodgepole pine forest. Many of these stands were old forest with several canopy layers, numerous large diameter trees, and some large woody debris. Douglas-fir forests were mixed with subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) up to 2,200 m. Above 2,000 m, spruce-fir forest occupied sites without recent fire.

Meadows and open shrub fields covered <3% of the area. Sagebrush-bunchgrass (*Artemisia* spp.-*Festuca idahoensis*) slopes were the most common open habitat below 1,850 m whereas *Carex* meadows and willow (*Salix* spp.) bogs occurred at

higher elevations. Aspen occurred in small clumps (usually <0.5 ha) below 2,100 m and covered <1% of the landscape.

For the Chamberlain study site, we classified the landscape by dominant overstory vegetation using color 1:5800 aerial photographs. Rank order of landscape coverage from most to least dominant were lodgepole pine, Douglas-fir, spruce-fir, mixed-conifer, meadow and shrub-field openings, and aspen. Lodgepole-pine forest covered over 50% of the Chamberlain study area.

Climate at Chamberlain Basin has a strong Pacific coastal influence during winter but follows continental patterns in summer (Finklin 1988). At 1,700 m elevation, Chamberlain Basin Guard Station receives 76 cm of precipitation per year (50% as snowfall) and snow depths reach 50-90 cm. At 2,150 m, 70% of precipitation is snowfall, and snow depths exceed 150 cm. The frost-free period at 1,700 m lasts 35-40 days. In July, maximum temperatures averaged 28° C with average minimums of 5° C; in February, daily temperature extremes averaged 5° C maximum and -20° C minimum at 1,700 m.

Methods

Small Mammal Trapping

Snap trapping.—Small mammals were sampled at 7 sites using muscum special snap traps baited with peanut butter and rolled oats set in a rectangular 9 x 10 grid (90 traps) with 15 m spacing. Traps were checked daily for 7 days. One or 2 grids were trapped at a time so the trapping sequence extended over a 6-week period in the spring. The order of trapping moved from low to high elevation sites so that the phenology of each site was similar at trapping time. Grids were trapped in the same order each year although several grids were added to the study during the 5-year investigation (grids were added as more field help became available during the study and the importance of spruce-fir forest as boreal owl foraging habitat became apparent). The first grid was begun 19 May in 1984 and 1985, 26 May 1986, 22 May 1987, and 23 May 1988.

In 1984, 1 grid was placed in each of 3 vegetation types: sagebrush-bunchgrass, lodgepole-pine forest, and old mixed-conifer forest. In 1985, these sites were trapped in the same order. A wet meadow, a second lodgepole-pine stand, and a mature Douglas-fir forest site were added in 1985

Statistical Analysis

Macrohabitat.—Broad habitat associations of small mammal species were examined by comparing the frequency of capture for each species across vegetation types. We examined simple frequency of capture values rather than employing a more complex model because the data did not fit the assumptions of more sophisticated estimators. We treated results from snap-trapping and pit-trapping separately. Neither method can give a completely accurate ranking of species abundance within various habitats. By using both methods we sought to sample a broad range of mammal species and rank the importance of various vegetation types for each species.

Microhabitat.—We examined the microhabitat characteristics of forests used by small mammals within the study area using a principal components analysis (PCA). For this analysis we first developed a forest vegetation ordination based on vegetative structural features measured at both the random locations and the trap locations (101 sites). This analysis included only forest sites because of the problems associated with examining disjunct gradients. For the PCA, we transformed the structural variables to Z scores (Pielou 1984) prior to analysis. This analysis defined the principal component

axes describing primary gradients of the forest habitats of the Chamberlain site.

After examining the ecological pattern of the habitat gradients defined by those principal components with eigenvalues > 1 , we compared the forest structure at the 14 forest pit trap sites to the number of mammals captured at each site. To do so, we calculated the Spearman rank correlation between the principal component scores and the abundance of each small mammal species. This analysis excluded pit trap sites in open habitats (wet meadow and sagebrush-bunchgrass). It would have been inappropriate to include these in the PCA because they are not part of the "forest" habitat gradient.

Results

Habitat Use and Relative Abundance

Comparison of sampling methods.—Snap trapping and pit trapping differ in sampling efficiency for different small mammal species (Williams and Braun 1983). We captured a broader array of species in pit traps than snap traps (Tables 1, 2). Pocket gopher (*Thomomys talpoides*), golden-mantled ground squirrel (*Spermophilus lateralis*),

TABLE 1. Number of individuals captured in 9 x 10 snap-trapping grids at 7 sites in Chamberlain Basin, Idaho, during 1984-88. Trap sites are labeled by dominant overstory vegetation. Each grid was run for 7 days during late May or early June for the number of years listed.

	Sage (4 yrs)		Wet meadow (3 yrs)		Lodgepole 1 ^a (4 yrs)		Lodgepole 2 ^b (3 yrs)		Douglas-fir (4 yrs)		Mixed conifer (5 yrs)		Spruce-fir (2 yrs)	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
<i>Sorex vagrans</i> and <i>S. cinereus</i>	0 ^c		16		4		1		0		1		71	
<i>Tamias amoenus</i>	18	0	1	0	3	0	4	0	1	0	4	0	0	0
<i>Claucomys sabrinus</i>	0	0	0	0	0	0	2	0	0	0	0	0	0	0
<i>Peromyscus</i> <i>maniculatus</i>	3	0	0	0	3	0	1	0	7	1	7	3	0	0
<i>Clethrionomys</i> <i>gapperi</i>	0	0	0	0	0	0	1	0	12	0	9	2	66	38
<i>Phenacomys</i> <i>intermedius</i>	0	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Microtus montanus</i> and <i>M. longicaudus</i>	7	2	5	5	0	0	0	0	0	0	0	0	0	0
<i>Zapus princeps</i>	2	0	1	0	8	0	0	0	0	0	3	0	0	0
Total # individuals per trapping year		8.0		9.3		4.7		3.0		5.5		5.8		88

^aLodgepole-pine forest with lush understory vegetation and some downed logs.

^bLodgepole-pine forest with dry understory and no downed logs.

^cShrews were not aged.

TABLE 2. Relative capture frequency of small mammals sampled using pit traps set year-round at Chamberlain Basin, Idaho, during 1985-88 in 7 vegetation types defined by dominant overstory. Values represent number of captures per 1000 trap-site nights. Three sites were trapped for each vegetation type except spruce bottom, where only 2 sites were trapped. Trap-site days in thousands are recorded in parenthesis. Variation in abundance across vegetation types is represented by the coefficient of variation (Zar 1974) which was calculated after standardizing capture frequency by trapping effort (capture frequency/effort).

Small mammal species	Sage (2.9)	Wet meadow (2.8)	Lodgepole (3.3)	Mixed conifer (3.3)	Douglas-fir (3.0)	Spruce bottom (2.3)	Spruce-fir (2.4)	Coefficient of variation
<i>Sorex vagrans</i> and <i>S. cinereus</i>	8.6	16.1	5.8	8.5	5.3	33.5	18.7	0.88
<i>Sorex palustris</i>	0	0.4	0	0	0	0	0	2.5
<i>Tamias amoenus</i>	2.1	0	2.7	5.5	2.0	0	0	1.11
<i>Spermophilus lateralis</i>	0	0	0	0.9	0	0	0	3.33
<i>Tamiasciurus hudsonicus</i>	0	0	0	0.3	0	0	0	3.0
<i>Glaucomys sabrinus</i>	0	0	0	0	0	0.4	0	3.0
<i>Thomomys talpoides</i>	1.4	1.1	1.5	0	0.3	0	0.4	0.91
<i>Peromyscus maniculatus</i>	3.8	0	1.5	3.0	0.7	2.2	1.2	0.74
<i>Clethrionomys gapperi</i>	0	0	2.7	1.5	8.3	13.9	21.7	1.29
<i>Phenacomys intermedius</i>	0	0	0.6	0.3	0	0	1.2	1.63
<i>Microtus montanus</i> and <i>M. longicaudus</i>	7.9	1.8	0	0	0	0	0.8	1.90
<i>Zapus princeps</i>	1.4	0.4	0.3	0	0	0.4	0	1.42
<i>Mustela erminea</i>	0	0	0	0	0	0.4	0	3.0
Total per 1000 trap nights	8.7	7.1	4.6	6.1	5.5	22.1	18.3	

red squirrel (*Tamiasciurus hudsonicus*), weasel (*Mustela erminea*), and water shrew (*Sorex palustris*) were captured in pit-traps but not snap traps. For each of these species except pocket gophers, however, only 1 to 3 individuals were captured during the entire study. Because of the size of the traps employed and because our traps were not placed in trees, neither trapping method was expected to efficiently sample mammals over ~150 g or arboreal species.

Considering terrestrial mammals less than 150 g, the pocket gopher was the species most differentially sampled by the 2 methods. Pit traps captured pocket gophers on 5 sites, whereas snap traps did not capture this species. For the 3 most frequently captured species, however, pit and snap trapping yielded similar results. Southern red-backed voles (*Clethrionomys gapperi*), shrews (*Sorex vagrans* and *S. cinereus*), and deer mice (*Peromyscus manica-*

tus) were the most frequently captured species by both methods (Tables 1, 2). To compare the 2 trapping methods, we examined capture rates (frequency of capture) for these 3 small mammals across vegetation types. Capture rates of southern red-backed voles in pit and snap traps were strongly related (Spearman rank correlation, $r_s = 0.94$). The 2 trapping methods also resulted in similar ranking for shrew abundance ($r_s = 0.75$). Capture rate for deer mice differed ($r_s < 0.10$) mainly because pit traps in Douglas-fir forests captured few mice, whereas the number of snap-trapped mice was highest for this habitat. Otherwise the rank order of the habitats was similar for snap and pit-trap samples of deer mice. Based on these results we concluded that the pattern of habitat use illustrated by the snap and pit trapping data represent real ecological patterns and not patterns driven by capture bias of the sampling methods.

Throughout the remainder of the paper we will not consider golden-mantled ground squirrels, red squirrels, flying squirrels (*Glaucomys sabrinus*), or weasels because neither sampling method is designed to effectively sample these species.

Relative abundance of small mammals.—Southern red-backed voles and shrews dominated the small mammal community at Chamberlain (Tables 1, 2). Numbers of shrews and southern red-backed voles captured in pit traps and snap traps were each at least 3 times the number of other small mammal species. The numbers of deer mice, *Microtus* spp., western jumping mice (*Zapus princeps*), yellow-pine chipmunks (*Tamias amoenus*), and pocket gophers were each similar in magnitude.

The number of small mammals captured (lumping all species) was greater in spruce-fir forest than other habitats. Number of individuals captured in spruce-fir forest was nearly double that of all other vegetation types. Fewer individuals were captured in lodgepole pine forest than other habitats (Tables 1, 2).

Broad scale habitat associations.—We combined *Sorex vagrans* and *S. cinereus* for discussion of distribution and abundance because a high proportion of shrews were not identified to species. In general, however, *S. vagrans* was more common in non-forested habitat while *S. cinereus* was the more common shrew in the spruce-fir forests. We captured shrews at all pit-trap sites, and variation in capture rates among habitats was low compared to other small mammals (Table 2). Shrews were more abundant in spruce-fir forests than other vegetation types. Based on pit-trap samples, shrews dominated the small mammal communities in lodgepole pine, mixed-conifer, and unforested habitats.

A water shrew was captured with a pit trap on a single site in a wet meadow. This site was inundated for several weeks each spring and was located within 50 m of a small perennial stream.

We found yellow-pine chipmunks in all habitats except spruce-fir bottoms and spruce-fir uplands. Chipmunks were only captured once at a wet meadow site (snap trapping). Capture rates were the highest in the drier habitats—sagebrush-bunchgrass (snap trapping) and mixed-conifer (pit trapping).

Pocket gophers were caught in all habitats except mixed-conifer and spruce bottoms. Dirt

mounds and "soil ropes" seen throughout the study area suggested that pocket gophers used all but the most rocky habitats. Pit-trap capture rates of pocket gophers were highest in lodgepole pine forest and sagebrush-bunchgrass habitats.

We captured deer mice in all vegetation types except wet meadow. Pit and snap-trap samples differed, however, in the rank order of deer mice captures across habitats. In pit-trap samples, deer mice were most frequently captured in sagebrush-bunchgrass habitats where they were the most frequently captured mammal. Deer mice were also frequently captured in mixed-conifer by pit traps, but rarely in Douglas-fir. Snap-trapping results showed Douglas-fir as the most important habitat for deer mice followed by mixed-conifer, lodgepole, and sagebrush-bunchgrass. During 2 years of snap trapping in the spruce-fir grid, no deer mice were captured.

Southern red-backed voles occurred in all forested vegetation types but capture rates were low in lodgepole pine and mixed-conifer forest. The species was absent from nonforested sites. In both spruce-fir and Douglas-fir forests the biomass of southern red-backed vole captures exceeded that of other small mammals. Southern red-backed voles were captured in both pit and snap traps more frequently in spruce-fir forest than in other types (Tables 1, 2). Average pit-trap capture rates across all years and sites were 2.2 times greater in upland spruce-fir than other types. Snap trapping indicated even larger differences in red-backed vole abundance between spruce-fir and other types; average snap trap capture rates in spruce-fir exceeded all other forests by an order of magnitude.

Heather voles (*Phenacomys intermedius*) were rarely captured (8 individuals in pit and snap traps combined), yet they were found in all forested vegetation types. No more than 3 individuals were captured at any single trap site (a single upland spruce-fir pit trap set); only a single individual was captured at other sites. These voles did not occur in any of the non-forested types.

Montane voles (*Microtus montanus*) and long-tailed voles (*M. longicaudus*) used narrower ranges of habitat than other common small mammal species. In both the pit and the snap traps, we caught *Microtus* spp. in non-forested habitats and a single spruce-fir upland site (Tables 1, 2). *Microtus* capture rates were higher at sagebrush-bunchgrass

sites where *M. longicaudus* was more frequent than in wet meadow where *M. montanus* was most common.

Western jumping mice were found in all habitats except Douglas-fir forest. Despite their relative scarcity across habitats, jumping mice were the most frequently captured species in 1 lodgepole pine site (Table 1). Traps within lodgepole pine where jumping mice were captured generally occurred near wet areas with lush understory vegetation.

Species richness among vegetation types.—We examined species richness among vegetation types using pit trap results (excluding golden-mantled ground squirrels, red squirrels, flying squirrels, or weasels). For this comparison we used pit trap results because this method sampled a wider range of small mammals (e.g. pocket gophers). In decreasing order, species richness was, lodgepole pine (7 species), spruce-fir upland (6), mixed-conifer (6), sagebrush-bunchgrass (6), Douglas-fir (5), wet-meadow (5), and spruce bottom (4).

Microhabitat Associations

In the preceding section we described broad habitat associations of small mammals. Below we will examine further the relationships between forest structure and small mammal capture rates.

Based on analysis of vegetation measurements from 101 forest sites we identified 6 predominant structural gradients of forest habitats available at Chamberlain. The predominant structural gradients were defined by PCA (Table 3). From 21 simple structural variables, PCA defined 6 components with eigenvalues >1, accounting for 75% of the overall variance. The seventh component accounted for less variance (4.75%) than would be expected for any one of the original variables.

We interpreted the principal components as follows:

1. Component 1 describes a complex gradient from highly structured, mature and older forest with many canopy layers to young or aggradation

TABLE 3. Six principal components derived from analysis of structural features measured at 101 plots in 4 forest vegetation types at Chamberlain Basin, Idaho, in 1985. Zero loading was 0.45 throughout.

Structural feature	Principal component					
	1	2	3	4	5	6
Basal area	0.668	-0.452	0.478			
Density trees 2.5-7.6-cm dbh		0.687				
Density trees 7.7-15-cm dbh	-0.733	0.481				
Density trees 15.1-23-cm dbh	-0.513			0.501		
Density trees 23.1-38-cm dbh				0.722		
Density trees 38.1-53-cm dbh	0.553					
Density trees >53-cm dbh	0.514	-0.487	0.177			
Density snags 2.5-38-cm dbh	-0.767					
Density snags >38-cm dbh					0.588	
Conifer cover 0-1 m	0.544	0.634				
Conifer cover 1.1-2 m	0.666	0.607				
Conifer cover 2.1-4 m	0.763					
Conifer cover 4.1-8 m	0.596					
Conifer cover >8 m			0.720	0.480		
Horizontal cover diversity	0.812					
Low conifer vertical diversity	0.605	0.745				
High conifer vertical diversity	-0.479		0.604			
Subshrub cover		0.467				
Grass cover					-0.555	
Forb cover						0.685
Eigenvalue	5.839	3.771	2.037	1.743	1.223	1.104
% variance explained	27.8	18.0	9.7	8.3	6.1	5.3
Cumulative %	27.8	45.8	55.5	63.8	69.9	75.2

stage forest with little vertical diversity. This component describes the overall physiognomy of the stand whereas subsequent components relate to individual features of forest structure (i.e., understory, overstory).

2. Component 2 defines a gradient with dense cover 0-2 m above the ground, numerous 2.5 to 15-cm-dbh trees and few large trees describing the positive end.

3. Component 3 defines a cline in occurrence of large trees (>53 cm dbh), high basal area, and upper canopy cover.

4. Component 4 defines a gradient in trees 15.1-38-cm dbh with a well developed upper canopy.

5. Component 5 describes a gradient with large snags (>38 cm dbh) and little grass cover on the positive end of the gradient.

6. Component 6 is a gradient in forb ground cover.

Using the first 6 principal components we compared forest structures measured at 14 forest pit trap sites to the number of mammals captured at each site. Spearman rank correlation between principal component scores and capture rate for 4 small mammal species suggested differences in habitat use (we considered $P < 0.10$ as sufficient evidence to suggest a relationship and $P < 0.05$ as strong evidence). In this analysis, we considered only those small mammal species captured in at least half the 14 forested pit trap sites.

Southern red-backed vole capture rates were positively related to complexity of forest structure (PC1) (Spearman Rank Correlation ($r_s = 0.61$, $P = 0.02$) but not related to other gradients (Table 4). Shrews appeared to respond positively to increased forest complexity, increasing number of canopy layers, forest age (PC1), and to sites with

out heavy grass cover but with large diameter snags (PC5). The presence of a complete upper forest canopy cover or high density of 15-38 cm dbh trees appeared associated with reduced shrew capture rate (PC4).

Deer mouse capture rate was not significantly correlated with any of the principal components suggesting that the mice responded to factors unrelated to the forest structure characteristics we measured or were simply ubiquitous in these forest habitats. The response of chipmunks to habitat structure contrasted with the other small mammals examined. The sign of correlations between chipmunks and principal components were opposite those of southern red-backed voles and shrews. Chipmunk captures were especially less numerous in forest with complex structure, high vertical diversity, and many large trees, or forests with dense cover 0-2 m above the ground (PC1 and PC2).

Discussion

Relative Abundance

Fifteen species of mammals were captured in pit or snap traps in Chamberlain basin but a majority of species were not common. Only shrews and southern red-backed voles were common and even these species were only common in spruce-fir forests.

Few studies of small mammals in subalpine forests in the Rocky Mountains have used trap grids or pit trapping comparable to ours. Williams (1955), Brown (1967), Campbell and Clark (1980), Ramirez and Hornocker (1981), and Millar *et al.* (1985) trapped with 1-3 transects rather than in a grid. Halvorson (1982) and Scrivner and Smith (1984) provide the most comparable studies from this region. Their results suggest that the

TABLE 4. Relationships (Spearman Rank Correlation) between small mammal capture rate and forest structure measured at 14 pit-trap sites. Forest structure was defined by principal component scores describing six gradients of forest structure from analysis of 101 forest sites including the 14 trapping locations. Significant correlations are highlighted ($*P \leq 0.10$, $**P \leq 0.05$).

Species	Principal Component					
	1	2	3	4	5	6
<i>Clethrionomys gapperi</i>	0.61**	0.38	0.08	-0.14	0.45	0.06
<i>Sorex vagrans</i> and <i>S. cinereus</i>	0.55**	0.11	-0.10	-0.49*	0.79**	0.18
<i>Peromyscus maniculatus</i>	-0.01	0.12	-0.18	-0.50	0.18	-0.24
<i>Tamias amoenus</i>	-0.58**	-0.68**	0.21	0.24	-0.36	0.01

abundance of voles on the spruce-fir snap-trap grid at Chamberlain are similar to other sites studied in the Rockies. On our most productive snap-trap grid (an old spruce-fir forest), we caught an average of 8.3 red-backed voles/100 trap nights during a week of trapping each spring for 2 years. Halvorson (1982) captured an average of 8.5 and 6.1 voles/100 trap nights on 2 timbered plots in Montana. Scrivner and Smith (1984) captured an average of 2.9 voles/100 station nights (they had 2 traps per station) on their old forest site in Area 1 and 0.7/100 station nights at the old forest site in Area 2 (Areas 1 and 2 were different study areas).

Neither Halvorson (1982) or Scrivner and Smith (1984) report capturing shrews. In both studies, however, more deer mice were captured than on any of the snap-trap grids at Chamberlain. On our Douglas-fir snap-trap grid we captured 0.3 deer mice/100 trap nights; more than on any other site. Halvorson (1982) reported an average of 1.8 and 2.3 deer mice/100 trap nights on 2 timbered plots. In Idaho mature grand-fir (*Abies grandis*) forest. Scrivner and Smith (1984) captured an average of 12.9 deer mice/100 station nights in Area 1, and 7.4/100 station nights in Area 2.

Raphael's (1988) study in subalpine forest in Wyoming produced a very similar list of species and relative abundance's as we found in Idaho despite the difference in methods (the Wyoming study placed trap stations 200 m apart along ~1.4 km transects in a large grid). In Wyoming, the rank order of small mammal captures across all sites was: southern red-backed vole, shrews (*Sorex cinereus*, *S. monticolus*, *S. hoyi* and *S. nanus*), deer mouse, chipmunks (*Tamias minimus* and *Tamias umbrinus*), western jumping mouse, voles (*Microtus montanus*, *M. longicaudus*), heather vole, golden-mantled ground squirrel, water shrew, weasel (*Mustela erminea*), northern pocket gopher, and house mouse (*Mus musculus*). Red squirrels were common in both Idaho and Wyoming but not sampled comparably. The species of shrews and chipmunks differed between Idaho and Wyoming and northern flying squirrels were absent from Wyoming. Otherwise, the rare occurrence of northern pocket gophers in the Wyoming sample is the most striking difference between our results and Raphael's (see Table 2).

Habitat Associations

Common species of small mammals at Chamberlain displayed relatively strong habitat associations

at either a macro-or microhabitat scale. Furthermore, despite broad overlap among species in habitats used, there were differences in the habitat where species were most common. *Microtus* voles were virtually confined to non-forested sites while southern red-backed voles and heather voles were not trapped in meadow or shrub habitats.

Southern red-backed voles and shrews were far more abundant in spruce-fir forest than any other habitat. These results corroborate patterns observed in other geographic areas (e.g. Raphael 1988, Ramirez and Hornocker 1981, Brown 1967, Millar *et al.* 1985). Others have suggested that red-backed voles are associated with characteristics of mesic, mature forests as a consequence of their food habits and need for moisture (Maser *et al.* 1978, Ure and Maser 1982). Microhabitat analysis for the red-backed voles at Chamberlain indicated an association with complex, mature forest structure which produce the lichen and fungi which this species feeds upon.

Deer mice occurred in all habitats except wet meadows. Other investigations in the Rocky Mountains have demonstrated the wide range of habitats used by this species (e.g. Williams 1955, Brown 1967, Halvorson 1982). This species' greater abundance in drier habitats—sagebrush-bunchgrass, mixed-conifer, and Douglas-fir—may be associated with the production of seeds by grasses and forbs which occur in these habitats. Although deer mice were captured in spruce-fir pit traps, these mice were not captured on the spruce-fir, snap-trap-grid during 2 years of trapping.

Heather voles were trapped in all forested habitats but were always rare. The pattern of broad habitat association (in some cases including non-forested sites) but low capture rates, seems to characterize this species in the Rocky Mountains (Millar *et al.* 1985, Brown 1967, Williams 1955). In contrast, high densities of heather voles have been found in jack pine monocultures with heavy ground cover of Ericaceous shrubs (Foster 1961, Naylor *et al.* 1985). The life history of this species is not understood, however, further study of heather vole demography and life history strategy could provide insight into mechanisms for persistence in small populations.

Yellow-pine chipmunks differed from red-backed voles, shrews and deer mice in their relation to microhabitat gradients. This species also differed from other small mammals in macrohabitat associations. Chipmunks were the most common mammal in sagebrush-bunchgrass sites (snap

trapping) but were also common in dry forest habitats (lodgepole pine and mixed-conifer).

Differences in species' habitat associations led to substantial differences in the structure of small mammal communities across vegetation types. Although lodgepole pine forest had the highest species richness (7) it had the fewest individuals captured in the snap trap sample. Furthermore, abundance of each species was quite similar in lodgepole pine. Mixed-conifer and Douglas-fir forests had similar species richness, abundance of individuals, and (based on both pit and snap trapping) similar mix of species. Wet meadow, which had a low species richness, differed most from the other sites in species composition. Spruce-fir forest stood out from other habitats in the abundance of small mammals and the degree of dominance of the community by shrews and red-backed voles. On the spruce-fir snap-trapping-grid, over 99% of all captures were shrews and red-backed voles. No other habitat was dominated by two species to this extent.

Conclusions

Our data corroborate the results of other investigations by demonstrating the relatively low abundance of small mammals in subalpine habitats of the Rocky Mountains. The abundance of mice and voles at Chamberlain paralleled pattern observed elsewhere in the Rockies but was low compared to studies in Scandinavia. The trapping rate at our most productive site was less than snap trap capture rates reported by Lofgren *et al.* (1986) and Korpimaki (1987*a,b*) during vole peaks during their studies of boreal owls in Sweden and Finland. Lofgren *et al.* (1986) captured 16.6 voles/100 trap nights during vole peaks and 1.4 during low years. Similarly, Korpimaki (1987*a,b*) captured up to 18 voles/100 trap nights in Finland during peak vole years. During all years, our trapping rates in habitats other than spruce-fir were lower than those observed by Lofgren *et al.* (1986) during low prey years.

Differences we observed in small mammals (e.g. species composition, species richness) among habitats suggests a mosaic pattern of small mammal communities in the Rockies. Subalpine forests in this region occur in a mosaic or patchwork of successional stages and species associations (Peet

1988, Knight 1994). Patches of lodgepole pine in various stages of succession are mixed among patches of spruce-fir forest. Patch sizes are generally small (10's to 100's of ha) leading to patchiness at the watershed scale. The relationship of small mammals with habitat conditions, then, results in frequent changes in small mammal communities within landscape areas less than 1000 ha.

The landscape mosaic of small mammal communities likely influences higher trophic levels. Many species of carnivores that occur in subalpine habitats are food limited and prey primarily on small mammals (e.g. boreal owls—Lofgren *et al.* 1986, Korpimaki 1987*a*; great gray owls—Duncan and Hayward 1994; American marten—Thompson and Colgan 1987). The value of each subalpine patch as foraging habitat for these carnivores will be determined, in part, by the small mammal community. Foraging habitat use, daily movement patterns, and population parameters of these carnivores may be affected by the landscape pattern of the small mammal communities.

Finally, variation in the species composition and structure of small mammal communities likely result in different consequences for the plant community in which they occur. While red-back voles frequently feed on *Bryoria* lichen and fungal sporocarps (Martell 1981), deer mice consume seeds, berries and insects (Martell and Macaulay 1981), and pocket gophers kill many conifer seedlings by consuming both above and below-ground parts (Crouch 1971). As the species composition of small mammal communities change among habitats the mammals will differentially effect the dominant overstory as well as understory.

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