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Small mammal habitat associations in poletimber and sawtimber stands of four forest cover types

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ABSTRACT

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Small mammal distribution was examined in poletimber and sawtimber stands of four forest cover types in northern New England: northern hardwoods, red maple, balsam fir, and red spruce-balsam fir. During 1980 and 1981, eight stands on the White Mountain National Forest, NH, were sampled with four trap types (three sizes of snap traps and one pit-fall) for 16 000 trap-nights. Trapping was conducted during four 5-day periods in June and July. A total of 1206 individuals of seven species - *Blarina brevicauda* (short-tailed shrew), *Sorex cinereus* (masked shrew), *Sorex fumeus* (smokey shrew), *Sorex hoyi* (pygmy shrew), *Clethrionomys gapperi* (boreal red-backed vole), *Peromyscus maniculatus* (deer mouse), and *Napaeozapus insignis* (woodland jumping mouse) - were captured. *Blarina brevicauda*, *S. fumeus*, and *N. insignis* were more abundant in hardwoods ($P > 0.001$). Only *P. maniculatus* was more numerous in softwoods ($P < 0.05$). *S. cinereus* was more abundant in fir than in spruce-fir stands ($P < 0.001$) and *S. hoyi* and *C. gapperi* did not occur differentially among habitat types. Possible causes of these relationships are the lower tree density and basal area and the greater amount of ground cover in hardwoods than in softwoods. Abundances of these seven species were typical, except that *S. hoyi* was notably more common than previously documented.

INTRODUCTION

The spatial distribution of small mammal populations is influenced by the patchiness of their environment. Patchy habitats provide more or less suitable conditions for various species according to their habitat preferences. Differences in species' densities among habitats reveal the importance of habitat suitability (Aulak, 1970; Mazurkiewicz, 1984). It is generally assumed that suitability of a habitat for a given species declines as that species' density increases above optimum, commonly resulting in dispersal to other less suitable habitats (Goertz, 1970; Hansson, 1977).

Small mammal distributions among the various forest cover types in New

England are not well understood. Some species are assumed to have wide habitat tolerances, e.g. *Peromyscus leucopus*; others are rare, unstudied, or local, e.g. some shrews, especially *Sorex hoyi* (DeGraaf and Rudis, 1986). Forests are managed by adjusting the compositions of type and timber size-class but comparisons of the relative habitat values of type and size-class have not been made for small mammals in New England. We sampled two timber size-classes (poletimber and sawtimber) in each of four common forest cover types, to evaluate their relative values as habitats for small mammals. The proportions of these cover types in the study area, which is 75% forested, are: northern hardwoods (46%), red maple (3%), balsam fir (8%), red spruce–balsam fir (5%). Seven other types — aspen, birch, red oak, oak–pine, balsam fir, red and white pine, red spruce and hemlock — together constitute 13% of the study area.

STUDY AREA

This study was conducted on the White Mountain National Forest (WMNF), New Hampshire (44°30′N, 71°15′W). The study area covers an area of approximately 20 km^2, and is bounded by low (970–1260 m) ranges of mountains to the north, east, south, and southwest. Elevation in the study area ranges from 330 to 1240 m. Most of the area was logged during the nineteenth century. Around the turn of the century, large fires burned much of the region, resulting in the extensive 90-year-old even-aged forest present at time of the study. Sawtimber stands (all types) constitute 65% of the area, poletimber stands 25%, and younger stands 10%. At higher elevations, red spruce (*Picea rubra*), balsam fir (*Abies balsamea*), and paper birch (*Betula papyrifera*) stands predominate; stands on lower slopes contain sugar maple (*Acer saccharum*), red maple (*A. rubrum*), yellow birch (*B. alleghaniensis*), and beech (*Fagus grandifolia*), with components of white spruce (*P. glauca*), red spruce, balsam fir, eastern hemlock (*Tsuga canadensis*), aspen (*Populus* spp.), and white ash (*Fraxinus americana*) on suitable sites. Valley bottoms support extensive stands of red spruce, white spruce, and balsam fir with associated alders (*Alnus* spp.) and aspens.

Northern hardwoods are composed of sugar maple, American beech (*Fagus grandifolia*), and yellow birch in varying proportions in the study area and occur widely in northern New England. These species comprise the basic hardwood type in northern New England, and occur to an elevation of 760 m on fertile, moist loamy soils. On drier sites, beech becomes more prominent. On wetter sites, the proportions of red maple and yellow birch increase, and beech is absent (Eyre, 1980). Striped maple (*Acer pensylvanicum*) and hobblebush (*Viburnum alnifolium*) are common in the understory throughout the study area.

In the red maple type, red maple is dominant or co-dominant; associates are yellow birch, balsam fir, and sugar maple. The type occupies moist to wet muck or peat soils in swamps, depressions of slow drainages, or along sluggish streams. It can be differentiated readily from northern hardwoods by the absence of beech and the increased proportion of yellow birch and red spruce.

Red spruce–balsam fir stands consist either of red spruce and balsam fir in approximately equal proportions or together they predominate in a mixture of associates — the composition varies depending on site and disturbance history. This type occupies moderately to poorly drained flats and well-drained to dry, shallow soils on steep, rocky, upper mountain slopes. Associates are red maple, paper and yellow birch, and aspens, white pine (*Pinus strobus*), eastern hemlock, and occasionally black spruce (*Picea mariana*) and tamarack (*Larix laricina*). Stands are usually dense; the ground is generally devoid of plants except for mosses or scattered seedlings of red spruce and balsam fir (Eyre, 1980).

In the balsam fir type, balsam fir is either pure or predominant and occurs on moist or wet-site soils. Common associates on the study area are paper birch, aspens, and northern white-cedar (*Thuja occidentalis*). The type occurs on moderately well-drained to poorly drained flats and in swamps. Pure stands commonly result from heavy cutting or blowdown.

METHODS

We selected eight stands of at least 16 ha from WMNF compartment records. Two softwood poletimber stands were comprised of trees of 10.0–22.0 cm diameter at breast height (dbh); two hardwood poletimber stands were of 10.0–30 cm dbh. Mean dbh of trees in two softwood sawtimber stands was at least 23 cm, and at least 31 cm in two hardwood sawtimber stands.

Stand features were measured on two randomly located 0.04 ha circular plots in each stand. Tree dbh was measured with a diameter tape. Basal areas were calculated. Per cent ground cover was estimated using a 15 cm $\times$ 2.5 cm sighting tube at 10 points along each random plot diameter. Numbers of shrubs and saplings more than 1 m high were recorded on 20 m^2 at cardinal intersects of the 0.04 ha plot perimeters.

A grid of five columns and 20 rows (divided into four five-row quarters) was established in each stand; trap stations (intersections of rows and columns) were 10 m apart. A combination of trap types was used to minimize bias from effects of species-specific trap susceptibility. Three sizes of snap-traps and one size of pit-fall trap were used; small — Mcgill Can't Miss Four-Way Mouse Traps, medium — Museum Specials, large — Mcgill Can't Miss Four-Way Rat Traps, and pit-fall traps made from plastic containers 28.6 wide cm $\times$ 28.0 cm deep. Two of the four trap types were used at each station; all trap combinations were replicated among quarters (Fig. 1).

Trapping was conducted concurrently in all stands by respective quarter

Quarter	Row	Column A	Column B	Column C	Column D	Column E
1	1	s-x-p	m-x-l	s-x-m	s-x-p	m-x-s
	2	m-x-s	s-x-p	m-x-l	s-x-m	s-x-p
	3	m-x-p	s-x-m	s-x-p	s-x-m	l-x-m
	4	m-x-s	m-x-p	s-x-m	s-x-p	s-x-m
	5	l-x-s	m-x-s	l-x-p	s-x-m	s-x-p
2	6	x	x	x	x	x
	7	x	x	x	x	x
	8	x	x	x	x	x
	9	x	x	x	x	x
	10	x	x	x	x	x
3	11	x	x	x	x	x
	12	x	x	x	x	x
	13	x	x	x	x	x
	14	x	x	x	x	x
	15	x	x	x	x	x
4	16	x	x	x	x	x
	17	x	x	x	x	x
	18	x	x	x	x	x
	19	x	x	x	x	x
	20	x	x	x	x	x

x- trap station
s- small snap
m- medium snap
l- large snap
p- pit-fall

10m

40m

Fig. 1. Trapping grid design showing stations and trap types (same for all quarters) used to study small mammals, White Mountain National Forest, NH, 1980–1981.

(e.g. quarter 1 traps were opened in all stands, then quarter 2 traps in all stands, and so on). Trapping was conducted for one 5-day period in each quarter during June and July 1980 and 1981. Intervals between periods were 8–14 days. Trap arrangement, schedule, and order of sampling among quarters was unchanged between years. The total number of trap-nights per stand was 2000 (100 stations per grid×2 traps per station×5 days×2 years), or 16 000 trap-nights total.

All traps were baited with peanut butter, bacon grease and rolled oats, replaced daily as needed. Traps were checked daily during trapping periods.

ANALYSIS

An analysis of variance (ANOVA) with split-plot design was used to test the effects of forest cover type–size class (C), mammal species (A), quarter pairs (Q), and year (Y), on number of individuals captured.

Split-plot design allows whole plots, to which one or more treatments are applied, to be divided into subplots to which one or more additional treatments are applied; thus each split plot becomes a block for the subunit treatments (Steel and Torrie, 1960). In this study, the design resulted in a three-level hierarchy (whole, split, and split–split) to appropriate parts of which the treatments were applied.

To clarify the associations of species and subsets of habitat types, e.g. hardwoods vs. softwoods or poletimber vs. sawtimber, single degree of freedom comparison tests were used (Cohen and Burns, 1976). These tests allowed further interpretation of significant differences shown by ANOVA through comparisons among the means or groups of means of the various cover types and size-classes. These comparisons were done for all species grouped, for the shrew species grouped, and for each species individually.

Duncan's New Multiple-Range Test (Steel and Torrie, 1960) was used to examine differences among the subclass means of the individual species captures with all habitats combined.

RESULTS

Two years' sampling yielded 1223 mammals captured; 1206 of these comprised the seven species included here (Table 1). The remaining 17 specimens comprised 10 other species, *Synaptomys cooperi* (1), *Microtus pennsylvanicus* (1), *M. chrotorrhinus* (1), *Lepus americanus* (1), *Tamiasciurus hudsonicus* (3), *Condylura cristata* (1), *Sorex palustris* (3), *Parascalops*

TABLE 1

Number of captures of small mammals in eight habitats in the White Mountains, NH, 1980–1981

Species	Hardwoods				Softwoods				Total
	Northern hardwoods		Red maple		Balsam fir		Spruce fir		
	Pole timber	Saw timber	Pole timber	Saw timber	Pole timber	Saw timber	Pole timber	Saw timber	
Blarina brevicauda	24	27	23	25	16	9	12	10	146
Sorex cinereus	20	27	27	43	29	57	34	15	252
Sorex fumeus	39	4	53	2	5	3	1	1	108
Sorex hoyi	3	3	7	4	7	2	3	5	34
Total shrews	86	61	110	74	57	71	50	31	540
Clethrionomys gapperi	18	19	11	15	19	25	16	19	142
Peromyscus maniculatus	16	30	10	34	53	34	54	29	260
Napeozapus insignis	69	24	34	55	16	19	26	21	264
Total nonshrews	103	73	55	104	88	78	96	69	666
Grand total	189	134	165	178	145	149	146	100	1206

breweri (1), *Tamias striatus* (1), *Glaucomys sabrinus* (2), and unidentified shrew (1) and vole (1), none of which is discussed further here.

Number of captures differed ($P<0.01$) among the following main and two-way sources: habitat type (C), animal species (A), habitat type×quarter pair (CQ), habitat type×animal species (AC), animal species×quarter pair (AQ), year×quarter pair (YQ), and animal species×year (AY); there were no differences by quarter (Q) or year (Y) (Table 2).

Species groups that differed ($P<0.05$, Duncan's new multiple range test), ranked in order of increasing abundance, are *S. hoyi*, *S. fumeus*, *C. gapperi* and *B. brevicauda*; and *S. cinereus*, *P. maniculatus* and *N. insignis* (Table 3).

Analysis of the AC interaction by single degree of freedom comparisons on grouped and individual species to clarify mammal-habitat associations is shown in Table 4. Because this analysis produced subclass means whereby the two sources were tested with different error variances, a weighted error term (E) was required (Damon and Harvey, 1987, p. 327), calculated as follows:

$$E=\frac{\text{MS error (a)}+(n_s-1)\text{ MS error (b)}}{n_s}$$

where n_s is the calculated degrees of freedom for appropriate pooled mean square; MS error (a) is the mean square error, whole-plot component; and MS error (b) is the mean square error, split-plot component. The weighted error variance for these tests was 0.172.

More *Blarina brevicauda* were captured in hardwoods than in softwoods ($P<0.01$). More *Sorex cinereus* were captured in the red maple type than in northern hardwoods ($P<0.05$) and in balsam fir than spruce–fir ($P<0.01$).

More *Sorex fumeus* were captured in hardwoods than in softwoods ($P<0.01$) and more were captured in poletimber stands than in sawtimber ($P<0.01$). Analysis of the interaction between cover type and size-class showed that the effect of size-class is primarily between poletimber and sawtimber stands of hardwoods ($P<0.01$), and that the cover type effect is between hardwood poletimber and softwood poletimber. Captures were more numerous in hardwood poletimber stands than in all others.

Capture of *Sorex hoyi* and *Clethrionomys gapperi* did not differ among forest cover types or between size-classes. More *Peromyscus maniculatus* were captured in softwoods than hardwoods ($P<0.01$), the only species to show this preference. Further analysis of the interaction indicated that this difference was only in poletimber stands ($P<0.01$).

More *Napaeozapus insignis* were captured in hardwoods than in softwoods ($P<0.01$). The significant interaction among the four hardwood stands obscured the relative effects of red maple and northern hardwoods. Within northern hardwoods, the poletimber stand contained more individuals than the sawtimber stand, whereas the opposite was true in red maple stands. Like-

TABLE 2

Sources of variation (ANOVA for seven species; split-plot design) in numbers of seven small mammals in eight habitats in the White Mountains, NH, 1980–1981

Source of variation[a]	d.f.	Mean square	F	Significance
Whole-plot				
Mean	1	129.860	712.55	
C	7	0.543	2.98	0.01
Q	3	0.384	2.11	
CQ	21	0.391	2.15	0.01
S(CQ)-error	768	0.182		
Split-plot				
A	6	4.930	28.89	0.01
AC	42	0.970	5.68	0.01
AQ	18	0.840	4.92	0.01
ACQ	126	0.344	2.02	0.01
SA(CQ)-error	4608	0.170		
Y	1	0.001	0.01	
YC	7	0.197	1.23	
YQ	3	0.609	3.79	0.01
YCQ	21	0.411	2.56	0.01
SY(CQ)-error	768	0.161		
Split-split plot				
AY	6	1.040	7.20	0.01
AYC	42	0.515	3.57	0.01
AYQ	18	0.630	4.37	0.01
AYCQ	126	0.478	3.31	0.01
SAY(CQ)-error	4608	0.144		
	11200			

[a]C, Forest type–size class; Q, quarter pairs; S, trap stations; A, animal species; Y, year.

TABLE 3

Groups of small mammals that differed[a] in abundance in forest habitats, White Mountain National Forest, NH, 1980–1981

	Animal species						
	S. hoyi	*S. fumeus*	*C. gapperi*	*B. brevicauda*	*S. cinereus*	*P. maniculatum*	*N. insignia*
Rank	1	2	3	4	5	6	7
Mean no. captures	0.002	0.006	0.008	0.009	0.015	0.016	0.016
Number captured[b]	34	108	142	146	252	260	264

[a]$P < 0.05$ — Duncan's new multiple range test (Steel and Torrie, 1960, pp. 107–109).
[b]Number of trap-nights 16 000.

wise, within sawtimber stands, red maple was used more than northern hardwoods whereas in poletimber stands northern hardwoods were used more than red maple.

TABLE 4

Differences[a] in use among forest habitats by small mammal species and groups, White Mountain National Forest, NH; there were no significant main effects between habitat combinations which are not listed

Species or group	Habitats compared	d.f.	Mean square	F	Significance
Blarina brevicauda	HARDWOOD[b]-softwood	1	1.6900	9.810	0.01
Sorex cinereus	Northern hardwoods-RED MAPLE	1	0.6613	3.838	0.05
	BALSAM FIR-spruce fir	1	1.7113	9.933	0.01
S. fumeus	HARDWOOD-softwood	1	4.840	28.094	0.01
	SAWTIMBER-poletimber	1	4.840	28.094	0.01
Peromyscus maniculatus	Hardwood-SOFTWOOD	1	4.000	23.218	0.01
Napaeozapus insignis	HARDWOOD-softwood	1	6.250	36.510	0.01
	Weighted error variance	>4000	0.172		
All seven species	HARDWOOD-softwood	1	1.418	7.798	0.01
	S(CQ)-error	768	0.182		
Four shrew species	HARDWOOD-softwood	1	2.326	12.412	0.01
	S(CQ)-error	768	0.187		

Hardwood, northern hardwood+red maple; softwood, balsam-fir+spruce-fir.
[a]Single degree of freedom comparisons (Cohen and Burns, 1976).
[b]Habitats in which species or groups were more abundant are indicated by capitals.

As might be expected from the above results, analysis of habitat use by all seven species grouped using single degree of freedom comparisons showed that hardwoods were used much more than softwoods ($P<0.01$). Within hardwood stands there was significant interaction because of the higher use of poletimber in the northern hardwood stand and slightly higher use of the sawtimber in the red maple stand.

Analysis of habitat use by grouped shrew species showed that more shrews were captured in hardwoods than in softwoods ($P<0.01$).

The mammal species–community association (AC) was examined in detail because it was the primary concern of this study. Of the other significant two-way interactions, the most interesting was the trend in abundance from 1980 to 1981 (AY). All four shrews increased whereas the non-shrews decreased. There was a steady decline in total captures through the four quarters in 1980 but not 1981 (YQ). All species except *P. maniculatus* declined from the first to second trapping quarter (AQ). The CQ interaction showed no consistent trends.

DISCUSSION

Blarina brevicauda has been reported to prefer hardwoods in the central and southern Appalachian Mountains (Kirkland, 1978; Dueser and Shugart, 1979). It has been reported as rare in eastern Canada (Morris, 1955) and absent in Maine softwoods (Richens, 1974). In our study, *B. brevicauda* occurred in both softwood types at approximately half its abundance in either hardwood type. Most hardwoods may be preferred habitats within its distribution (Banfield, 1974; Getz, 1961).

Blarina brevicauda is known to select areas with fallen logs, slash, rock and other debris (McKeever, 1952; see Kirkland, 1978); forest type may be important only as a modifier of microclimate (Lovejoy, 1970). In southeastern Michigan, *Blarina* occurred only in those habitats in which burrow air was always saturated with water vapor (Pruitt, 1959). Hamilton (1943) noted *B. brevicauda* to be most abundant in habitats with heavy leaf mold; this substrate is more prevalent in hardwoods than in conifer stands (Kirkland and Griffin, 1974). Perhaps humidity was higher in the hardwoods as a result of their denser understory and ground cover.

Sorex cinereus is the most widely distributed shrew in North America, occupying all moist woodlands within its range (Brown, 1967). Logs, stumps, and ground covers that help to maintain humidity are associated with this shrew (Getz, 1961). Microhabitat characteristics that increase soil moisture are probably key components in habitat occupancy by *S. cinereus*.

Sorex fumeus, likewise, occurs primarily in shady damp woods, typically of a northern hardwood type (Banfield, 1974). Seldom found in dry woodlands (Hamilton and Whitaker, 1979), it requires deep, loose leaf litter (Burt, 1957); nests are located in or under rotted logs or stumps (Godin, 1977). We found that *S. fumeus* used hardwood poletimber stands preferentially. However, none of the other species that favor moist sites displayed an affinity for poletimber stands. *Sorex fumeus* is generally considered to be uncommon (Richens, 1974), but in this study it was as common as *S. cinereus* and *C. gapperi*.

Sorex hoyi, generally considered to be rare or very rare, showed no affinity for a particular cover type or size-class. The 34 captures in this study (all taken in pit-fall traps; specimens deposited in Museum of Zoology, University of Massachusetts, Amherst) represent an important sample and render the results for this species noteworthy. In his extensive review of the genus, Long (1972) examined 250 specimens, the majority of those available; his own work yielded 29 more. The results of our work suggest that *S. hoyi* is perhaps more common than is generally believed. *Sorex hoyi* is reported to occur in many habitats: grassy openings in coniferous forest (Godin, 1977), marsh/forest interface (Prince, 1941; Spencer and Pettus, 1966), boreal forest, beech–maple woodlands, and highly disturbed sites — sandy blowouts, cut-over forests, flooded areas, and even cultivated areas (Wrigley et al., 1979). Such a range of habitats suggests commonness rather than rarity. Many studies use snap traps, to which *S. hoyi* may react negatively or which may be too large to take this shrew consistently.

Clethrionomys gapperi prefers cool, moist forest conditions, coniferous, mixed, or deciduous (Miller and Getz, 1972; Banfield, 1974; Godin, 1977; Hamilton and Whitaker, 1979). Rotting logs and stumps, exposed roots and loose litter are associated with high abundance of this vole (Gunderson, 1959). Water, either free or contained in succulent plants, is apparently a key habitat requirement (Getz, 1968). *Clethrionomys gapperi* showed no differential abundance among habitat types in our study; adequate water was probably available in all. *Clethrionomys gapperi* was more abundant in younger (seedling and sapling) than in older stands of northern hardwoods in West Virginia (Healy and Brooks, 1988).

Peromyscus maniculatus is known to have broad ecological tolerances across its enormous range (Hamilton and Whitaker, 1979). This species is less abundant in seedling than in older stands of northern hardwoods in West Virginia (Healy and Brooks, 1988). The subspecies reported on here, *P.m. gracilis*, primarily utilizes coniferous or northern hardwood types; the reasons for its marked abundance in softwood poletimber in this study are not clear. *Peromyscus leucopus* was not encountered in this study; the difference in occurrence among habitats shown by *P. maniculatus* was not the result of competition from a congener. Competition between *P. maniculatus* and *P. leucopus* can limit the habitat distribution of either (Baker, 1968); dominance between *P.l. noveboracensis* and *P.m. nubiterrae* is site specific, not species specific (Wolff et al., 1983). The greater use of softwood stands in this study is typical for northern New England (Godin, 1977), although not necessarily for other parts of its range.

Napaeozapus insignis inhabits spruce–fir and hardwood–hemlock stands in North America. Its range coincides with the combined ranges of eastern hemlock and balsam fir (except in the boreal forest–tundra ecotone) (Whitaker and Wrigley, 1972), although Brower and Cade (1966) found no preference for any particular species of woody plant cover. *Napaeozapus insignis* has been reported both to prefer waterside habitats (Preble, 1956; Brower and Cade, 1966; Banfield, 1974) and to show no preference for habitat near water (Whitaker, 1963). This species' habitat distribution is either poorly understood or it shows great geographic variation. Shrubs and woody ground cover also have been associated with *N. insignis* (Whitaker, 1963); Lovejoy (1973) reported highest captures at sites with these characteristics and high levels of invertebrate food. He also noted a preference for fallen logs, slash, and other cover. Results of the present study show a greater abundance in deciduous cover than previously reported. Greater densities of shrubs and ground cover in deciduous stands are probably important characteristics favoring *N. insignis*, but do not account for greater use of young northern hardwoods and mature red maple stands.

GROUPED SPECIES

The greater abundance of the seven species as a group and of the four shrew species in deciduous cover types may be related to moisture. Although no reports are available that evaluated the preferences of small mammals as a group between hardwoods and softwoods, studies reporting on individual species usually include the importance of high humidity or soil moisture. In our study, components such as ground cover that tend to increase moisture were more abundant in hardwood types (Table 5). Microhabitat characteristics such as fallen logs, rocks, and litter depth probably differed among habitats; and the specific features influencing species abundance may vary among habitats. However, Gore (1986) found no relationship between small mammals and microhabitat features within old-growth northern hardwoods in the White Mountains of New Hampshire.

SAMPLING TRENDS AMONG SPECIES AND YEARS

The most notable differences between 1980 and 1981 were the increase in shrews and the decrease in mice. Possible reasons include the following:

(1) an increase in shrew food availability and/or reproduction as a result of climatic influences,

(2) removal of nonshrews in 1980 may have influenced shrew population levels in 1981,

(3) observed differences are normal fluctuations caused by a variety of factors that cannot be evaluated in this 2-year study.

Rainfall during the warm part of the year can be a very important regulator of the general level of metabolism in soil–litter communities, and thus modify the availability of food of animals that feed on invertebrates in soil or litter (Crapo and Coleman, 1972). Precipitation on the study area was greater in 1981 than in 1980. Increases in rainfall may have influenced both insects and other invertebrates that shrews feed upon — Smith et al. (1974) analyzed small mammal population fluctuations in an eastern hardwood forest, and suggested that such may be the case with *B. brevicauda*. Moist conditions would increase this shrew's food base, but this would not explain the declines in non-soricids. In fact, higher moisture would probably also favor *C. gapperi* (Getz, 1961, 1968) and probably *N. insignis*.

Species composition changes caused by removal trapping, the second possibility, may have occurred. Although there is documentation of exclusion or competition between species, e.g. *C. gapperi* and *M. pennsylvanicus* (Morris, 1955; Clough, 1964), *P. maniculatus* and *P. leucopus* (Baker, 1968; Wolff et al., 1983), *C. gapperi* and *P. maniculatus* (Merritt, 1981), *N. insignis* and *C. gapperi* (Brower and Cade, 1966), interspecific displacement between the shrews and rodents studied here has not been reported. Because these two groups differ greatly in diet and ecology, competition for food sources or habitat would seem unlikely.

The third possibility is perhaps most likely, although a 2-year sample is probably insufficient to address small mammal composition and population

TABLE 5

Mean (S.D.) values of stand characteristics of eight stands (two samples per stand), White Mountain National Forest, NH, 1980–1981

	Forest cover type and timber size-class							
	Northern hardwoods		Red maple		Balsam-fir		Spruce-fir	
	Sawtimber	Pole	Sawtimber	Pole	Sawtimber	Pole	Sawtimber	Pole
Trees > 10.0 cm dbh ha^{-1}[a,c]	774.4	663.7	641.6	575.2	1769.0	1283.2	1172.6	1415.9
	(219.0)	(219.1)	(187.7)	(31.2)	(125.2)	(62.6)	(281.6)	(500.6)
Basal area (m^2 ha^{-1})[a,b,c]	17.0	39.2	15.8	26.3	33.4	55.4	37.6	42.0
	(7.2)	(2.2)	(5.9)	(4.1)	(5.4)	(1.2)	(7.4)	(11.7)
Shrubs or saplings ha^{-1}	1273.2	875.3	2896.6	843.5	1448.3	286.4	859.4	1687.0
	(180.0)	(27.5)	(1395.5)	(377.8)	(382.7)	(225.1)	(900.3)	(810.3)
Ground cover (%)[b,c]	47.5	47.5	42.5	60.8	22.5	52.5	25.0	32.5
	(3.5)	(10.6)	(3.5)	(7.1)	(10.6)	(17.7)	(7.1)	(17.7)

[a]Significant cover type effect, ANOVA 3, 8 d.f.; $P<0.01$.
[b]Significant size-class effect, ANOVA 3, 8 d.f.; $P<0.04$.
[c]Significant difference between hardwoods and softwoods, ANOVA 1, 8 d.f.; $P<0.02$. Significant difference between hardwoods and softwoods, ANOVA 1, 8 d.f.; $P<0.02$.

trends. Significant changes in numbers and species composition of small mammals occurred during a 6-year study of upland and hardwood forests in South Carolina (Smith et al., 1974), but causes and effects could not be identified despite the length of the study. Over an 11-year study, Grant (1976) found that peak numbers of *Peromyscus* and *Clethrionomys* did not coincide or exhibit regular recurrence, nor was either related to habitat characteristics. These two species were negatively associated in New York (Kirkland and Griffin, 1974) and were rarely found together in Michigan (Ozoga and Verme, 1968). Grant (1976) believed that part of the reason for these varied results is that some study areas probably contain a greater variety of habitats, i.e. conditions conducive to habitat segregation, and that habitat preferences are likely to be pronounced only at low densities, if at all. Densities probably varied among study areas.

The almost five-fold increase in *S. hoyi* from 1980 ($N=6$) to 1981 ($N=28$) was the most notable change for a species. Because of the paucity of information about this species, population fluctuations are not well documented. One possibility may involve the removal of *S. cinereus*. Both species are small insectivores; and competition for food may occur; Ryan (1986) reported a high degree of dietary overlap between sympatric populations of *S. hoyi* and *S. cinereus* in Michigan. Perhaps *S. cinereus* is dominant over *S. hoyi* because of larger size and greater abundance. Captures of *S. hoyi* in 1981 were relatively high and distributed evenly throughout the trapping period. Removal of *S. cinereus* may have allowed an increase in *S. hoyi* reproduction and/or activity levels.

The large *N. insignis* sample ($N=49$) in early June 1980 (trapping quarter 1) in one habitat type, northern hardwood poletimber, was unique to that quarter and habitat and was probably the result of some peak in intraspecific activity, e.g. breeding. In a 2-year study in northwestern Maine, nearly the entire catch of *N. insignis* was obtained from one trapping period in early July from a single hardwood site. Twice as many jumping mice were captured in the first year than in the second; the capture rate was greatest in the first trapping period (Richens, 1974).

None of the habitats in this study had common boundaries, so movement from one to another could not be evaluated. In Poland, a study of the rodent communities of four biotopes (habitats) which had common borders showed that the conditions for rodents were very similar in alder wood, pine wood, and willow brushwood; it was concluded that a high degree of patchiness may promote enrichment of local rodent faunas in forest ecosystems (Banach, 1987).

MANAGEMENT CONSIDERATIONS

Responses of small mammals to timber harvesting have been reported for northern coniferous forests (Monthey and Soutier, 1985; Clough, 1987) and hardwoods (Lovejoy, 1970; Kirkland, 1977). The major findings of the present study potentially useful to forest managers are that the seven species as a group and the four shrews as a group showed significantly greater abundance in hardwoods. In predominantly coniferous forests, retention of hardwood stands will probably enhance small mammal faunas. This differential habitat use by a complex of six of the seven most common species has not been documented previously. A possible cause is the higher moisture in hardwoods as a result of ground cover/microhabitat conditions, but the sampling of microhabitat variables was insufficient to clarify reasons for habitat use by species or for variation in their abundance among the habitat types.

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