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Small-mammal abundance at three elevations on a mountain in central Vermont, USA: a sixteen-year record

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Abstract

As part of a study of forest resilience to gypsy moth (*Lymantria dispar*) defoliation, small mammals were sampled with live (box) and pitfall traps for 16 years at three elevations on a mountain in west-central Vermont, USA. The more mesic, lower-slope location had the most diverse small-mammal community. White-footed mice (*Peromyscus leucopus*) were the most commonly captured small mammal at all locations, but less so at the lowest elevation. Southern red-backed voles (*Clethrionomys gapperi*), eastern chipmunks (*Tamias striatus*), and northern short-tailed shrews (*Blarina brevicauda*) were also regularly captured over the 16 years. Captures of all species showed considerable year-to-year variation. During the study, white-footed mouse density ranged from 3.7/ha (lower-slope June 1984) to 93.4/ha (mid-slope, July 1985). Over the 16 years, median density estimates across locations ranged from 12 to 19/ha in June and from 25 to 32/ha in July. Annual fluctuations in mouse abundance were synchronous across elevations, probably in response to regional-scale fluctuations in acorn production. In addition to those for white-footed mice, standardized capture rates are presented for the three other common species, and time to first capture is presented for 11 infrequently encountered species. The study demonstrates the importance of long-term surveys to properly characterize a small mammal community. © 1998 Elsevier Science B.V.

Keywords: White-footed mice; Red-backed voles; Eastern chipmunks; Northern short-tailed shrews; Annual population dynamics

1. Introduction

Small mammals, including Soricidae and Muridae, are ubiquitous in forest ecosystems (Lautenschlager et al., 1997) and are important to many forest ecosystem functions: dispersing seed, preying on many forest insect pests, and serving as prey items for predatory vertebrates (Sullivan, 1990; Elkinton et al., 1996; Ostfeld et al., 1996). However, long-term ecological information on population dynamics and community structure of forest floor small mammals is limited.

Mice of the genus *Peromyscus* are widespread across North America (Baker, 1968; Hooper, 1968; Smith, 1989) and across New England (DeGraaf and Rudis, 1987). They are among the most common, if not the most common small mammal in the north-eastern deciduous forest (Godin, 1977). Nevertheless,

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reports of long-term monitoring of populations of *Peromyscus* are scarce. Ostfeld (1988) used published data from 12 studies to characterize variability in *Peromyscus* populations through time. Of these, the longest reported study included ten annual surveys; studies were generally much shorter, three to five years. More recently, Krohne et al. (1988) trapped six to seven years (site dependent) at four sites; Kaufman et al. (1995) reported a six-year trapping effort; Kesner and Linzey (1997) analyzed a nine-year weekly nest box record; and Wolff (1996) reported a 14-year trapping effort. Variation in *Peromyscus* populations through time has generally been reported as low (Ostfeld, 1988; Fryxell et al., 1998). *Peromyscus* populations have been described as moderately fluctuating but non-cyclic (Krohne et al., 1988). Population changes, when they occur, are frequently a consequence of changes in food availability (Elkinton et al., 1996; Wolff, 1996; Jones et al., 1998).

Reports of the long-term monitoring of forest-dwelling small mammal species other then *Peromyscus* are even less common (Connell and Sousa, 1983; Ostfeld, 1988). Fryxell et al. (1998) report a 43-year study that described temporal dynamics of eight small mammal species in Ontario: deer mice (*P. maniculatus*) were consistently the most abundant; variation in abundance of all species was intermediate, typical of small mammals in general; abundance of only one species, the rarely caught northern flying squirrel (*Glaucomys sabrinus*) was suggestive of cyclic population dynamics; and all species showed evidence of synchronized population fluctuations over time. Grant (1976) conducted an 11-year study of small mammal populations in northern hardwoods forests at Mont St. Hilaire, Quebec. Nine species accounted for one-third of the captures and the remaining two-thirds were *Peromyscus* sp. Getz (1989) reported modest multi-year population fluctuations in a 14-year record of northern short-tailed shrew (*Blarina brevicauda*) surveys in three grassland habitats in Illinois.

We report the results of 16 years of small mammal trapping at three structurally and compositionally distinct forest habitats along an elevational gradient on a mountain in west-central Vermont, USA. The study was begun to ascertain and compare small mammal density, diversity, and predator impact on gypsy moth (*Lymantria dispar*) dynamics within forest stands either susceptible or resistant to defoliation by gypsy moth (Valentine and Houston, 1979; Houston and Valentine, 1985; Smith, 1985, 1989). Subsequent to that study, sampling of small mammals was continued to help assess long-term patterns in population change with particular emphasis on geographic variation in gypsy moth and white-footed mouse (*P. leucopus*) interrelationships. We describe annual density variations in white-footed mice, and relative abundance of three other common species, and time to first capture for 11 infrequently encountered species.

2. Study site and methods

2.1. Study site

The study was conducted on Salisbury Ridge, a southwest spur ridge of Bryant Mountain in Salisbury, Addison County, in west-central Vermont (W 73° 05′ 15″; N 43° 56′ 15″). The upper-slope forest at the top of the ridge, at 340 m elevation, was composed of white oak (*Quercus alba*) and northern red oak (*Q. rubra*) (Fig. 1(A). The mid-slope forest, about 240 m was dominated by white oak and chestnut oak (*Q. prinus*) (Fig. 1(B)). The forest at the lower-slope, approximately 200 m elevation, was dominated by red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), and northern red oak (Fig. 1(C)). The lower-slope forest was on a mesic site whereas the mid- and upper-slope forests were on more xeric sites (Houston and Valentine, 1985).

2.2. Small-mammal trapping

In the lower- and mid-slope habitat, a 7×7 trapping grid with 15 m spacing, was established. In the upper-slope habitat, because of topographic constraints, a 4×12 trapping grid, also with 15 m spacing, was established. A single Sherman live trap (7.5×7.5× 30 cm) was used at each of the trapping stations on the grids. At odd-numbered trapping stations, a pitfall trap (28 cm diameter×28 cm depth) was installed. Live traps were baited with peanut butter and oatmeal; pitfall traps were unbaited.

The slope distance between the center of the lower- and mid-slope trapping grids was approximately

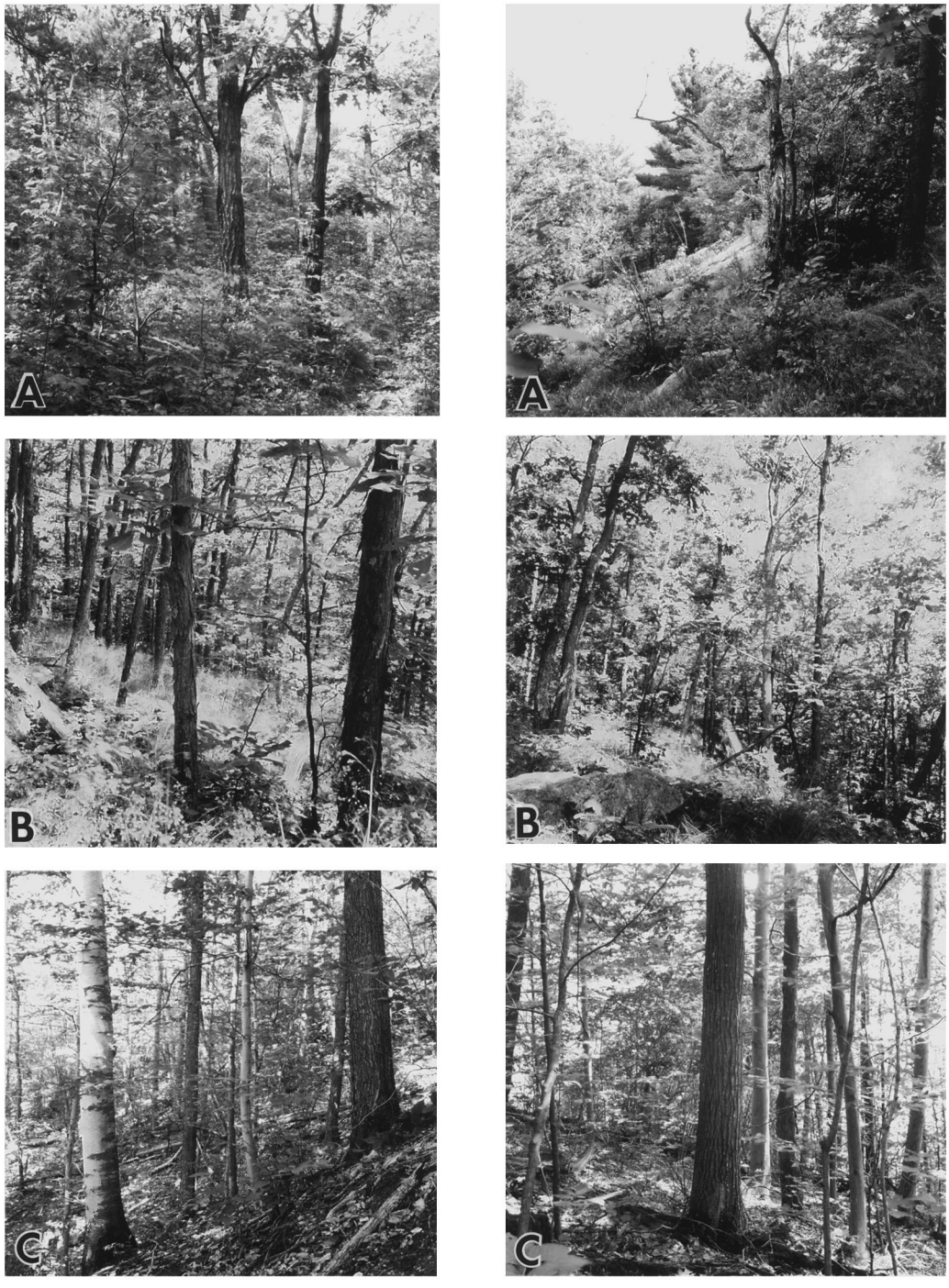

Fig. 1. Photographs showing the vegetative structure and life-form composition of the upper- (A), mid- (B), and lower-slope (C) habitats, Salisbury Ridge, VT, 1996.

150 m; and 175 m separated the centers of the mid- and upper-slope trapping grids. The approximate distance between the adjacent grid lines of the lower- and mid-slope trapping grids was 60 m, with 110 m between adjacent lines of the mid- and upper-slope grids.

Two trapping sessions, one in early summer, generally in late June, and another in mid-summer, generally in late July, were conducted in each of the 16 years. For the first 12 years, traps were monitored for five consecutive days for each session. For the final four years, each session was four days in length. Traps were checked once a day. Trapped animals were identified to species, sex, and age class, and before being released at the point of capture, each animal was uniquely numbered by toe clipping for individual identification.

2.3. Vegetation surveys

Over- and understory vegetation composition and structure were surveyed at the beginning of the study (1979) to characterize the habitat composition and structure and again in 1996, two years after the last small-mammal trapping, to assess change in habitat composition and structure. In 1979, overstory vegetation (trees$\geq$2.5 cm diameter at breast height [dbh]) was sampled on 36 5 m$\times$5 m plots, systematically established at 10 m intervals along four transects within the small-mammal trapping grid and across contours. Only species and dbh were recorded. Understory herbaceous and woody-stemmed vegetation was sampled on 1 m$\times$1 m plots nested within the southwest corner of the larger vegetation plot. Data included counts by species and height class. In the upper-slope habitat, 35 nested vegetation sampling plots were established along two transects because of topographic constraints.

In 1996, overstory vegetation was sampled on 250 m^2 circular plots located at ten systematically selected trapping stations. Data included species, dbh, and whether alive or standing dead. Understory vegetation was sampled on 244 m^2 circular plots located at even-numbered trapping stations. Data included percent cover by life form (i.e., forbs, grass, ferns, moss, lycopodium, woody-stemmed, and vines), a tally of coarse-woody debris (CWD) greater than 10 cm in diameter and in contact with the ground, and a count of individual plants by species and height class, or percent cover, if a colonial or mat-forming growth form, and percent exposed rock cover.

2.4. Analysis

Standardized species capture rates were calculated by dividing the number of individuals captured by the number of trap nights (TNs), after adjusting the number of TNs for sprung traps and traps occupied by other species. No effort was made to distinguish residents from transients. We assumed the mix of residents and transients on the trapping grid and in the sample reflected the regional mix of these residency categories. Diversity of the total capture of small mammals for each elevation was calculated using the Shannon–Weaver index (Poole, 1974: 391–395).

Densities of white-footed mice were estimated using CAPTURE (Otis et al., 1978; White et al., 1982). The estimate of the population size was based on the model and estimator recommended by CAPTURE (Elkinton et al., 1996). Density was estimated by dividing the estimate of population size after adjusting the trap-grid area by 0.5 the mean-maximum distance between recaptures. There were insufficient numbers of captures/recaptures to estimate density for any species other than white-footed mice.

Over- and understory vegetation data was summarized by elevation. Cover percentages were arcsine transformed prior to calculating summary statistics (Zar, 1974: 185–186).

3. Results

3.1. Small mammals

We captured 2 685 individuals, representing 16 species in 11 096 trap nights during the study (Table 1). Seven species were captured in the first year of the study while additional species were captured in subsequent years, through year 15 (Table 1). With 1995 individuals captured, white-footed mice were the most common small mammal species in all habitats and in all years. The northern short-tailed shrew was the second most common; 253 individuals were captured. Other species with more than 100

Table 1
Total and pitfall trap (in parenthesis) captures of small-mammal by species and elevational habitat, Salisbury Ridge, Vermont, 1979–94

Species	Lower-slope	Mid-slope	Upper-slope	Year to first capture
White-footed mouse	582 (5)	717 (10)	696 (3)	1
Southern red-backed vole	123 (6)	5 (2)	4 (1)	1
Eastern chipmunk	84 (0)	61 (0)	46 (0)	1
Woodland jumping mouse	3 (0)			8
Southern bog lemming		4 (4)	5 (3)	1
Southern flying squirrel	3 (0)	3 (0)	5 (0)	3
Red squirrel	4 (0)	2 (0)		4
Meadow vole	2 (2)	1 (1)		7
Northern short-tailed shrew	117 (13)	59 (6)	77 (11)	1
Masked shrew	9 (6)	5 (5)	2 (2)	1
Smoky shrew	28 (25)	4 (2)	3 (3)	1
Unknown shrew species	13 (7)	1 (0)	10 (0)	
Hairy-tailed mole		1 (1)		5
Grey squirrel	1 (0)			13
Star-nosed mole	2 (1)	2 (2)		12
Long-tailed shrew		1 (1)		15
All species	971 (65)	866 (34)	848 (23)	

captures were eastern chipmunks (*Tamias striatus*), 191, and southern red-backed voles (*Clethrionomys gapperi*), 132.

Species with few total captures were woodland jumping mice (*Napaeozapus insignis*), southern bog lemming (*Synaptomys cooperi*), southern flying squirrel (*G. volans*), red squirrel (*Tamiasciurus hudsonicus*), meadow vole (*Microtus pennsylvanicus*), masked shrew (*Sorex cinereus*), smoky shrew (*S. fumeus*), hairy-tailed mole (*Parascalops breweri*), grey squirrel (*Sciurus carolinensis*), star-nosed mole (*Condylura cristata*), and long-tailed shrew (*S. dispar*) (Table 1).

Species richness and the composition of small mammal captures were similar in the lower- and mid-slope habitats over the study (Table 1). Species diversity was highest in the lower-slope habitat ($H'=0.573$) and similar in the mid-slope ($H'=0.308$) or upper-slope ($H'=0.312$), where the white-footed mouse dominated the captures. Species richness was lowest in the upper-slope habitat. The four major species were captured in each of the three elevational habitats, though the southern red-backed vole was a minor component of the captures of the two higher habitats. The differences in composition and richness among the habitats were in the occurrence of minor species (Table 1).

Pitfall trap captures contributed less than 5% of total captures (Table 1). Shrews were the only species with a substantial proportion (24%) of captures occurring in the pitfall traps. Over 80% of the captures of the smaller masked and smoky shrews were in pitfall traps. The largest number of pitfall trap captures occurred in the lower-slope habitat, reflecting the greater proportion of shrews in the total small mammal captures in this habitat. Because of the relatively low numbers of pitfall captures, these data were not included in subsequent analysis.

White-footed mouse densities, estimated by CAPTURE, ranged from 3.7/ha in the lower-slope habitat in the June trapping session of 1984 to 93.4/ha in the mid-slope habitat in the July trapping session of 1985 (Fig. 2). Except for the spring session in the upper-slope habitat, 1985 estimated densities were the greatest of the 16-year record for both sessions and all habitats. Density estimates could not be made for three spring trapping sessions (1988 and 1990 in the lower-slope habitat and 1990 in the mid-slope habitat) due to insufficient numbers of captures/recaptures. Mouse density estimates were typically lower in the June trapping session (median value of 18.2/ha) than in the July session (28.7/ha) and in the lower-slope habitat (14.8/ha) than the mid- (22.5/ha) and upper-slope habitats (27.8/ha). Estimates of mouse density were

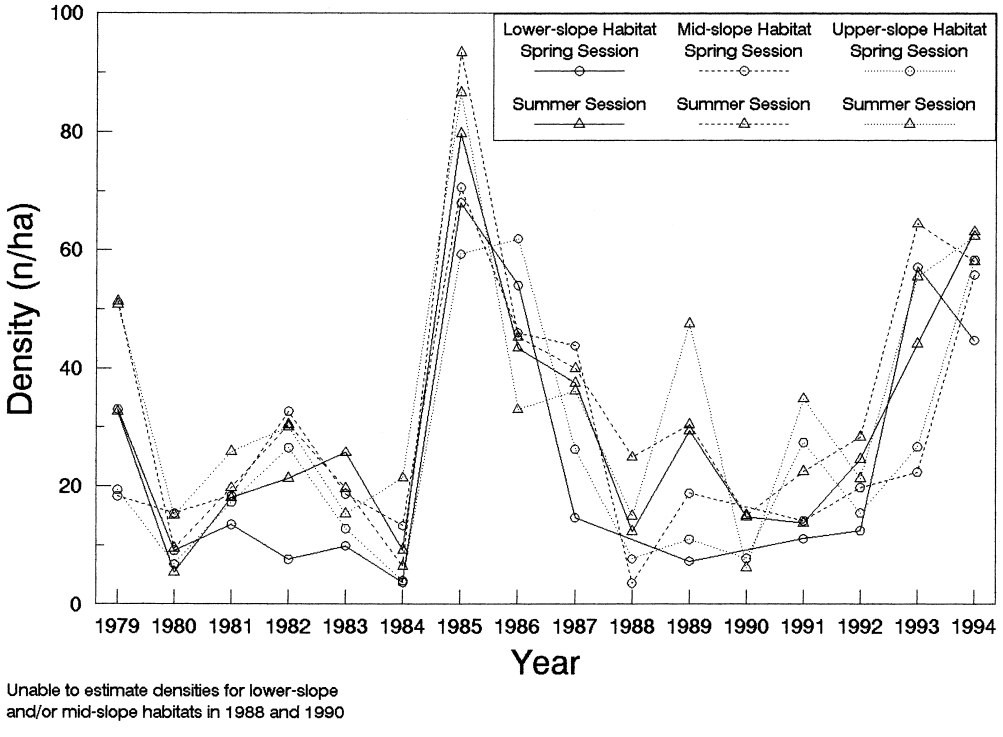

Fig. 2. Mean white-footed mouse densities by year, trapping session, and elevational habitat, Salisbury Ridge, VT, 1979–94.

highly correlated (r=0.957, p<0.001) with the number of individual captured mice (i.e., minimum number alive).

Annual variation in mouse densities was generally synchronous over the three habitats with low estimated densities occurring in 1980, 1984, 1988, 1990 (Fig. 2). Annual density estimates were correlated among the three habitats (Pearson correlations and associated Bonferroni-corrected probabilities between lower- vs. mid-slope habitat: r=0.706, P=0.071; lower- vs. upper-slope: r=0.812, P=0.006; and mid- vs upper-slope habitat: r=0.886, P<0.001 in the June session and between lower- vs. mid-slope habitat: r=0.941, P<0.001; lower- vs. upper-slope: r=0.88, P<0.001; and mid- vs upper-slope habitat: r=0.915, P<0.001 in the July session). The s measure of temporal variability of mouse densities (standard deviation of the $\log_{10}$ of density estimates; Connell and Sousa, 1983; Ostfeld, 1988) was less than 0.5 for all elevational habitats (lower=0.397, mid=0.317, upper=0.354 in the June session and lower=0.311, mid=0.305, upper=0.29 in the July session), indicating fluctuating, but non-cyclic populations.

Southern red-backed voles were captured almost exclusively in the more mesic, lower-slope habitat (Table 1). A small number of voles were captured in the mid-slope habitat in 1987 and 1994 and in the upper-slope habitat in 1994 (Table 2). Standardized red-backed vole capture rates followed a general four-year 'cycle' with high capture rates in 1982, 1986, and 1994. However the s measure of variability was 0.3, identifying a fluctuating but non-cyclic population. Red-backed vole capture rates did not vary synchronously with those of mice.

Standardized eastern chipmunk capture rates differed among the habitats. The lower-slope habitat had the largest median annual capture rate (1.3/100 TNs), with the mid-slope habitat having an intermediate rate (0.6) and the upper-slope having the lowest rate (0.3). Chipmunk capture rates peaked in 1981 and were relatively high for the following two years (Table 2). Standardized capture rates of northern short-tailed shrews differed considerably among the habitats.

Table 2
Standardized captures of individual small mammals per 100 trap nights by year, elevational habitat [a], and species, Salisbury Ridge, VT, 1979–94

Year	Habitat	White-footed mouse	Southern red-backed vole	Eastern chipmunk	Northern short-tailed shrew	Other species
1979	L	11.0	0.5	0.3	2.9	0.6
	M	11.4	0.0	0.3	0.3	0.0
	U	12.1	0.0	0.0	0.4	0.0
1980	L	3.9	0.5	1.7	0.3	0.0
	M	4.4	0.0	0.5	0.2	0.0
	U	6.1	0.0	0.2	0.8	0.0
1981	L	8.3	3.0	2.6	1.4	0.3
	M	11.7	0.0	5.7	0.3	0.0
	U	9.7	0.0	3.7	0.8	0.3
1982	L	6.2	5.1	0.5	0.0	0.0
	M	11.3	0.0	1.1	2.7	0.5
	U	11.4	0.0	1.5	1.1	0.0
1983	L	8.6	3.2	2.5	2.1	0.0
	M	9.8	0.0	2.5	0.0	0.0
	U	9.6	0.0	2.4	2.3	0.0
1984	L	2.6	0.0	1.3	1.2	0.5
	M	3.8	0.0	0.2	0.4	0.0
	U	4.7	0.0	0.9	0.5	0.3
1985	L	21.1	1.0	0.0	6.3	0.3
	M	25.4	0.0	0.5	0.3	0.0
	U	40.1	0.0	0.0	7.5	2.2
1986	L	15.4	5.3	0.7	2.1	0.5
	M	17.2	0.0	2.8	1.0	0.0
	U	13.3	0.0	0.2	1.0	0.2
1987	L	9.5	1.5	0.2	1.3	0.3
	M	14.1	0.4	1.2	1.3	0.0
	U	11.6	0.0	0.2	0.3	0.2
1988	L	2.8	0.3	0.2	0.0	0.0
	M	5.5	0.0	0.8	0.0	0.0
	U	5.2	0.0	0.4	0.0	0.0
1989	L	8.5	2.1	3.2	1.6	0.4
	M	10.2	0.0	0.2	0.0	0.0
	U	8.0	0.0	0.0	0.0	0.0
1990	L	6.0	0.6	1.9	4.7	4.8
	M	8.5	0.0	0.6	0.0	0.0
	U	13.1	0.0	0.6	0.7	0.0
1991	L	4.7	0.0	1.3	2.7	0.9
	M	8.5	0.0	0.3	0.0	0.0
	U	11.0	0.0	0.0	1.8	0.0
1992	L	6.3	0.3	2.7	3.9	0.8
	M	9.5	0.0	0.6	1.8	0.5
	U	9.0	0.0	0.9	1.8	1.1
1993	L	15.5	2.1	3.4	4.3	0.8
	M	15.4	0.0	1.1	7.7	1.4
	U	15.4	0.0	0.3	4.0	0.0
1994	L	12.9	5.6	0.7	1.0	0.0
	M	15.7	0.3	0.0	0.6	0.0
	U	19.7	0.7	0.0	1.9	0.0

[a] Plots are [L]ower-, [M]id-, and [U]pper-slope habitats.

Table 3
Average number of trees≥2.5 cm diameter at breast height per hectare by species/species group, elevational habitat, and year, and the average number per hectare, basal area (BA), and quadratic stand diameter (QSD) of all species by habitat and year, Salisbury Ridge, Vermont

Species	Lower-slope		Mid-slope		Upper-slope	
	1979	1996	1979	1996	1979	1996
Pine	0	0	23	47	43	95
Red maple	422	476	11	47	343	320
Sugar maple	137	88	0	3	0	4
Birch	667	90	0	0	0	0
Hickory	0	4	800	243	143	55
American beech	354	348	0	0	0	0
White ash	11	88	0	7	100	62
Aspen	46	24	0	0	0	0
Black cherry	0	0	0	60	0	207
White oak	11	12	686	283	429	244
Chestnut oak	0	0	354	283	0	18
Red oaks	160	112	171	163	514	320
Other deciduous	343	796	57	37	414	113
Unknown	11	0	0	0	0	0
All species						
#/ha	1554	1988	1680	1183	2071	1444
BA (m^2/ha)	24.8	24.7	18.8	12.1	19.5	14.4
QSD (cm)	14.3	12.6	11.9	11.4	10.9	11.3

The median annual capture rate in the lower-slope habitat was 1.9/100 TNs, greater than that for the mid- (0.3) or upper-slope habitats (0.9). Standardized short-tail shrew capture rates varied with no obvious pattern among habitats and years (Table 2). Pitfall trap captures for the smaller masked and, in particular smoky, shrews were much greater in the lower-slope habitat (Table 1).

3.2. Vegetation

The lower-slope forest was dominated by northern hardwoods (beech-maple-birch), with a major red oak component (Table 3). No conifers were present. Total basal area remained constant over the study but the density of trees increased 28% and the average stand diameter decreased from 15.3 to 14.5 cm. At the beginning of the study, aspen (*Populus* sp.) constituted 16% of the total basal area, but only 3% of the total number of trees. By the end of the study, aspen had all but disappeared from the stand. All other species, except sugar and red maples, generally declined in dominance over the course of the study. Changes in composition and structure in the lower-slope habitat were likely most affected by a diameter-limit timber harvest that occurred in 1983. The harvest focused on oaks greater than 25 cm in diameter. The stand had been previously harvested in 1973 to the same standards.

The total understory foliage cover in the lower-slope habitat was less extensive than in the mid- and upper-slope habitats (Table 4). Forbs were the dominant life form in this habitat, followed by woody-

Table 4
Average percent cover by life form and elevational habitat, Salisbury Ridge, Vermont, 1996

Life form	Lower-slope	Mid-slope	Upper-slope
Forbs	18.9	23.4	25.6
Grass	3.3	26.6	25.2
Ferns	5.3	0.8	6.2
Moss	9.4	9.7	13.5
Lycopodium	0.8	0.0	0.0
Woody-stemmed vegetation	11.7	43.0	52.9
Vines	0.4	0.4	0.0
Total foliage cover [a]	24.1	61.8	70.0
Rock	16.5	36.7	22.0

[a] Life-form percentages do not sum to total foliage cover due to layering.

Table 5
Understory plant density by species and elevational habitat for the ten most numerous species, Salisbury Ridge, Vermont, 1979

Lower-slope			Mid-slope			Upper-slope		
Species	Life form [a]	Plants/ m^2	Species	Life form	Plants/ m^2	Species	Life form	Plants/ m^2
Aralia nudicalulis	H	3.7	*Vaccinium vacillans*	S	17.3	*Vaccinium angustifolium*	S	32.9
Acer rubrum	T	2.5	*Gaylussacia baccata*	S	14.8	*Antennaria* sp.	H	18.2
Aster sp.	H	2.3	*Amelanchier* sp.	T	4.9	*Gaylussacia baccata*	S	6.1
Polygonatum biflorum	H	2.1	*Solidago* sp.	H	3.1	*Amelanchier* sp.	T	4.4
Corylus sp.	T	6.9	*Vaccinium angustifolium*	S	2.8	*Aronia* sp.	T	4.4
Hamamelis virginiana	S	1.9	*Aralia nudicalulis*	H	2.3	*Helianthus* sp.	H	2.8
Desmodium sp.	H	1.6	*Antennaria* sp.	H	2.0	*Polygonatum biflorum*	H	2.1
Lysimachia quadrifolia	H	1.3	*Aster* sp.	H	1.9	*Solidago* sp.	H	1.7
Smilacina racemosa	H	1.3	*Helianthus* sp.	H	1.8	*Vaccinium vacillans*	S	1.3
Viburnum acerifolium	S	1.3	*Polygonatum biflorum*	H	1.5	*Lysimachia quadrifolia*	H	1.2
All species		27.8	All species		62.7	All species		84.0

[a] Life form codes: [H]erb, [S]hrub, [T]ree.

stemmed vegetation. The understory of the lower-slope was different from that of the two higher elevational habitats with less grass and woody-stemmed plant cover. Ericaceous shrubs were not common in the lower-slope habitat, unlike in the upper habitats (Table 5). Exposed rock cover in the lower slope was considerably less than in the mid-slope habitat and minimally less than the upper-slope habitat. Twelve pieces of CWD were tallied on nine of the 24 understory-survey plots. The average cover of CWD was 218 cm^2/m^2.

The mid-slope habitat had the lowest total overstory density and basal area of the three habitats (Table 3). The mid-slope forest was almost pure oak-hickory, with white and chestnut oak dominating over the course of the study. Both species declined in density over the study, presumably due to gypsy-moth defoliation and subsequent mortality. In 1996, chestnut oak density and basal area were significantly greater in mid-slope habitat than in either the lower- or upper-slope habitats. Eastern white pine (*Pinus strobus*) constituted a small but increasing component of the stand. Because the two oaks dominated the stand, the total-stand basal area and density declined over the study. The average stand diameter increased slightly from 13.6 to 14.2 cm over the study.

The total understory foliage cover of the mid-slope habitat was greater than the lower-slope but similar to the upper-slope habitat. The understory life-form composition of the mid-slope habitat was similar to that of the upper-slope habitat (Table 4). The understory cover was dominated by woody-stemmed vegetation, with major forb and grass cover. Low-bush blueberry species (*Vaccinium* sp.) and huckleberries (*Gaylussacia baccata*) were numerous in the mid-slope habitat (Table 5) and widespread, occurring on over 70% of the vegetation survey plots. The mid-slope habitat had much less fern cover than the other habitats. Exposed rock was more extensive in the mid-slope habitat than in the other two elevational habitats. No CWD was observed on the understory-survey plots.

The upper-slope habitat was also dominated by white and red oaks (Table 3). Both species declined in density over the study, most likely due to gypsy-moth defoliation and mortality. Conifers, composed mainly of eastern white pine but with a small component of pitch pine (*P. rigida*), were a small but increasing component of the stand. Total basal area and density declined over the study and the average stand diameter remained essentially constant at 11.8 cm.

The total understory foliage cover in the upper-slope habitat was the most extensive of the three elevational habitats (Table 4). The upper-slope understory consisted predominantly of woody-stemmed vegetation, but with major forb and grass cover. As with the mid-slope habitat, low-bush blueberries were numerous (Table 5) and wide spread, occurring on over 80% of the vegetation survey plots.

Rock cover was intermediate in extent. Six pieces of CWD were surveyed on three of the 24 understory-survey plots. The average cover of CWD was 49 cm^2/m^2.

4. Discussion

4.1. Small mammal community

Over the 16 years of trapping, most small mammal species expected to occur in these mixed-hardwood habitats in west-central Vermont were captured. However, many infrequently captured species would have been missed in short-term monitoring. After three and five years, we captured eight and ten species, respectively, of the 15 species captured over the study.

Even after 16 years, two additional small mammal species that could reasonably be expected to occur at the location were not captured. The woodland or pine vole (*M. pinetorum*) and deer mouse (*P. maniculatus*) have been reported from southern and central Vermont in deciduous forests (Godin, 1977; DeGraaf and Rudis, 1987). Identification of *Peromyscus* was made by pelage coloration rather than the more exact but demanding examination of salivary amylase (Parren and Capen, 1985), so it is possible that some *P. maniculatus* individuals may have occurred in the sample. Other species reported from central Vermont use different habitats. The pygmy shrew (*S. hoyi*) may use more moist habitats and the northern flying squirrel (*G. sabrinus*) and rock vole (*M. chrotorrhinus*) may use higher elevation habitats (DeGraaf and Rudis, 1987).

The more mesic, lower-slope habitat supported a more diverse small mammal community than the more xeric mid- and upper-slope habitats. While the species richness was comparable between the lower- and mid-slope habitats, diversity (H') was enhanced in the lower-slope habitat by the lesser dominance of white-footed mouse captures (60% of all captures), compared to 82% of all captures in the mid- and upper-slope habitats, and to the greater numbers of red-backed voles and shrews, species sensitive to soil moisture conditions (DeGraaf and Rudis, 1987). There was also more coarse-woody debris in the lower-slope habitat, a common vole habitat component (Getz, 1968; Miller and Getz, 1977). The higher median capture rates of eastern chipmunk in the lower-slope habitat agree with Bowers (1995) that this species prefers an open-understory and closed-overstory habitat. The lower-slope habitat had lower total understory foliage cover (Table 4) and greater overstory density and dominance (Table 3) than the upper habitats.

Capture data may not accurately represent true small mammal composition because of trapping biases due to differing size and behavior of individual small mammal species (O'Farrell et al., 1994; Jones et al., 1996). However, as trapping methods were standard among the three elevational habitats of this study, these data can be used for inter-habitat comparisons.

4.2. White-footed mouse

White-footed mice dominated the captures in all habitats, though to a lesser degree in the lower-slope habitat, in every year. The three habitats were structurally and compositionally distinct. The lower-slope habitat was a mesic, mixed-hardwoods stand whereas the upper two habitats were more xeric and dominated by oaks. The dominance of the mouse across the habitats demonstrated that it is a forest habitat generalist, a description supported by reviews of habitat use by this species (Godin, 1977; DeGraaf and Rudis, 1987).

White-footed mouse capture rates and estimated densities varied synchronously in time across the three elevations despite differences in structure and vegetation composition among the habitats. Minimal movement between capture grids and habitats was detected from recaptures of marked individuals. These results concur with the conclusions of Krohne and Burgin (1990), who suggested that the presence of a single, overriding regulatory factor such as an abundance of forage resources accounts for demographic homogeneity at finer scales.

Annual fluctuations in white-footed mouse densities have been shown to be closely correlated to the previous year's hard mast, generally acorn, production (Elkinton et al., 1996; Ostfeld et al., 1996; Wolff, 1996). Acorn production was not monitored in this study. While total oak basal area differed minimally among the three habitats, total oak density differed considerably (Table 2). The species composition of oaks also differed among the habitats, with red oaks

dominant in the lower-slope habitat, where there also was a major white oak component. Chestnut and white oaks dominated in the mid-slope, and red and white oaks were dominant in the upper slope.

Differences in oak composition and diameters can result in differences in potential acorn production. Generally, potential acorn production is related to tree diameter, with larger-diameter trees having greater per unit basal area production (Goodrum et al., 1971). The larger average diameter oaks in the lower-slope habitat have greater potential acorn production than the smaller diameter trees in the upper habitats. By having a mixture of white and chestnut (mid-slope) or white and red (upper-slope) oaks, and greater densities of oaks in both habitats, the higher altitude habitats have an increased probability of a regular and plentiful acorn crop. In mixed-oak stands, good acorn production by one species often offsets poor production by another species, and exceptional acorn crops occur when two or more species have good crops (Goodrum et al., 1971).

Acorn production was described as 'good' or 'excellent' in northwestern Vermont in 1984 in annual subjective surveys of mast production (per. comm. S. Darling, Department of Fish and Wildlife, Pittsford, VT). White-footed mouse densities were the highest of the 16-year study the following year. Production for other years between 1978–87 were described as 'fair' or occasionally 'good'. No regional data on acorn production in northwestern Vermont were available for the years 1989–94. Location-specific acorn production data from Mendon, VT, approximately 35 km to the south, was considered 'excellent' in 1990, 'good' in 1989, 1991, and 1993, and 'poor' in 1992 (per. comm. S. Darling, Department of Fish and Wildlife, Pittsford, VT). This annual pattern in acorn production does not correspond with our mouse density estimates (i.e., mouse densities were not high in 1991 [Fig. 2]) following an 'excellent' acorn crop in 1990), implying that patterns in acorn production may not be consistent over larger areas.

The population densities of white-footed mice on Salisbury Ridge, Vermont between 1979–94 were similar to results from other long-term trapping studies. Peak densities exceeding 80 mice per hectare, as observed in 1985, were also reported by Wolff (1996) from a 14-year record at a Virginia site and by Krohne et al. (1988) from a 6-year record from a site in Ohio. In both studies, the peak was attained only once over the duration of the study and fell precipitously the following year. Krohne et al. observed that populations of forest-dwelling *Peromyscus* populations fluctuate moderately on a multi-annual time scale, that the magnitude of the fluctuations fall within a relatively narrow range of s, and concluded that these values are similar to those reported for noncycling microtines. The same observations can be made of and conclusions drawn from the *Peromyscus* data from the 16-year record from Salisbury Ridge.

Variation in annual mouse capture rates within the three elevational habitats was larger than variation among the habitats. The maximum difference in mouse capture rates among habitats was 2.3:1 in 1991 between the upper- and lower-slope habitats, only a third or less of the maximum difference in annual capture rates within a habitat. Efforts at detecting differences in mouse densities or at monitoring the response of mice to habitat disturbances need to consider the effects of annual variation in mouse abundance on sample size and power.

5. Conclusions

Populations of white-footed mice appeared to fluctuate at two spatial scales. There was a synchrony in annual densities or capture rates across all three elevational habitats, despite their differences in vegetative composition and structure. Other studies have shown that food resources, namely oak mast, have a controlling influence on mouse populations. Oaks were common or dominant in all habitats. Acorn production was not monitored in the study but it was likely that regional-scale temporal patterns in acorn abundance controlled mouse populations on the Ridge.

At the finer spatial scale, mouse capture rates differed among the habitats. The lower-slope habitat had much lower mouse capture rates than the higher altitude habitats. At the within-habitat scale, the lower-slope habitat had a more open understory which could result in increased predation risk. The lower-slope also had a lesser density of blueberries and huckleberries, which can be an important summer food resource (Smith, 1989). Finally, the lower-slope habitat had a lesser oak component in the overstory,

with a smaller potential acorn crop compared to the upper two habitats.

This study demonstrates the importance of long-term surveys to characterize and/or assess the characteristics of small-mammal communities. Common species are detected in the first years but new species were being captured in the last years of this 16-year effort. Quantification of abundance for the assessment of differences among habitats (or treatments) or for the detection of change requires a commitment of several years. Even for the white-footed mouse, the most abundant species in the small-mammal community, a three- to five-year trapping effort would not reliably detect differences that were identified by the 16 years of data. For less abundant species, the requirement for long-term trapping is necessary.

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