

# Habitat Associations of Bat Species in the White Mountain National Forest

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## ABSTRACT

Very little is known about the forest habitat associations of the nine bat species (*Lasiurus cinereus*, *L. borealis*, *Lasionycteris noctivagans*, *Eptesicus fuscus*, *Pipistrellus subflavus*, *Myotis lucifugus*, *M. septentrionalis*, *M. leibii*, and *M. sodalis*) present in the White Mountain National Forest (WMNF). Timber management is the dominant form of habitat manipulation in the WMNF. Anabat II detectors were used to survey the flight activity of bat species in four age-classes (regeneration, sapling/pole, mature, and commercially overmature) of northern hardwood and spruce/fir forest stands. These vegetative classifications are appropriate to the current management structure of the WMNF. Prototype software was used to objectively identify unknown echolocation sequences in a statistically predictable manner. Non-myotids were identified to species, and myotid species were identified to genus. The results of our survey provide a baseline description of species distribution and bat community structure associated with managed forests in the northeastern United States.

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## INTRODUCTION

A baseline description of the habitat use of bats, treating all species as a composite, exists in the WMNF (Krusic 1995). However, very little is known of the distribution of individual bat species, or community structure associated with forested habitats. There are nine bat species present in the WMNF: *Lasiurus cinereus* (hoary), *L. borealis* (red), *Lasionycteris noctivagans* (silver-haired), *Eptesicus fuscus* (big brown), *Pipistrellus subflavus* (eastern pipistrelle), *Myotis lucifugus* (little brown), *M. septentrionalis* (northern long-eared), *M. leibii* (eastern small-footed), and *M. sodalis* (Indiana) (Krusic 1995; Sasse 1995). The status of four species is of concern in New Hampshire: *M. sodalis* is considered endangered, while *P. subflavus*, *M. septentrionalis*, and *M. leibii* are designated as species of concern (U.S. Forest Service 1986).

The study of species that make up communities leads to an understanding of their interaction within the ecosystem, and provides an insight into the likely consequences of alterations to the system through environ-

mental change or habitat manipulation (Findley 1993). Bats are heterothermic mammals, consequently, gestation and spermatogenesis are highly dependent on temperature (Kunz 1982). It is possible that long-term study of species' community structure may provide an early indication of the effects of any climate change due to global warming. Habitat manipulation in the WMNF is achieved primarily through timber management at the stand level. Consequently, change in forest structure at this scale is the most proximate habitat alteration likely to affect bats.

The purpose of this study was to compare the relative habitat use and community structure of bat species in four different stand age-classes (regeneration, sapling/pole, mature, and commercially overmature) of two forest types in the WMNF. The study investigated only the nocturnal flight activity of bat species during the summer, approximately 25% of the year. Although this is a small proportion of a bat's life cycle in terms of time, it is the only period that bats are dynamic members of the ecosystem (the rest of the time they are roosting or hibernating). It is also when bats forage to acquire energy and nutrients to raise young, and to maintain a positive energy balance for summer and overwinter survival.

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## MATERIALS AND METHODS

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**Study Area** The WMNF, located in north-central New Hampshire and southwestern Maine (Figure 1), encompasses 304 050 ha, of which 139 300 ha (46%) are available for habitat manipulation through timber management (U.S. Forest Service 1986). Nearly 97% of the WMNF is forested, this being representative of the surrounding New England states that average over 80% forest land (DeGraaf et al. 1992). New England forests are unique in their domination by northern hardwood tree species: i.e., *Acer* spp. (maples), *Fagus* spp. (beech), and *Betula alleghaniensis* (silver birch) (Hornbeck and Leak 1992). Weather conditions in the WMNF are highly varied and location-specific due to differences in aspect and elevation (approximately 130–2300 m). The average temperature and rainfall, June to August in Grafton County, New Hampshire (43° 59'N, 71° 41'W) is 17.7°C and 93.2 mm, respectively (Quinlan et al. 1987).

**Habitat Types** Vegetative classification of forested areas was based on stand age-class, as designated by the White Mountain National Forest Management Plan (U.S. Forest Service 1986). Sites representative of four age-classes of both hardwood and softwood forest types were selected; regeneration (0–9 yrs), sapling/pole (10–59-yr hardwood, 10–39-yr softwood), mature (60–119-yr hardwood, 40–89-yr softwood), and overmature (>119-yr hardwood, >89-yr softwood). Softwood stands were predominantly of the spruce/fir forest type (*Picea rubens* (red spruce) and *Abies balsamea* (balsam fir)). Hardwood stands were comprised predominantly of northern hardwood tree species (*Acer* spp., *Fagus* spp., and *Betula alleghaniensis*) and *P. rubens*. In combination, these forest types cover over 60% of the WMNF (U.S. Forest Service 1986). To sample the required range of age-classes, sites were located in both managed and unmanaged areas of the forest.

In the WMNF, softwood regeneration is encouraged by group cutting,

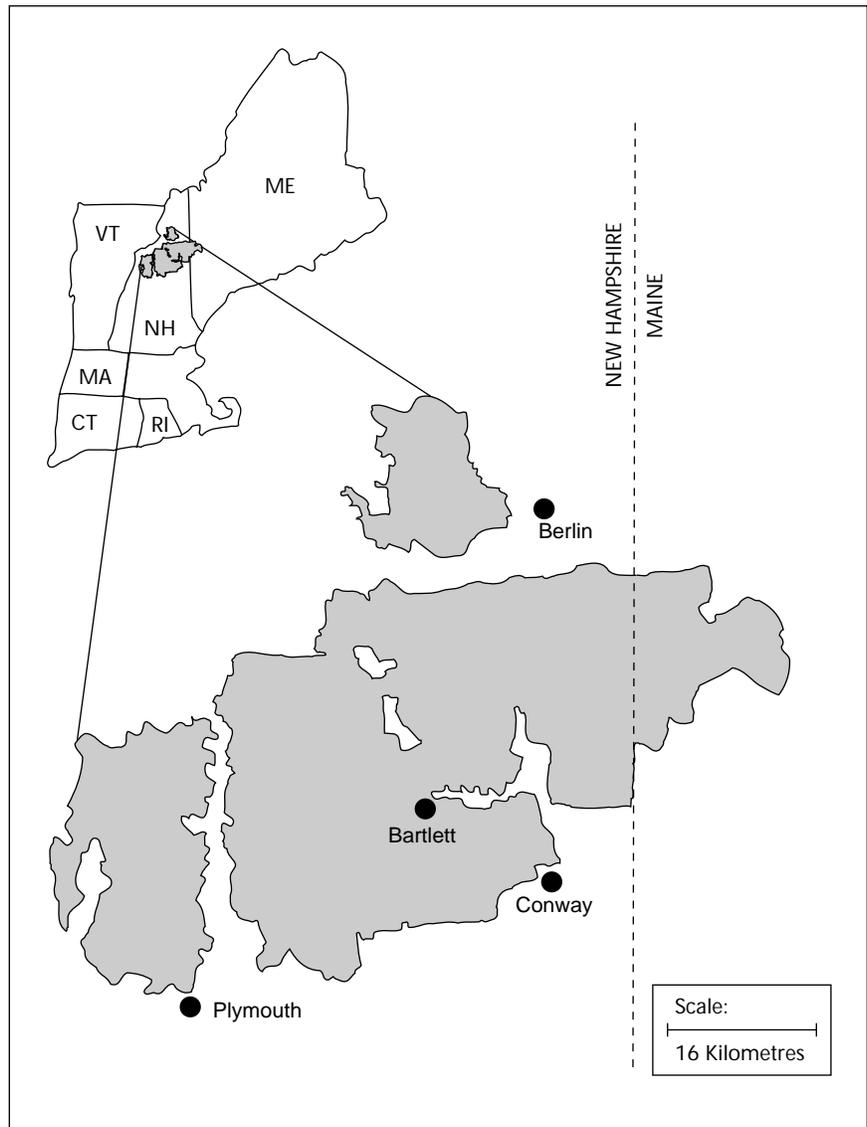


FIGURE 1 Location of study area; the White Mountain National Forest, New Hampshire and Maine.

an uneven-aged management system that creates a series of proximate cuts, 0.1–0.8 ha in area, surrounded by mature forest (U.S. Forest Service 1986). Clearcutting refers to the harvest of almost all trees on an area of at least 1 ha (Hunter 1990). Bat species' activity associated with hardwood regeneration was surveyed in clearcuts (max. 12.1 ha, mean 7.3 ha; U.S. Forest Service 1986). Bat species' activity in stands of softwood regeneration was surveyed in group cuts.

Each forest stand surveyed was selected to include a habitat "feature," identified as a road/trail, moving water, or still water. If no habitat feature was available (6 of 36 sites), contiguous forest was sampled. In combination, a forest stand and the habitat feature at its edge were identified as a sampling "site." Sites were selected from Forest Service inventory maps

and confirmed by field inspection. Sites were located randomly, subject to the logistical limitations of deploying all detectors in one evening.

#### Equipment and Sampling Procedure

We used four broadband Anabat II detectors (Titley Electronics, Australia) to survey the relative activity of foraging and commuting bats associated with selected habitat types. Voice-activated cassette recorders (Panasonic, model RQ-L317) were used to store this information on magnetic tape, allowing multiple systems to be operated simultaneously. Each detector system was placed in a weatherproof housing.

Prior to this study, the detection volume of Anabat units was estimated and standardized using an ultrasonic pet flea collar (Krusic 1995). Based on these estimates, detectors deployed at the forest edge and forest interior of each site were spaced over 50 m apart to ensure independent sampling. Surveys were conducted on nights that were subjectively determined to have low wind speeds and minimal precipitation and conditions that ensured a minimum of background noise on tape. Sites were sampled from approximately 30 minutes before sunset until 30 minutes after sunrise; recording systems remained active throughout the night.

On each survey night, four sites were sampled, either at the habitat feature or within the forest. Each site was of the same forest type, but differing age-class. This allowed direct comparison of species' habitat use among age-classes of the same forest type, independent of nightly variations resulting from weather conditions and/or insect abundance. Sites sampled on a single night were designated as a sampling "group." Five groups were established in hardwood forest and four in softwood. Throughout June to August 1994, each group was sampled once at the habitat feature, and three times in the forest interior.

#### Species Identification

Prototype computer software was developed to identify bat species' echolocation calls in an objective and statistically predictable manner. The software analyzed broadband detector output, and automatically classified bat calls based on a multivariate discriminant function derived from characteristics of positively identified calls. Six parameters were used to describe search-phase echolocation structure: call duration, characteristic frequency (i.e., frequency of minimum slope), maximum frequency, minimum frequency, average frequency, and time between calls. Identifications were made at the resolution of a pass, defined as a sequence of more than 2 echolocation calls (Thomas 1988) recorded as a bat flew through the air-space sampled by the Anabat detector. During software validation, composite analysis of passes correctly classified the five non-myotid species (*E. fuscus*, *L. borealis*, *L. cinereus*, *L. noctivagans*, and *P. subflavus*) with 100% accuracy. Identification accuracy of Myotid species ranged from 42% (*M. leibii*) to 85% (*M. septentrionalis*). Consequently, *Myotis* species were identified to genus only, resulting in pass classifications of 97% accuracy. The software classified a pass as "unknown" if any of the six parameters were more than two standard deviations from the mean values for all species. Data are presented as measurements of species activity, calculated as the number of passes/detector/night.

#### Data Analysis

The GLM (General Linear Model) module of Systat for Windows (v. 5.0, Wilkinson et al. 1992) was used for ANOVA, MANOVA, mean separations (Tukey's test) and simple linear correlations. Counts of bat echolocation

passes were square-root-transformed before analysis to correct for non-homogeneous variance (Zar 1984). Back-transformed least squares means are reported and used to plot all figures. Chi-square test of homogeneity (Zar 1984) was used on original counts to test for differences in bat community structure between habitat types.

## RESULTS

### Distribution of Bat Species

A total of 4479 echolocation passes were recorded. Abundance of pass identifications, independent of recording location, were in the order of: *Myotis* species (n = 1852) > *L. borealis* (n = 761) > *E. fuscus* (n = 652) > *P. subflavus* (n = 584) > unknown (382) > *L. noctivagans* (n = 138) > *L. cinereus* (n = 110).

**Habitat features** There was a significant difference between the distribution of all species groupings at the forest edge (habitat feature) and forest interior ( $p < 0.001$ ,  $df = 22$ ). All species were identified most commonly at habitat features (Figure 2). The distributions of *E. fuscus* ( $p = 0.02$ ,  $df = 3$ ,  $\bar{X} = 6.79$  passes/detector/night), *L. borealis* ( $p < 0.001$ ,  $df = 3$ ,  $\bar{X} = 9.59$  passes/detector/night), *P. subflavus* ( $p < 0.001$ ,  $df = 3$ ,  $\bar{X} = 6.30$  passes/detector/night), and *Myotis* species ( $p = 0.02$ ,  $df = 3$ ,  $\bar{X} = 21.44$  passes/detector/night) were significantly different among habitat feature types (Figure 3). The activity of each species group was greatest over still water.

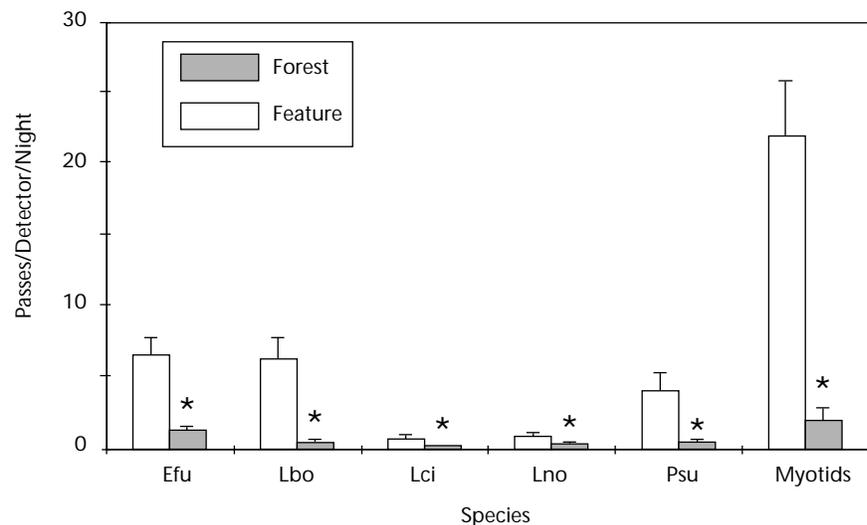


FIGURE 2 Relative bat species activity (LS mean plus one standard error) at the forest edge (habitat feature) and forest interior, White Mountain National Forest, 1994. Efu *Eptesicus fuscus*; Lbo *Lasiurus borealis*; Lci *Lasiurus cinereus*; Lno *Lasionycteris noctivagans*; Psu *Pipistrellus subflavus*; Myotids species of the genus *Myotis* (*M. lucifugus*, *M. septentrionalis*, *M. leibii*, and *M. sodalis*). \* (in all figures) represents a significant difference ( $P \leq 0.05$ ) between sampling sites for the species indicated.

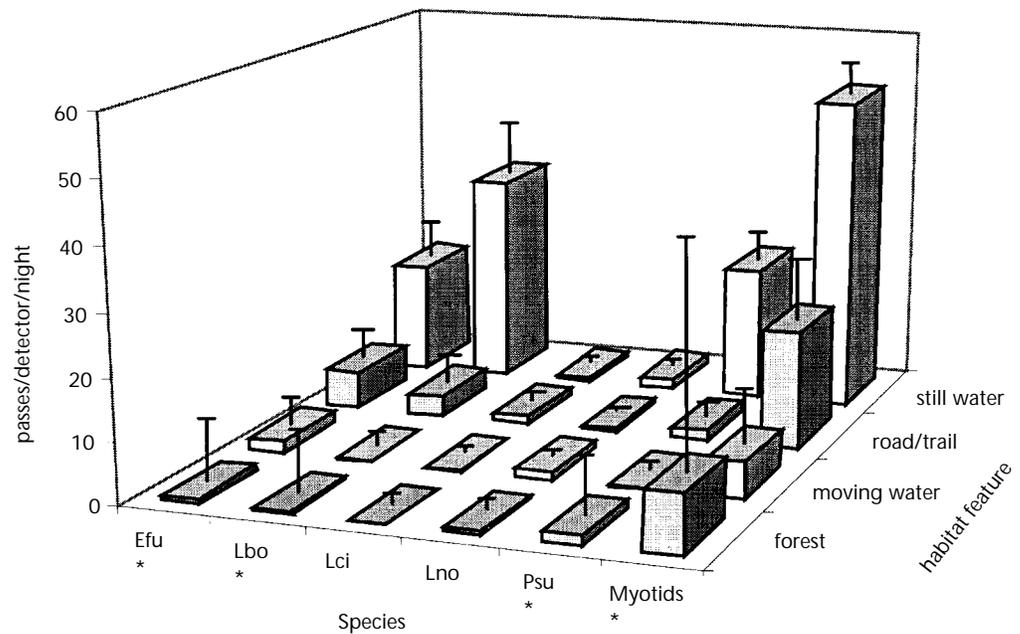


FIGURE 3 Relative bat species activity (LS mean plus one standard error) among habitat features identified in the White Mountain National Forest, 1994.

In contrast, activity of *L. borealis*, *P. subflavus*, and *Myotis* species was lowest over moving water, and that of *E. fuscus*, *L. cinereus*, and *L. noctivagans* lowest in contiguous forest.

**Forest-interior** There was no difference in the activity of *E. fuscus* ( $p = 0.17$ ,  $df = 1$ ), *L. borealis* ( $p = 0.14$ ,  $df = 1$ ), *P. subflavus* ( $p = 0.77$ ,  $df = 1$ ), or *Myotis* species ( $p = 0.23$ ,  $df = 1$ ) between hardwood and softwood forests. In contrast, *L. cinereus* ( $\bar{X} = 0.34$  passes/detector/night in hardwood,  $\bar{X} = 0.07$  in softwood) and *L. noctivagans* ( $\bar{X} = 0.65$  passes/detector/night in hardwood,  $\bar{X} = 0.17$  in softwood) used hardwood more than softwood forest ( $p < 0.02$ ,  $df = 1$ ). Within the hardwood forest type, *L. borealis* ( $p < 0.001$ ,  $df = 3$ ), *P. subflavus* ( $p < 0.001$ ,  $df = 3$ ), and *Myotis* species ( $p < 0.000$ ,  $df = 3$ ), were differentially distributed among age-classes (Figure 4). These same species were distributed unevenly among different age-classes of the softwood forest type, as was *E. fuscus* ( $p < 0.002$ ,  $df = 3$ , Figure 5).

Within both forest types, all species were found most commonly in areas of regeneration (Figures 4 and 5). Within the regeneration age-class, *L. borealis* ( $\bar{X} = 4.00$  passes/detector/night), *E. fuscus* ( $\bar{X} = 2.47$ ), *L. noctivagans* ( $\bar{X} = 0.92$ ), and *L. cinereus* ( $\bar{X} = 0.72$ ) were recorded most frequently in clearcuts (hardwood regeneration), while *Myotis* species ( $\bar{X} = 12.00$  passes/detector/night) and *P. subflavus* ( $\bar{X} = 6.30$ ) were most abundant in group cuts (softwood regeneration).

#### Community Structure

**Habitat features** Species richness was equal among habitat features, in that all species were recorded at each feature type (Figure 3). Community

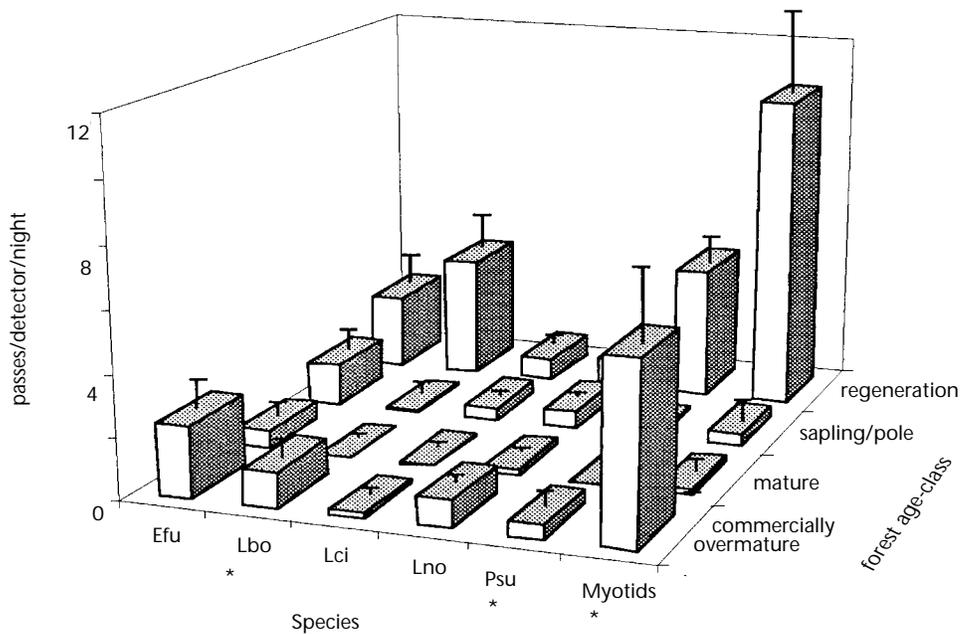


FIGURE 4 Relative bat species activity (LS mean plus one standard error) among four stand age-classes of the hardwood forest type, White Mountain National Forest, 1994.

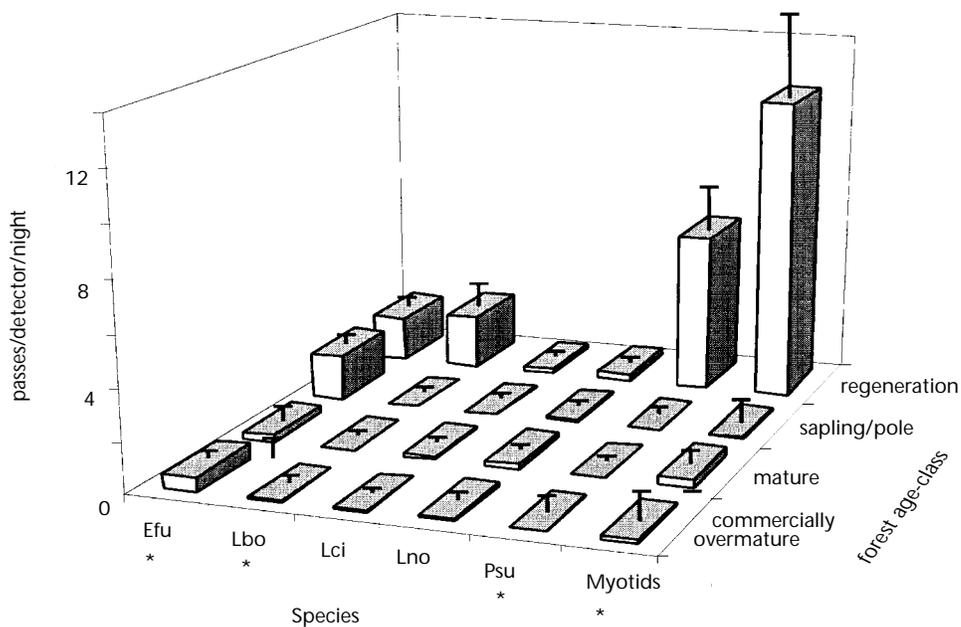


FIGURE 5 Relative bat species activity (LS mean plus one standard error) among four stand age-classes of the softwood forest type, White Mountain National Forest, 1994.

structure, or species assemblage (i.e., a composite evaluation of species richness and relative activity of each species), was unequal among habitat features ( $p < 0.001$ ,  $df = 15$ ). Pairwise comparison indicated similarity in species assemblage at moving water and forest habitats ( $p = 0.32$ ,  $df = 5$ ), and at road/trail and moving water habitats ( $p = 0.10$ ,  $df = 5$ ). All other pairwise comparisons resulted in significant differences in community structure between habitat feature types ( $p < 0.001$ ,  $df = 5$ , Table 1). Still water was the habitat feature where the greatest activity of each species was recorded (Figure 3).

**Forest-interior** In hardwood forest, all species were recorded in each age-class except mature, where *P. subflavus* was absent (Figure 4). Pairwise comparisons of community structure indicated differences among all age-classes ( $p \leq 0.001$ ,  $df = 5$ , Table 2). Most frequent activity was recorded in areas of regenerating hardwood ( $\bar{X} = 5.6$  passes/detector/night, Figure 4).

TABLE 1 Pairwise comparisons, using chi-square test of homogeneity, of species' community structure among habitat features (White Mountain National Forest, 1994).

	Moving water		Still water		Road/trail	
	$X^2$	$P$	$X^2$	$P$	$X^2$	$P$
Forest	5.4	0.321	73	<0.001	24.9	<0.001
Moving water			43.1	<0.001	0.4	0.095
Still water					223.6	<0.001

TABLE 2 Pairwise comparisons, using chi-square test of homogeneity, of species' community structure among different stand age-classes of the hardwood forest type (White Mountain National Forest, 1994).

	Sapling/pole		Mature		Overmature	
	$X^2$	$P$	$X^2$	$P$	$X^2$	$P$
Regeneration	160	<0.001	83	<0.001	57	<0.001
Sapling/pole			162	<0.001	137	<0.001
Mature					57	<0.001

TABLE 3 Pairwise comparisons, using chi-square test of homogeneity, of species' community structure among different stand age-classes of the softwood forest type (White Mountain National Forest, 1994).

	Sapling/pole		Mature		Overmature	
	$X^2$	$P$	$X^2$	$P$	$X^2$	$P$
Regeneration	193	<0.001	93	<0.001	77	<0.001
Sapling/pole			192	<0.001	178	<0.001
Mature					192	<0.001

In softwood forest, all species groups were present in regeneration and commercially overmature areas, but *P. subflavus* was not recorded in the sapling/pole or mature age-class (Figure 4). Pairwise comparisons indicated differences between the community structure of all age-classes ( $p \leq 0.001$ ,  $df = 5$ , Table 3). Most frequent activity was recorded in areas of regenerating softwood ( $\bar{X} = 5.1$  passes/detector/night, Figure 5).

## DISCUSSION

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### Species Distribution

Factors that may influence the presence, abundance, and activity of a bat species in a habitat include the physical structure of the habitat, microclimate, availability of prey and water, proximity to roost sites, exposure to predators, and competition. The relationship between species and the physical structure of habitat has been investigated by a number of authors (e.g., Findley and Wilson 1982; Norberg and Rayner 1987; Fenton 1990; Saunders and Barclay 1992). Much of this work has been reviewed and summarized by Fenton (1990). The ability of a bat species to use a structural habitat type may depend on its mechanical and perceptual adaptations (Fenton 1990). Manoeuvrability, speed, and endurance of a species is determined by wing morphology—specifically, wing loading and aspect ratio (Norberg and Rayner 1987). In general, bats with low wing loading and low aspect are manoeuvrable, and predictably well adapted for avoiding obstacles in close-forested environments. Bats adapted for open-area foraging, where speed and endurance is an advantage and manoeuvrability is less critical, tend to have higher aspect ratios and wing loading (Norberg and Rayner 1987). Perception of prey and obstacles and the ability to distinguish between the two are dependent upon the echolocation characteristics of the species (Fenton 1990). In general, bats with short, high-frequency FM call structures and short interpulse intervals are better adapted for foraging in forested habitat, whereas those with long, lower-frequency CF calls and long interpulse intervals are adapted for open areas. Fenton (1990) notes that bat species adapted for foraging in open areas are not able to forage effectively in edge or closed habitats. Bats adapted to exploit edge habitat are capable of foraging in open habitat, but not in closed forest habitat; and bats adapted for closed habitats can also forage along edges or in open areas.

Regardless of morphological characteristics, some bats may be absent from a habitat because of physiological limitations due to microclimate. New England represents the northern limit of several species in our study. Consequently, these species may be at physiological and/or competitive disadvantage in the mountain habitats of the WMNF. Cool microclimate may limit the local distribution of species with populations that extend much further north. For example, Barclay (1991) suggested that the absence of female *Myotis lucifugus* from Rocky Mountain regions with low ambient temperatures was due to relatively high energy requirements of these bats during maternity periods. A similar pattern of predominantly male *M. lucifugus* during early summer months was found during mist netting in the WMNF (Krusic 1995).

On a landscape scale, the WMNF is primarily forested habitat. As a result, we would not expect open-area species to be the predominant bat species in our study area. *Lasiurus cinereus* and *Lasionycteris noctivagans* are both migratory bats (van Zyll de Jong 1985). The wing morphology required for long-distance flight is high aspect ratio and high wing loading; the same characteristics that favour open-area foraging (Findley and Wilson 1982). Based on our own recordings and information in the literature (Fenton and Bell 1981; Barclay 1986), search-phase calls for *L. cinereus* are low-frequency (18 kHz), long (10 ms) CF calls with a long interpulse interval (300 ms). *Lasionycteris noctivagans* calls have an initial FM component with a long (9 ms), low-frequency (25 kHz) CF tail and a moderately long (167 ms) interpulse interval (Barclay 1986; Fenton 1990; Krusic 1995). Thus, both species appear well adapted for foraging in open areas, a habitat that was limited in our study area. Although overall activity of both species was low, they were detected most frequently in hardwood clearcuts—the largest open areas of the habitats we surveyed. Both species were also recorded in sapling/pole sites, but it is likely that they were foraging or commuting above the canopy.

*Pipistrellus subflavus* was nearly absent from all forest age-classes except clearcut and group-cut clearings, where it was relatively abundant. The only habitat feature used frequently by *P. subflavus* was open water. This pattern suggests that it may be adapted for foraging in small, open areas or along edges. These observations are supported by the call structure of *P. subflavus*, which is typical of an open-area forager. The call has two strong harmonics with an initial FM component and an extended CF tail, the CF part of the first harmonic is at about 20 kHz, the second harmonic is at about 40 kHz, the duration of the call is 7.8 ms and the interpulse interval is 189 ms (MacDonald et al. 1994; Krusic 1995). Although its echolocation characteristics may preclude the species from using forest habitats, it appears that its flight characteristics allow enough manoeuvrability to negotiate even small openings. While New Hampshire is close to the northern extreme of the range of *P. subflavus*, its relative abundance in forest openings and over ponds suggests that climate and energy demand do not exclude the species from the WMNF. *Pipistrellus subflavus* is the only species that was totally absent in recording from mature age-class stands of either forest type, and from softwood sapling/pole stands. Thus, this species appears to be most selective of the type of habitat that it uses.

The distribution of *Lasiurus borealis* among the forest types, age-classes, and features of our study area was quite similar to that of *P. subflavus*. Red bats were very active over still water, in softwood group cuts, and hardwood clearcuts. Unlike *P. subflavus*, there was significantly more *L. borealis* activity in overmature hardwood than in mature or sapling/pole areas. This relatively open, deciduous forest may provide roost sites for the species. Fenton (1990) classifies *L. borealis* as a “long-range” bat that targets prey from relatively large distances. This is consistent with a species that feeds in more open areas rather than cluttered forests. The echolocation calls of *L. borealis* are higher frequency (39 kHz) than other open-area species in our region, and the interpulse interval is intermediate (110 ms) (Krusic 1995). The call structure has an initial FM component with a CF tail. Call length is 8.2 ms. Our own recordings have shown the

call structure of *L. borealis* to be variable in shape, frequency, and duration of the CF component (Krusic 1995). This plasticity may allow *L. borealis* to feed efficiently in open areas, and also manoeuvre through open forest to avoid predators or to find roost sites.

The relatively high activity of *E. fuscus*, and its presence in all surveyed habitat types, indicate it to be a generalist species in our study area. It was recorded with nearly equal activity in all hardwood forest age-classes except mature forest. In softwood it was most active in the openings of group cuts and sapling/pole habitats. It used roads and trails and still water, but activity was relatively low over streams. Wing loading and aspect ratio of *E. fuscus* is intermediate (Fenton 1990) in relation to other species. Fenton and Bell (1981) illustrate the call structure of *E. fuscus* with an initial FM component and a CF tail at 28 kHz with a duration of about 7 ms. Our own recordings indicate that *E. fuscus* calls become shorter (5.5 ms) and lose their CF tail when foraging along trails and roads in forested areas (Krusic 1995). Perhaps the intermediate wing morphology and the flexibility in echolocation allows *E. fuscus* to exploit a larger range of habitat types and successfully capture a wider variety of prey.

Activity of *Myotis* species was recorded most frequently throughout the forest. Although this group was identified to genus only, it is likely that the majority of echolocation passes were produced by *M. lucifugus*. Previous mist-netting in the study area indicated a predominance of this species (75% of individuals trapped). The second most common myotid, *M. septentrionalis*, represented only 0.07% of all bats netted. Only single individuals of *M. leibii* and *M. sodalis* were captured (Krusic 1995). Additionally, the echolocation calls of *M. septentrionalis* have a low intensity, making this species largely undetectable using the Anabat system. Despite differences in bat activity indicated by mist-netting and detector surveys (Kunz and Brock 1975), it is likely that very few of the *Myotis* echolocation passes were emitted by species other than *M. lucifugus*. Myotids have very low wing loading and wing aspect ratio, and predictably, are very manoeuvrable (Barclay 1991). The call structures of all myotids in our area are very similar. All are high-frequency (46–55 kHz) FM calls of short duration (2–4 ms) with short interpulse intervals (66–80 ms) (Fenton and Bell 1981; Krusic 1995). On the basis of wing morphology and call structure, *M. lucifugus* appears to be well adapted for foraging in close forest habitats, yet this is unlikely to preclude them from also foraging in open areas (Fenton 1990). The results of our study are consistent with this prediction. *Myotis* spp. were the most common bats at all habitat features and in nearly all age-classes of both forest types.

#### Community Structure

The community structure of bats within a given habitat depends upon resource availability, the amount of overlap in resource requirements and competitive relationships among the species. If, as Fenton (1990) suggests, physical habitat structure excludes some species from closed forest, we would expect the greatest species diversity in open habitats. Overall, this prediction is supported by our results. Forest openings, resulting from cutting, had most frequent activity of the greatest number of species. Larger openings, such as clearcuts and ponds, had greater activity of all species than did smaller openings, such as group cuts or trails and streams. The high activity of species over still water may result not only

from the presence of an opening, but from the availability of water, and perhaps an abundance of insect prey.

Frequent activity of bat species in areas of recent timber harvest contrasts other studies of bat habitat use in forested areas (e.g. Thomas 1988; Carey 1989; Perkins and Peterson 1993 in the western United States; and Dennis and Brazil 1995 in Newfoundland). These studies indicate species' preference for older forest age-classes, and in some cases, avoidance of clearcuts. It is possible that the small size of timber harvests in the WMNF (mean 7.3 ha, maximum 12.1 ha) encourages the presence of bat species due to a proportionally high amount of edge per unit area and associated high insect densities (Rydell 1989). Additionally, the age of commercially overmature stands in our study area (>89-yr softwood, >119-yr hardwood) is approximately equal to the age of mature stands (approximately 100 yrs) in Douglas-fir forests of the United States where bat activity has consistently been found to be low (e.g., Thomas 1988; Carey 1989). Within unharvested forested habitat in our study area, greatest activity was recorded in overmature hardwood stands. A recent study of *Myotis septentrionalis* in the WMNF suggests that overmature hardwood stands provide important roosting habitat for bats (Sasse 1995).

Concentration of activity of each species group at the forest edge (Figure 2) may also indicate the importance of linear landscape elements to foraging bats, possibly for commuting and navigation across the landscape (Limpens et al. 1989). In contrast to Limpens' study, where linear habitat features protrude from the surrounding agricultural landscape, such features are often set within a predominantly forested landscape in the northeastern United States. As a result, they are likely to provide relatively uncluttered commuting "highways" and foraging areas.

Forest management implications from this study are that forest openings, water sources, linear elements, such as trails and forest roads, and overmature hardwood forest stands may provide the mosaic of habitats that encourage bat use and diversity. In contrast, closed forested areas, especially softwood stands and younger hardwood stands, are not heavily used by foraging bats.

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