SECTION IV FORAGING

Surveying Forest-Bat Communities with Anabat Detectors

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ABSTRACT

Surveying bat populations and activity with ultrasonic bat detectors is a widespread practice in microchiropteran field research. We conducted tests on two aspects of bat detector use: vertical deployment of detectors and identification of species by call. The number of bat calls recorded from simultaneous bat detector surveys, conducted at tree canopy-level and at ground-level with Anabat II detectors, were compared. Ground-level surveys sampled significantly more bat calls than canopy-level surveys at a forest-interior site, but there was no difference between levels at a pond-edge site. The mean number of calls obtained from the forest-interior and pond-side sites were not different. This counter-intuitive result may be a function of small sample size. Vocalizations from captive individuals of seven different bat species were recorded with the Anabat II detector system and analyzed with the Anabat V computerized sonagraph. Although Nested Random Effects ANOVA of bat calls exhibited significant interspecific variation, Discriminant Function Analysis was unable to adequately distinguish between the calls of most species in this study. Discrimination between the calls of different species was confounded by variation in call characteristics among individuals and among the vocalizations of individuals. These results may apply only to calls of captive individuals from populations inhabiting our research area. However, if the intra-individual variation we observed is characteristic of the vocalizations of free-flying bats of most species, identification of bats by call is a questionable research method.

INTRODUCTION

The use of ultrasonic sound detectors, or "bat detectors," as a means of surveying bat activity and populations has attained widespread use in microchiropteran field studies (Kunz and Brock 1975; Fenton and Bell 1981; Thomas and West 1988). The Anabat II Detector[1] is a relatively new,

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[1] Produced and marketed by Titley Electronics Pty. Ltd., P.O. Box 19, Ballina, N.S.W. 2478, Australia.

broad-band bat detector that has the advantage of being readily set-up for automated sampling (Hayes and Hounihan 1994). Prior to a planned deployment of Anabat II detectors in a study of bat-habitat relationships in the southeastern U.S., we conducted preliminary tests on two factors that could considerably influence the results of ultrasonic surveys of bat abundance and diversity.

First, we were concerned that there might be differences in sampling results between detectors deployed at the canopy-level and those deployed at ground-level, and that such differences might vary across habitat types. Thomas and West (1989) suggested that sampling at both levels whenever possible is a sound practice, but offered no empirical data to support that reasoning. Because we perceived that there is a scarcity of quantitative data about bat detector deployment, nor any information concerning their use in forests of the southeastern U.S., we tested the hypothesis that detectors deployed on the ground and in the tree canopy would provide similar results.

Second, because the nocturnal nature of bats often makes visual identification of species rather difficult, the use of ultrasonic bat detectors to discriminate between species on the basis of calls is an enticing concept (Fenton and Bell 1981; Fenton et al. 1983; Fullard 1989). Anabat V software[2] uses bat calls recorded with the Anabat II detector to generate a computerized sonagraph, making call analysis a much less burdensome prospect. Combined with the ease of automation, the Anabat V software makes the Anabat II system an attractive option for field biologists. There has, however, been some discussion regarding inconsistencies and unreliability in species identification with bat detectors in general (Thomas et al. 1987). Specific discussions, particularly those in the electronic medium (notably Batline), about species identification with Anabat II detectors have argued both for and against its reliability in this task. Testing the utility of Anabat II detectors as a tool for species identification was an obvious initial step in our research.

METHODS AND MATERIALS

Level of Detector Deployment Comparison

Two Anabat II detectors were employed in this study. One was assigned to canopy surveys and the other to ground surveys. Both Anabat II detectors were connected to CTR-76 Radio Shack cassette tape recorders. Only one Anabat II delay switch was available, which was used in canopy surveys. The Anabat II detector and other equipment used for canopy surveys were nested in a 20 cm × 18 cm × 10 cm plastic container with a hole cut in one side to accommodate the protruding Anabat II microphone. This package was then secured in a 23 cm × 20 cm × 15 cm open-faced box made of ~0.30-cm-thick welded aluminum, with the microphone protruding through the plane of the open box-face. The Anabat II detector and cassette player used for ground surveys were not placed in any container.

2 Ibid.

Two survey sites were chosen in close proximity to pond L009 in the Palustris Experimental Forest of the Evangeline Ranger District, Kisatchie National Forest, Louisiana, U.S.A. Each survey site was a tree that offered an adequately uncluttered branch at between 10 m and 13 m above ground-level. One site was located in the forest interior at least 20 m from the nearest edge, while the other site was located at the edge of the L009 pond. Both sites were located in a mixed stand (i.e., *Pinus palustris* (long-leaf pine), *P. taeda* (loblolly pine), *Celtis laevigata* (hackberry), and *Quercus marilandica* (blackjack oak)) and were separated by ~300m. Conifers dominate the canopy.

Sampling began 25 July 1995 and continued as opportunity to visit the survey area allowed through 15 October 1995. Surveys were initiated anywhere from one-half hour before to an hour and forty-five minutes after official sunset. Only one ultrasonic survey was conducted per night, except for a few occasions when both sites were surveyed in random order. Sampling was not carried out during rainfall, except on 13 October 1995, when a very light, intermittent drizzle fell throughout the survey period. Temperatures during surveys varied from ~18°C to ~30°C, winds were light, and humidity was generally high.

For each survey, the canopy-level detector equipment was hoisted with a rope 10+ m into the canopy, while the ground-level detector was placed directly below it. Detectors were deployed in the same spot for each survey. The ground-level detector in the forest-interior was propped at about a 30° angle, while the pond-side ground-level detector, which was placed about 90 cm up the side of an earthen dike, was propped at about 10°. The pond-side detectors were always pointed towards the pond, while the forest-interior detectors were haphazardly oriented depending on which direction the canopy-level detector was pointing after being hoisted into the canopy. Both detectors were set to sensitivities of 3 to avoid interfering noises from frogs and insects. Ground-level and canopy-level surveys were conducted simultaneously for 45-minute periods.

Vocalizations recorded during these surveys were classified as calls if they met the criteria of having two sequential signals of varying frequency, separated by no more than one second. This classification is subjectively based on what we recognized as a bat call from previous experience with the equipment. The one-second delineation for division of vocalizations into calls is an artifact of the Anabat II Delay Switch, which ends recordings one second after the last signal is detected.

The number of calls recorded at each level was tallied for each survey, and a difference between ground-level and canopy-level was calculated. The mean difference between canopy and ground was not normally distributed, and was tested for departure from zero using a Wilcoxon Signed Rank Test for paired data. The number of calls recorded at each level was compared between sites using a Wilcoxon-Mann-Whitney Test for unpaired data.

Analysis of Species Discrimination

Seven species of bats were mist-netted over various waterways in the Evangeline, Vernon, and Kisatchie ranger districts of the Kisatchie National Forest during the spring, summer, and fall of 1995. These seven species were: *Lasiurus borealis* (red bat), *L. seminolus* (seminole bat), *Nycticeius humeralis* (evening bat), *Pipistrellus subflavus* (eastern

pipistrelle), *Eptesicus fuscus* (big brown bat), *Myotis austroriparious* (southeastern Myotis), and *Corynorhinus rafinesquii* (Rafinesque's big-eared bat). Calls from these individuals were recorded using an Anabat II detector, a CTR-76 or CTR-96 Radio Shack cassette tape recorder, and, at times, the Anabat II delay switch. With the exception of some *C. rafines-quii* at a roost site, bats were recorded while they were being held in a wire (2.5 cm × 2.5 cm mesh) cage or flying free in a 4 m × 4 m × 3.5 m screen tent.

Calls were down-loaded through the Anabat V Zero Crossing Analysis Interface Module (z-CAIM) onto a 386 computer for analysis with the Anabat V sonagraph. Recordings from four individuals were randomly chosen for each species, except *M. austroriparious* (only three individuals were available) and *C. rafinesquii* (calls recorded at the roost site could not be assigned to specific individuals). Three calls from each individual were randomly selected, as well as 15 pulses from each call.

Each randomly selected pulse was measured for five characteristics: maximum frequency, midpoint frequency, minimum frequency, slope, and duration. Midpoint frequency of pulses was calculated as the frequency at the midpoint of vocalization. Slope was calculated as the difference between the maximum and minimum frequencies, divided by the duration. These characteristics were chosen for analysis because they were readily obtained or calculated from the Anabat V read-out. We used midpoint frequency rather than the average frequency calculated by the Anabat V program, because these average frequency values seemed at times nonsensical, especially for frequency-modulated calls without any flat areas. In addition to treating pulses as individual observations, we also took means for all five measurements of a call's pulses and used these to characterize the call. We analyzed calls this way in an attempt to reduce the effect of variation in pulse characteristics and improve species identification.

The call and pulse measurements for all species, except *C. rafinesquii*, were subjected to Nested Random Effects ANOVA. *C. rafinesquii* was left out of this analysis, because most of the calls for this species were taken from a roost site and could not be assigned to individual bats. The Nested Random Effects procedure partitions the variation in a call and pulse measurements among possible sources of differentiation, such as differences between species and differences between individuals. This analysis identifies those characteristics with a high percentage of interspecific variation relative to intraspecific and intra-individual variation. Measurements of pulse and call characteristics for all species were then submitted to Discriminant Function Analysis (DFA), in an attempt to calculate linear relationships from the data that would provide species identification. Resubstitution was used to cross-validate the power of DFA to correctly discriminate between species' calls. All analyses in this study were performed with SAS (SAS Institute Inc. 1989).

Level of Detector Deployment Comparison

Ground-level surveys in the forest-interior detected significantly more calls than did canopy-level surveys (Table 1). There was no significant difference between levels at the pond-side site (Table 1). This indicates a higher level of bat activity lower in forested habitat than at the canopy level, although less clutter at ground-level than canopy-level is another possible factor influencing results. There was, however, considerable shrub growth in the forested habitat, leading us to consider the former hypothesis as more likely.

There was a tendency for surveys at the pond-side to detect more calls than surveys in the forest-interior, although this trend was not statistically significant at any level (Table 2). This result indicates that levels of bat activity at the pond-site and forest-interior are not very different, which runs counter to our observations that bats in central Louisiana tend to heavily use waterways for feeding and drinking. The result, however, may have been a sampling artifact. Failure to reject the null hypothesis could be a function of the small sample sizes used in this analysis (Table 2).

TABLE 1 *The sample sizes, median differences, interquartile ranges (IQR), Wilcoxon Sign Rank value (*s*), and* p-*value associated with a comparison between ground-level and canopy-level detector surveys.*

Site	n	Median differences	IQR	s	p
Forest-interior	10	1.5	0–1	10.5	0.03
Pond-side	7	0	0–1	1.0	0.75

TABLE 2 *The sample sizes, median differences, interquartile ranges (IQR), Wilcoxon-Mann-Whitney (*s*) values, and* p-*values associated with a comparison between sites of number of calls recorded at each level.*

Level	Site	n	Median	IQR	s	p
Ground	forest-interior	9	3.00	0–4	49.5	0.90
	pond-side	6	3.50	0–4		
Canopy	forest-interior	8	0.50	0–1.5	37.0	0.81
	pond-side	5	0.00	0–4		

Analysis of Species Discrimination

Nested Random Effects ANOVA for bat calls revealed two variables, maximum frequency and midpoint frequency, that exhibited a large amount of interspecific variation. Minimum frequency, duration, and slope showed less interspecific variation, but rather large amounts of either inter-individual variation or error variation (Figure 1). For example, 78.1% of the variation in maximum frequency can be accounted for by differences across species lines. This is a strong indication that maximum frequency might be a useful factor in species discrimination. However, because interspecific variation is negligible (0.00%) for the variable minimum
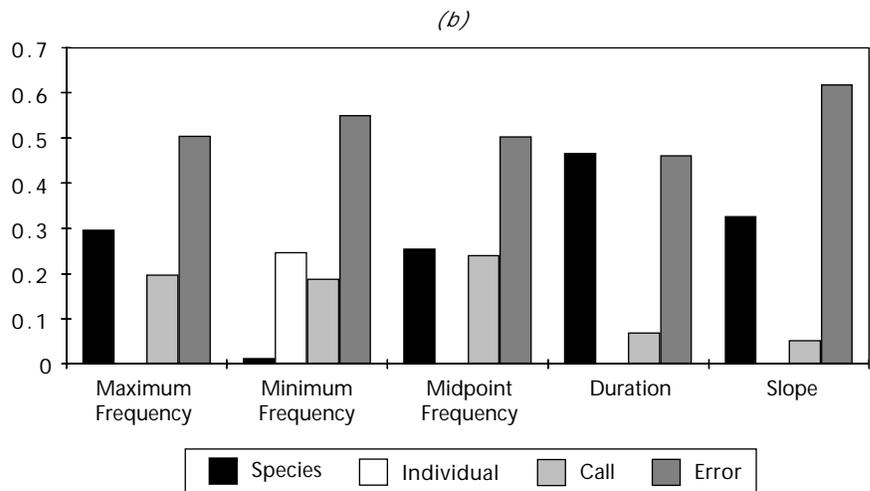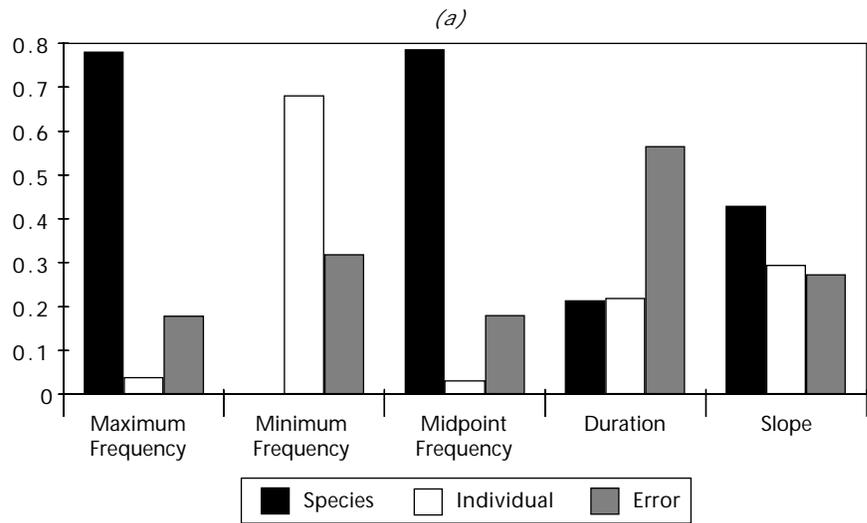
(a)

(b)

FIGURE 1   *(a) The proportion of total bat-call variation assigned by Nested Random Effects ANOVA to each potential source of variation. Error is equivalent to the variation among an individual's calls. (b) The proportion of total bat pulse variation assigned by Nested Random Effects ANOVA to each potential source of variation. Error is equivalent to the variation among a call's pulses.*

frequency, there is virtually no hope that this variable can be used to identify species. Such a large proportion of variation at the intra-individual or call level strongly suggests some potential for measurement overlap between the different species. Variation in pulse characteristics is similar to variation in call measurements, except for slope and duration, which exhibit relatively more interspecific variation (Figure 1).

The Multivariate Analysis of Variance (MANOVA) component of DFA indicated that there were significant differences ($p < 0.001$) among bat species for the call and pulse characteristics that we measured. DFA was able
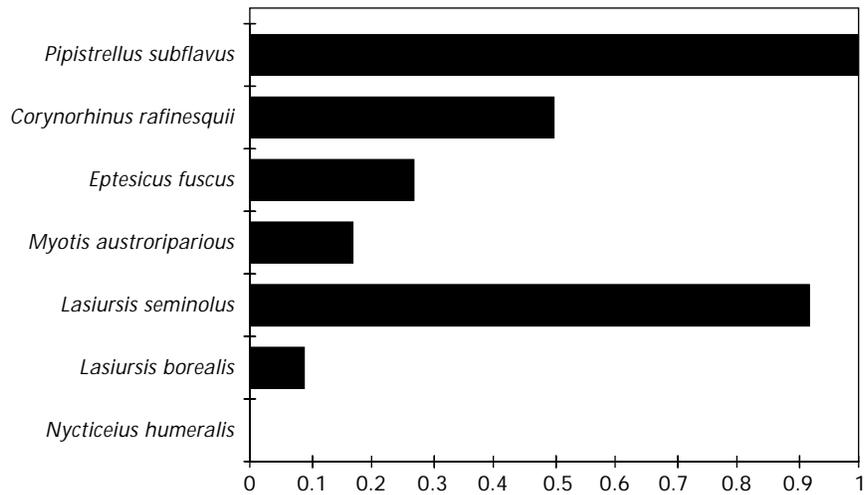
FIGURE 2 *The proportion of correct assignment of bat calls to their proper species using Discriminant Function Analysis, cross-validated by Resubstitution. There is no representation for the number of calls incorrectly identified to each species.*

to adequately discriminate the calls of *P. subflavus* and *L. seminolus* from other bats' calls, but was unable to distinguish between the other five species (Figure 2). DFA for pulse measurements was not nearly as successful, and is not reported herein. While DFA was able to correctly classify *P. subflavus* 12 out of 12 times and *L. seminolus* 11 out of 12 times, it is important to note that some bats were misclassified as *P. subflavus* and *L. seminolus*. One *E. fuscus* and two *L. borealis* calls were identified as *P. subflavus* and, likewise, six *N. humeralis*, two *L. borealis*, three *M. austroriparious*, and one *C. rafinesquii* were classified as *L. seminolus*. These errors, which are not depicted in Figure 2, suggest the call and pulse characteristics used in this study do not lend themselves to reliable classification of species.

DISCUSSION

Level of Detector Deployment Comparison

If further analysis of differences in sampling between canopy-level and ground-level bat detector surveys supports the trends exhibited by our data, then some interesting hypotheses come to the fore. In forested habitat, bat activity may be higher below the tree canopy than in the tree canopy. This would seem logical in light of recent reports that foraging in the forest-interior is minimal (Thomas and West 1989). Bats that may simply be commuting from one edge site to another, or from a roost site to an edge, may prefer flying in the relatively uncluttered space between the shrub canopy and tree-limb canopy. This may be especially true for fast-flying, less manoeuvrable bats with a high wing loading and aspect ratio (Norberg and Rayner 1987). Bats foraging for insects over a pond or meadow, on the other hand, probably exhibit relatively more vertical movement. This may be an explanation for the lack of significant differences between levels at the pond-side site.

Aside from higher sampling yields with ground-level detectors, researchers may benefit from not having to place detectors at the canopy level, which can be both troublesome and frustrating. Ropes become tangled, unwound, or stolen, batteries die unobserved, and detector knobs may be jolted into new positions. Ground-level surveys are simply much easier to conduct.

Ecological partitioning on a vertical basis is important to consider when exclusively conducting ground-level surveys of bat activity (Barclay and Bell 1988). One potential solution is to increase the angle at which the detector is propped, so as to cover a greater vertical range.

Analysis of Species Discrimination

Our results showed that there are significant interspecific differences in bat-call characteristics, but that these differences were insufficient in providing discrimination among bats of seven species indigenous to central Louisiana. Because the general applicability of our results is unknown, it is important to include the caveat that our findings may only pertain to captive bats in our specific locality. When conducting research on an animal trait, such as a bat vocalization, that varies not only in its uses (hunting echolocation, travelling echolocation, intraspecific communication, etc.), but perhaps also between localities and genealogical groupings, it is worrisome to project findings beyond the immediate boundaries of the study. For example, if *P. subflavus* calls show a great deal of variability across its range, due to adaptation in response to varying abiotic conditions or, perhaps, to different bat community constituencies, the discriminant function calculated in this study may well be invalid for *P. subflavus* elsewhere. Likewise, calls recorded from captive bats can differ from those of free-flying individuals.

When bat researchers attempt species discrimination with Anabat II detectors, or perhaps any brand of detector, some variables will be more useful than others (Thomas et al. 1987). However, there is little agreement regarding what variables may be of particular use as species discriminating factors. For instance, our data suggest that maximum frequency shows a great deal of interspecific variation, while minimum frequency holds little promise as a discriminating call characteristic. Thomas et al. found that the maximum frequency is too prone to atmospheric attenuation to be reliable, while minimum frequency showed promise in species identification. These conflicting results may be a function of differences in experimental design, equipment, or locality. Certainly, species discrimination with bat detectors is only further obfuscated by these concerns.

DFA was able to reliably identify two species, *P. subflavus* and *L. seminolus.* On the other hand, DFA also misclassified a number of calls from other species as belonging to one of these two bats. Other scientists working with Anabat II detectors in the field have purportedly experienced greater success with species discrimination than we have. This preliminary study should not be taken as a final word on the effectiveness of Anabat II detectors. Our method of collecting bat calls from captive bats in cages and tents may have added two confounding factors to the data set: (1) bats recorded while experiencing abnormal circumstances, (2) bats recorded while being held in two very different housings (cage and screen-tent). Likewise, different researchers may have chosen different variables to measure, or used entirely different protocols for analysis and

discrimination. Furthermore, ineffectiveness of Anabat II detectors in species discrimination does not diminish other potential uses of the Anabat II system, such as automated field surveys of bat activity.

We feel that the large amount of intraspecific variability that seems to exist in bat calls argues strongly for large sample sizes and quantitative approaches to species discrimination with bat detectors. If species discrimination protocols that rely on very small samples (i.e., three or four calls) do not fully capture the range of variation in call characteristics, they may be prone to misidentification of species with overlapping call structures. Subjective identification of bat calls may lack the reproducibility that gives power to quantitative approaches, such as DFA. Possible procedures that may improve species discrimination are analysis of only certain types of calls (i.e., CF or FM), and creation of sets of species with similar call characteristics for identification of groups. Some initial attempts on our part to employ these procedures did not improve discrimination.

Prior to deployment of Anabat II detectors in field studies, researchers should carefully consider what data they must collect. While the Anabat system may be very useful in surveying general bat activity, it may not be suited to surveys for specific species. Future quantitative studies of free-flying bat calls are needed to more closely approach a conclusion on this matter.

ACKNOWLEDGEMENTS

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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.

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 hetero-thermic 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.

MATERIALS AND METHODS

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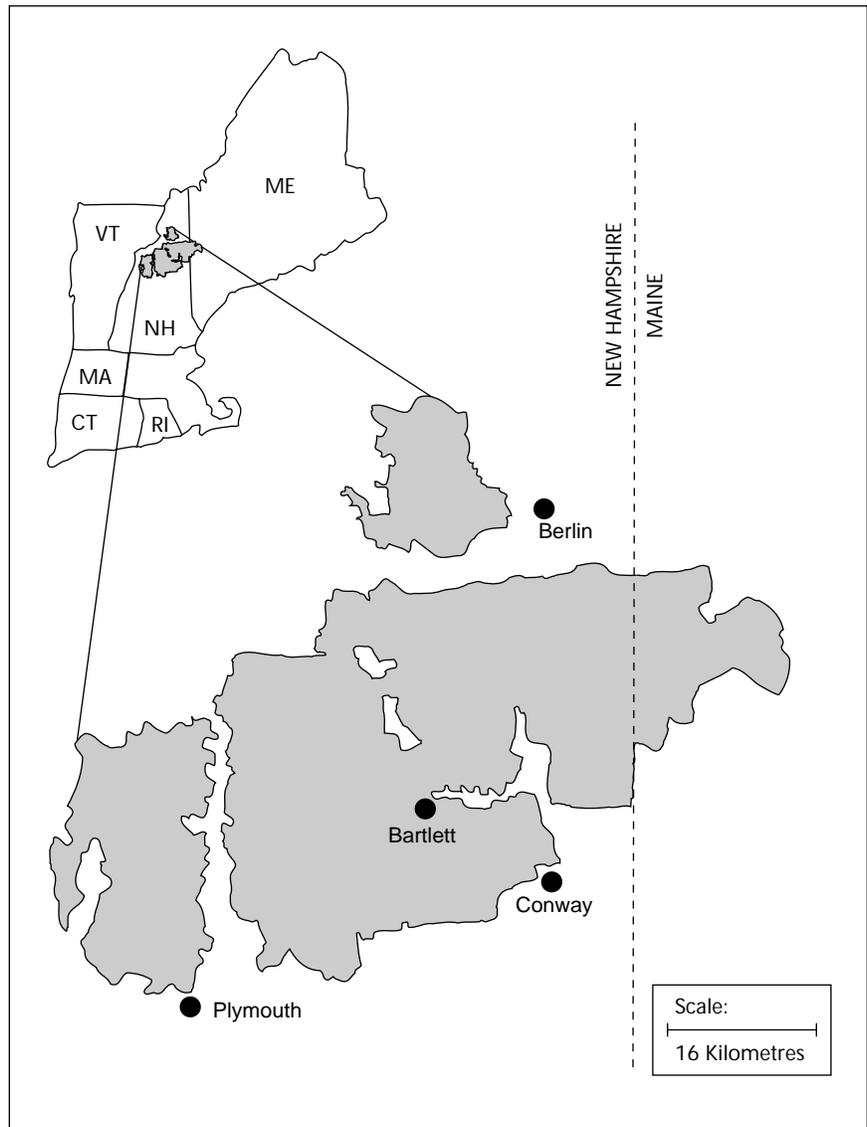
FIGURE 1   *Location of study area; the White Mountain National Forest, New Hampshire and Maine.*

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 airspace 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.
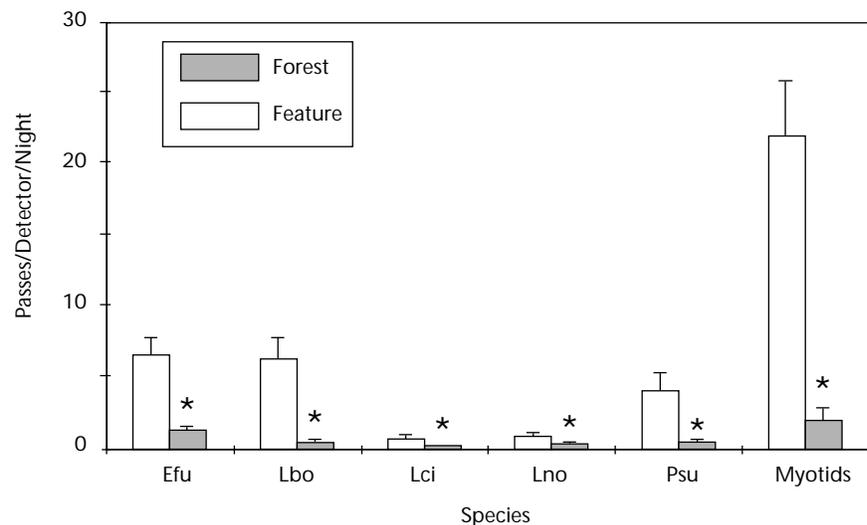
FIGURE 2   *Relative bat species activity (LS mean plus one standard error) at the forest edge (habitat feature) and forest interior, White Mountain National Forest, 1994. Efu Eptesicus fuscus; Lbo Lasiurus borealis; Lci Lasiurus cinereus; Lno Lasionycteris noctivagans; Psu Pipistrellus subflavus; Myotids species of the genus Myotis (M. lucifugus, M. septentrionalis, M. leibii, and M. sodalis). * (in all figures) represents a significant difference (P ≤ 0.05) between sampling sites for the species indicated.*
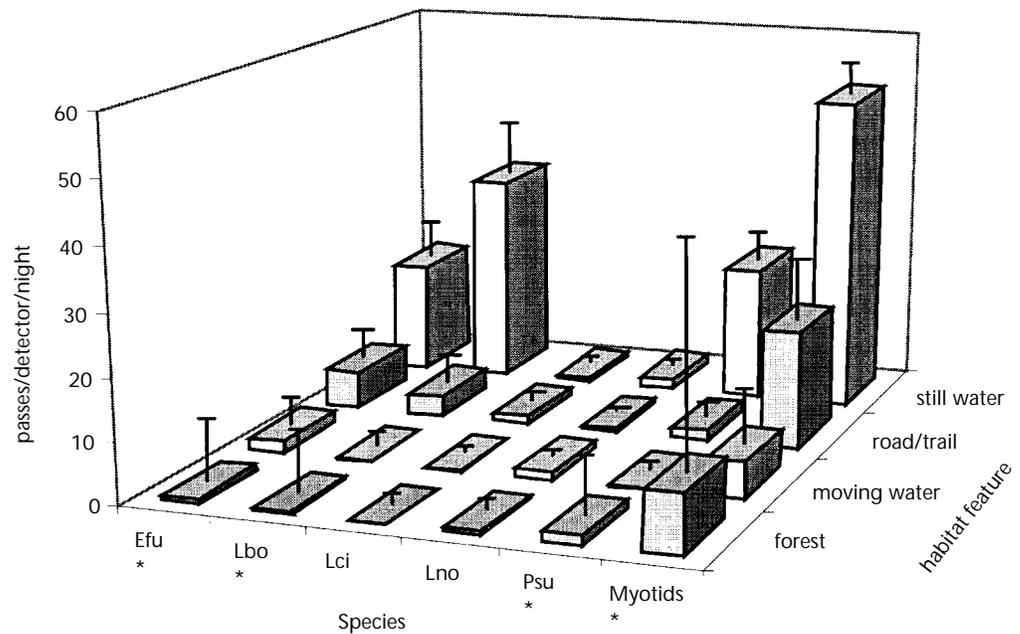
FIGURE 3   *Relative bat species activity (LS mean plus one standard error) among habitat features identified in the White Mountain National Forest, 1994.*

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.*
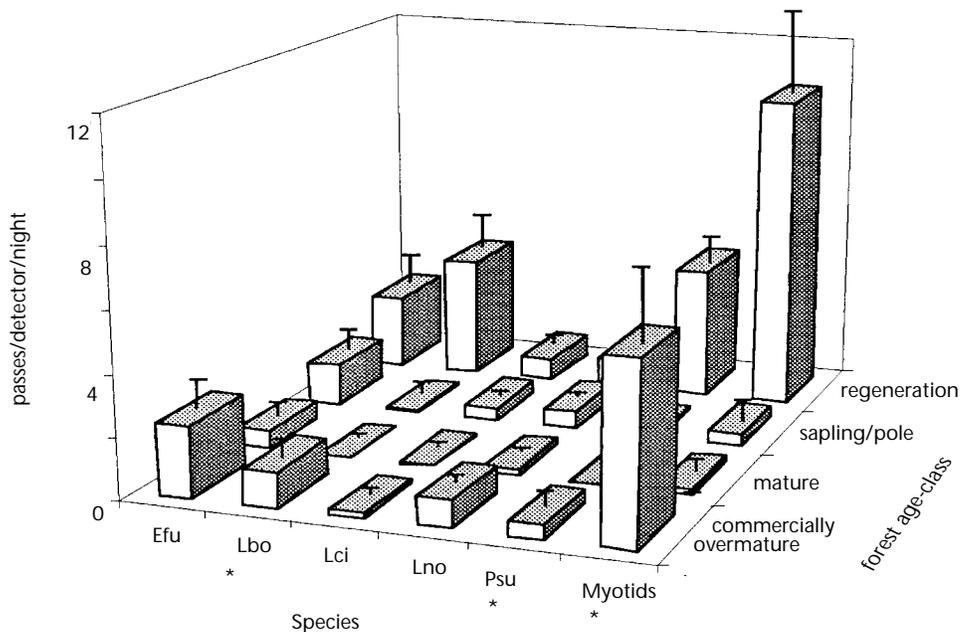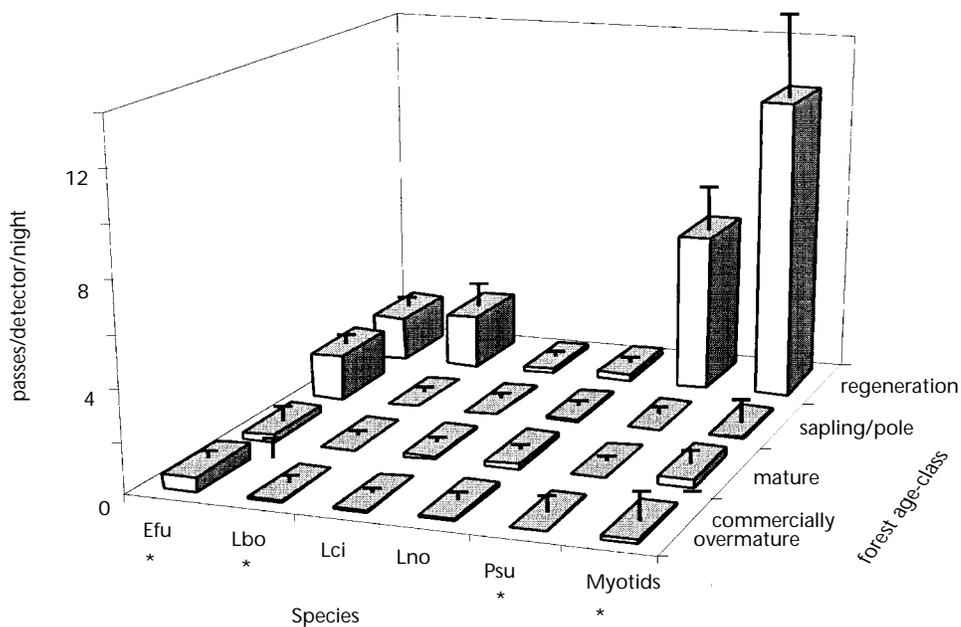

FIGURE 5   *Relative bat species activity (LS mean plus one standard error) among four stand age-classes of the softwood forest type, White Mountain National Forest, 1994.*

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 ($\overline{X} = 5.6$ 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 ($\overline{X}$ = 5.1 passes/detector/night, Figure 5).

DISCUSSION

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 loose 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. lucifigus*. 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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The Physical Nature of Vertical Forest Habitat and its Importance in Shaping Bat Species Assemblages

PAUL A. BRADSHAW

ABSTRACT

Recent work on forest-dwelling bat species has stimulated interest in how the composition of these faunas is derived and maintained. Resource limitation and competition do not appear to be important, but forest structure may be a primary influence in shaping bat communities.

Old-growth forests differ from younger forests in that they exhibit greater structural heterogeneity. They may be perceived as habitat volumes containing discrete layers, each with its own peculiar structural characteristics. For bats, the ability to fly allows movement into different, structurally distinct microhabitats, through vertical shifts between forest layers. Hence, vertical structural complexity may be an important habitat feature for forest-dwelling bats.

I quantified vertical forest structure by measuring profiles of foliage density. Increasing foliage density can be viewed as decreasing uncluttered space within which a flying animal could manoeuvre. Small, interspecific differences in wing morphology should have important implications for manoeuvrability and agility, which may be reflected in interspecific microhabitat associations. I made predictions about bat activity, based on eco-morphology, regarding vertical microhabitat association for sympatric species in three forest types on the west coast of Vancouver Island, British Columbia. Predictions were tested using ultrasonic detectors and mist nets set at three heights, corresponding to the canopy, understorey, and shrub layers.

Here, I outline the theoretical framework, and attempt to elucidate how functional relationships between habitat structure and bat community structure may be determined. I also present preliminary results from this ongoing study.

INTRODUCTION

Habitat structure may influence the distribution of organisms in three ways: by imposing a physical constraint on movement, by creating a

scattered pattern of resource distribution, or by altering microclimates. The extent to which they influence animal communities can vary as a function of habitat structural complexity (Brown 1991). Bats are the only true flying mammals, and this method of locomotion is sensitive to variations in habitat structural complexity (McKenzie and Rolfe 1986). This sensitivity may be reflected in patterns of microhabitat use. Here, I outline a preliminary study, and propose future work, examining the functional role of vertical habitat structure in influencing the arrangement of bat species assemblages in three coastal, temperate, old-growth forests.

Habitat structure develops in three dimensions. Typically, structure is measured horizontally, quantifying habitat heterogeneity, and vertically, quantifying habitat complexity (Alpert 1991). In terrestrial environments the extent of the vertical dimension of habitat structure may encompass three orders of magnitude. In rock-surface lichen communities this dimension is measured in a few millimetres, while in some temperate coniferous forests, it extends through 100 metres. In forests, particularly old-growth forests, vertical structural complexity is not homogeneous. Stratification is evident in the form of distinct layers, such as the canopy, understorey, and shrub. They can be viewed, simplistically, as having habitat edges that run in the horizontal plane. For forest-dwelling bats, vertical stratification in forest structure may be an exploitable habitat feature. By short, vertical movements into different forest layers, rapid shifts between structurally distinct microhabitats should be possible and may be advantageous. Determining to what extent bats use this dimension of forest structure, and how its use differs between species, is the principal objective of this study. The aim is to elucidate three-dimensional patterns of habitat use by insectivorous bats, be that for the purposes of feeding, roosting, and/or commuting to preferred foraging sites. By viewing forest habitats as a complex volume of space, exploitable in three dimensions, a more pervasive understanding of how bats use this habitat may be developed.

The functional role of habitat structure in shaping community structure is not easily determined. Relationships are complicated by numerous confounding factors, all of which conceivably influence the composition of bat communities. For instance, the physical structure of a habitat is not necessarily the principal determinant of community structure. Competition between organisms for limited resources may be more important. However, there is little evidence that resource competition, particularly for prey, actually occurs in bat communities (Findley 1993). Bat community structures are also influenced by latitudinal effects (Schum 1984; Willig and Selcer 1989), longitude (Heller and Volleth 1995), and by stochastic processes (Willig and Moulton 1989). At smaller spatial scales, additional confounding factors are introduced. For example, not all species within the community are equally sensitive to the same structural variables. Also, different aspects of forest structure may be important during different times of the year. This may vary between species, sexes, and even individuals. Variables of habitat structure are multifarious. Not all are readily quantifiable, and time constraints preclude assessing all of the ones that are. Variables that are important may be ignored, or simply not recognized as being ecologically relevant to bats. In addition, the spatial and temporal scales at which habitat structure is examined may not be appro-

priate to reveal functional relationships. Bats, as important agents in nutrient cycling in the forest, have the potential to modify their surrounding habitat structure.

By focusing on the potentially strong relationship between flying ability, microhabitat association, and vertical habitat structure, the confounding effects of unmeasured and unmeasurable variables can be mitigated. Examining vertical forest structure within an ecomophological framework may allow functional relationships between habitat structure and community composition to be determined. For flying mammals the ecomorphological premise states that interspecific differences in wing morphology translate into ecological differences, particularly in foraging style. Strong relationships between form and function have been demonstrated in some bat faunas (McKenzie et al. 1995). Detailed studies of flight morphology in bats (e.g., Fenton 1972; Norberg 1981; Aldridge 1986; Norberg and Rayner 1987; Saunders and Barclay 1992) have illustrated how relatively small, interspecific differences in wing morphology and body size can have important implications for flight style and consequently foraging behaviour. By quantifying habitat structure in terms of the amount, or density, of material obstructing flight space (hereafter termed clutter), and determining correlations between bat activity and microhabitats of differing clutter density, functional relationships may be demonstrated. Comparing vertical structure and vertical bat activity between several forest types and exposing patterns and relationships allows an estimation of the general applicability of the findings at larger spatial scales.

Defining Habitat Structure

Habitat structure is comprised of abiotic and biotic elements. Abiotic structure affects most bat species on a seasonal time scale, where winter hibernacula are located in caves, and year round for species that use abiotic roosting sites (e.g., *Corynorhinus townsendii*). For the most part, biotic structural influences (i.e., plant material) are more relevant to bat communities. However, abiotic habitat structures, such as soil horizons, topography, and local geology, have indirect effects on animal communities by influencing the growth and distribution of plant species, thereby influencing biotic structure. There are horizontal, vertical, and scale elements to the development of habitat structure (Brown 1991). Here, I focus on vertical structure, and assess differences in bat activity with height in reference to vertical profiles of foliage density.

Ecomorphology and Habitat Structure

It is clear that not all bat species are capable of exploiting vertical structural complexity to the same extent. Species differ in wing morphology and body size, which dictate manoeuvrability and flight style. Manoeuvrability can be quantified as the volume of space required for a flying bat to change direction during flight at a constant speed (Norberg and Rayner 1987). Bats display a great variety of wing sizes and shapes, which follow some general trends. Larger, faster-flying species are characterized by long, narrow wings. At the opposite end of the spectrum are smaller, slower-flying species that have short, broad wings. Wing design can be defined mathematically as ratios of certain morphological measurements. Wing loading (body mass divided by total wing area) and aspect ratio (wing span divided by wing area) are mathematically derived indicators of flying ability. They are closely related to agility, stalling speed, and manoeuvrability. Bats with long, narrow

wings typically have high wing loadings and high aspect ratios. They have high relative stalling speeds and are less manoeuvrable. Species with short, broad wings have low wing loadings and low aspect ratios, have low stalling speeds, and are highly manoeuvrable.

Based on this understanding of how morphology reflects manoeuvrability I make predictions regarding microhabitat associations. In essence, this is a test of the theory of ecomorphology, or "morphology as the cast of the ecological mould" (Findley 1976). Data on wing morphology and ear length, for all the bat species known to be present in the study region, were taken from the literature (Norberg and Rayner 1987). An index, composed of the sum of the following values—ear length divided by body mass, wing loading, and aspect ratio—was determined for all species in the sample. This index is an approximation of a species' ability to negotiate a complex and physically cluttered habitat, what I have termed clutter tolerance. Long ears, relative to body size, are characteristic of species associated with cluttered habitats (e.g., *Myotis evotis, Corynorhinus townsendii*). Indices for all species were put in rank order (Figure 1). I assumed in constructing this index that all measured morphological variables are equally important in dictating microhabitat preferences, so that a proportionate change in any one variable would alter with equal significance the ability of a species to cope with clutter. The predictive power of the clutter tolerance index is limited in that it relates purely to possible microhabitat associations. Small, highly manoeuvrable bats would be expected to show an equal association with highly cluttered habitat and open habitat. Furthermore, caution should be employed when relying on simplistic approaches in predicting ecological characteristics based on morphometric data (Norberg and Rayner 1987; Saunders and Barclay 1992). Present designs may not necessarily reflect optimal adaptations to current environments, and phylogenetic constraints should not be discounted in the analysis of flight performance.
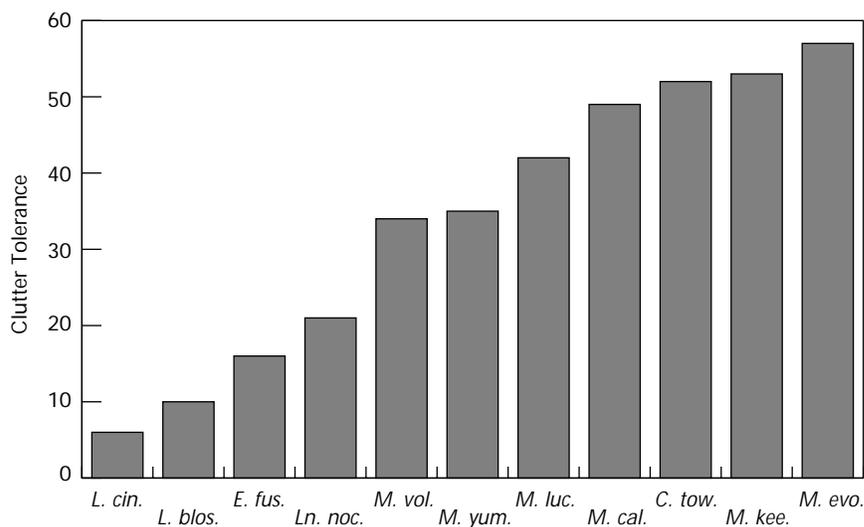

FIGURE 1 *Ranked clutter tolerance index for 11 northwestern Nearctic bat species. Indices were determined by summing three morphological variables associated with flight style.*

Vertical Stratification of Ancient Forests

Old-growth forest (over 200 years old, Kirk 1992) is distinct from younger forest in displaying greater vertical structural heterogeneity (Arsenault and Bradfield 1995). This dichotomy is pronounced in the wet, highly productive regions of the Pacific Northwest. In the western hemlock (*Tsuga heterophylla*) forests of coastal British Columbia, small, localized disturbances, the result of winter storms and lightning strikes, characterize the disturbance regime. This is reflected in the uneven age structure of these forests. These localized events, coupled with a successional process that involves a wide diversity of tree species with differing shade tolerances (Terborgh 1985; Hunter 1990), combine to mould the structure of the forest habitat volume, creating vertical stratification in forest structure. Forest stratification is typified by an upper layer of overstorey, or canopy, one or more subdominant layers composed of younger stems of the canopy trees, and mature trees of other species that fail to reach the canopy, constituting the understorey (Spurr and Barnes 1980). In essence, vertical structural complexity results from a combination of factors, including the longevity and large size of the dominant conifers, plant species' richness, and long-rotation, localized disturbance (Arsenault and Bradfield 1995).

Summary of Objectives

1. Assess the vertical distribution of foraging activity by vespertilionid bats in three coastal, old-growth forest types on Vancouver Island, British Columbia.
2. Determine habitat structure (in particular vertical structure) differences between the forest types.
3. Determine if vertical habitat structure can be functionally linked to bat community composition, through correlational analysis of microhabitat association and vertical forest structure.
4. Compare predicted, interspecific vertical microhabitat associations with observed distributions.

MATERIALS AND METHODS

This study is being conducted at two main sites: the Carmanah watershed (48° 64′N, 124° 61′W), and Rocky Point (48° 37′N, 123° 72′W). Both study sites are within old-growth forest that has never been logged or managed. Two biogeoclimatic zones are represented (Table 1).

Anabat II ultrasonic detectors, set at three heights in the forest along vertical transects, were used to sample bat activity. Detectors were used in combination with delay switches and tape recorders to enable the automated recording of bat calls.

Five sample trees were selected at each of three old-growth forest sites. The selection of trees was not random. Emergent canopy trees were preferentially selected so that equipment could be raised above the main canopy layer if desired. In addition, trees were selected for their accessibility to static line, or fixed rope, climbing techniques, which precluded a random approach. All sample trees were at least 30 m apart, the maximum distance being 300 m.

Suitable high branches, with adequate clearance to ground level, were selected. Trees were climbed by a professional arborist who attached

TABLE 1 *Biogeoclimatic zones, representative flora, and local climatic means for two of the forest types sampled.*

Site	Stand type	Biogeoclimatic zone	Mean annual temp. (range)	Mean annual precip. (range)	Representative flora
Carmanah Valley	Sitka spruce (*Picea sitchensis*)	Coastal western hemlock (cwh), subzone: very wet; hypermaritime (vh)	8.2°C	2951 mm	Western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) dominate the open canopy. Salal (*Gaultheria shallon*), red huckleberry (*Vaccinium parvifolium*), and salmonberry (*Rubbus spectabilis*) dominate the moderately well-developed shrub layer.
Rocky Point	Douglas-fir (*Pseudotsuga menziesii*)	Coastal Douglas-fir (cdf)	9.2 to 10.5°C	647 to 1263 mm	Redcedar–Grand fir–Foamflower association. Tree stratum consists of Douglas-fir (*Pseudotsuga menziesii*), grand-fir (*Abies grandis*), western redcedar (*Thuja plicata*), bigleaf maple (*Acer macrophyllum*), and western flowering dogwood (*Cornus nuttallii*). Western redcedar occurs in the understorey.

Source: Meidinger and Pojar, 1991.

pulleys to selected branches, so that equipment could be raised and lowered from the ground. This eliminated any unnecessary damage to the tree from frequent climbing trips to place and retrieve detectors. Pulleys were approximately 45 m above the ground within the forest canopy. Three detectors, enclosed in plastic, watertight containers, with ultrasonic microphones exposed, were set at three levels along each vertical transect: canopy (45 m), understorey (25 m), and shrub (1.5 m, Figure 2). On any night, all detectors were oriented to point in the same direction, although this direction changed from transect to transect. Detectors were left activated for the entire night. The light-sensitive switch, a feature of the Anabat II system, was not used, as it frequently failed to record early and late bat activity due to high relative light levels during twilight. Each Anabat detector and delay switch were powered by a single, 12-volt, sealed, rechargeable battery (Powersonic model PS–1270). This allowed continuous sampling for up to five nights. The detectors were lowered each day and moved to another transect (i.e., a different tree), audio-cassette tapes were replaced, and the digital clocks in the delay switches were resynchronized. To reduce the influence of sampling bias due to differing sensitivities between individual detectors, all sensitivity dials were set at 6, and detectors were rotated between levels after each sample night.

Mist nets were set over watercourses and within the forest to determine the species composition of the local bat fauna. Bats caught in nets were removed and identified to species, then morphological measurements were taken and an outline of an extended right wing was traced onto graph
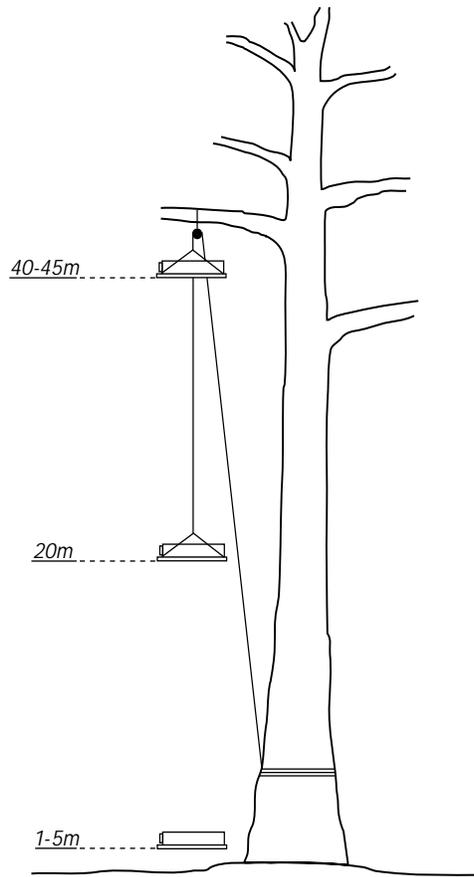
FIGURE 2 *Positioning of bat detectors along a vertical transect at each sampling tree.*

paper. This allowed measurement of wing area and wingspan. The bats were then weighed and marked with a chemi-luminescent tag (Buchler, 1976) affixed between the scapula with skin cement. Each tagged bat was released in an open area so that recordings of calls could be made using an Anabat detector connected to a tape-recorder. This provided a set of reference calls used to identify species, or species groups.

Vertical profiles of foliage (clutter) density were constructed, following MacArthur and Horn (1969). An SLR camera equipped with a 205-mm zoom lens attached to a tripod was used to generate cross-sections of vertical forest structure. At each sampling point eight transects, separated by increments of 45°, were set from the base of the stem running 30 m into the surrounding forest, creating eight radii of a circle with a diameter of 60 m, the centre being the sample tree. Along each transect a profile was measured every 5 m, producing six profiles per transect and a total of 48 for the sampling plot. All types of plant material, including twigs and branches, were included in the profile. There is no salient reason to consider any type of plant matter less or more important in obstructing bat flight.

Bat activity was measured as the number of bat passes. A bat pass was any call sequence that included two or more pulses (Garcia and Barclay 1993). Call sequences were classified as either a commuting pass or a

foraging pass. Sequences were designated as commuting passes if they lacked the characteristic increasing pulse repetition rate associated with a foraging attempt, or "feeding buzz."

Recordings of bat calls will be analyzed, using Anabat 5.2 software, and compared with reference recordings made of known species, to determine the species or species group to which the call most closely resembles.

RESULTS

Sampling was conducted on a total of 55 nights between June and August 1995, resulting in a total of 165 detector-nights. Of these, 25 sampling nights were at Carmanah Valley (69 detector-nights, some detector-nights were excluded due to equipment failure), and 21 nights at Rocky Point (63 detector-nights).

Mean foliage density with height for both Rocky Point and Carmanah (Figure 3) indicate distinct structural differences. At Rocky Point, foliage density is concentrated at the canopy level, approximately 35–50 m, whereas in Carmanah, foliage density is distributed more evenly, with

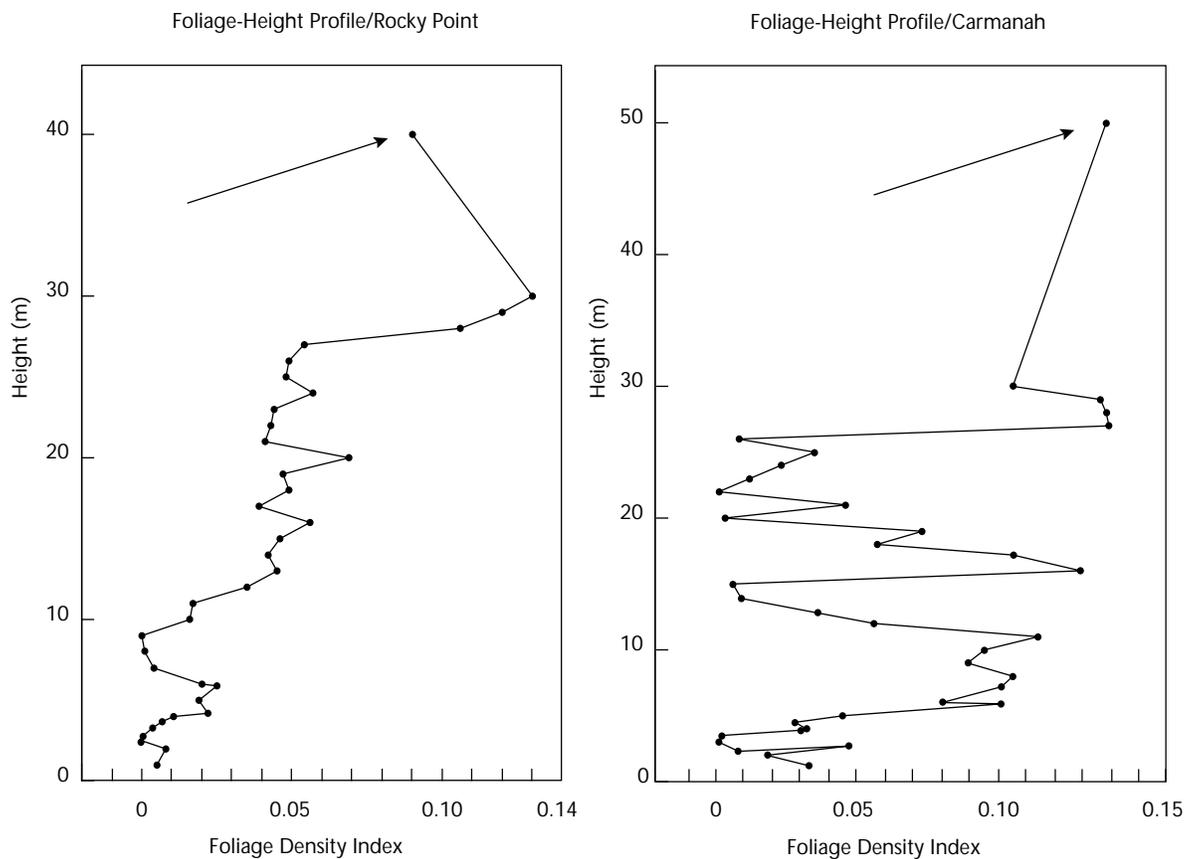Foliage-Height Profile/Rocky Point   Foliage-Height Profile/Carmanah

FIGURE 3   *Mean foliage density vertical profiles for both forest types (n = 16; n = 23). Points highlighted by arrows represent approximate mean densities of foliage between 30 and 70 metres.*
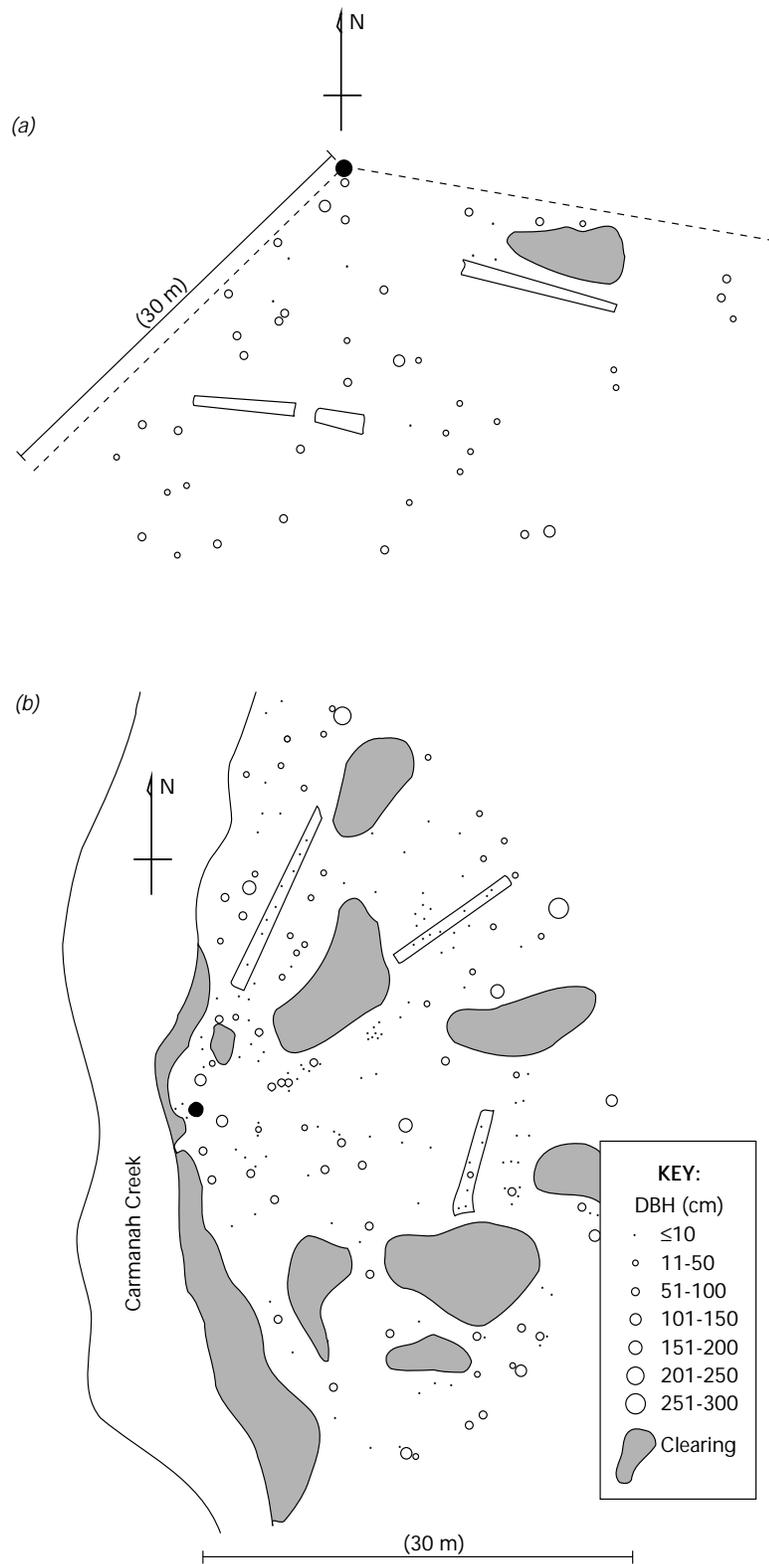
FIGURE 4 *Representative 30-m-radius plots for (a) Rocky Point and (b) Car-manah Valley. Filled circles are sampling trees. Open circles are live or dead stems.*

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peaks of density in the understorey and canopy. This agrees closely with personal observations of the vertical structure of these forest types, and is partly the result of differences in stand age structure between these forest types. Rocky Point sample plots (CDF, Coastal Douglas-fir (*Pseudotsuga menziesii*) zone) are characterized by a marked consistency of stem DBH (diameter at breast height), implying an even age structure (Figure 4a). Carmanah plots (CWH, Coastal Western Hemlock (*Tsuga heterophylla*) zone) display a wide range of stem DBH, and have a higher basal area ($B = 0.005454 * D^2$) per unit area, reflecting the well-developed understorey of this forest (Figure 4b).

Nightly bat activity patterns show marked differences between forest types. At a broad level, when forest types are compared, there is considerably more activity at Rocky Point. If height in the forest is considered, then distinct patterns appear. At Rocky Point, activity is concentrated in

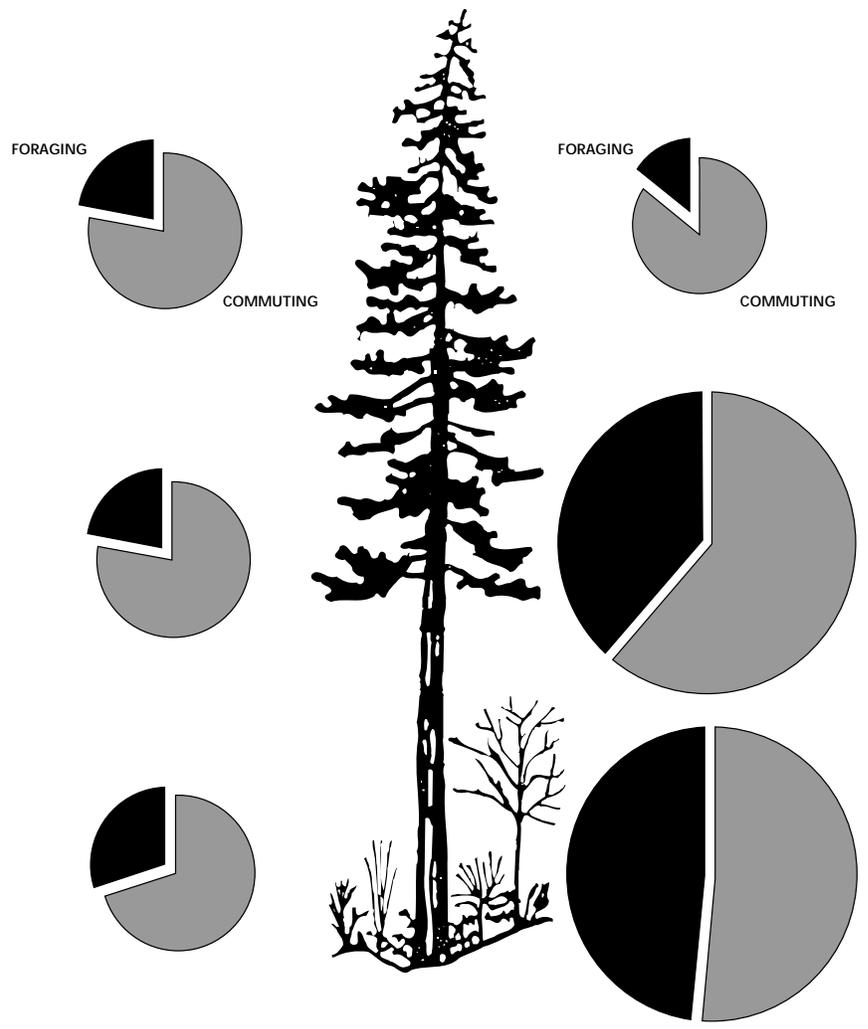**CARMANAH VALLEY (Sitka spruce stand)**   **ROCKY POINT (Douglas-fir stand)**

FIGURE 5   *Vertical bat activity for both forest types (132 detector-nights). Diameters of pie-charts represent percentage of the total activity for all sites.*

the shrub and understorey, with considerably less activity in the canopy. Foraging activity exhibits a general trend of decreasing with increasing height at Rocky Point (Figure 5). Carmanah sites do not display this apparent relationship. Both total activity and foraging activity remain relatively constant with height, although at the same approximate intensity as canopy activity at Rocky Point.

Foraging activity is not constant throughout the night at either site. Distinct peaks appear in the first hour after sunset for both forest types. However, foraging activity drops and remains low in Carmanah, whereas several further successive peaks in activity occur at Rocky Point (Figures 6a, b).

DISCUSSION

My results are preliminary and have not been statistically assessed. It would be premature to make any firm conclusions about the patterns of
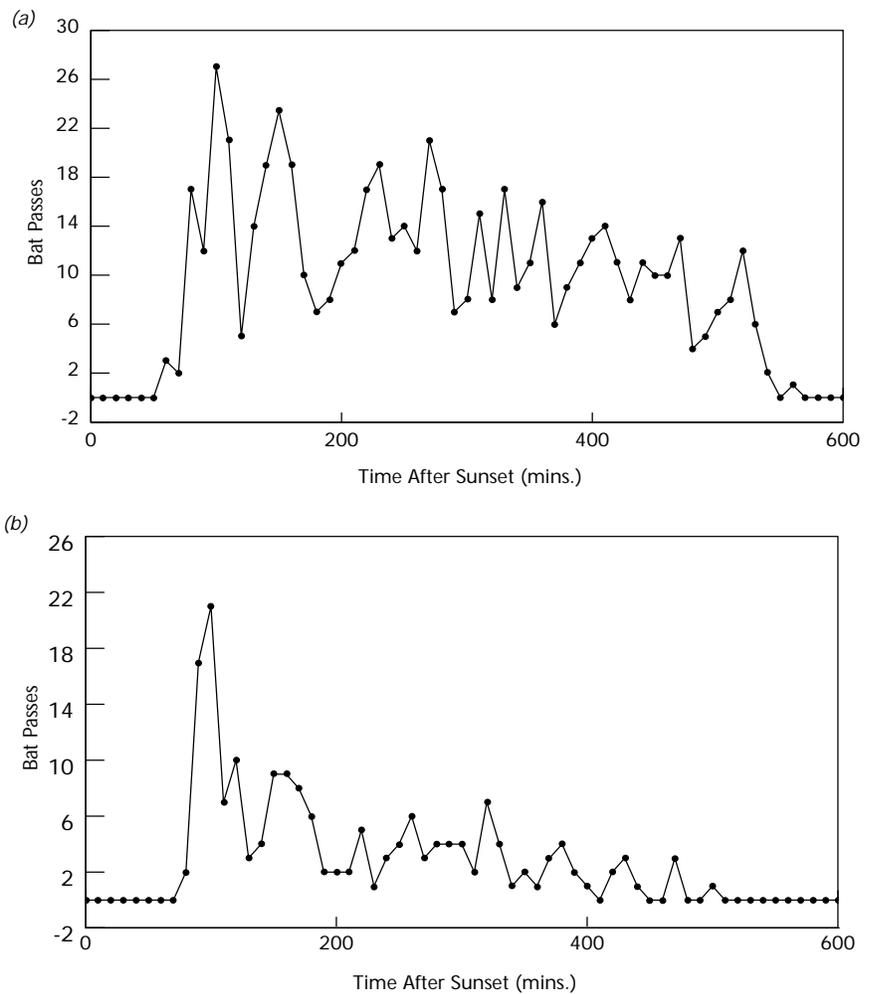

FIGURE 6   *Summed foraging passes with time after sunset for (a) Rocky Point and (b) Carmanah Valley.*

bat activity that have emerged so far. However, a broad pattern of vertical differences in activity is evident. The open structure of the Douglas-fir forest type harbours more bat activity, whereas the structurally more complex western hemlock forest of the Carmanah Valley has relatively lower levels of bat activity. Whether or not these apparent differences in activity, between and within forest types, reflect differences in bat community structure, is yet to be determined. Two pieces of evidence do, however, corroborate the hypothesis that differences between forest types are the result of different associated bat species assemblages. First, mist netting in both forest types (Rocky Point n = 25 nights; Carmanah n = 13 nights) resulted in the capture of 54 bats (all at ground level), distributed among five species. At Rocky Point the following species were trapped: *Myotis lucifugus*, *Myotis californicus*, *Myotis evotis/keenii*, *Lasionycteris noctivagans*, and *Corynorhinus townsendii*. At Carmanah only two species were trapped: *M. lucifugus* and *M. californicus*. Second, patterns of foraging activity after sunset (Figure 6a) at Rocky Point, typified by an initial large peak in activity followed by successively smaller peaks until dawn, imply the superimposing of nightly activity patterns of several species. Further research and analysis of current data will be undertaken to determine if these findings are consistent.

At present there is a paucity of information regarding the vertical distribution of bat foraging activity with respect to forest structure, for any forest type, but in particular for temperate forests. In the coastal regions of the Pacific Northwest, and for temperate regions in general, this gap in our understanding of habitat use is considerable. Developing a more pervasive, three-dimensional understanding of habitat use is an important research goal. Old-growth forests provide a unique opportunity to construct a "baseline" behavioural and ecological knowledge of minimally disturbed habitats and communities. If, in the future, a fully informed and effective reconstruction of damaged habitats is to be undertaken, or habitat reserves are to be created, this baseline knowledge will be invaluable.

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SECTION V **EFFECTS OF FOREST HARVESTING**

Managed Forests in the Western Cascades: The Effects of Seral Stage on Bat Habitat Use Patterns

JANET L. ERICKSON AND STEPHEN D. WEST

ABSTRACT

Timber harvest and stand-management practices have restructured the forest landscape of the Pacific Northwest. To investigate the impact of such practices on bats and other wildlife, a research project funded through the Washington State Timber, Fish and Wildlife Cooperative was initiated in 1992. As part of this project, we conducted a stand-level survey of bat activity within managed forests during the summers of 1993 and 1994. To assess patterns of habitat use across a gradient of managed forest conditions, we selected six replicates from each of four distinct, post-harvest seral stages: clearcut (2–3 yrs); pre-commercially thinned (12–20 yrs); young, unthinned (30–40 yrs); and mature (50–70 yrs) stands. Using Anabat II bat detectors, each site was monitored for bat activity on six nights throughout each summer. The number of detections recorded were not significantly different between years, but were different among seral stages. Overall, activity levels were low, with 46.2% of the nights having no detections. The highest detection rates were in clearcut stands while young, unthinned stands had no detections. Members of the genus *Myotis* were detected within all stand types except young, unthinned stands, but were most often detected in mature stands. Calls of big brown bats (*Eptesicus fuscus*), silver-haired bats (*Lasionycteris noctivagans*), and Townsend's big-eared bats (*Plecotus townsendii*) were recorded most often in clearcuts, but never in mature stands.

INTRODUCTION

Among mammals of their size, bats are unique in having long lives, low reproductive rates, and relatively long periods of infant dependency (Findley 1993). This combination of characteristics places them at risk of population decline in the presence of habitat alteration (Soule 1986). In western Washington, where approximately 3.9 million ha of forest is managed for timber harvest, there is growing concern over the status of forest-dwelling bats. Mitigating for effects of timber management activities is

difficult due to a lack of knowledge concerning bat response to forest age and structure (Christy and West 1993).

In 1983, the U.S. Forest Service's Old Growth Wildlife Habitat Program (OGWHP) was initiated to determine the degree to which wildlife, including bats, were associated with old-growth Douglas-fir (*Pseudotsuga menziesii*) stands. Using ultrasonic detection, Thomas and West (1991) monitored bat activity over a broad range of unmanaged forest conditions in the southern Washington Cascade and Oregon Coast ranges. In Washington, detection rates were 2.5 to 9.8 times greater in old growth (200+ yrs) than in younger stands (35–195 yrs). These findings suggest that old growth is an important habitat for forest-dwelling bats, and that its conversion to younger, managed stands may be detrimental to bat populations.

Recognizing the need to extend research from unmanaged to managed stands, a project funded through the Washington State Timber, Fish and Wildlife Cooperative was initiated in 1992 to investigate the impact of forest management on bats and other wildlife. Here, we describe results from a stand-level survey of bat activity within intensively managed forests in the western Cascade Range during the summers of 1993 and 1994.

METHODS

Study Area

Field work was conducted during the summers of 1993 and 1994 in managed forests located in the Western Hemlock Zone (Franklin and Dyrness 1973) of the Cascade mountains. This is the most extensive vegetation zone in western Washington and the most important in terms of timber production. The area is characterized by wet winters and dry summers with annual precipitation ranging from 800 mm at low elevations to over 3000 mm at high elevations (Franklin and Dyrness 1973). Average monthly precipitation over the period of this study was 0.68 mm in 1993 and 0.61 mm in 1994.

Study sites were located on intensively managed forest lands owned by the Champion International Corporation and the Weyerhaeuser Company. The primary management activities included timber production by staggered-set clearcutting as well as the operations associated with this type of harvesting (road building, competing vegetation management, conifer planting, and pre-commercial and commercial thinning). The last significant old-growth in the study area was converted to second-growth plantations in the mid-1980s, and the forests are currently harvested at a rotation of 50–60 years.

To assess patterns of habitat use by bats across a gradient of managed forest conditions, we selected six replicates from each of four distinct, post-harvest seral stages: clearcut (2–3 yrs); pre-commercially thinned (12–20 yrs); young, unthinned (30–40 yrs); and mature (50–70 yrs) stands for a total of 24 sites. Clear-cut stands were 2–3 years post-harvest with seedlings of Douglas-fir 1 to 2 m high. Weedy invaders, such as bracken fern (*Pteridium aquilinum*), red alder (*Alnus rubra*), and Canada thistle (*Cirsium arvense*), were consistently associated with these sites. Pre-commercially thinned sites were 10–13 year-old Douglas-fir stands within

which light still reached the ground between trees. The understorey consisted primarily of bracken fern, sword fern (*Polystichum munitum*), elderberry (*Sambucus racemosa*), and other forbs and grasses. Young, unthinned stands were 30–40 years old, with high tree density representing a wide range of stem diameters. Light interception was high with little vegetative growth on the forest floor. Mature forest sites were 51–62 years old, commercially thinned stands dominated by Douglas-fir or western hemlock (*Tsuga heterophylla*). Other tree species present included western redcedar (*Thuja plicata*), red alder, vine maple (*Acer circinatum*), and big leaf maple (*A. macrophylum*). Understorey vegetation was dominated by salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), sword fern, and red huckleberry (*Vaccinium parvifolium*).

The Bat Fauna

The area west of the Cascade Range crest in Washington is believed to support 11 species of bats (Barbour and Davis 1969; Thomas and West 1991). These include seven species of *Myotis* (*M. californicus*, *M. evotis*, *M. keenii*, *M. lucifugus*, *M. thysanodes*, *M. volans*, and *M. yumanensis*), big brown bats (*Eptesicus fuscus*), silver-haired bats (*Lasionycteris noctivagans*), Townsend's big-eared bats (*Plecotus townsendii*), and hoary bats (*Lasiurus cinereus*). At present, four of the *Myotis* species are on the Washington state monitor-species list (*M. evotis*, *M. keenii*, *M. thysanodes*, and *M. volans*). In addition, Townsend's big-eared bat is designated as a species of special concern, and is being considered for federal listing under the Endangered Species Act. Basic population information for many of these species, such as distribution, seasonal occurrence, and range is lacking, but all potentially occur in the study area.

Sampling Design

Ultrasonic detection is a relatively simple but effective way to monitor habitat-use patterns of bats. The automated detectors we used (Anabat II detectors and delay switches; Titley Electronics, Ballina, N.S.W., Australia) consist of a divide-by-n circuit board that counts the waves in the ultrasonic signal and constructs a new wave at the rate of one-for-n. This brings the signal into the range of human hearing and is compatible with cassette-tape storage. A sound-activated tape-recorder stores the bat passes as they occur along with time announcements entered at the time of detection.

Following the sampling protocol developed in the OGWHP (Thomas and West 1991), a detector was left in place for two consecutive nights then rotated to another site. We visited each stand at least three times for a minimum of six nights monitored in each. Samples at each site were spread over a 2–3 month period from mid-July to mid-September. On any given night, one to five of the 24 sites were monitored. Sampling began at dusk (approximately 2045 h) and continued for eight hours. No sites were sampled in heavy rain due to the decrease in bat activity associated with precipitation (Erkert 1982) and continual triggering of the detector system by raindrops.

Within a site, we placed a detector one metre from the ground and oriented it 30° from horizontal at a location greater than 100 m from the stand edge. Variation in recording conditions among heavily forested sites was minimized by placing the detector in a small gap within the stand. The same detector location was used each time a site was sampled.

Analytical Procedures

A detection, or bat pass (Fenton 1970), was operationally defined as two or more pulses recorded as a bat flew through the airspace sampled by the microphone. To compare habitat use among seral stages, bat activity was indexed as the average number of detections per night within each site. Nightly activity patterns were evaluated as the number of bat detections per 30-minute interval. High-repetition-rate "feeding buzzes," associated with an attack on prey, were identified as feeding activity (Griffin 1958).

The analysis of detections occurred at two levels. First, calls were summed regardless of species to determine the general distribution of detections among sites and trends in activity patterns. Second, calls were grouped into "call categories" using zero-crossing analysis and signal processing software (Anabat II, Titley Electronics, Ballina, N.S.W., Australia). The software displays the echolocation call as a function of frequency and time (sonagram) allowing each detection to be analyzed, edited, and saved as a file.

Because the echolocation calls of certain species were not distinguishable, detections were grouped into categories based on similar call characteristics. These could be associated with a particular species or group of species based on comparisons to calls of known identity. A library of known bat calls was created for this purpose using recordings made from free-flying bats, and from call characteristics obtained from the literature (Fenton and Bell 1981; Thomas and West 1989). For this study, six categories of call types were recognized. These were associated with the following species: Type 1, big brown bat; Type 2, hoary bat; Type 3, silver-haired bat; Type 4, Townsend's big-eared bat; Type 5, *Myotis* group (*M. californicus, M. evotis, M. keenii, M. lucifugus, M. thysanodes, M. volans*); and Type 6, *Yuma myotis*.

Vegetation Sampling

As part of the broader research program, overstorey and understorey vegetation was sampled at each of the 24 sites during the summer of 1993. For purposes of this study, we tallied live trees by species and diameter at breast height (DBH) within twelve 12-m² plots and thirteen 45-m² plots on each site. Trees <10 cm and 10–50 cm DBH were recorded within the 12-m² plot, while trees 50–100 cm DBH were counted within the 45-m² plot. Stumps and snags were counted by species, diameter class (<10 cm, 10–50 cm and >50 cm DBH), height class (<1.5 m, 1.5–15 m and >15 m), and decay class (1–3, from hardest to most decayed, modified from Maser et al. 1979). Only stumps and snags >50 cm DBH were recorded within the 45-m² plots. All other classes were recorded within the 12-m² plot. Sampling criteria conformed with standard protocols established for the OGWHP.

Statistical Analysis

Mean detection rates were calculated for all species combined, all members of the genus *Myotis*, all non-*Myotis* species, and each call category. Differences between years and among seral stages were examined using a two-way ANOVA. When significant results were obtained, Tukey's pairwise comparison tests were used to locate the differences. Mean values for the vegetation characteristics were determined for each seral stage. Data were analyzed using SYSTAT (Wilkinson 1992) with a significant level of $\alpha = 0.05$ unless otherwise indicated. Means ± SE are presented.

Vegetation   Young, unthinned stands had the highest mean density of trees <50 cm DBH, while trees >50 cm DBH reached highest densities in mature stands (Table 1). Large snags >15 m in height were found only in pre-commercially thinned and mature stands, with the latter having significantly greater densities.

Effect of Seral Stage   We monitored bat activity for over 2500 hours during 1993 and 1994, resulting in 967 echolocation calls recorded. Each site was sampled on six nights in each year with the exception of one pre-commercially thinned stand that was not sampled in 1994.

The mean number of detections per night did not vary significantly between years (p = 0.4; n = 47 ANOVA), with an average of 3.75 (0.84) detections per night in 1993 and 3.07 (0.79) in 1994. Significant differences were found, however, among seral stages ($p < 0.001$; n = 47 ANOVA; Figure 1). Clearcuts accounted for 57% of all detections, while young, unthinned stands had none. Pre-commercially thinned and mature stands had

TABLE 1   *Means of vegetation characteristics for each seral stage where CC = clearcut, PCT = pre-commercially thinned, YU = young unthinned, and M = mature.*

Characteristic	CC $\bar{x}$(se)	PCT $\bar{x}$(se)	YU $\bar{x}$(se)	M $\bar{x}$(se)
Stumps				
<10 cm DBH	6.697 (0.504)	18.222 (5.375)	28.987 (5.654)	44.36 (7.016)
10–50 cm DBH, <1.5 m tall	5.873 (0.347)	6.307 (0.872)	5.013 (1.244)	2.027 (0.494)
>50 cm DBH, <1.5 m tall	23.692 (1.117)	10.807 (2.062)	11.923 (1.919)	8.063 (1.848)
Snags				
10–50 cm DBH, 1.5–15 m tall	0.057 (0.036)	0.318 (0.089)	0.582 (0.198)	2.585 (0.661)
>50 cm DBH, 1.5–15 m tall	2.448 (1.165)	3.128 (0.814)	1.075 (0.207)	1.268 (0.353)
10–50 cm DBH, >15 m	0	0.138 (0.068)	0.110 (0.051)	0.582 (0.218)
>50 cm DBH, >15 m	0	0.013 (0.013)	0	0.207 (0.076)
Standing trees				
Trees <10 cm DBH, >3 m tall	0.208 (0.148)	14.253 (6.716)	16.515 (6.298)	5.030 (1.000)
Trees 10–50 cm DBH, >3 m tall	0.013 (0.013)	13.388 (0.906)	22.193 (2.566)	6.653 (1.348)
Large dominant trees 50–100 cm DBH	0	0.142 (0.126)	1.652 (0.379)	18.67 (3.81)

intermediate detection rates accounting for 14% and 30% of all detections respectively. Overall, activity levels were low, with 46.2% of the nights having no detections.

Use of seral stages differed among species groups. We detected *Myotis* within all stand types except young, unthinned stands, but they were most often detected in mature stands. In contrast, detections in clearcuts accounted for the majority of non-*Myotis* detections (81%). Big brown bats, silver-haired bats and Townsend's big-eared bats were not recorded in mature stands. Of the six call categories, the *Myotis* group, Yuma myotis, and hoary bat were the only ones detected in all three seral stages where bat use was recorded. However, all 14 hoary bat detections within the mature seral stage were recorded in one site on the same night (Table 2).

Activity Patterns

Bat activity was not uniformly distributed throughout the night, with activity peaking during the first two hours following sunset. Within clearcuts, non-*Myotis* species gradually increased in activity and peaked between 2215 and 2245 h, followed by variable but consistently low activity (Figure 2a). This pattern was largely driven by detections attributed to the
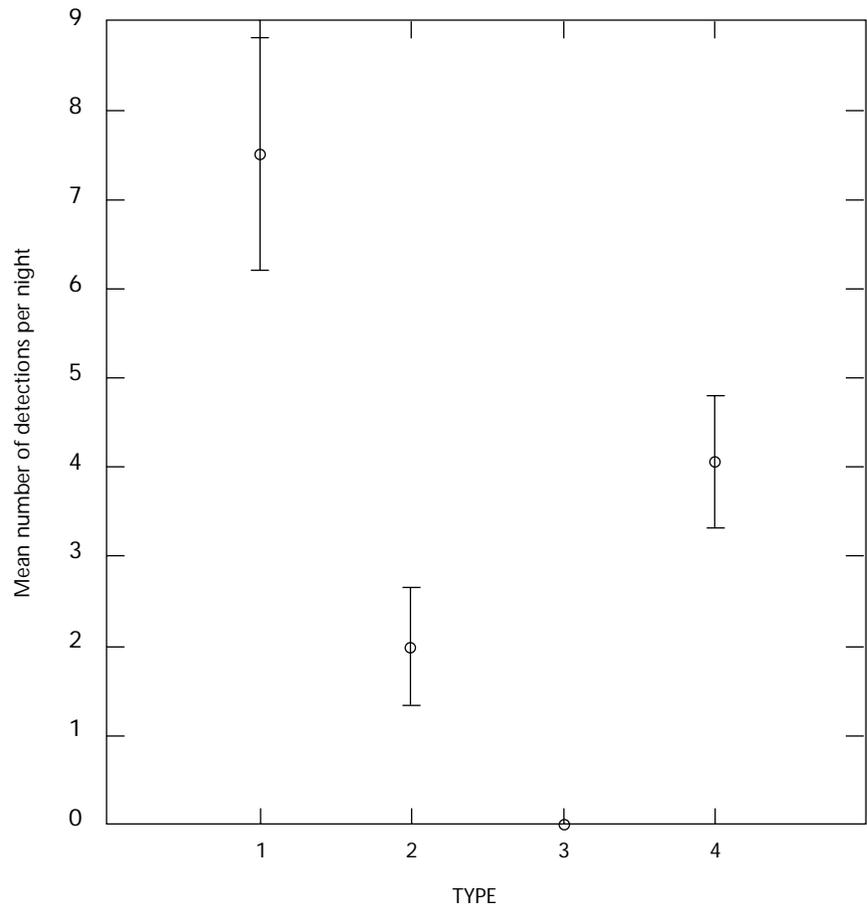

FIGURE 1 *Mean number of detections per night where 1 = clearcut, 2 = pre-commercially thinned, 3 = young unthinned, and 4 = mature stands.*

Mean detection rates for bats in clearcut (CC), pre-commercially thinned (PCT), young unthinned (YU), and mature (M) stands. Where ANOVA was significant, means not significantly different from each other are indicated with letters: α = 0.05).

Species	CC $\bar{x}$(se)	PCT $\bar{x}$(se)	YU $\bar{x}$(se)	M $\bar{x}$(se)
Big brown bat	0.808 (0.185)	0.031[a] (0.021)	0[a]	0[a]
Silver-haired bat	2.327 (0.627)	0.407[a] (0.164)	0[a]	0[a]
Townsend's big-eared bat	0.113[a] (0.056)	0.031[a] (0.021)	0[a]	0[a]
Hoary bat	0.587[a] (0.267)	0.150[a] (0.080)	0[a]	0.194[a] (0.194)
Myotis group	2.093[a] (0.580)	0.405[b] (0.157)	0[b]	1.959[a] (0.532)
Yuma *Myotis*	0.788[abc] (0.329)	0.394[ab] (0.210)	0[bc]	0.910[a] (0.224)
All *Myotis spp.*	1.107[ab] (0.262)	0.408[ac] (0.160)	0[c]	1.266[b] (0.248)
All non-*Myotis*	0.834 (0.200)	0.154[a] (0.061)	0[a]	0.053[a] (0.039)
Total	7.504[a] (1.300)	1.989[bc] (0.652)	0[b]	4.058[c] (0.738)

silver-haired bat. *Myotis* spp. followed a similar pattern, but peaked between 2145 and 2215 h (Figure 2b). Mature stands had elevated activity during the first hour after dusk (2045–2145 h), with a smaller secondary peak near sunrise (0515 h), while activity in pre-commercially thinned stands was more evenly distributed throughout the night (Figure 3).

Feeding activity was very low within all stands. Of the 967 detections, only 13 were identified as feeding activity. Clear-cut stands had the highest number of feeding buzzes (n = 10), which were recorded for both non-*Myotis* and *Myotis* spp. The three feeding buzzes detected in mature stands were all identified as *Myotis* spp.

DISCUSSION

Patterns of Habitat Use

Bat activity within a habitat is primarily related to the availability of foraging and roosting resources. Although commuting bats also contribute to activity levels, the differences in habitat use among seral stages observed in this study are likely related to the differential availability of these resources.

Patterns of activity of insectivorous bats have often been interpreted in relation to the availability of prey (Kunz 1973; Erkert 1982). Several studies have documented insect abundance to be higher in clearings than in
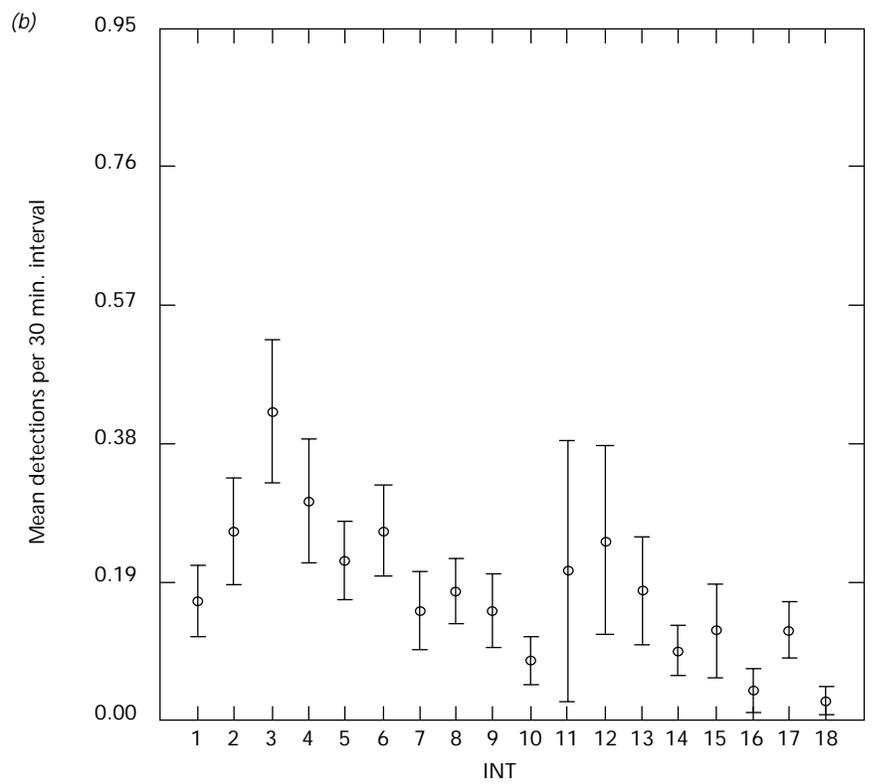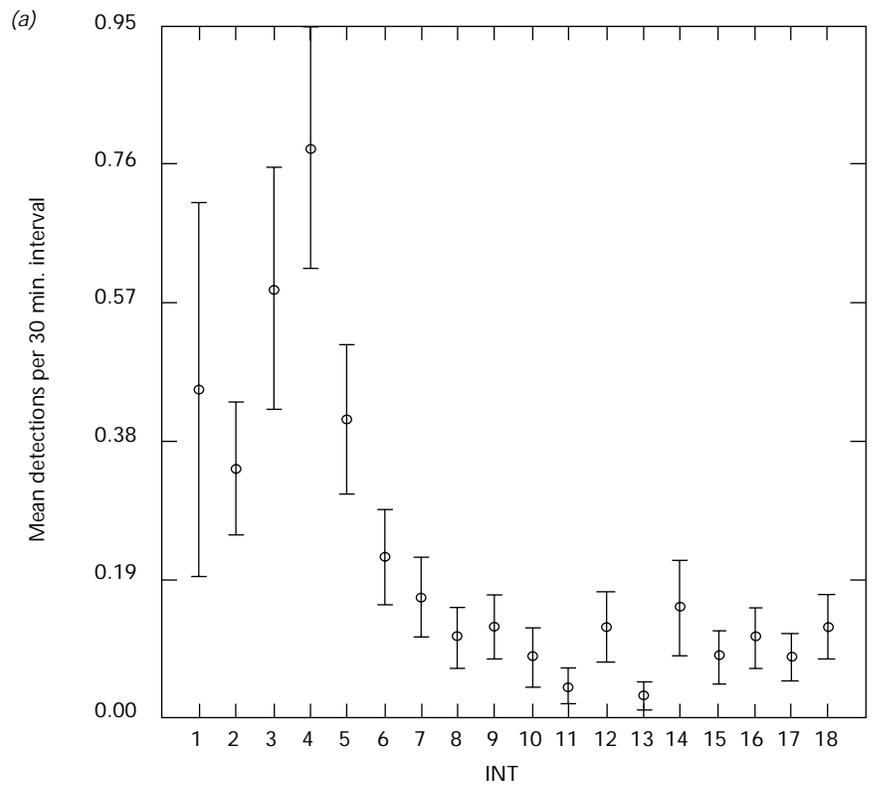
(a)

(b)

FIGURE 2 *Mean number of detections per interval in clear-cut stands for (a) all non-*Myotis *bats and (b) all members of the genus* Myotis.
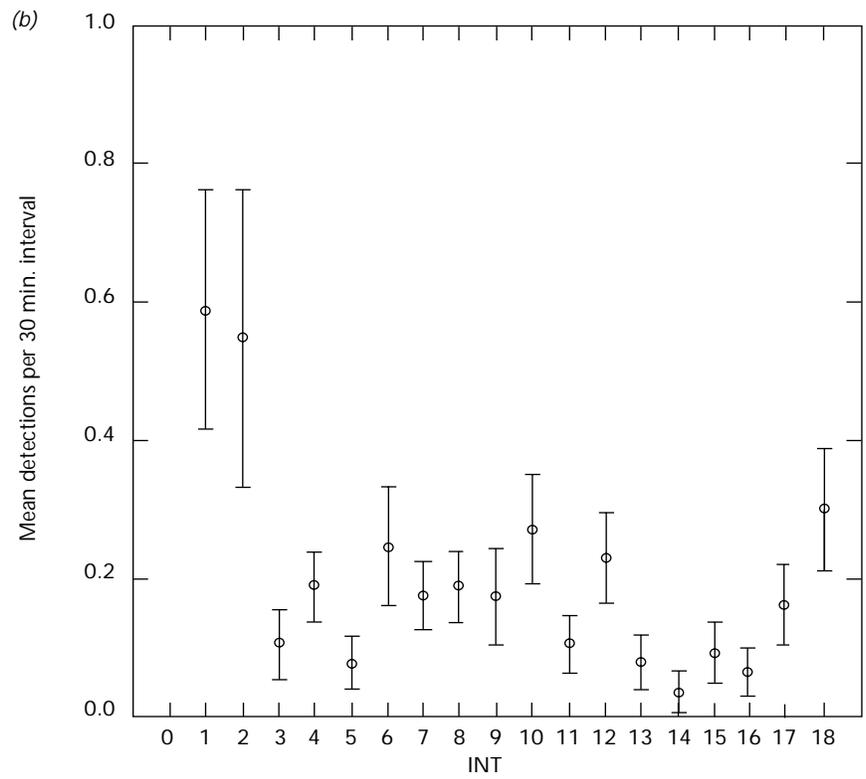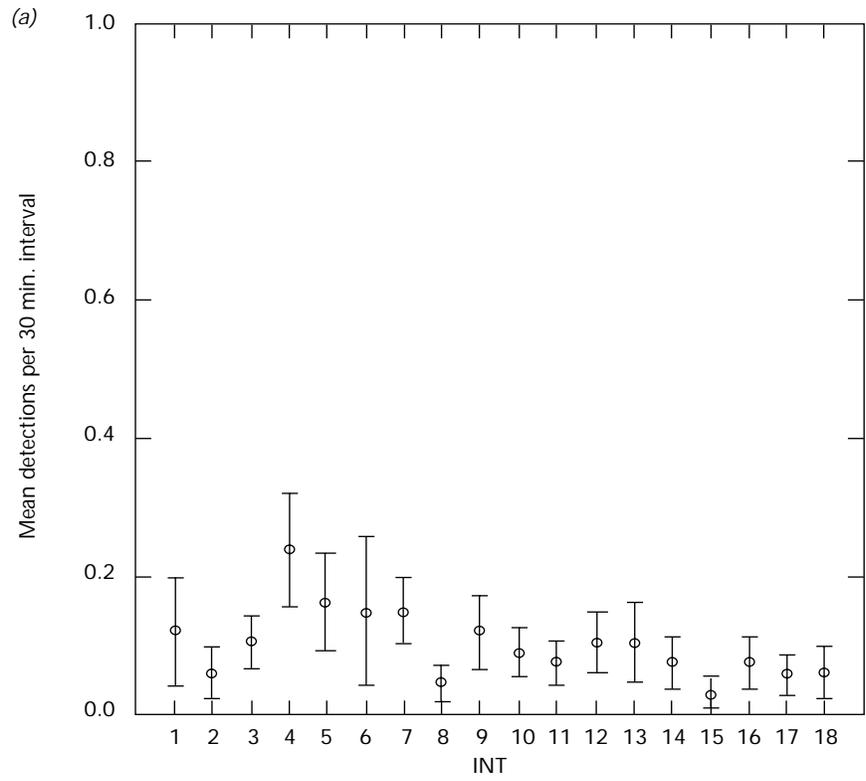
(a)

(b)

FIGURE 3 *Mean number of detections per interval in (a) pre-commercially thinned and (b) mature stands.*

surrounding habitats (Lunde and Harestad 1987; de Jong 1994). Within this context, the high detection rate, presence of feeding buzzes, and low abundance of roosting structures within clear-cut stands suggest these sites were used for foraging.

Although we detected bats in each call category, other studies have documented the avoidance of clearings by certain species. When de Jong (1994) compared habitat preferences of four species of bats in Uppsala, Sweden, two of them (*M. brandti* and *M. nattereri*) were found to significantly avoid open habitats. Similarly, in British Columbia, Lunde and Harestad (1986) found that *Myotis lucifugus* avoided clear-cut areas. In general, smaller species of bats closely follow edges and avoid open areas, whereas larger species readily use clearings (Limpens et al. 1989). The grouping of species (i.e., *Myotis* group) during call analysis in this study masks individual species' response to clearcuts, but at least some species of *Myotis* used clear-cut stands frequently.

The pre-commercially thinned and young, unthinned seral stages had little or no activity. The absence of activity in young, unthinned sites indicates that these stands are unsuitable habitat for forest-dwelling bats. Although a high density of snags was present, these were typically small-diameter Douglas-fir whose lack of crevices and hollows make them unlikely roost sites. In addition, tree density within these stands may be too high for most bat species to negotiate given the limitations of their sonar systems and flight capabilities. Such impediments to flight may be particularly challenging to newly volant bats (Constantine 1966).

Mature sites had the second-highest detection rates, and were the only seral stage to have a secondary peak in activity during the early morning hours. This activity pattern is similar to that described by Thomas and West (1991) for old-growth stands (185–200+ yrs) of the southern Washington Cascades. They concluded that these peaks of activity after sunset and before sunrise, coupled with low foraging rates, indicated that bats were dispersing away from roosts located in old-growth and commuting elsewhere to feed. If Thomas and West's interpretation of the observed activity patterns are accurate, it would appear that at least *Myotis* spp. can also roost in mature second growth. Large trees (50–100 cm DBH) and snags (>50 cm DBH and >15 m tall), which are "roost-type" trees for certain species in Washington (Christy 1993; Campbell 1993), were most abundant in these stands. Suitable roosting conditions may not be present for all forest-dwelling species, however, as infered by the absence of calls for the big brown bat and silver-haired bat within the mature stands.

Unfortunately, specific roost characteristics of forest-dwelling bats are poorly known, and it is currently impossible to measure roost availability within the mature stands for most species (but see Campbell 1993). With recent advances in the miniaturization of radio-transmitters, however, radio-tracking of small bats has become feasible and presents the only practical means of gathering information on roost-site characteristics. Results from recent radio-telemetry studies in the Pacific Northwest (Christy 1993; Campbell 1993) concur with findings in other regions of the world, with bats preferentially roosting in the largest and oldest trees available (Taylor and Savva 1988; Lunney et al. 1988; this volume). These results suggest that retention and recruitment of appropriate snags in managed forests may prove effective in encouraging bat presence in other-

wise unsuitable habitat. More radio-tracking studies are needed, however, to provide additional information on roost-site characteristics and the availability of appropriate roosts in second-growth forests.

Because bats are highly mobile animals, restricting interpretation of habitat selection to the stand level will limit our understanding of bat habitat associations. Consideration must also be given to the influence of the surrounding landscape. Reduction in forests having large snags and trees will not only affect roost availability, but may also increase the distance between roosting, foraging, and drinking sites. The additional energy costs of increased travel may be of particular importance to reproductive females (Kunz 1987). As forests are fragmented, certain species that avoid crossing large openings when foraging or commuting (Limpens and Kapteyn 1991) may be restricted from accessing distant resources. For some bat species, corridors have proven valuable, not only as hunting habitats, but also as travel corridors between roosting and foraging areas (de Jong 1994). The spatial patterns and corridors among stands will be an important consideration in designing future landscapes appropriate for bats.

Limitations of Ultrasonic Detection

Although ultrasonic detection has been used successfully in the field to identify bats based on species-specific call characteristics (Fenton 1970; Fenton and Bell 1981; Fenton 1982), it is important to emphasize that this technique relies on several assumptions: that species will consistently use the same call under a variety of conditions, that calls are equally detectable in different habitats, and that comparisons to reference recordings obtained from a limited geographic region are sufficient to identify field detections over broader regions. Evidence suggests that some bats may vary properties of their calls under different environmental conditions (Schrumm et al. 1991) and across geographical regions (Thomas et al. 1987). To date, variation in call structure is poorly understood, but call variability seems sufficiently high to warrant caution in species identification. Future call analysis will be facilitated by obtaining high-quality reference recordings from multiple individuals of each species under a variety of environmental conditions to determine the extent of natural variation present. Such a library is currently being compiled by the authors and other researchers for bats of the Pacific Northwest. In spite of its limitations, ultrasonic detection is rapidly becoming a valuable tool for surveying free-ranging bats. It is the most appropriate method for assessing patterns of distribution and activity on a large scale, and eliminates many of the problems associated with extracting ecological data from trapping studies (Thomas and West 1989).

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The Influence of Logging Riparian Areas on Habitat Utilization by Bats in Western Oregon

JOHN P. HAYES AND MICHAEL D. ADAM

ABSTRACT

We monitored bat activity using Anabat II bat-detector systems in three riparian areas that had partially been clear-cut logged in western Oregon. Total bat activity averaged 4.1 to 7.7 times higher in wooded areas than in adjacent logged areas. Activity in wooded areas was almost exclusively *Myotis* species; non-*Myotis* species, especially *Lasionycteris noctivagans*, accounted for a substantial amount of the activity in logged habitats. Different levels of activity between the habitat types could be the result of differences in insect prey populations in the two habitats. More Lepidopterans, more large-bodied insects, and fewer small-bodied insects were captured in the wooded habitat than in the logged habitat. Differences in bat-community composition in the two habitats could be due to differences in the morphology and echolocation call structure of the bat species. Other hypotheses that might explain differences in activity include differences in risk of predation, competitive interactions, or behavioural or evolutionary constraints. Our findings indicate that forest-management activities in riparian areas can influence patterns of habitat use by bats.

INTRODUCTION

Many species of bats use riparian areas. The importance of riparian areas to bats, especially *Myotis* species, as foraging habitat has been documented in several studies (e.g., Brigham et al. 1992; Furlonger et al. 1987; Lunde and Harestad 1986; Thomas 1988; Thomas and West 1991). Bats also depend on riparian areas as a source of free water for drinking (Cross 1988). Despite the importance of riparian areas to bats, there is little information documenting the influence of alteration of riparian habitat on bat populations. Kurta and Teramino (1992) suggested that urbanization results in decreased activity of bats over riparian areas. There is almost no information available concerning the influence of forest-management activities in riparian areas on bats (Christy and West 1993).

In western Oregon, extensive management activities are being implemented or considered in forested riparian areas. Much of the focus of riparian-area management in the Pacific Northwest is ecological restoration

aimed at enhancing or restoring anadromous fish habitat; anadromous fish may be keystone species in Pacific Northwest aquatic systems (Willson and Halupka 1995), and have declined or become extirpated in several stream systems (Frissell 1993). Following historic logging activities, many riparian areas in western Oregon were recolonized by red alder (*Alnus rubra*) that may be succeeded by shrub communities (Hibbs 1987). Neither alder- nor shrub-dominated riparian areas in western Oregon are likely to provide the long-term input of large woody debris into streams necessary to provide high-quality freshwater habitat for anadromous fish. In contrast, riparian areas with large conifers are likely to provide adequate inputs of woody debris to provide quality fish habitat. One of several proposed strategies to establish conifers in alder-dominated riparian areas is to clear-cut patches to the stream edge, and plant conifers in the clearcuts.

In this paper, we examine influences of logging in riparian areas on activity of bats in western Oregon.

METHODS

We selected three, third-order streams in western Oregon for study: Bark Creek (T11S R7W Sect. 30; 44° 35′N, 123° 35′W) and Buttermilk Creek (T10S R8W Sect. 31; 44° 40′N, 123° 42′W) in the Coast Range Mountains, and Ames Creek (T14S R1E Sect. 9, 10, and 15; 44° 38′N, 122° 41′W) in the western foothills of the Cascade mountains. Clear-cut logging was conducted at the study sites during spring and early summer 1993. At Bark and Buttermilk creeks, clearcutting was conducted along 90 m of the stream and in the adjacent upslope forest stand; at Ames Creek clearcutting was conducted along 180 m of the stream and in adjacent upslope forest stands. Overstorey vegetation in wooded portions of the riparian areas is dominated by red alder with scattered big-leaf maple (*Acer macrophyllum*) and occasional conifers.

At each study site, we established one station to monitor bat activity in wooded habitat and one in logged habitat. The two stations were equidistant from the forest-clearcut edge. We chose locations along the streams to maximize reception of bat echolocation calls, avoiding areas with sharp bends in the stream and areas with vegetation that might obstruct sound reception. Distances from the stations to the habitat edge varied from 40 to 75 m. Each monitoring station was situated within 3 m of the stream, with the detector microphone oriented along the major axis of the stream.

We monitored bat activity using an Anabat II bat-detector system according to methods described by Hayes and Hounihan (1994). With this system, bat echolocation calls, the time of night, and a calibration tone are recorded on audio tape as bats fly over or near a monitoring station. Bat detectors were set at a sensitivity of six to minimize stream and insect noises and to minimize detecting bats flying in adjacent habitats.

Because of substantial temporal variation in bat activity between nights, we paired activity by night in our comparisons. We eliminated nights when detectors at one or both stations malfunctioned and nights when rain or insect noise filled audio tapes at one or both monitoring stations before the end of the night. Bat activity was successfully monitored over both the

logged and wooded sections of the stream for 12 nights between 9 August and 2 September 1993, and 9 nights between 9 May and 7 September 1994 at Bark Creek; for 15 nights between 28 July and 23 September 1993, and 13 nights between 9 May and 14 September 1994 at Buttermilk Creek; and for 6 nights between 30 August and 7 September 1994 at Ames Creek. Because of high levels of bat activity, audio tapes from the wooded area at Bark Creek were filled with bat calls by 2320 h on 10 May 1994 and by 0332 h on the night of 7 July 1994; we used data on bat activity for the portion of these nights when both detector systems were operational.

We randomly selected 10 nights from Bark Creek and 10 nights from Buttermilk Creek to assess taxon-specific responses in activity levels to habitat structure. We used the Anabat computer software program (version 4.2a) to examine time-frequency plots of echolocation pulses recorded on these nights to attempt to classify bat calls taxonomically. Due to considerable overlap in the characteristics of echolocation pulses emitted by species of bats in this geographical region (Hayes and Cross, unpublished data), we did not attempt to classify calls by species. We classified calls as *Myotis* or non-*Myotis* on the basis of the shape and frequency of echolocation pulses.

To supplement the echolocation data, we set mist nets at various locations for five nights at Bark Creek. We identified and released all captured bats at the site of capture.

We sampled insect populations using 10-watt, black-light traps (Bioquip, Santa Monica, California) powered by 12-volt gel cells. We set a 12-volt timer (Real Goods, Ukiah, California) so that the traps would operate for a three-hour period beginning 30 minutes after official sunset. Insects were collected in alcohol. We positioned traps in the forested and logged habitats approximately 10 m from the bat-monitoring stations, about 1.5 m off the ground. Insect populations were sampled between 10 August and 15 September 1994 for 9 nights at Bark Creek and for 7 nights at Buttermilk Creek. We identified the insects we collected by order and tallied them by body length into one of three size classes: 0 to 5 mm, 5 to 10 mm, and over 10 mm. Insects were oven-dried for at least 24 hours and weighed.

To account for temporal variability in insect data, we paired data by night. We performed a paired *t* test using PROC MEANS of the SAS statistical software package for personal computers (version 6; SAS Institute, Inc. 1985) to test whether the difference between the number or biomass of insects captured in the two habitat types was significantly different from zero. Because of small sample sizes, some size classes were combined for analysis.

RESULTS

Total Bat Activity

More echolocation calls were recorded in the forested habitat than in the logged habitat at each study site. The number of calls recorded in a night in the forested habitat averaged 7.7 times higher than those recorded in the logged habitat at Bark Creek (Figure 1a), 4.7 times higher at Buttermilk Creek (Figure 1b), and 4.1 times higher at Ames Creek (Figure 1c).
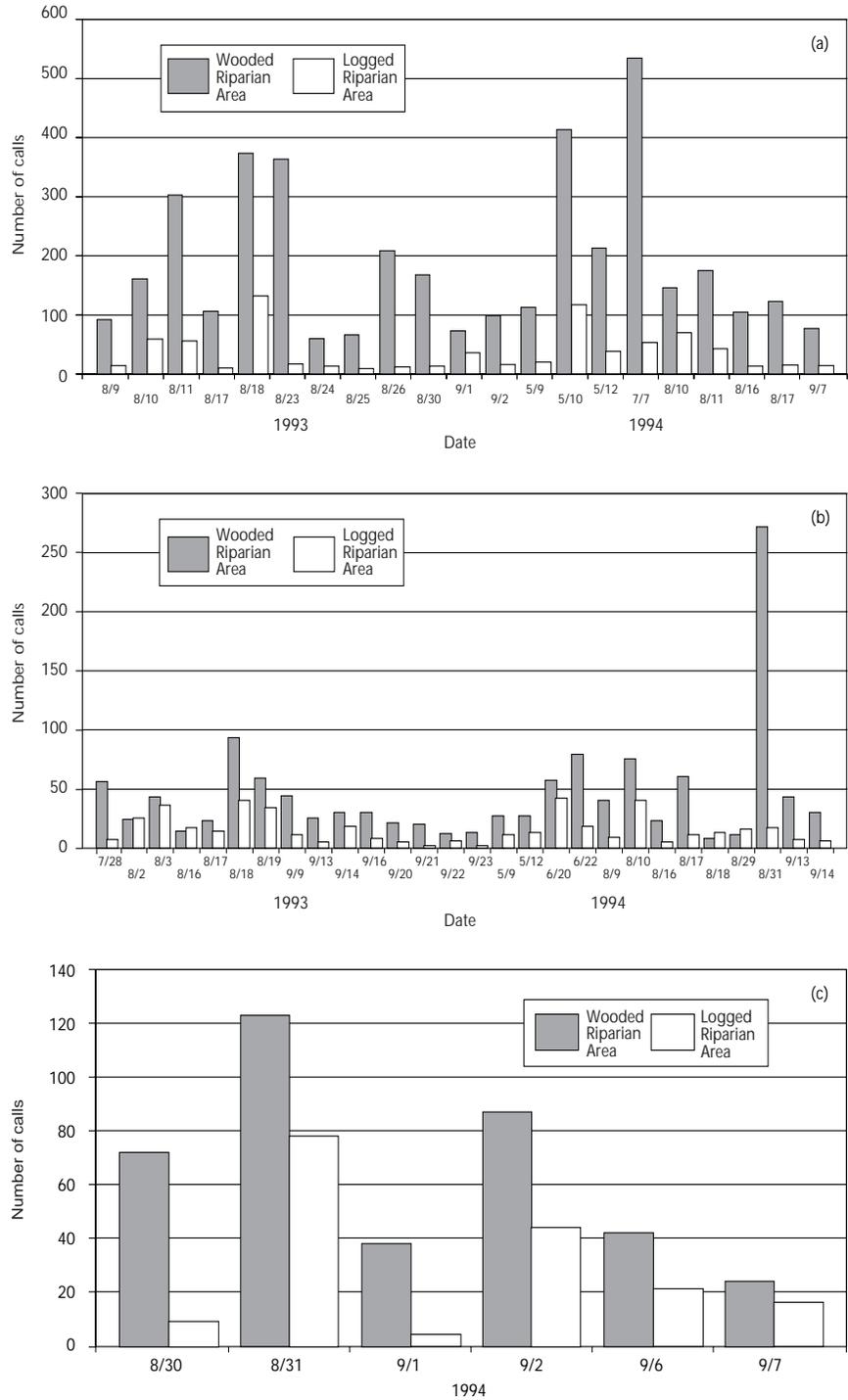
FIGURE 1   *Total number of bat calls recorded in wooded and logged habitat at (a) Bark Creek, (b) Buttermilk Creek, and (c) Ames Creek.*

The number of calls recorded in the wooded habitat exceeded those in the logged habitat during all nights at Bark Creek and Ames Creek, and during 24 of 28 nights at Buttermilk Creek. On each of the four nights for which greater number of calls were recorded in the logged habitat at Buttermilk Creek (2 and 16 August 1993, 18 and 29 August 1994), extremely low levels of activity were recorded in the wooded habitat, whereas numbers recorded in the logged habitat on those nights were more typical. Activity levels in the wooded habitat during two of these nights (18 and 29 August 1994) were the lowest ever recorded in wooded habitat during this study.

Levels of activity varied substantially between nights. Activity levels on consecutive nights in the wooded habitat varied by a factor of 6. For example, numbers of bat calls recorded on four consecutive nights (23 to 26 August 1993) in the wooded habitat at Bark Creek were 363, 59, 65, and 208. Relative differences in activity in the logged habitats were even greater, although the absolute differences were smaller. Activity levels on non-consecutive nights varied even more. The number of calls recorded in the wooded habitat varied from 7 to 270 at Buttermilk Creek and from 24 to 123 at Ames Creek. The minimum number of calls recorded in the wooded habitat at Bark Creek was 59; 413 calls were recorded by 2320 h on 10 May 1994, and 534 calls were recorded by 0332 h on 7 July 1994 when the tapes were filled at the wooded habitat at Bark Creek.

Although we did not collect detailed or quantitative data on behavioural patterns of bats using the wooded and logged habitats, anecdotal observations suggest that bats were functionally using the habitat types differently. Bats in the wooded habitat were frequently seen travelling in one or more circuitous routes through the wooded riparian area; an individual bat would repeatedly travel this pathway several times before leaving the immediate vicinity. In contrast, the bats that were occasionally seen in the logged habitat did not have a similar flight pattern. *Myotis* bats observed in the logged habitat apparently flew through the logged habitat *en route* from one wooded area to another. We did not observe a sufficient number of non-*Myotis* bats to comment on their behaviour patterns.

Species-Specific Responses

In the 10 nights at Bark Creek and 10 nights at Buttermilk Creek for which echolocation calls were classified as *Myotis* or non-*Myotis*, there were a total of 2,434 calls; 1,637 of these were of adequate quality to be taxonomically classified (Table 1). Of 1,263 identifiable calls in the wooded habitats, only 1 (<0.1%) was identified as non-*Myotis*. This call was probably emitted by a *Lasionycteris noctivagans*. Non-*Myotis* calls were more prevalent in logged habitats; 6.2 and 29.4% of identifiable calls in the logged habitats at Buttermilk Creek and Bark Creek, respectively, were emitted by species other than *Myotis*. The majority of these calls appeared to be from *Lasionycteris*, but some may have been from *Eptesicus fuscus* or *Lasiurus cinereus*.

Mist Netting

We captured 18 bats during 5 nights of mist-netting on Bark Creek: 6 California *Myotis* (*Myotis californicus*), 5 Yuma *Myotis* (*M. yumanensis*), 3 little brown *Myotis* (*M. lucifugus*), 1 long-eared *Myotis* (*M. evotis*),

1 long-legged *Myotis* (*M. volans*), and 2 silver-haired bats (*Lasionycteris noctivagans*).

Insect Abundance

A total of 2,021 insects were captured in the light traps (Table 2). The number and biomass of insects we captured differed between the wooded and logged habitat for some orders and size classes. In general, insects with body lengths greater than 5 mm were more abundant in wooded habitats and those with body lengths less than 5 mm were more abundant in the logged habitats. Lepidopterans were more numerous and contributed more biomass in wooded habitats than in logged habitats, although the biomass for large Lepidopterans did not significantly differ among the habitats.

TABLE 1 *Number of bat calls classified as* Myotis, *non-*Myotis, *or unidentified, recorded during 10 nights at Bark Creek and 10 nights at Buttermilk Creek.*

Study site	Habitat	*Myotis*	non-*Myotis*	Unidentified	Total
Bark Creek	wooded	971	1	434	1406
Bark Creek	logged	161	67	101	329
Buttermilk Creek	wooded	291	0	182	473
Buttermilk Creek	logged	137	9	80	226

TABLE 2 *Number and biomass of insects captured in light traps at Bark and Buttermilk creeks.*

Order	Size (mm)	Logged		Wooded	
		Number	Biomass (g)	Number	Biomass (g)
Lepidoptera	<10	34	0.100	77***	0.276**
	>10	108	2.981	165**	4.036
Diptera	<5	532	0.063	470	0.066
	>5	21	0.045	17	0.047
Coleoptera	<5	386**	0.132**	24	0.042
	>5	4	0.370	9	0.463
Trichoptera	<5	17*	0.016	2	0.005
	>5	29	0.151	57*	0.352
Hymenoptera	<10	7	0.015	7	0.001
	>10	18**	0.559	3	0.174
Other[a]	all sizes	19	0.017	15	0.020
Total	<5	959**	0.236***	516	0.126
	5–10	76	0.205	140**	0.414*
	>10	140	4.011	190*	4.944

[a] Includes the orders Homoptera, Hemiptera, Ephemeroptera, Neuroptera, Collembola, and Psocoptera.

Asterisks next to a number denote that the value is significantly larger than the corresponding value from the other habitat type at $p < 0.10$ (*), $p < 0.05$ (**), or $p < 0.01$ (***).

Bat Response to Logging

Logging substantially reduced the total amount of bat activity in riparian areas. The magnitude of the influence that logging had on bat activity at these sites was unexpected for two reasons. First, the size of the disturbance (90 or 180 m of stream) is relatively small in relation to the distances that bats travel in the course of a night. Second, the species of bats using these riparian areas are widespread and use geographically and ecologically diverse habitats. The species at our study sites occur in more open habitats in other areas, including over large streams that have minimal cover from adjacent vegetation, and in very open areas, including deserts.

Decreased activity of *Myotis* species in the logged habitat might partially be explained by differences in insect populations. Observations of greater levels of foraging activity over riparian areas than in adjacent upslope areas (Lunde and Harestad 1986; Thomas 1988; Thomas and West 1991) has led to speculation that open water may be critical foraging habitat for some species of bats in Pacific Northwest forests (Christy and West 1993). Assessing insect availability is problematic, and any insect sampling method has biases (Kunz 1988; Whitaker 1994). Although sampling biases complicate interpretation of the insect data, our data suggest that insect populations differ between the two habitat types. In general, large insects appeared to be more abundant in the wooded habitat than in the logged habitat. In addition, size classes of some insect taxa significantly differed between habitats. Large Trichopterans and Lepidopterans of all size classes were more abundant in the wooded habitat than in the logged habitat. Lepidopterans are a major component of the diet of all species of *Myotis* in our study area, and Trichoptera was identified as a component of the diet of *M. lucifugus* and *M. californicus* in western Oregon (Whitaker et al. 1977).

The differences in the proportions of *Myotis* and non-*Myotis* calls in the two habitat types indicate that the influence of habitat alterations differs among bat taxa. Activity levels of *Myotis* species are substantially reduced following clearcutting of alder-dominated riparian areas along small streams. In contrast, activity levels of non-*Myotis* species, primarily *Lasionycteris*, were considerably higher in the logged habitat than in the wooded habitat. The interaction between habitat structure and differences in the morphology and echolocation call structure of the bat species may partially explain differences in activity levels of different bat species in the wooded and logged habitats. The morphology and typical echolocation calls emitted by *Lasionycteris noctivagans* allows it to forage more effectively than *Lasiurus cinereus* for small prey over short distances (Barclay 1986), but *L. noctivagans* is probably a less effective forager in densely forested, highly cluttered riparian areas than are the smaller-bodied *Myotis* species using steep-frequency, modulated echolocation calls (Neuweiler 1989).

Other factors that may have influenced habitat-related differences in activity levels include competitive interactions among bat species, behavioural or evolutionary constraints, and relative risk of predation. Demonstrating specific causal effects would be difficult at best.

Bat populations responded to the habitat alterations relatively rapidly. We began monitoring bat activity at Bark Creek and Buttermilk Creek

within two to three months of when logging was completed. Dramatic differences in activity levels between the two habitat types were evident from the onset of our monitoring, and the differences persisted for at least two years. Longer-term responses are not known. It is likely that differences in activity levels will persist for several years until trees in the logged habitat attain sufficient height to allow bats to fly beneath the tree canopies, but this remains speculative.

Scope and Limitations

Bat detectors are useful tools to assess activity levels of bats, but have limitations that must be understood to interpret the results. First, the number of bats using an area is not directly measured; the data provide only an index to activity. Second, the sensitivity of bat detectors differs among bat species because of species-specific differences in intensity and frequency of calls. Comparisons can be made between habitats within a taxon, but the data may provide only a poor estimate of relative activity levels between taxa. In addition, habitat structure may influence receptivity of bat detectors; highly cluttered environments may impede sound transmission resulting in relatively fewer detections for a given level of activity. The degree to which this influences comparisons of bat activity between habitats is not known. In our study, habitat-related differences in detector receptivity were probably of minor or no influence as the bat detectors were oriented towards relatively open areas over streams in both habitats. If habitat structure influenced detector receptivity in our study, receptivity would be greater in the less cluttered, logged habitats. Our estimates of differences in total activity and activity of *Myotis* species between habitat types would be conservative; differences in estimates of activity for non-*Myotis* species between habitat types could be inflated. Finally, temporal variation in bat activity along streams is high. We accounted for temporal variation in our study by pairing all comparisons by night.

Our ability to reliably classify bat echolocation calls by species is hampered by high variation in echolocation pulse characteristics emitted by bats within a species, and by considerable overlap in characteristics of pulses emitted by different species (Hayes and Cross, unpublished data). Intraspecific variation in calls may also result from differences in foraging habitat (Brigham et al. 1989); if substantially different call structures are used in the more open, logged habitat versus the more cluttered, wooded habitat, classification of echolocation calls would be confounded and could result in misclassification of some calls. Further taxonomic resolution could reveal additional patterns that have important management and conservation implications.

All of our work was conducted on third-order streams with alder-dominated riparian areas in the Oregon Coast Range. Results from larger streams, conifer-dominated riparian areas, or other geographic areas might be different. Although we have not formally studied other systems, anecdotal observations suggest that habitat alteration of larger streams and conifer-dominated riparian areas would influence bats differently than those we reported here. In comparison to the systems we examined, bats seem to use more strata in riparian areas dominated by conifers along larger streams, the physical structure in these streams do not impose the same limitations for large-bodied and fast-flying bats, and most of the activity along large streams appears to be in areas that are not covered by

forest canopies. In the absence of research, it is difficult to speculate how bats would respond to habitat alterations in these systems.

Conservation and Management Implications

Our findings indicate that forest-management activities in riparian areas can have important consequences for patterns of habitat use by bats. The population-level consequences of decreased activity levels resulting from clear-cut logging of riparian areas are not clear. However, if the practice was widespread, it is likely that populations of some species of bats would be affected.

The influence of management activities on one resource, species, or community must be weighed against its influence on others. Riparian-area restoration activities may be an important component of plans to improve the long-term survival of anadromous fish runs in the Pacific Northwest. Benefits to one species or resource must be weighed against possible impacts on other species, including bats, in developing management strategies.

Future Research

Clear-cut logging represents one end of a spectrum of forest management activities being considered or implemented in riparian areas. We plan to begin additional research to examine the influence of other forest management activities, such as thinning riparian-area forests and maintenance of different sizes of uncut buffer strips along streams, on bat activity.

Finally, this work represents one piece of a host of studies we are conducting to examine the influence of forest management activities on bat populations in the Oregon Coast Range. Additional work on temporal variation in activity patterns, use of day and night roosts, foraging patterns of bats, and the influence of forest management on these activities are underway or planned for the near future.

ACKNOWLEDGEMENTS

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Habitat Selection by Bats in Fragmented and Unfragmented Aspen Mixedwood Stands of Different Ages

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ABSTRACT

To determine if bats prefer certain ages of aspen mixedwood forest for roosting and foraging, and to predict the impacts of logging on bats, we compared the relative abundances and foraging activities of bats in young, mature, and old stands in 1993 and 1994, using bat detectors. In 1994, we also assessed post-logging bat abundances in two of the mature and two of the old stands. We tracked radio-tagged *Myotis lucifugus* and *Lasionycteris noctivagans* to roost trees, which we measured and compared to a random sample of wildlife trees. Mean total activity of all bats was significantly greater in old than in young or mature stands. It also appeared greater in unfragmented than fragmented stands, but not significantly so. All 27 roost trees were in old forests. Bats preferred tall (mean: 22.0 m), newly dead *Populus* spp. with heart rot and low leaf cover (mean: 27%). Tree-roosting colonies were small (4–63 bats) and transient. Bats likely select trees large enough to house colonies and provide suitable temperatures, and these trees are only available in old stands. Roost preference likely explains observed activity patterns. To sustain bat populations in these forests, old stands must be retained and roost sites preserved by managing the forest at the stand level.

INTRODUCTION

Habitat selection by bats is generally considered to be driven by roosting and foraging requirements (Fenton 1990) and may be the product of interactions between the two (Kunz 1982). The availability of suitable roost sites is likely a primary factor in determining a bat's choice of a habitat (Kunz 1982). Bats choose roosts that provide protection from predators (Fenton et al. 1994), and suitable thermal environments, given metabolic and reproductive demands (Hamilton and Barclay 1994). Foraging habitat may be dictated by the morphology and echolocation call type of bats; some bats cannot forage in highly cluttered environments and must forage in more open areas (Aldridge and Rautenbach 1987; Norberg and Rayner 1987). Within this limitation, prey availability is probably the

strongest influence on habitat selection (Fenton 1990; Saunders and Barclay 1992), and competition (Fenton 1990) or predation (Barclay 1989) are likely not as important.

Roost availability may influence foraging habitat, leading some bats to forage in poorer-quality habitat (Geggie and Fenton 1985), particularly if commuting is costly, but there is some evidence that bats travel long distances from roosts to foraging grounds (e.g., Brigham 1991; de Jong 1994). Unfortunately, few studies examine the relative influences of foraging and roosting requirements on habitat selection by bats or look at differences within habitats, such as forests, although forests potentially provide both roosting and foraging opportunities to bats.

Forests differ in structure and composition with age, location, and disturbance. In particular, because forests of different ages may vary in stem density (Thomas et al. 1988) and openness of the canopy (Oliver and Larson 1990; Lee et al. 1995a), and thus clutter, they may differ in their suitability as foraging habitat for bats. Roosting opportunities may also depend on forest age, as the number of trees of appropriate size (Mannan et al. 1980) and decay, and the number containing cavities (Rosenberg et al. 1988; Newton 1994) and other shelter for bats, may differ. Bats, therefore, may prefer certain forests over others. For example, there is evidence that bats prefer older forests to younger ones (Perkins and Cross 1988; Thomas 1988). Disturbances within forests may influence bat habitat selection in that they create openings for foraging (e.g., Crome and Richards 1988), but also remove potential roost trees.

The effects of major disturbances, such as commercial harvesting, on bats are potentially two-fold. First, in the short term, forest fragmentation may create more open areas, particularly edge habitat, for foraging, but may cause a loss of roost trees. Second, forest harvest may truncate the age distribution of the forest by selectively removing older trees, and thus may represent a loss of preferred habitat, especially for roosting. The overall effects of fragmentation may reflect a combination of the predicted negative impacts on the availability of roost trees, and possible improvements to foraging habitat.

Historically, anthropogenic disturbances in the aspen mixedwood forest of northern Alberta were limited to roads and seismic exploration (Stelfox 1995). However, much of the aspen mixedwood forest in Alberta was recently allocated to timber harvest companies. Current harvest practices, which generally involve clearcutting, impose a 70-year rotation on the forest (Stelfox 1995). Approximately 20% of the forest to be harvested is older than 70 years (Alberta Forestry, Lands and Wildlife 1985). It is predicted that a change in age structure will occur in these forests due to logging (Stelfox 1995), and thus there is some concern for the future of bat populations.

The aims of our study were, therefore, (1) to determine whether bats are found primarily in certain ages of aspen mixedwood forest, and whether their use of the forest for foraging and roosting varies with stand age; and (2) to determine the immediate impact of forest fragmentation on bat abundance, roosting, and foraging. This study is unique in that it is one of the first studies to examine bat habitat selection in forests on the basis of both foraging and roosting criteria, and to study bat abundance and behaviour in the same stands pre- and post-logging. By considering

these factors, we can gain a better understanding of the use that bats make of the boreal forest, and of general principles of bat habitat selection that we can use to recommend the preservation of forest features essential to bats.

METHODS AND MATERIALS

We conducted this study in the aspen mixedwood forest to the northwest and northeast of Lac La Biche, Alberta, between 54° and 55°N, and 111° and 113°W. This forest is dominated by *Populus tremuloides* (trembling aspen), and *Picea glauca* (white spruce) in upland mesic areas. The range of ages currently found in the forest is 0–150+ years, with few young stands (Stelfox 1995).

In the summers of 1993 and 1994, we worked in or near 12 pyrogenic stands selected by the Alberta Environmental Centre (AEC): four young (20–30 yrs), four mature (50–65 yrs), and four old (>120 yrs; Stelfox 1995). Each stand contained six randomly placed sites of 100 m radius. Thus, the design included four stands of six sites in each age, or 72 sites in total.

Effect of Stand Age and Fragmentation on Bat Abundance and Foraging

In 1993, no harvesting had occurred in the area. In the winter of 1994, two mature stands and two old stands were fragmented by logging: half the sites in each of these stands (3 of 6 sites) were incorporated into approximately 30-ha clearcuts. The remaining mature and old stands, and all the young stands, were left intact as controls. "Logging" refers to the removal of trees at the *site* level, and "fragmentation" refers to the removal of trees from certain parts of *stands*. "Unfragmented" refers to the control stands that were left intact in 1994.

In each summer, we sampled one site per night, randomizing the site order, but ensuring that we monitored at least one site per stand in every four-week period. In 1994, we also ensured that we monitored one logged site each week. To evaluate bat diversity, abundance, and activity in each site, we identified and counted bat echolocation passes using QMC bat detectors during a two-hour period beginning 15 minutes after sunset. To differentiate between species groups, we set one detector at 25 kHz and one at 40 kHz. The number of passes detected per unit time, or bat activity, is an index of the relative use of, or abundance in, each site, and can be compared among sites (Thomas 1988).

In each site, we established a transect through the site centre, along which we monitored activity at stations for 20-minute periods. In unlogged sites, this transect crossed areas of differing canopy cover. In logged sites in 1994, we sampled three habitats: centre of the cutblock, edge of the cutblock, and forest surrounding the cutblock. We located the site centre (now in the clearcut) and identified the nearest edge, usually 100–250 m away. We then established a sampling position 50 m into the forest (perpendicular to the edge). We monitored bat activity at the centre of the cutblock for 20 minutes, while our assistant monitored activity in the forest. We then monitored at the edge for 20 minutes before returning to our original positions. This cycle continued for the two-hour monitoring period. Both 25 and 40 kHz were monitored at all times. In half the sites

in each age, we started the monitoring cycle at the edge, and in the other half, in the centre/forest. A given observer monitored the centre at some sites and the forest at others.

To determine foraging activity in the different ages and treatments, we also used the bat detectors. When bats attack insects, they increase the repetition rate of their echolocation pulses (Fenton and Bell 1979). We recorded the resultant "buzz" as we monitored passes.

Roost Selection

To obtain bats for radio-telemetry (and also enhance species identification), we caught bats in mist nets placed in gaps and cutlines within unlogged stands perpendicular to the edge of logged sites. In 1994, we radio-tracked 14 bats carrying 0.67-g radio-transmitters (Hamilton and Barclay 1994) to their roost trees. All bats weighed >8 g, and were female. We preferentially tagged lactating and pregnant females.

We tracked each individual for one to two weeks, usually locating her roost tree every other day, and noting her general position each day. For measurements of residency time and distance between roosts, we only used trees for which we could ascertain arrival and departure date. We used the maximum number of days an individual could have resided in a given tree.

For roost trees, we recorded tree species, height, and diameter at breast height (DBH). We assigned trees to a decay class based on the condition of the top, number of branches, amount of bark, and presence of rot. We measured the percentage of leaf remaining, percentage of bare trunk, canopy class (based on the number and size of branches remaining), and canopy depth. We also recorded the roost type, entrance dimensions, and height on the tree.

At sunset, we observed a roost tree for 45–60 minutes, counted the number of bats that emerged, and noted bat behaviour at the tree. We recorded the direction, duration, and approximate distance (based on signal strength) of flight by the radio-tagged bat using radio-telemetry.

We also measured a random sample of wildlife trees, defined as live and dead trees with any sign of decay (M. Nietfeld, pers. comm.), having a minimum DBH of 10 cm, maximum lean of 45°, minimum height of 1 m, and a scar, hole, crack, or piece of loose bark at least 1×2 cm in entrance size. To obtain this sample we used a T^2 method (Krebs 1989). In each site, we identified points 25 m from site centre at bearings of 0°, 120°, and 240°, and located the nearest wildlife tree within a 25-m radius of the point. We searched for a second tree in a 25-m radius hemisphere from the first tree. For each tree, we recorded the same characteristics as for roost trees.

STATISTICAL ANALYSES

Effect of Stand Age

Because activity in hour 1 and hour 2 in both years was not normally distributed, we proceeded in two stages for each year's data to assess differences in activity among stand ages. First, we considered only "occurrence": whether bats were present (one or more passes detected) or absent in stands of different ages. For 1993 data, we fitted a transformed logistic response function to the proportion of sites per stand in which bats were

present (Neter et al. 1985) before performing an ANOVA with age as the main effect. We then compared activity between different pairs of ages using a t-test on the least squares mean proportion of sites per stand. In 1994, due to lower sampling intensity, we used a chi-squared test to evaluate differences in occurrence among stand ages. Based on the 1993 results (see below), we first compared young stands to mature stands. If there was no significant difference, we pooled data from young and mature stands and compared the pooled data to data from old stands. In both years, we analyzed each hour separately and repeated the procedure on data for *Myotis* and *L. noctivagans*.

In the second stage of analysis, for each year we contrasted total bat activity among ages in hours 1 and 2 for sites in which bats were present. We conducted ANCOVA on log-transformed data with age as a main effect, stand nested within age, and ambient temperature and date as covariates. We specified a random term for stand. We conducted pairwise t-tests to determine which ages differed in mean activity using $\alpha = 0.017$ as the level of significance (Zar 1984). There were insufficient data to conduct this test for *Myotis* or *L. noctivagans*.

To determine if foraging activity differed among ages, we used a chi-squared test to compare the observed number of feeding buzzes to the expected number (based on sampling intensity) among ages. We conducted this test for total *Myotis* and *L. noctivagans* buzzes in each year.

Roost Selection

There were no clear differences between the species' selection of any tree characteristic (Table 1; ANOVA: $0.003 < F < 0.41$, $0.53 < p < 0.95$), and thus values for the two species were pooled in subsequent analyses. Because all roost trees were found in old stands, we compared continuous variables of roost trees and random wildlife trees in old stands using a stepwise discriminant functions analysis (DFA). For this analysis, we used only three random trees per site. We then conducted a canonical discriminant functions analysis on the same data with the significant variables.

For top condition, presence of rot, edge size, canopy class, and roost type, we compared roost to all old-stand random wildlife trees with chi-squared tests. We used randomization tests to compare decay class, bark condition, distance from edge, and tree species of roost trees to those of random trees.

Effect of Fragmentation

To determine if bats preferred certain habitats within logged sites, we compared bat activity (passes per hour) in the different habitats in 1994 with two-way ANOVA, with stand and habitat as main effects, and Tukey's tests. We used inverse-transformed data in all cases, except old stands in hour 2.

The effect of fragmentation on activity in fragmented stands should be viewed in the context of the general increase in bat activity from 1993 to 1994 (see Results). To control for year-to-year differences, we compared the magnitude and direction of the change in number of captures or passes, from 1993 to 1994, between treatments. In other words, fragmentation affected bat activity only if the amount of the change in treated sites from 1993 to 1994 differed from that of control sites.

We compared bats' use of unlogged sites in fragmented stands to that of sites in unfragmented stands with two-way ANOVA, with year and

TABLE 1

Tree and roost characteristics	*Myotis lucifugus* n = 16 trees	*Lasionycteris noctivagans* n = 11 trees	F	P
Tree				
DBH (cm)	41.0 ± 1.88	42.5 ± 3.46	0.41	0.53
Tree height (m)	22.3 ± 1.70	22.1 ± 2.25	0.003	0.95
Distance to canopy (m)	−0.2 ± 1.29	1.10 ± 0.98	0.41	0.53
Percent bark	93.1 ± 2.62	95.5 ± 1.42	0.11	0.74
Canopy depth (m)	3.84 ± 1.30	4.00 ± 2.00	0.03	0.86
Percent leaf	26.9 ± 8.90	27.3 ± 12.1	0.06	0.82
Percent bare trunk	71.6 ± 4.44	65.5 ± 7.21	0.11	0.74
Tree distance (m)[1]	1050 ± 251.7 (n = 9)	280 ± 66.3 (n = 5)	—	—
Roost				
Roost height (m)	11.4 ± 1.27 (n = 17 roosts)	11.0 ± 1.36 (n = 11 roosts)	0.03	0.86
Roost width (cm)	7.37 ± 0.91 (n = 16)	5.18 ± 1.05 (n = 11)	—	—
Residency (days)	3.67 ± 0.56 (n = 6)	2.67 ± 1.20 (n = 3)	—	—
No. of bats	15.3 ± 4.55 (n = 16)	9.10 ± 2.27 (n = 10)		0.83[2]

[1] Tree distance is the horizontal distance between consecutive roost trees.

[2] Mann-Whitney test.

— Not calculated.

stand treatment as main effects, and site as a nested effect. The interaction indicated whether stand treatment affected bat activity. In some cases we used Mann-Whitney tests to compare the effect of fragmentation on the difference in activity between years.

All values are expressed as means ± S.E. unless otherwise stated. Means and S.E.'s for log-transformed activity data were back transformed, resulting in asymmetrical S.E.'s. We used $\alpha = 0.05$ as the level of significance unless otherwise stated.

RESULTS

We confirmed the presence in all stand ages of *L. cinereus* (hoary bat), *L. noctivagans*, *E. fuscus* (big brown bat), *Myotis lucifugus*, and *Myotis septentrionalis* (northern long-eared bat). Most (70–75%) of the echolocation activity was from *Myotis* spp., followed by *L. noctivagans*, *E. fuscus*, and *L. cinereus*.

The total number of passes was greater in 1994 than in 1993 in the first two hours of the night in sites sampled in both years (1111 versus 763 passes). This change was due primarily to increased bat activity in old stands. In old stands, total passes increased from 647 in 1993 to 1076 passes in 1994, although the difference was not significant (ANOVA: $F = 2.21$, df = 1,10, $p > 0.1$). Total activity in mature and young stands remained low over both summers.

Effect of Stand Age In both years, relative total abundance of bats was greater in old stands than in mature or young stands in hour 1; in hour 2, there were no significant differences in any case. In 1993, the occurrence of total bats was

significantly higher in old stands (82%) than in young stands (39%; overall $F = 6.64$; df = 2,9; $p < 0.05$, $t = 3.3$; df = 9; $p < 0.01$; Figure 1), but did not differ significantly from that of mature stands (68%; $t = 1.36$; df = 9; $p > 0.2$). In 1994, the difference in occurrence between young and mature stands was not significant (Yates' $\chi^2 = 0.01$; df = 1; $p > 0.9$), but it was significantly higher in old sites (11 of 12 sites, 92%) than in young and mature sites combined (17 of 32 sites, 53%; Yates' $\chi^2 = 4.1$; df = 1; $p < 0.05$; Figure 2).

The pattern of occurrence of *Myotis* spp. in different stand ages was similar to that of total bats (Figures 1 and 2). In 1993, the occurrence of *Myotis* was significantly greater in old stands (75%) than in young stands (21%; $t = 3.3$; df = 9; $p < 0.01$; overall $F = 6.0$; df = 2,9; $p < 0.025$) in hour 1. In 1994, the occurrence of *Myotis* in old sites (10 of 12, 83%) was significantly greater than in the other ages combined (5 of 32 sites, 16%; Yates' $\chi^2 = 14.92$; df = 1; $p < 0.001$). The occurrence of *L. noctivagans* was low in all stand ages in both years (Figures 1 and 2). There were no significant differences in either year, although occurrence appeared greatest in old stands in 1994.

In 1993, when bats were present, old stands appeared to have greater total bat activity, but differences were not significant (Figure 3). In 1994, activity differed significantly among stand ages ($F = 39.9$; df = 2,4; $p < 0.005$). Old stands had significantly higher mean total passes per hour (55.0) than either young (1.6; $t = 7.97$; df = 20; $p < 0.001$) or mature stands (2.1; $t = 7.05$; df = 20; $p < 0.001$) in hour 1.

Foraging activity was generally low in most sites, although it was high in a few sites near large gaps. We heard a total of 127 buzzes in 129 hours (0.98 buzzes per hour) in 1993, and 74 buzzes in 88 hours (0.84 buzzes per hour) in 1994. In both years, total foraging activity was greater than expected in old stands and lower than expected in young and mature stands combined (1993: $\chi^2 = 53.5$; df = 1; $p < 0.001$; 1994: $\chi^2 = 167.0$; df = 1; $p < 0.001$; Figure 4). *Myotis* foraging activity was also significantly greater in old stands in both years (1993: $\chi^2 = 69.2$; df = 2; $p < 0.001$; 1994: $\chi^2 = 147.8$; df = 2; $p < 0.001$), as was *L. noctivagans* foraging activity (1993: $\chi^2 = 7.91$; df = 1; $p < 0.005$; 1994: $\chi^2 = 24.0$; df = 1; $p < 0.001$).

Roost Selection

In 1994, we observed 15 trees used by 10 female (one pregnant, four lactating, three non-reproductive, one unknown) *M. lucifugus*, and 11 trees used by six female *L. noctivagans* (two pregnant, one lactating, two post-lactating, and one juvenile). A total of 26 roost trees, all *Populus* spp., and all in old stands, were measured. Mean roost tree height and DBH were 22.3 m and 41.0 cm for *M. lucifugus* and 22.1 m and 42.5 cm for *L. noctivagans*.

Myotis lucifugus and *L. noctivagans* both roosted predominantly (19 of 28 roosts) in deep cavities that appeared to have originated as cracks, scars, or knot holes; these roosts held the largest colonies (6–60 bats; 15 roosts). Two *M. lucifugus* roosts (of two and four bats) were under loose bark, both in trees of decay class D3 and D4. Mean, median, and maximum colony sizes of *M. lucifugus* were 15.3, 7.5, and 60 bats, respectively, and of *L. noctivagans* were 9.1, 7.0, and 24 bats, respectively (Table 1). Mean roost height was 11.4 m for *M. lucifugus* and 11.0 m for *L. noctivagans*.
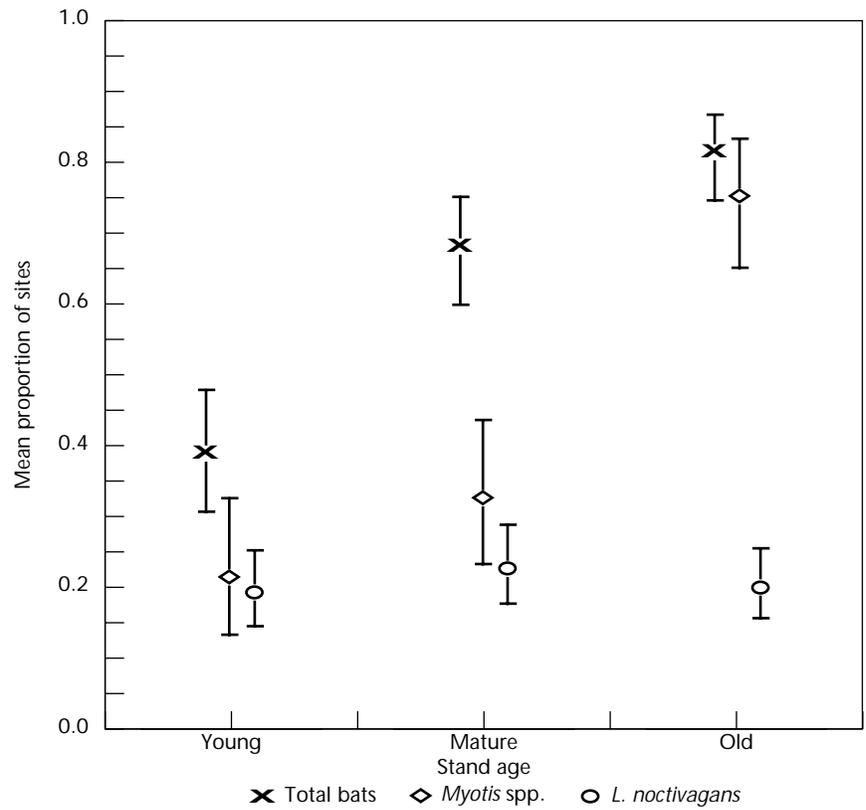
FIGURE 1 *The mean (± S.E.) proportion of sites in aspen mixedwood stands of different ages in which at least one bat was detected in hour 1, 1993. Means and S.E.s were calculated from log-transformed data, and thus S.E.s are asymmetrical. n = 4 stands/age, and from 4–6 sites/stand.*
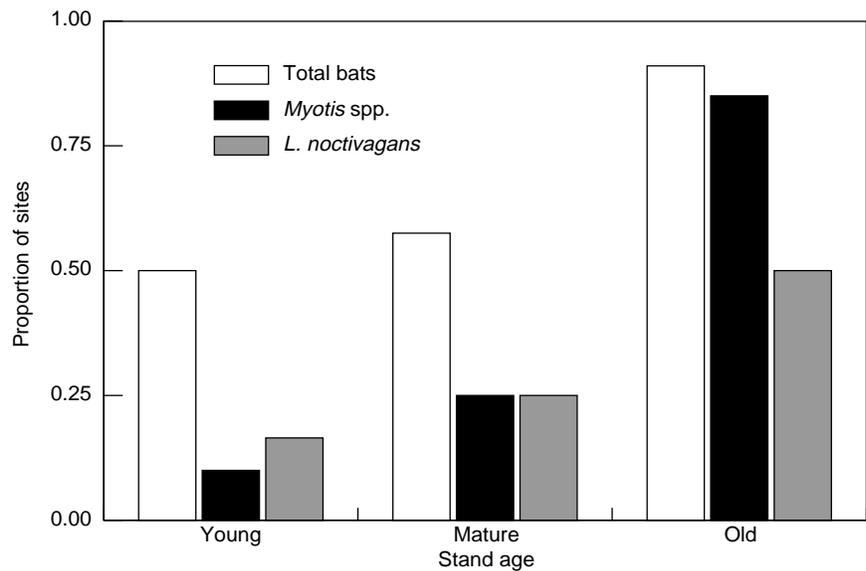

FIGURE 2 *The proportion of sites in aspen mixedwood stands of different ages in which at least one bat was detected in hour 1, 1994. Young: n = 20, Mature: n = 12, Old: n = 12 sites.*
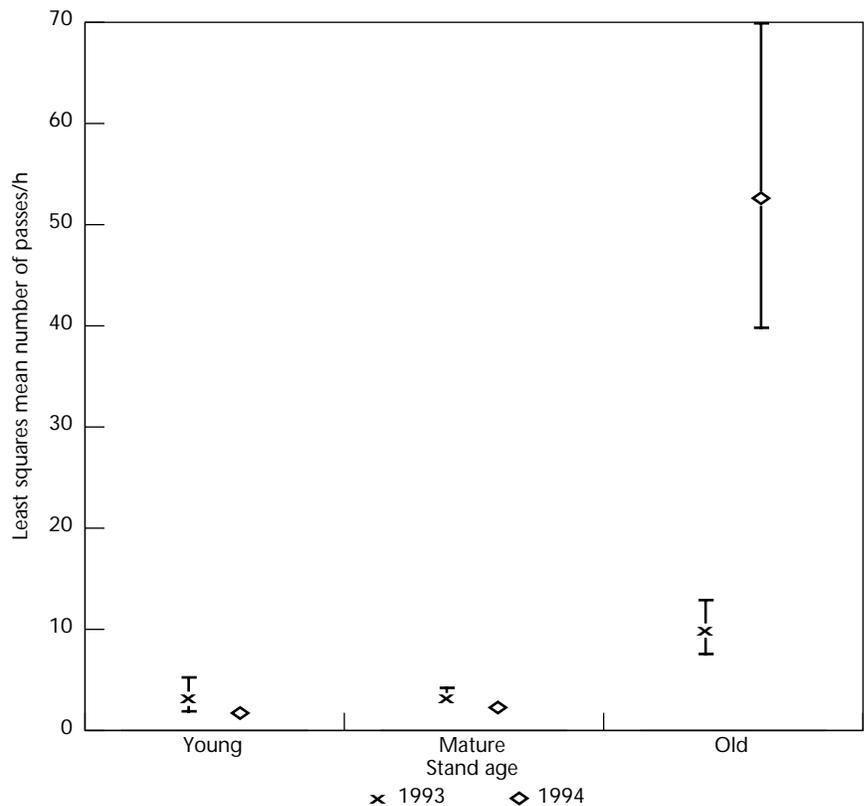
FIGURE 3 *Least squares mean number (± S.E.) of total bat passes per hour detected in aspen mixedwood stands of different ages in 1993 and 1994. Means are based only on sites in which at least one bat was detected, and calculated from log-transformed data, thus S.E.s are asymmetrical. 1993 Young: n = 7, Mature: n = 16, Old: n = 21; 1994 Young: n = 10, Mature: n = 7, Old: n = 11.*

Colonies were transient (mean residency time: 3.3 ± 1.6 days). Bats did not remain together, as individuals from a colony moved to different trees. Bats often moved several hundred metres between roost trees (mean distance: 775 ± 710 m, n = 14).

Tree height and percentage of leaf significantly discriminated between roost and random trees in old stands; the former explained 11.9% and the latter 22.2% of the variation between the two groups. Roost trees tended to be taller and of a lower percentage of leaf than old-stand random trees. The classification error rates for random and roost trees were 29.6% and 29.9%, respectively, for a total of 29.7%. Roost trees were also taller, and had a lower percentage of leaf than random trees in young and mature stands (Table 2, Figure 5). Random trees in these ages were also of lower DBH, were further below the canopy, and tended to be more cluttered.

Roost trees were more likely to have rot than were old-stand random trees (Yates' χ^2 = 4.61; df = 1; $p < 0.05$). Few trees in mature, but many trees in young stands showed evidence of rot (Figure 6). Bats preferred trees of decay classes D1 and D2 (G = 12.6, $p < 0.025$, Figure 7), and of moderate canopy class (χ^2 = 6.40; df = 2; $p < 0.05$), given their low abundance among old random trees, and indeed, wildlife trees in all ages.
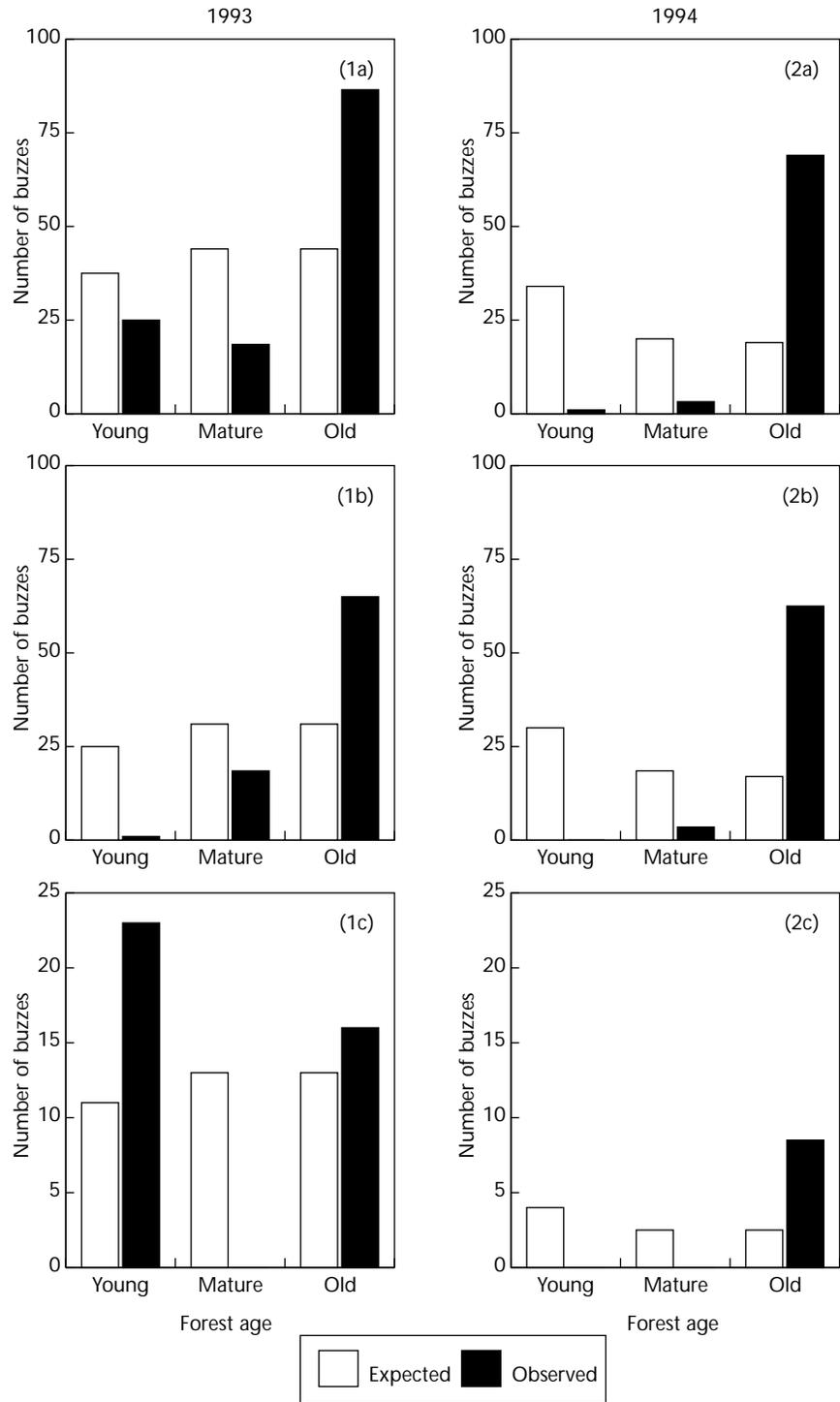
FIGURE 4 *Comparison of observed to expected (based on sampling effort) number of feeding buzzes for different species groups in young, mature, and old aspen mixedwood stands. In each year: (a) total, (b)* Myotis *spp., (c)* L. noctivagans.
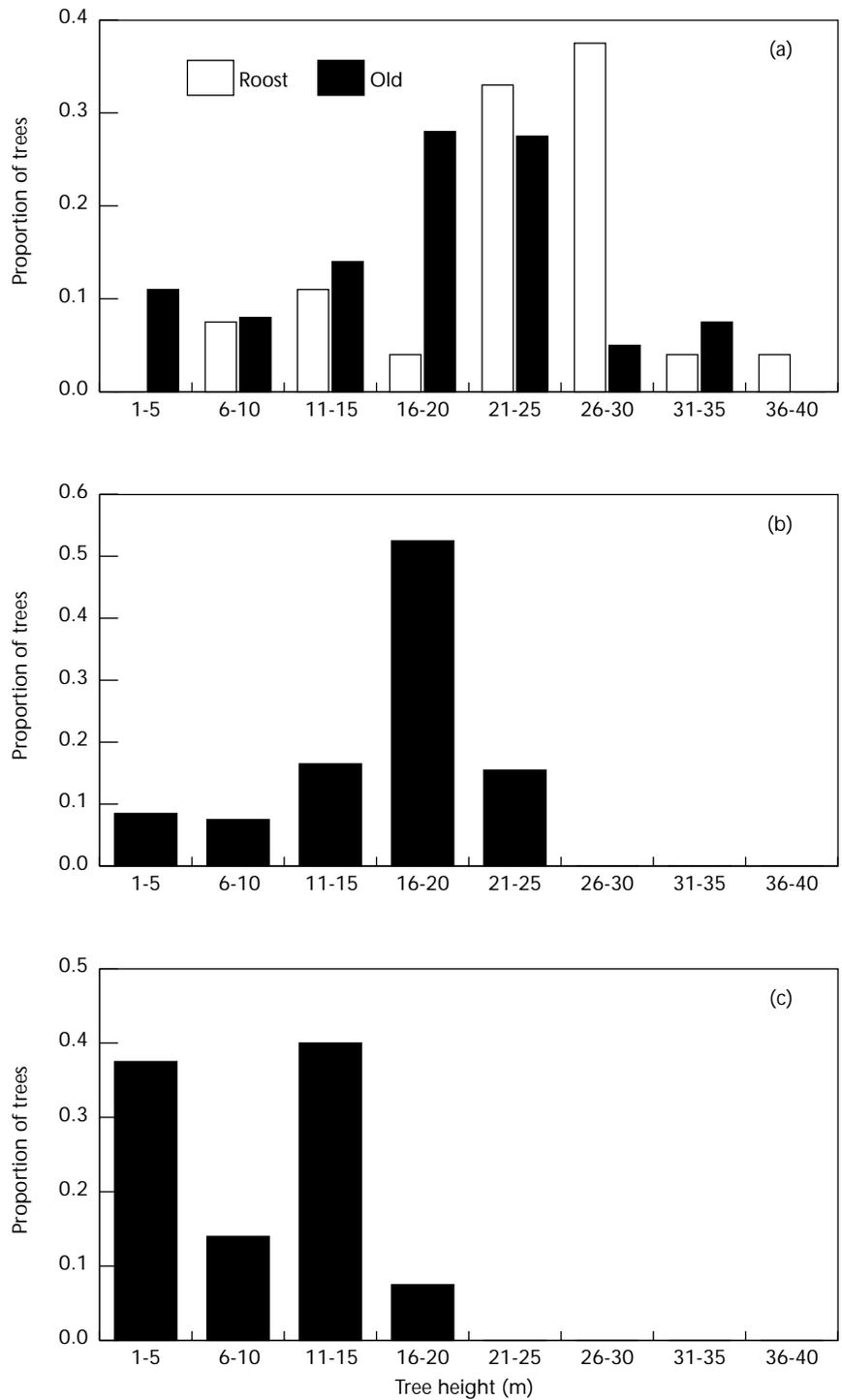
FIGURE 5 *Relative proportions of trees of different heights in samples of (a) roost trees, and random trees in old, (b) mature, and (c) young aspen mixedwood stands. Roost: n = 27, Old: n = 64, Mature: n = 127, Young: n = 112. For old sites, I included only the first random tree at each bearing; for young and mature sites, I included both trees.*
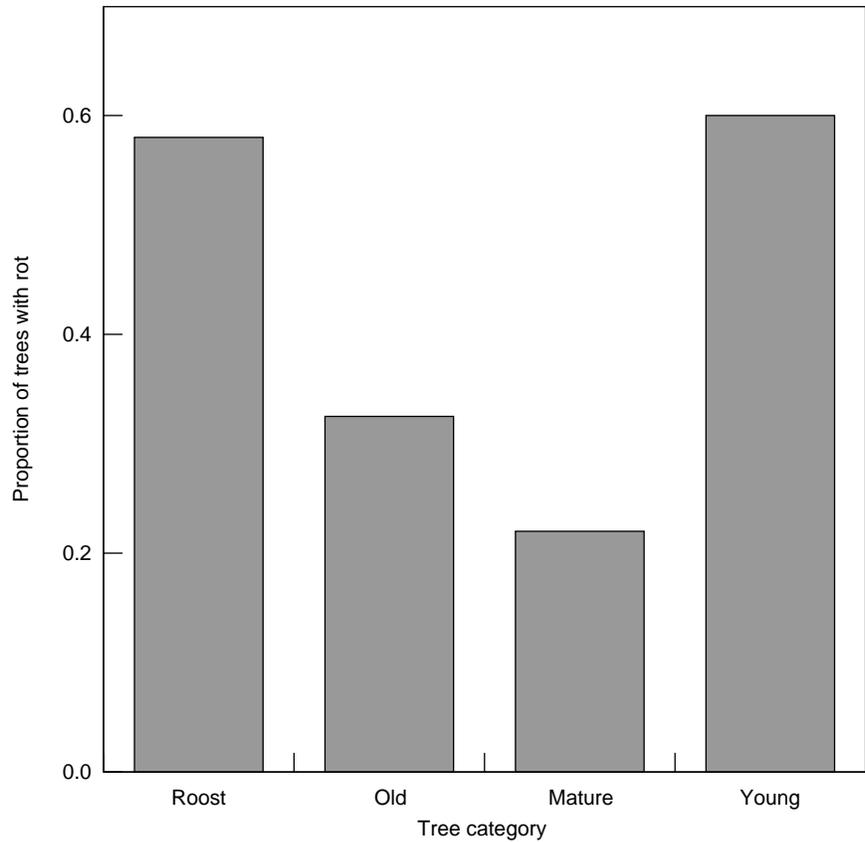
FIGURE 6   *Relative proportions of trees with rots in samples of (a) roost trees and random trees from old, (b) mature, and (c) young aspen mixedwood stands. Roost: n = 27, Old: n = 127, Mature: n = 127, Young: n = 109. In all ages, I included both trees sampled at each bearing in each site.*

Effect of Fragmentation

In logged sites, bats appeared to prefer the edge habitat in both mature (Figure 9) and old stands, followed by centre, then forest. We could not draw any statistical conclusions for old stands; given the low numbers of bats detected in the forest and the centre, activity was not normally distributed within these classes. In mature stands, activity among habitats differed significantly ($F = 5.07$; df = 2,14; $p < 0.025$); bats were more active along the edge than in the forest.

Activity following fragmentation was either reduced, although not significantly, or remained unchanged compared to activity in unfragmented stands. In general, there was a tendency for activity in control stands to increase more than in fragmented stands from 1993 to 1994 (Figure 10a). Total activity in mature stands showed a different pattern from that of other species and ages, in that it decreased slightly in both control and fragmented stands (Figure 10b).
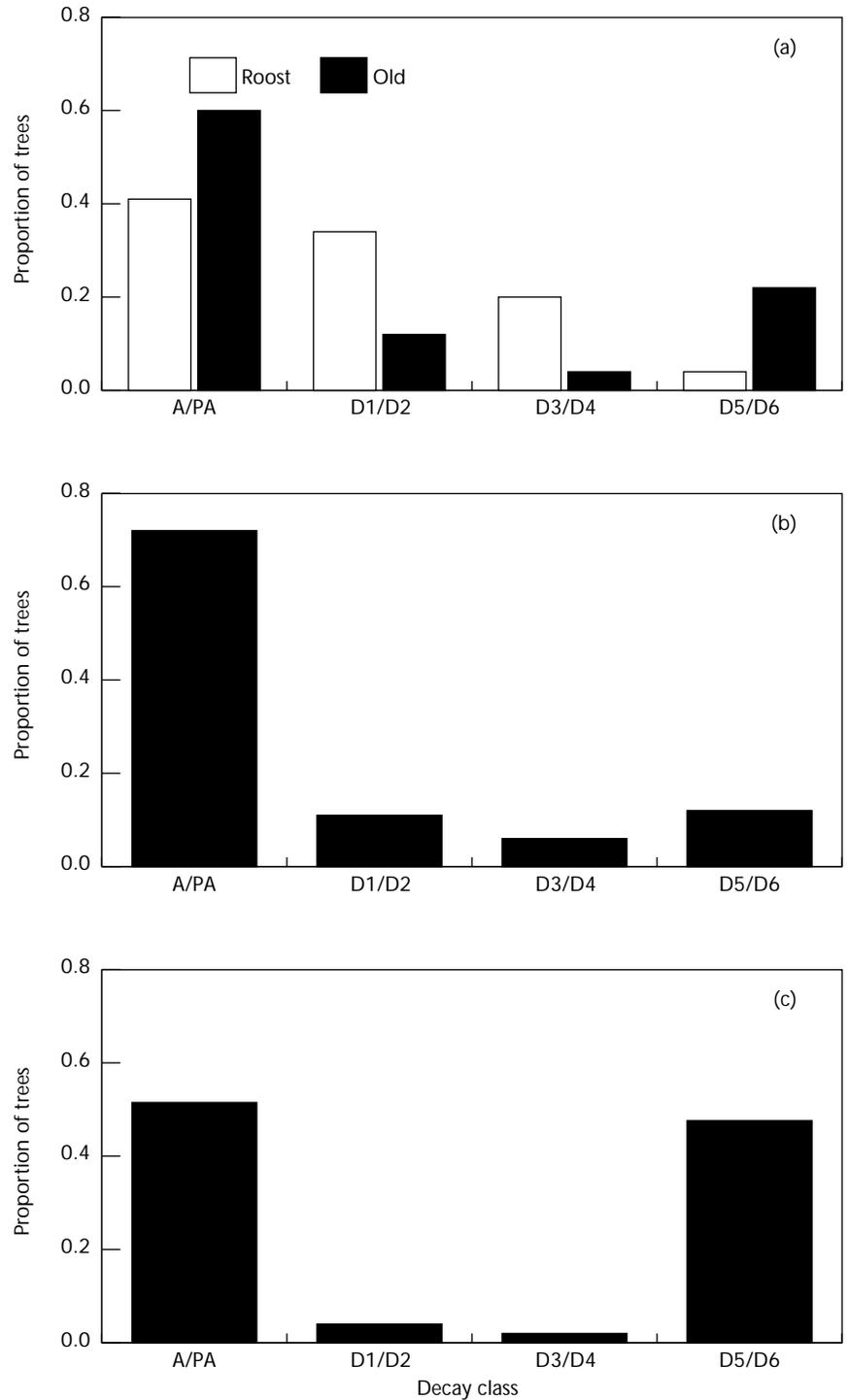
FIGURE 7 *Relative proportions of trees in different decay classes in samples of (a) roost trees, and random trees from old, (b) mature, and (c) young aspen mixedwood stands. Roost: n = 27, Old: n = 127, Mature: n = 127, Young: n = 112. In all ages, I included both trees sampled at each bearing in each site.*
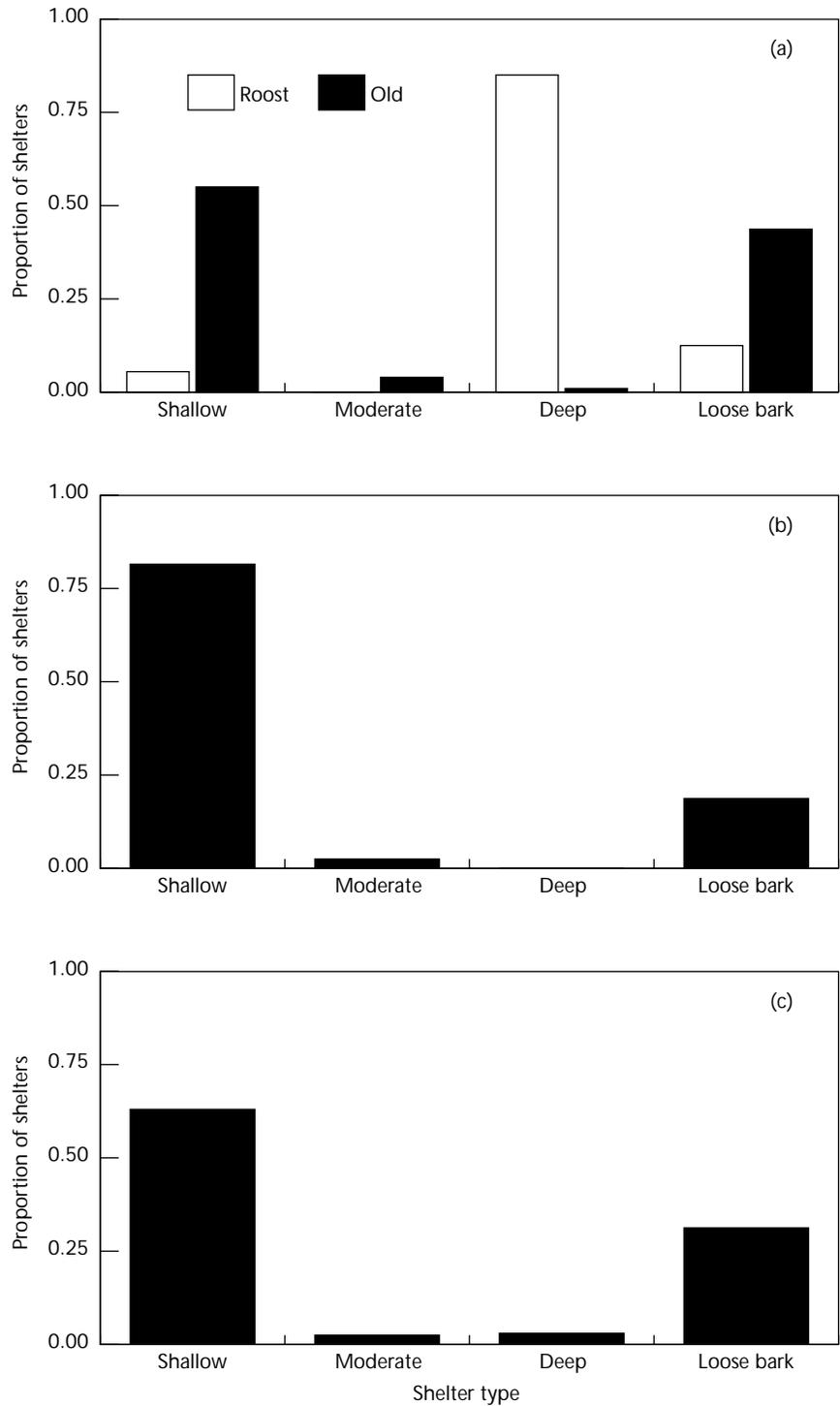
FIGURE 8 *Relative proportions of different types of shelter (based on depth and type) found in (a) roost trees, and random trees in old, (b) mature, and (c) young stands. Cavities and cracks: shallow (1–10 cm deep), moderate (11–20 cm deep), deep (>20 cm). Loose bark: 2–50 cm deep. Roost: n = 25, Old: n = 284, Mature: n = 219, Young: n = 179 shelters.*
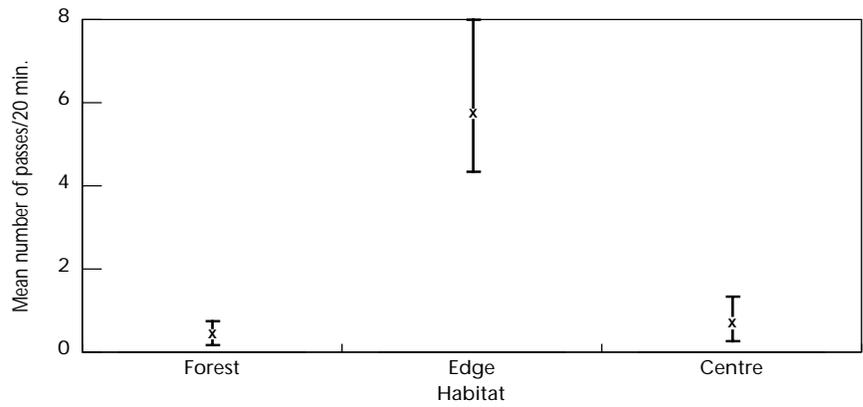
FIGURE 9   *Mean (± S.E.) number of passes/20 minutes detected in different habitats of logged sites in mature aspen mixedwood stands, 1994. Means and S.E.s were calculated from inverse-transformed data, thus S.E.s are asymmetrical. n = 6 sites/habitat.*
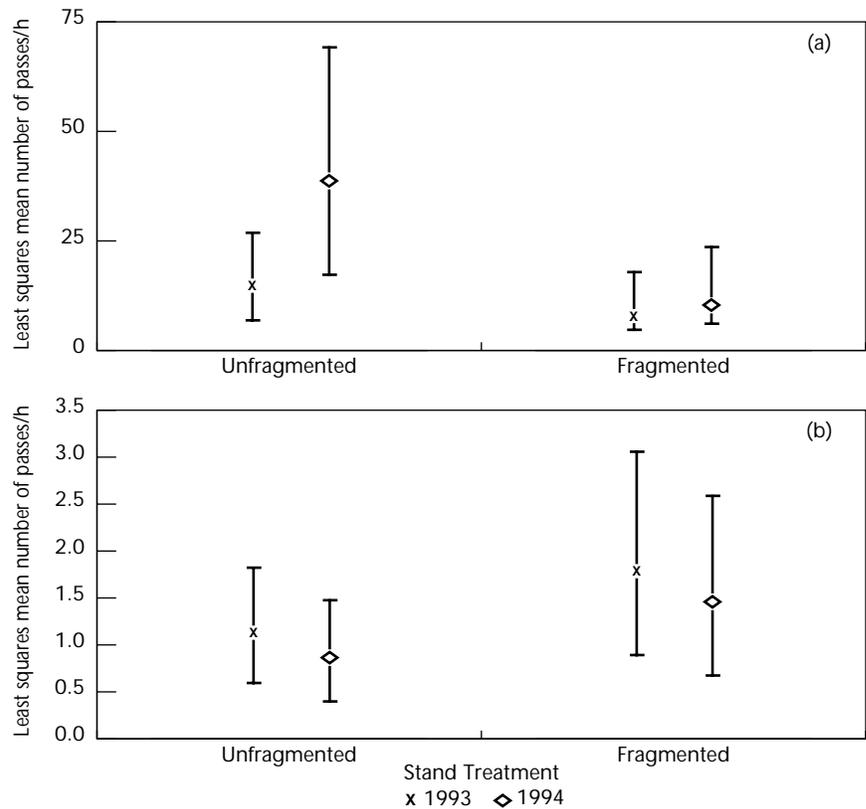
FIGURE 10   *Least Squares Mean (± S.E.) number of total passes per hour detected in unfragmented and fragmented (a) old and (b) mature aspen mixedwood stands in hour 1 in 1993 and 1994. In 1993, fragmented stands had not yet been logged. Means and S.E.s were calculated from log-transformed values, and thus S.E.s are asymmetrical. Unfragmented: n = 11, Fragmented: n = 6 sites/year. There were two stands in each treatment; in fragmented stands, only the unlogged sites were included.*

Effect of Stand Age

Bat occurrence in both years, and activity in 1994, were highest in old stands, indicating that bats prefer this forest age. In 1994, occurrence was higher in old stands than in both the other ages, while in 1993 it was greater in old stands than in young, but not mature stands. In both years, *Myotis* occurrence in old stands was greater than that in mature stands. Lower 1993 temperatures may have depressed bat abundance and activity by reducing reproductive success (Fenton et al. 1980; Lewis 1993), the number of bats in flight (Grinevitch et al. 1995), and duration of flight (Barclay 1985; Rydell 1989a), diminishing sample size and making it more difficult to detect differences in abundance among stand ages.

Old forests may contain habitat features required by bats, particularly *Myotis* spp., that are not present in any other ages. Foraging opportunities may be greater in old aspen mixedwood forests due to reduced clutter (Lee et al. 1995a), or perhaps greater insect densities. Old stands have lower densities of trees; they also have more gaps (Lee et al. 1995a), and thus more edges, which are often used by bats (Barclay 1985, 1991; Furlonger et al. 1987; this study). Old stands have greater densities of large wildlife trees (see below and Lee et al. 1995a and b), and thus also offer better roosting opportunities than young and mature stands.

The higher numbers of total and *Myotis* passes and buzzes indicate that many bats are attracted to old stands for foraging. Many *Myotis* spp., including *M. lucifugus*, prefer to forage in open areas (Barclay 1991; Saunders and Barclay 1992), particularly if prey abundance is greater there (Brigham et al. 1992). In particular, *M. lucifugus* forages along the edge of vegetation (Furlonger et al. 1987; Kalcounis and Brigham 1995), and thus may use gaps present in old stands.

Availability of foraging opportunities in old stands may not be the driving factor in the selection of this stand age by bats, given the presence of other foraging sites, such as lakes, in our study area. Some bats, especially *M. lucifugus* (Barclay 1991; Saunders and Barclay 1992) often prefer water bodies to other habitats, and will travel several kilometres to them from roosts (Brigham 1991; de Jong 1994). Alternatively, bats may not leave the forest, but forage over bogs, puddles, and small clearings in the forest. Regardless, the low number of buzzes detected suggests that the stands themselves may not be of great importance for foraging. At this point, we cannot completely elucidate the role of foraging behaviour in attracting bats to old stands, but roost-site selection may be more important.

We found bat roost trees only in old stands. Comparison of characteristics of roost and random trees in old stands showed that female bats selected deep cavities in tall aspen trees that were of a low percentage of leaf, early decay class, and moderate canopy class, and with rot. In young and mature stands, few wildlife trees matched these criteria. In particular, in young and mature stands, most wildlife trees were short and small, and of inappropriate decay class. Thus, potential roost trees were scarce in these ages. Random trees in old stands best matched roost trees in terms of height, DBH, and decay class.

We focused on roosts used by female bats because selection of a warm (McNab 1982), protected, maternity roost environment is critical to bats'

reproductive success. Bats selected trees and roosts which reflected these factors: roosts in tall, large trees with rotten centres that can be accessed through deep cavities are likely warm, spacious, and protected from predators. For example, roosts in large trees may have thicker walls, and thus extra insulation, than those of small DBH, resulting in more stable roost temperatures (Sluter et al. 1973). Trees of early decay classes also generally have firm wood, which lessens their chance of blowdown, and improves insulation (Desch and Dinwoodie 1981), as does live wood (Humphrey et al. 1977).

Deep cavities, high in trees, also provide thermal and social benefits and may offer protection from predators. Loose bark pieces could not hold the numbers of bats found in some cavities. Cavity roosts may have more stable and/or warmer temperatures, and be more humid (McComb and Noble 1981) than loose bark, which is thin in aspen.

Bats switched roost trees often, despite the potential costs in terms of lost social interactions and familiarity with an area (Lewis 1995). Roost switching may be important for maintaining healthy populations, as it may enable bats to reduce predation (Fenton et al. 1994) and parasitism (Lewis 1993), and use different microclimates (Lewis 1995). Suitable trees may be at such low density in young and mature stands that bats are unable to find sufficient alternate roosts.

If presence of cavities, and tree height, size and decay class are the most important features selected by bats, then the more abundant roosting opportunities of old stands may explain why we found roost trees in old stands only. Furthermore, there are several indicators that roost trees are limited, even in old stands. First, as noted, even in old stands some of the features selected by bats are not common (e.g., tall trees). Second, the decay classes selected by bats are short-lived in aspen systems: D1 lasts a maximum of 10 years, and D2, an additional 10 (P. Lee, pers. comm.). Third, bats travelled long distances between alternate roosts. Given their apparent scarcity, roost trees may drive habitat selection in aspen mixedwood forests. Another explanation is that bats select old stands as the best combination of both roosting and foraging opportunities. However, the fact that differences in foraging opportunities (e.g, presence of gaps) among stand ages were less striking than differences in roosting opportunities, supports the first idea.

Effect of Fragmentation

Any changes in bat abundance in forests following fragmentation reflect the combined impact of harvesting on roosting and foraging habitat. This impact is manifested at different levels within fragmented stands. By examining the habitat choices made by flying bats within logged sites, the effect on foraging habitat can be examined. On the other hand, comparisons of intact portions of fragmented stands with unfragmented stands help clarify the impact on roosting habitat.

We predicted that fragmentation would increase foraging and commuting habitat through the creation of edges. Within logged sites, bats generally preferred the edge of cutblocks to the forest or the centre of a clearcut. For foraging, edges may represent the best combination of several factors when compared to open clearcuts or dense aspen forest. Edges are less cluttered than forests, making foraging and commuting easier and serving as a navigational corridor (Limpens and Kapteyn 1991). Also,

insect abundance and density may be higher along edges, particularly the lee edge, than in open habitat (Lewis 1970) or in the forest (Toda 1992). Even when insect abundance is higher in open areas, some bats choose to forage near the edge, perhaps to avoid predation (Estrada et al. 1993; de Jong 1994).

The effects of the loss of roost trees are most likely to be seen by comparing unlogged sites in fragmented stands to those in unfragmented stands. In these sites, there is unlikely to be a flurry of activity resulting from changes in foraging opportunities; activity more likely represents bats commuting to roost trees and foraging in the forest. If roost trees are limiting, and the bat population is affected by their loss following fragmentation of the stand, then activity will diminish.

Total and *Myotis* activity levels in unlogged sites in fragmented stands did not change statistically following fragmentation, although there was a slight decrease in activity. These trends may represent a decrease in bat activity or perhaps abundance due to a loss of roost trees, even at this early date following fragmentation. Other animal species that depend on roost trees, particularly cavity trees, are less abundant in fragmented than unfragmented stands (birds—Franzreb and Ohmart 1978; Keller and Anderson 1992; red squirrels—(*Sciurus vulgaris*) Wauters et al. 1994).

As in the other levels of comparison, the lack of statistical differences between stand treatments may result from the great variability in bat activity between sites, and/or the lack of time since fragmentation. With time, logged sites may become more profitable as foraging grounds, as vegetation and insects flourish, and bats are attracted to fragmented areas. However, it is unlikely that foraging areas are in short supply in and near the aspen mixedwood forest, at least in old stands. If roost trees are limiting, by contrast, and thus the dominant factor in bat habitat selection, the trend towards a decrease in bat abundance in fragmented stands may become significant. Over time, it is likely that more roost trees will be lost from the system, for several reasons. As more forest is logged, the number of current roost trees and new recruits from which to draw will be reduced. Tree mortality and tree fall increases with decreasing patch size (Chen and Franklin 1992), and logging disrupts the replacement of snags (Cline et al. 1980) and cavity trees (Tidemann and Flavel 1987). If trees currently in early decay stages are not replaced in the next 10 years, a loss of roost trees and a decrease in bat populations at the stand level may occur.

The use of fragmented forests by bats is a product of roosting and foraging opportunities. It appears that neither was strongly affected by fragmentation in the short term, and thus bat activity and abundance remained statistically unchanged. However, little of the aspen mixedwood forest has been logged to date. In the future, it is likely that localized foraging habitat (along edges) will become more profitable, while roosting habitat in fragmented forests becomes impoverished. This loss of roosting habitat may be exacerbated by increased isolation of patches if old forests are not connected to other patches, as bats appear to avoid open areas (de Jong 1994). If roost trees are limiting in this system, and thus dominate habitat selection, it is likely that a decrease in bat abundance will occur.

Before suggesting ways to accommodate bats in managed forests, it is important to recognize the limitations of our study. First, it was conducted in a subset of stands in the aspen mixedwood forest, and may not fully represent conditions in other areas of this forest. Second, the data were only collected over a two-year period and cannot fully address the long-term consequences of forest harvesting. Third, there remain outstanding questions with respect to the importance of roosting and foraging sites in the aspen mixedwood forest. With these limitations in mind, we propose the following issues for consideration:

1. Old stands are important to bats, especially in terms of roost trees. Decreased amounts of old growth in aspen mixedwood forests may lead to declines in bat abundance. Connecting remnant patches of old growth via other forested areas that provide shelter for commuting bats may improve the suitability of such patches for bats.
2. Bats preferred to roost in large, open cavities on average 10 m above the ground in dying or newly dead *Populus* spp. (especially aspen) of at least 20 m height and 35 cm DBH. Moreover, individual bats used several of these trees within a two- to three-week period. If roosting behaviours are not accommodated by retaining such trees within patches of old growth, bat populations may decline.
3. Bats preferred edges (and avoided open areas) as foraging and commuting habitat. In planning the size of cutblocks, the ratio of edge to open area should be considered. Cutblocks with relatively great amounts of edge are likely to provide better bat-foraging habitat.

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Habitat Use by Bats in Fragmented Forests

scott d. grindal

ABSTRACT

Habitat disturbance associated with forest harvesting has various effects on wildlife. To assess the impact on bats, I used ultrasonic detectors to monitor relative habitat use by bats in disturbed forested sites and riparian areas. In addition, I experimentally tested the effect of spatial clutter on the foraging activity of bats. My results suggest that habitat use by foraging bats varies depending on a combination of spatial clutter and prey availability. In forested areas, clear-cut edges appeared to be preferred foraging sites. However, much greater foraging rates were observed in habitats associated with lakes. Activity patterns and prey availability levels in forest suggested that this habitat type may be important for roosting and as a source of prey. Therefore, the creation of preferred foraging habitat by forest harvesting must be balanced with the removal of other requirements (e.g., tree roost sites), as well as protection of primary foraging areas (lakes).

INTRODUCTION

Habitat may be disturbed in a number of ways. Intensive agriculture alters large areas of habitat. Wildfires may also affect large areas, and are thought to be regulating influences in some ecosystems. Forest harvesting is another form of habitat disturbance, and is now one of the major kinds of large-scale disturbances occurring in forest ecosystems.

In the past, the forest industry has not had the best reputation for considering forest resource values, other than timber. However, recent emphasis has been placed on non-timber forest values, such as wildlife. Forest companies now protect wildlife habitat, including wildlife trees, which are saved for their potential shelter and food. Yet, problems still exist with integrating forestry practices and wildlife habitat requirements in an ecosystem context (Hunter 1990).

Large-scale habitat disturbances cause abiotic changes in the environment (e.g., direct loss of habitat or changes in microclimate conditions). Changes in abiotic conditions may in turn affect biotic components of the environment, such as prey availability, competition between and within species, or predation rates. These changes resulting from habitat disturbances may then affect animals in a number of ways, depending on the nature of the disturbance, and on the ecology of the particular species

(Pickett and White 1985). For example, forest harvesting may have positive, negative, or neutral impacts on wildlife, affecting such things as foraging success, which may in turn influence population dynamics. Previous studies suggest that some animals may benefit from forest harvesting (Sparks et al. 1994), whereas others may be negatively influenced (Chubbs et al. 1992). For other species, there appears to be no dramatic impact on their ecology (Medin 1986).

Unlike many other vertebrates, there is a limited amount of information on the effects of forest harvesting on bats. Most of the previous work on the ecology of bats has been conducted in caves or human-made structures, and very little is known about what role bats may play in a forest ecosystem, and the effects of large-scale disturbances.

Two basic requirements of bats are roosting and foraging habitat. Roosting habitat provides areas for shelter during the day and for reproduction, whereas foraging habitat provides for energy and nutrient requirements. If bats have specific tree-roost requirements, then forest harvesting would have an obvious negative impact on roosting ecology. However, the impact of forest harvesting on the foraging ecology of bats is not as evident. Forest harvesting creates openings in the forest, and previous studies suggest that gaps and the resulting edge habitat are important foraging areas for some bat species (Fenton 1990).

For my purposes, forest harvesting results in three distinct habitat types. The first are clearcuts, which represent disturbed habitat where the majority of the vegetation is removed. The second is edge, which represents the boundary between clearcuts and the remaining forest. The third is forest, which represents undisturbed habitat.

As a result of forest harvesting, bats are presented with a choice of the three different habitat types. Bats may select certain foraging habitats depending on the physical nature of the habitat and/or the prey availability found there. Habitat selection may also be determined to some extent by the ecomorphology of the animal. Ecomorphology can be defined as aspects of an organism's ecology that may be dictated by certain morphological features (Findley 1993).

For bats, I have used three characteristics to describe their ecomorphology. The first is the size of the bat, which will determine the size of prey that can be consumed. The second is wing loading, which deals with the mass and wing area of bats. These two characteristics can be used to predict habitat use by bats over a continuum ranging from large, fast-flying bats to small, slow-flying bats that are more agile. The third characteristic is echolocation, which is the mechanism that bats use to perceive their environment and search for prey (Griffin 1958). Different bats produce different frequencies of echolocation, which allows for varying trade-offs between such things as range of detection and resolution (Norberg 1987; Norberg and Rayner 1987). That is, large, fast-flying, less manoeuvrable bats tend to have echolocation that permits long-range detection of objects (over 5 m), but with a relatively coarse resolution of environmental detail. These bats should be limited to relatively open habitat. In contrast, small, slow-flying, agile bats have echolocation that permits fine resolution of the environment, but at a short range (1–2 m). These bats should be able to fly and navigate in more cluttered or environmentally complex habitats, but not be restricted to them.

Predictions   Insects are the exclusive prey of bats in Canada (van Zyll de Jong 1985), and this prey base may vary between different habitats. I hypothesized that the foraging activity of different types of bats should vary depending on the degree of spatial complexity of a habitat (i.e., clutter; Figure 1), and on prey availability. Specifically, dealing with only the degree of clutter of a habitat, I predicted that the open-adapted bats (large, fast-flying, less manoeuvrable) should be limited to clear-cut areas, with reduced activity in the more cluttered habitat of the forest. In contrast, clutter-adapted bats (small, slow-flying, and more manoeuvrable) should not be limited to specific foraging areas, and therefore should display relatively equal activity patterns across the three habitat types (see also Fenton 1990).

The purpose of my study was to monitor habitat use by foraging bats in areas associated with forest harvesting and in riparian habitat. In addition, I experimentally tested the effect of spatial clutter on the foraging activity of bats.
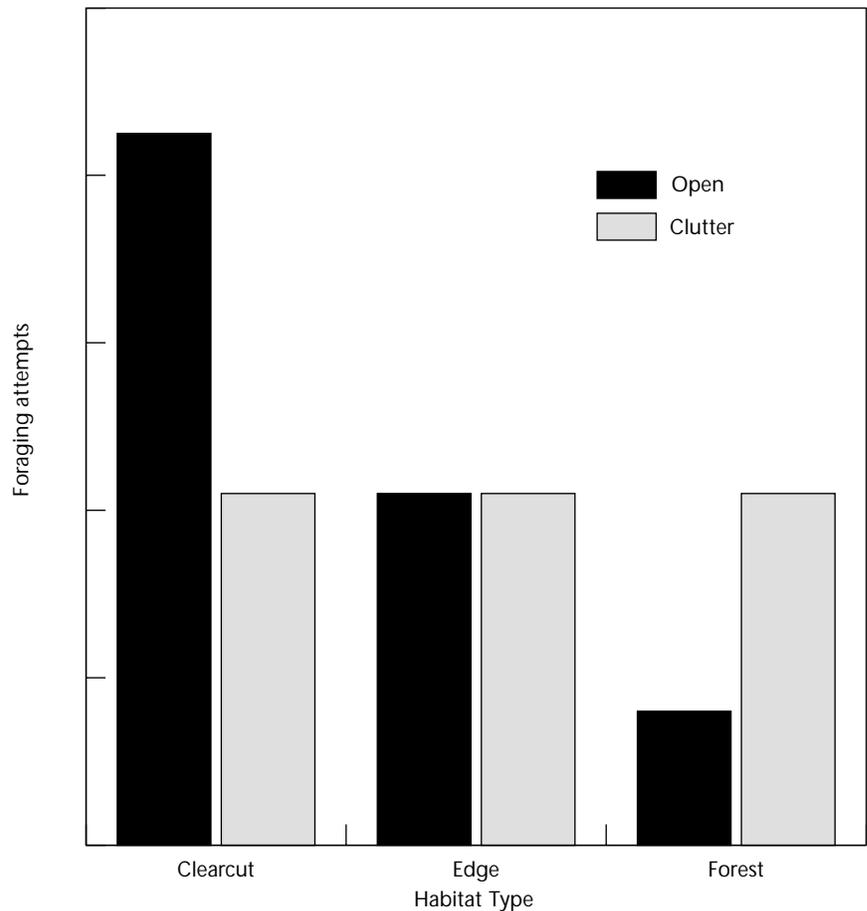

FIGURE 1   *Predicted foraging activity for open-adapted bats (open) and clutter-adapted bats (clutter) in the three habitat types associated with clearcuts. Note that the predicted values are relative, not absolute.*

Study Site   The study took place during the summers of 1993–1995 in the West Arm Demonstration Forest in the southern interior of British Columbia. The study site is approximately 14,500 ha, encompassing five watersheds that drain into Kootenay Lake. The area is dominated by conifers, and elevation ranges from 540 m at Kootenay Lake to 1800 m in the subalpine.

Sampling of Clearcuts   To monitor relative bat activity in habitat types associated with clearcuts, I used Mini-2 ultrasonic bat detectors (Ultra Sound Advice, U.K.) for 90 minutes after sunset (Pacific Standard Time). The detectors were connected to micro-cassette recorders to allow for multiple sampling, as well as transcription of bat activity over certain time periods.

Overall bat activity was separated into two activity types: commuting and foraging. Commuting activity was identified by a steady series of echolocation calls (two or more consecutive pulses; Thomas 1988), emitted when bats are searching for prey or travelling. Foraging activity was identified by a rapid series of echolocation calls or a "feeding buzz," produced when bats make a feeding attempt (Griffin 1958).

Bat activity was separated into two species groups as either clutter-adapted (detectors set at 40 kHz) or open-adapted (detectors set at 25 kHz) bats. The two groups were differentiated based on the frequency setting of the detectors, as well as pulse repetition rate (Thomas and West 1989). Bats that were expected in the study area were categorized as either clutter-adapted (*Myotis californicus*, *M. evotis*, *M. lucifugus*, *M. septentrionalis*, *M. volans*, *M. yumanensis*) or open-adapted (*Eptesicus fuscus*, *Lasionycteris noctivagans*, *Lasiurus cinereus*; Nagorsen and Brigham 1993).

To assess insect availability, I used light-suction traps (Kunz 1988) paired with bat detectors. Insect biomass was determined by drying a representative sample of insects to a constant mass at room temperature. The mean mass for each insect order was then multiplied by the number caught in each habitat type per sample night.

On a sample night, one pair of bat detectors (40 and 25 kHz) and a light-suction trap were placed in each of the three habitat types associated with clearcuts (clearcut, edge, and forest). To maintain independence of observation and eliminate any edge effects (Sisk and Margules 1993), bat detectors and insect traps were placed at least 50 m into forest and clearcut habitat types. Samples were taken randomly throughout the summers of 1993 and 1994.

Clutter Sampling   To experimentally test for the effect of spatial complexity of a habitat on the foraging activity of bats, I constructed areas of artificial clutter, or "clutter boxes." These clutter boxes consisted of a cube-shaped area extending from the edge of a clearcut (30 m along the edge of the clearcut × 20 m out from the edge × 18 m above the ground). The spatial clutter consisted of over 5500 m of suspended twine for each clutter box (one vertical line every 1 m). Foraging activity and insect availability were monitored using a similar protocol as in the clearcut sampling. Bat detectors and insect traps were placed inside the clutter box (treatment), and farther along the edge of the same clearcut (control). Two complete set-ups

(treatment and control) were constructed. Samples were taken at approximately weekly intervals throughout the summer of 1995.

Lake Sampling

To assess the importance of riparian habitat, I sampled bat foraging activity in lake areas. A similar protocol was used as in the clearcut sampling (i.e., centre of the lake, edge of the lake, and adjacent forest). However, detectors in the centre of the lake were placed in plastic containers and floated out onto the lakes in small inner-tubes. Samples were taken in July 1994, and at approximately monthly intervals throughout the summer of 1995.

Statistical Analyses

I used Kruskal-Wallis one-way analysis of variance (Zar 1984) to examine the effect of bat type and habitat type on foraging activity and insect availability (excluding bat type for the latter). In cases of a significant effect, I conducted non-parametric multiple comparisons (Dunn procedure; Zar 1984). Proportional data were arcsine-transformed prior to statistical analysis. Spearman Rank correlation tests were used to examine the relationship between insect availability and foraging activity. I used a rejection level of 0.05 in all cases.

RESULTS

Clearcut Sampling

I collected 693 hours of bat activity data in the three habitat types on a total of 77 nights. These data consisted of 192 foraging attempts and 2024 commuting passes. Habitat type had a significant effect on overall bat foraging activity (Figure 2, Table 1). Foraging activity was significantly greater along the edge than in the clearcut or forest habitat for clutter-adapted bats. Open-adapted bats showed a similar pattern, except that foraging activity did not differ significantly between the clearcut and edge. As predicted, open-adapted bats foraged significantly more than the clutter-adapted bats in the less spatially complex habitat type of the clearcut. However, foraging activity between the two bat types did not differ in the other two habitat types.

Both types of bats foraged infrequently in the forest. In 231 hours of observation, I recorded no foraging attempts by open-adapted bats in the forest, and only one by a clutter-adapted bat. However, commuting activity was recorded in the forest, suggesting that bats do use this habitat type (Figure 3). Commuting activity in the forest peaked between 20 to 30 minutes after sunset, then remained consistently low (Figure 3). Commuting activity in the edge and clearcut tended to be greater, and peaked later, than activity in the forest. A similar trend was observed for foraging activity, with the exception of only a single foraging attempt recorded in the forest.

I sampled for a total of 432 hours using insect light-suction traps on 48 nights during 1994. In all, this sampling resulted in the capture of 2424 insects. Habitat type had a significant effect on insect availability (Figure 4). Total insect biomass was significantly less in clearcut than edge or forest habitats (for both, $H = 4.01$, df $= 1,96$, $p < 0.05$), and did not differ significantly between the edge and forest ($H = 0.09$, df $= 1,96$, $p > 0.05$). Total mean insect biomass from all habitat types contained predominantly

Variable	Clearcut sampling			Lake sampling		
	df	H or q	p	df	H or q	p
Bat type						
Clearcut/lake						
Open vs. clutter	1,154	6.59	**	1,24	10.11	**
Edge						
Open vs. clutter	1,154	0.0037	>0.5	1,24	1.08	>0.1
Forest						
Open vs. clutter	1,154	1.0	>0.01	1,24	0.032	>0.5
Habitat type						
Open						
Edge vs. forest	1,154	21.44	***	1,24	21.44	***
Edge vs. clearcut/lake	1,154	3.22	>0.05	1,24	2.82	>0.05
Clearcut/lake vs. forest	1,154	11.75	***	1,24	13.46	***
Clutter						
Edge vs. forest	1,154	17.19	***	1,24	20.82	***
Edge vs. clearcut/lake	1,154	14.95	***	1,24	7.3	**
Clearcut/lake vs. forest	1,154	0.33	>0.5	1,24	28.18	***

H represents test values for main effects; q represents test values for multiple comparisons (Dunn's test) when appropriate; ** = $p < 0.01$, *** = $p < 0.001$. See figures 2 and 7.

Diptera (61.5%) and Lepidoptera (36.5%), with smaller amounts of Hymenoptera, Trichoptera, Neuroptera, Coleoptera, and Hemiptera (combined 2.0%). Mean insect biomass was not significantly correlated to foraging activity (Spearman, $r = -0.03$, $p > 0.5$).

Clutter Sampling

In the experimental sites, I collected 34 samples on 17 nights. Mean foraging activity in the clutter box was significantly less than along the edge for clutter-adapted bats ($H = 6.44$, df = 1,34, $p < 0.02$), but not for open-adapted bats ($H = 0.0$, df = 1,34, $p = 1.0$; Figure 5). Mean insect biomass collected did not differ between the treatment and the control ($H = 0.058$, df = 1,34, $p = 0.81$; Figure 6).

Lake Sampling

I sampled nine different lakes on 12 nights. Foraging activity in lake areas showed similar patterns to that of the clearcut. Foraging activity by both bat types was significantly greater in the lake and edge habitat than in the forest (Figure 7, Table 1). In particular, foraging activity in the centre of the lake by clutter-adapted bats was significantly greater than open-adapted bats (Figure 7, Table 1), or in the other habitat types. Mean foraging activity for all habitat types associated with lakes was approximately 39 times greater than for those associated with clearcuts.
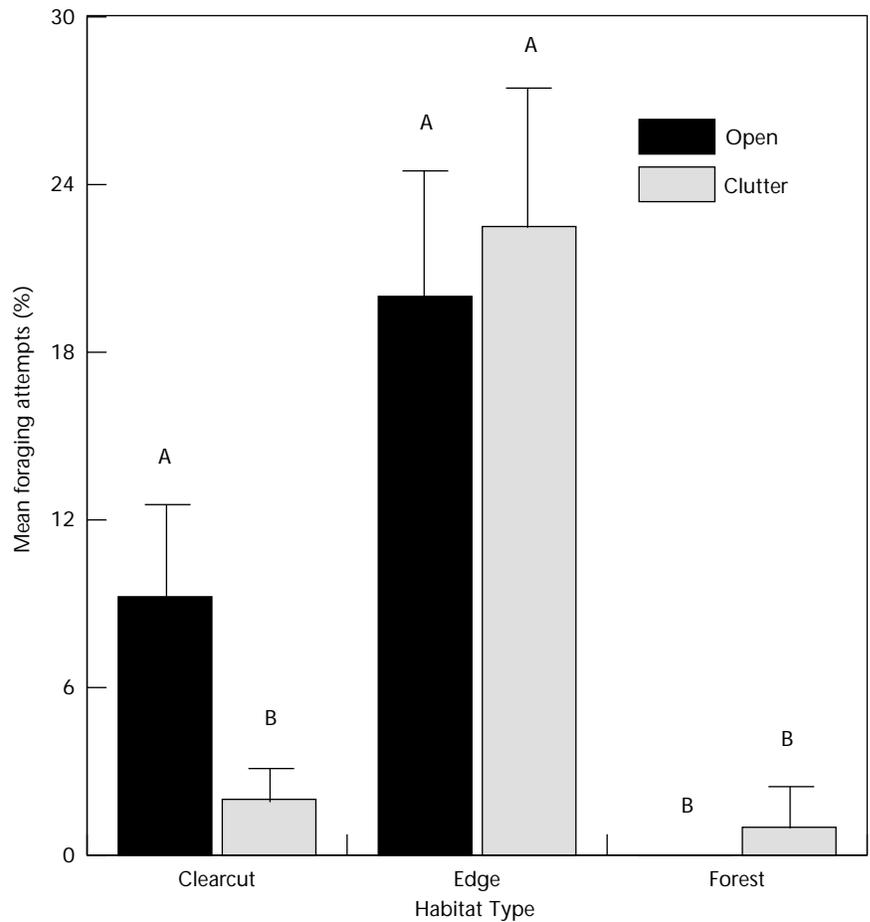
FIGURE 2 *Mean (+ 1 SE) foraging activity per hour for open-adapted bats (open) and clutter-adapted bats (clutter) in the three habitat types associated with clearcuts. Within each habitat type, and between habitat types for the same bat type, means with the same letter are not significantly different (p > 0.05). See Table 1.*
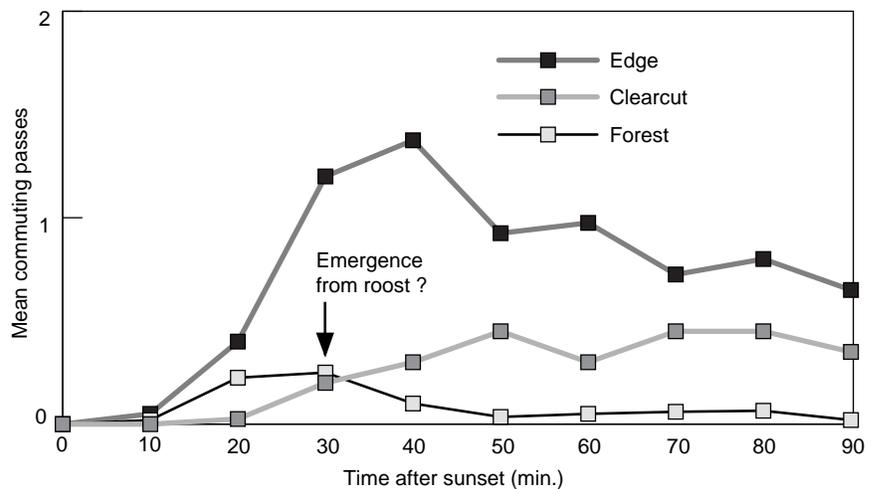

FIGURE 3 *Mean commuting activity over time for the three habitat types associated with clearcuts. Bat types were combined.*
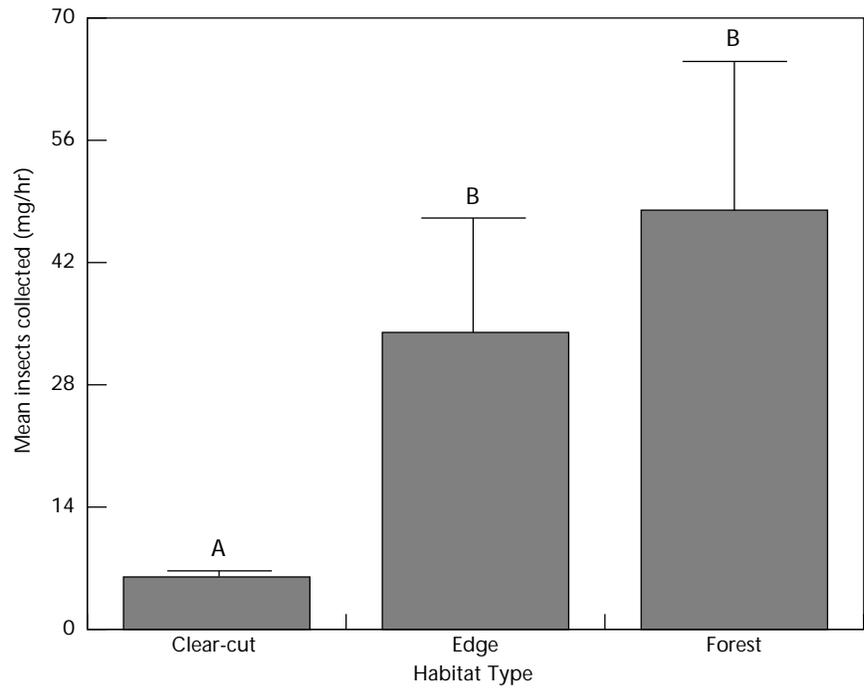
FIGURE 4 *Mean (+ 1 SE) insect biomass collected per hour in the three habitat types associated with clearcuts. Means with the same letter are not significantly different (p > 0.05).*
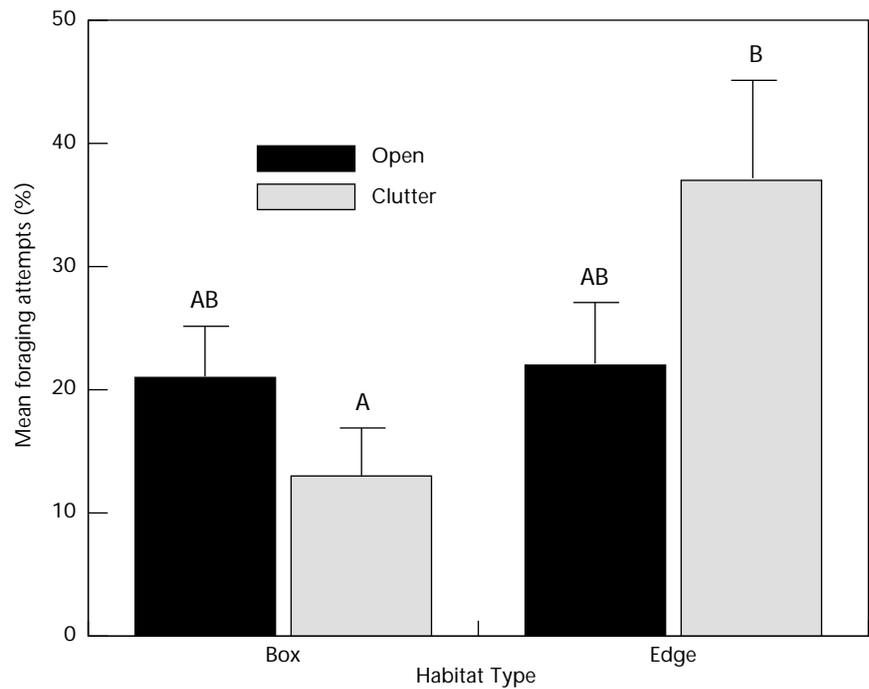

FIGURE 5 *Mean (+ 1 SE) foraging activity per hour for open-adapted bats (open) and clutter-adapted bats (clutter) in the clutter box and edge. Within each habitat type, and between habitat types for the same bat type, means with the same letter are not significantly different (p > 0.05).*
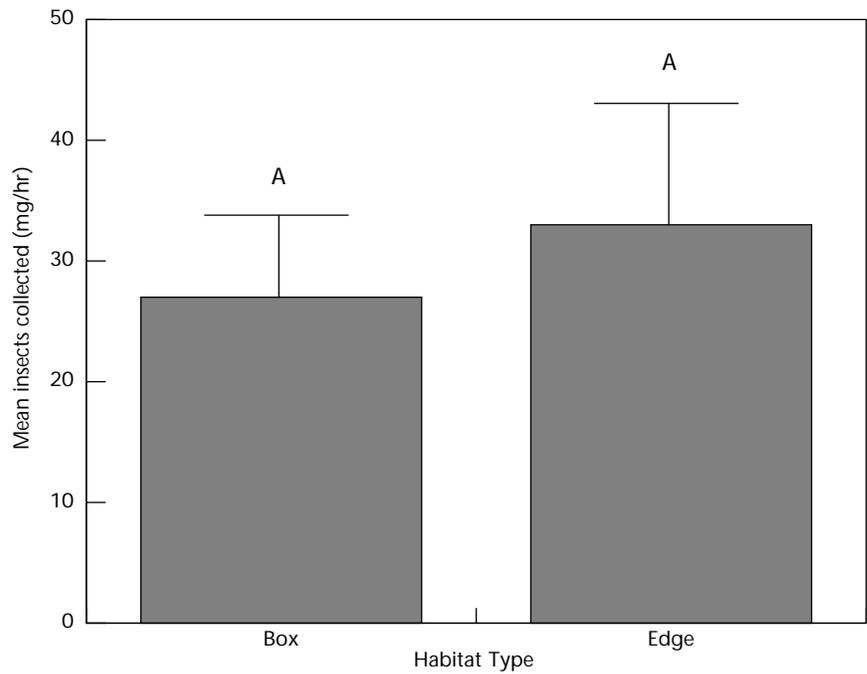
FIGURE 6   *Mean (+ 1 SE) insect biomass collected per hour in the clutter box and the edge. Means with the same letter are not significantly different (p > 0.05).*
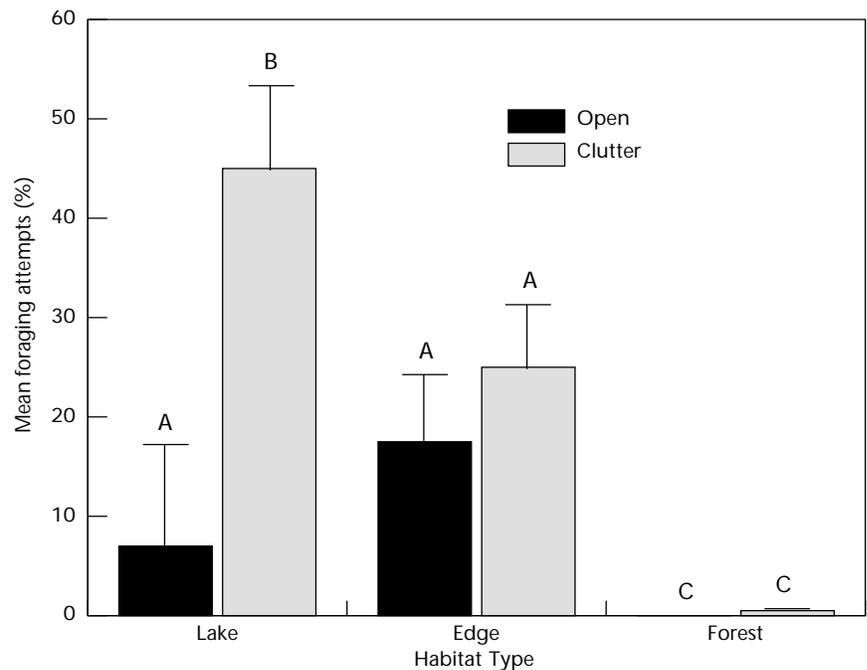

FIGURE 7   *Mean (+ 1 SE) foraging activity per hour for open-adapted bats (open) and clutter-adapted bats (clutter) in the three habitat types associated with lakes. Within each habitat type, and between habitat types for the same bat type, means with the same letter are not significantly different (p > 0.05). See Table 1.*

Sampling of Clearcuts

My results support the hypothesis that foraging activity of different types of bats varies depending on a combination of habitat structure and prey availability. The patterns observed between the open and clutter bats within each habitat type were as I predicted. Open-adapted bats were significantly more active than clutter-adapted bats in clearcuts, with similar trends for the other habitat types. However, the results between habitat types were not as predicted. Foraging activity was significantly greater on the edge than in the clearcut or forest habitats. Edge may be preferred because of the nature of its vertical structure, which is a relatively unique landscape-form in a forest, and may be used as a navigational reference or flight corridor by bats. There was reduced foraging in the clear-cut areas, yet this habitat type may be important for the larger open-adapted bats, because few obstructions are encountered there. The low activity observed in the forest suggests that this habitat is not an important foraging area for either group of bats, perhaps because of the greater spatial complexity that may make flight and foraging energetically more expensive for bats (Aldridge and Rautenbach 1987; Norberg and Rayner 1987).

The second part of my hypothesis stated that bat activity in the different habitat types should vary depending on prey availability. That is, bats should be most active where there are the most prey. However, my results did not support this prediction. Bat activity was not correlated with insect availability. The edge and forest had significantly greater total insect biomass than the clearcut, which may explain the high bat activity along the edge of clearcuts. Forest habitat appears to be an important source of prey, but may not be an important foraging area for bats because of the greater environmental clutter associated with it. That is, even though there were high prey resources in the forest, the greater degree of clutter prevented bats from using this prey source. Therefore, the preference of bats for edge habitat may be due to a combination of high prey resources, associated with the forest, and the structural nature of edge that provides a navigational reference or flight corridor.

Minimal foraging activity was observed in the forest (i.e., only one foraging attempt recorded in two years). However, commuting activity was detected, suggesting that bats were active in this habitat type. What, then, were bats doing in the forest? Bats roost in hollows or under loose bark of trees (Nagorsen and Brigham 1993). The commuting activity in the forest may be associated with the emergence of bats from their roosts as they travel to other foraging areas. Commuting activity in the forest peaked 30 minutes after sunset, then remained consistently low. This peak in activity may represent the time when bats emerged from their roosts and commuted to foraging areas. This suggests that although the forest habitat may not be an important foraging area, it may be important for roosting.

Clutter Sampling

My results suggest that the artificial clutter affected the foraging activity of bats. Prey availability between the treatment and the control did not differ, indicating that only the spatial complexity of the habitat type was manipulated. As expected, clutter-adapted bats foraged less within the clutter box than along the control edge. In contrast, the open-adapted

bats did not seem to be affected by this degree of spatial complexity. This is surprising, as I expected the open-adapted bats to be most dramatically influenced by the artificial clutter, due to their ecomorphological characteristics. That is, the faster, less manoeuvrable flight and relatively coarse resolution of echolocation calls of the open-adapted bats would limit them to more open habitat. I suspect that the clutter boxes were not large enough to properly sample the open-adapted bats, and that the bat detectors were actually monitoring open-adapted bats flying outside the clutter box. This may have occurred because, relative to clutter-adapted bats, open-adapted bats generally produce more intense echolocation calls of lower frequencies that travel greater distances (Griffin 1971).

Lake Sampling Riparian areas appear to be primary foraging areas for bats, with much greater foraging rates observed there than in forest-harvested areas. My results suggest that the centre and edge of lakes are important foraging areas, particularly for clutter-adapted bats. Greater activity by clutter-adapted bats may reflect the prey availability associated with lakes. That is, smaller flying insects that emerge from the surface of the water may only be perceptible and available to the clutter-adapted bats, equipped with their slower, more manoeuvrable flight and finer resolution of echolocation calls.

CONCLUSIONS

My results suggest that habitat use by foraging bats depends on the spatial complexity of a habitat type in combination with prey availability. The disturbance associated with forest harvesting appears to create preferred habitat for foraging bats, particularly for large bats that may be restricted to open habitat. My data suggest that edge and clear-cut habitats are preferred, and that forest habitat is not an important foraging area. However, the forest habitat may be important as a prey source for bats, as well as for potential roosting habitat. Furthermore, lake habitat, and most likely other riparian areas, appear to be primary foraging areas for bats, and need to be managed accordingly. Therefore, there must be balance between the creation of beneficial feeding areas along clear-cut edges, and the requirements for prey resources and suitable roosting sites, associated with forest habitat.

ACKNOWLEDGEMENTS

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Partial Cutting and Bats: A Pilot Study

MARK PERDUE AND J. DOUGLAS STEVENTON

ABSTRACT

We conducted a preliminary study of bat presence and activity, using ultrasonic detectors, in two intensities of partial cutting compared to clearcuts and uncut forest. The study was conducted in coast-interior transitional forests at the Date Creek silvicultural systems research site in northwestern British Columbia. The presence of bats in the study area was confirmed, and bat use (indexed by number and length of detections) of partial-cut treatments was at least as great as for the uncut forest. Bats were also detected in clearcuts, but at a lower rate. We tentatively conclude that the creation of openings in dense forest favours bat travel and foraging. Studies of roost-site requirements in relation to partial cutting are needed.

INTRODUCTION

Partial cutting is often advocated as a means of maintaining habitat for forest-dwelling wildlife while allowing extraction of timber. We examined the influence of two intensities of partial cutting on bat use of forest stands as compared to their use of uncut forest and clearcuts. The expectation was that partial cutting would maintain or, by the creation of canopy openings, actually improve travel and foraging potential for bats.

The objectives of this pilot study were (1) to determine if bats are present in the treatment units, (2) to conduct a preliminary assessment of bat activity in partial-cut treatments versus uncut and clearcut treatments, and (3) to assess priorities for further study of bats and the effects of partial cutting.

MATERIALS AND METHODS

The study was conducted from May to August 1995 at the Date Creek silvicultural systems study site in northwestern British Columbia (55° 22'N, 127° 50'W). These forests are transitional in climate, flora and fauna being between coast and interior types, and are in the moist-cold Interior Cedar-Hemlock biogeoclimatic subzone (Meidinger and Pojar 1991).

Four harvest treatments were applied to various sites in the fall and winter of 1992–93: (1) clearcutting with retention of scattered deciduous trees, (2) a heavy removal partial cut (approximately 60% of stand volume removed) using a combination of openings (0.1 to 0.5 ha) with single-tree to small-group selection, (3) a light removal partial cut (approximately 30% of stand volume removed) as either single stems or small groups, and (4) no harvesting. There were four replicates (each approximately 20 ha in size) of each treatment in a randomized block design across four site/age combinations: mesic, 350-year-old forest; mesic, 140-year-old forest; mesic-submesic, 140-year-old forest; and mesic-subhygric, 140-year-old forest. The treatments created distinct differences in stand density and degree of canopy removal (Figure 1).

We examined bat activity using ultrasonic detectors (Ultra Sound Advice, s-25), focusing on bat use of forest openings in the four treatments. The question we examined was: is the probability of hearing a bat, or the length of time bats were heard, influenced by size of opening or density of openings created by the treatments?

From air photos, four canopy openings were randomly selected for sampling in each treatment unit (a total of 64 sample points). For clearcuts (one large opening), or if distinct openings were not available in the uncut treatments, random sample points were used. The selected sample sites were sampled in random order (only during good weather) between late May and early August.

Ultrasonic detector microphones were located in the centre of the opening, mounted pointing vertically, 1 m above the ground. Using a timer and tape-recorder, detectors monitored bat echolocation calls for 50 minutes, 25 minutes before and after official twilight. The two parameters of bat use we analyzed were (1) the number of 50-minute samples with bat detection (presence/absence), and (2) the total length of time that bats were heard (activity) on the four, 50-minute tapes from each treatment unit. We were not able to distinguish between bat species, but we believe most or all were *Myotis* spp.

Due to the data significantly contradicting the assumptions for ANOVA, we examined the influence of treatments on the number and length of
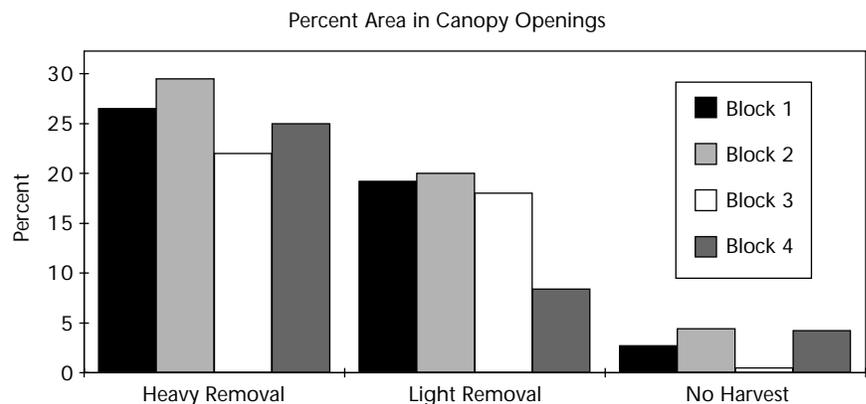

FIGURE 1   *Area (%) in canopy openings by harvest treatment and block (ecosystem/age combinations).*

detections using Friedman's non-parametric test for randomized blocks (Sokal and Rohlf 1981). This method tests for consistent ranking of treatments among experimental blocks. The influence of individual opening size and weather variables on the length of time that bats were heard, and on the probability of detecting a bat, were examined by regression and logistic regression. For this pilot study we used $p < 0.10$ as our criterion for significance.

RESULTS

Bats were detected in all treatments. Although the total number of samples with a detection varied by treatment (Figure 2), the ranking of treatments was not consistent across blocks ($p = 0.437$). Thus, we cannot conclude that treatment affected simple presence or absence of bats. Bat activity as indexed by length of detections (Figure 3), in contrast to presence or absence, was significantly different between treatments ($p = 0.086$). The order of the treatments (greatest use to lightest use) based on mean rank was: heavy removal, light removal, uncut, and clearcut.

None of the variables examined by logistic regression or standard regression (opening size, opening perimeter, temperature, humidity, individual bat detector) showed a significant relationship ($p > 0.10$) to either the probability of detecting bats, or the length of time that bats were heard. The proportion of detections with "feeding buzzes" showed the same pattern as for length of detections, but the sample size was too limited for statistical analysis.
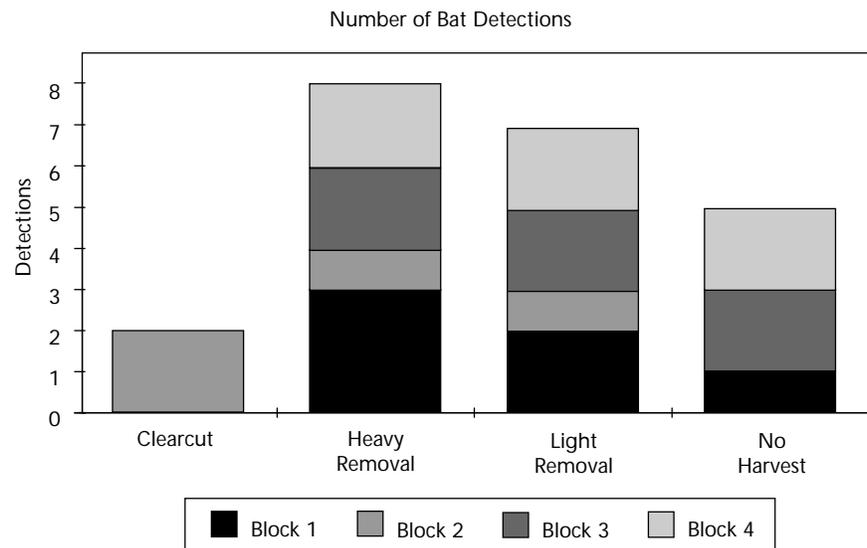
Number of Bat Detections

FIGURE 2   *Number of 50-minute samples with a bat detection by harvest treatment and block (ecosystem/age combinations). Friedman's randomized block design test of treatment differences p = 0.437.*
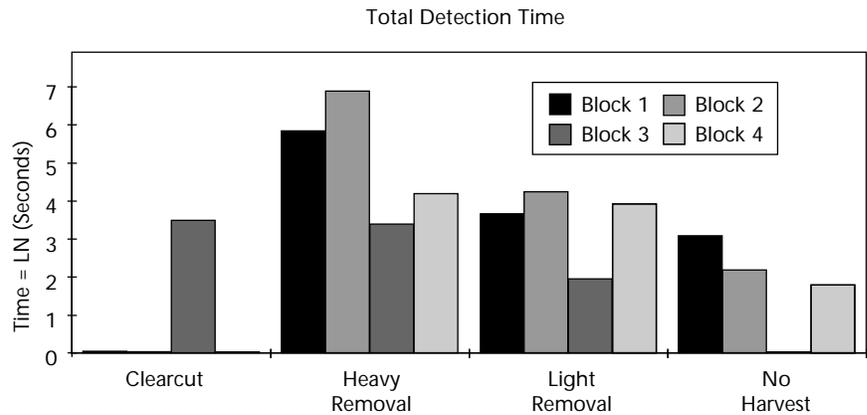
Total Detection Time

The total length of time that bats were detected by harvest treatment and block (ecosystem/age combinations). For illustration, time is presented as the natural log of total time (seconds). Friedman's randomized block design test of treatment differences p = 0.086.

DISCUSSION

The creation of canopy openings by partial cutting appears to favour bat foraging and travel as indexed by the length of time that bats were heard. We conclude that the partial cuts were at least as suitable as uncut forest or clearcuts. We suggest that the highest priority for further study is to determine species-specific roosting requirements. Partial cutting, while apparently maintaining or improving foraging habitat, reduces the abundance of potential roosting structures, such as snags.

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Effects of Timber Harvest on Bat Activity in Southeastern Alaska's Temperate Rainforests

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STEPHEN W. LEWIS

ABSTRACT

Five species of bats occur in southeastern Alaska's coniferous rainforests: *Myotis lucifugus*, *M. californicus*, *M. volans*, *M. keenii*, and *Lasionycteris noctivagans*. Over 42% of the high-volume timber in southeastern Alaska has been harvested, raising concern about wildlife habitat and conservation. We studied bat activity in old-growth forests, riparian areas, closed-canopy, second-growth forests, and clearcuts on Prince of Wales and Revillagigedo islands using ultrasonic bat detectors. Bats foraged in riparian areas, and activity patterns in this habitat differed during lactation and post-lactation. Bat calls detected in old-growth forests consisted primarily of commuting activity. Bats fed in clearcuts, but activity was low. Bat activity in second-growth was very low. Activity levels and nightly activity patterns make it clear that conservation of old-growth forests and riparian areas is essential for continued viability of the southeastern Alaska bat community. Diet and reproduction of *M. lucifugus* in these temperate rainforests differed from that reported at lower latitudes. Preliminary diet information for *M. keenii* and *M. volans* in southeastern Alaska is also presented. Over 300 caves have been surveyed in southeastern Alaska's 1,769 km² of karst terrain. Evidence of bats occupying these caves is widespread, and seasonality of that occupation is just beginning to be assessed. We provide evidence that neither clearcuts, nor second-growth forests provide habitat characteristics essential to most southeastern Alaska bats during the summer. This study also provides strong evidence that old-growth forests and riparian zones provide habitat characteristics needed by bats.

INTRODUCTION

Microchiropteran bats are long-lived nocturnal insectivores with low reproductive rates and non-cyclic populations (Findley 1993). These characteristics allow bats to achieve constant population levels in stable habitats, but may make them vulnerable when habitat is modified. Many bat populations have suffered decline, and some are threatened or endangered

(Tuttle 1979; Lowe et al. 1990; Speakman et al. 1991), due in part to habitat alteration (Lowe et al. 1990; Adam et al. 1994). The southeastern Alaska bat community consists of five species. *Myotis californicus*, *M. volans*, *M. keenii*, and *Lasionycteris noctivagans* reach the northern limit of their range in southeastern Alaska. *Myotis lucifugus*, the most commonly encountered bat species in southeastern Alaska, also occurs in more northerly parts of Alaska and Canada (Youngman 1975; Hall 1981; Parker et al. unpublished data).

Over 42% of the most productive forests (timber volume classes 6 and 7) in southeastern Alaska had been harvested by 1990 (United States Department of Agriculture 1991, 1993), and extensive harvesting continues. To determine whether southeastern Alaska forests are important bat habitat, we compared relative bat activity levels in high-volume, old-growth forests, riparian areas, clearcuts, and closed-canopy, second-growth forests. We also analyzed the nightly pattern of bat activity and relative feeding activity. Preliminary data were collected on bat diets, *M. lucifugus* reproduction, and seasonal bat occupation of caves.

METHODS

Study Area

This study was conducted in southeastern Alaska from 29 May through 28 August 1993. Southeastern Alaska is the wettest and coldest part of the north-temperate coniferous rainforest zone (Walter 1985). This ecosystem stretches from 54° to 60°N latitude, and includes the Alexander Archipelago and a narrow strip of mainland coast. The coastal mountain range and glacier fields isolate the region geographically and climatologically from nearby British Columbia and south-central Alaska (Figure 1).

Study sites were on northern, central, and southeastern Prince of Wales and western Revillagigedo islands at 55° to 56°N latitude (Figure 2). Prince of Wales, the third-largest island in the United States, covers 4557 km². Karst topography is well developed over much of northern and central Prince of Wales Island. This karst landscape has many caves and crevices, and contains some of the most productive forests on the island (Aley et al. 1993). Study sites were on harvested and unharvested areas of karst as well as non-carbonate lands (Table 1). Revillagigedo Island is approximately one-half the size of Prince of Wales Island and has little karst. Study sites on this island were on non-carbonate terrain. Heavy rains occur in all seasons throughout the study area. Annual precipitation varies from 4064 mm on western Revillagigedo Island to 2032 mm on northern Prince of Wales Island (Hartman and Johnson 1978).

Forest Habitats Monitored

Habitats investigated were (1) old-growth forests dominated by western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), and red cedar (*Thuja plicata*); (2) riparian areas (edge of streams or ponds 10–25 m wide, Table 1) within these forests; (3) closed-canopy, second-growth forests harvested 25–70 years ago; and (4) forests clearcut-harvested 5–17 years ago in which the canopy had not yet closed. Six sites in each of the four habitat types were monitored. The 24 study sites were all >16 ha and at elevations <250 m. Dominant overstorey (tree) and understorey (shrub

Alexander Archipelago

Canada
United States

N

Prince
of Wales
Island

Revillagigedo
Is.

Ketchikan

United States
Canada

Alaska

Map Location

Queen Charlotte
Islands

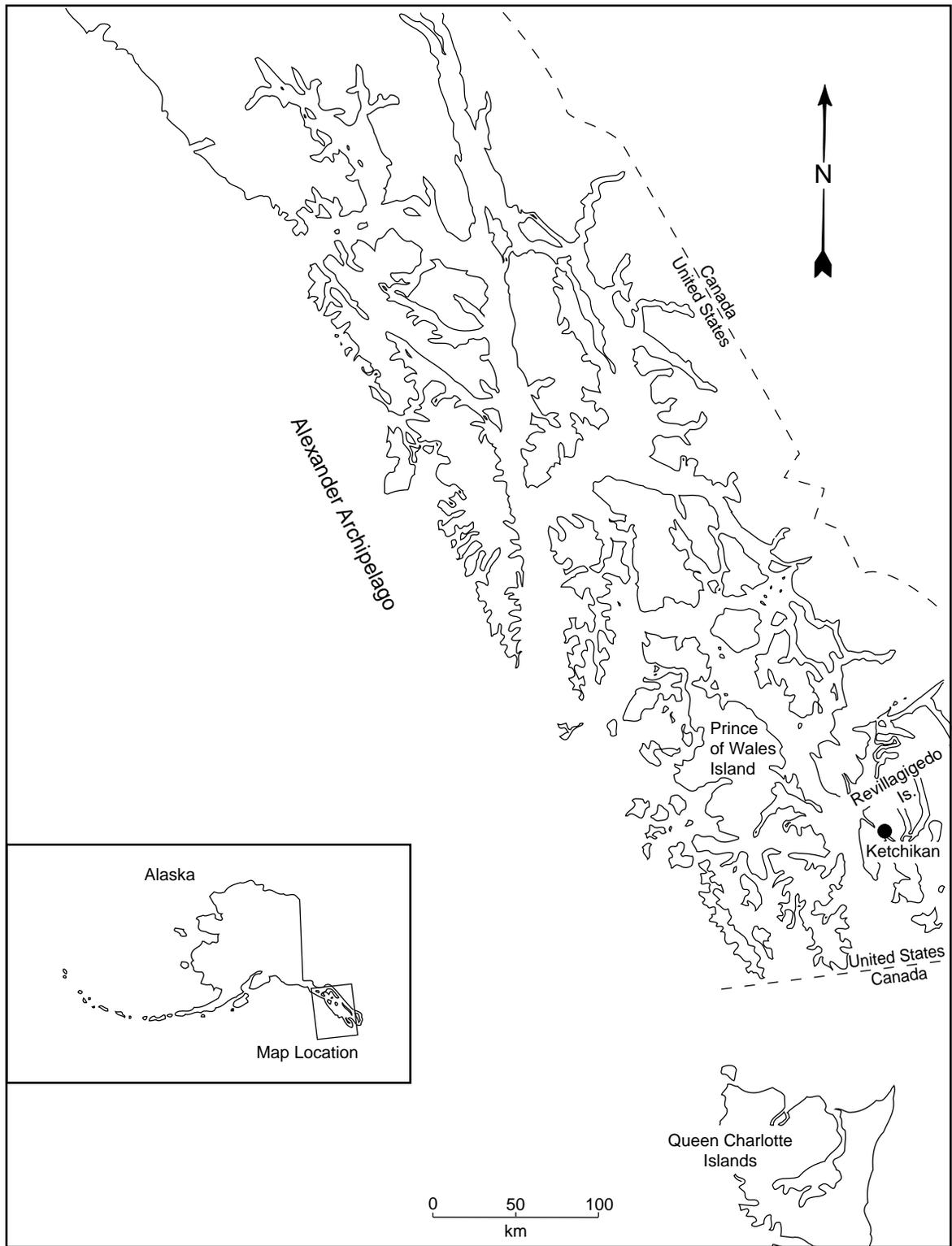0   50   100
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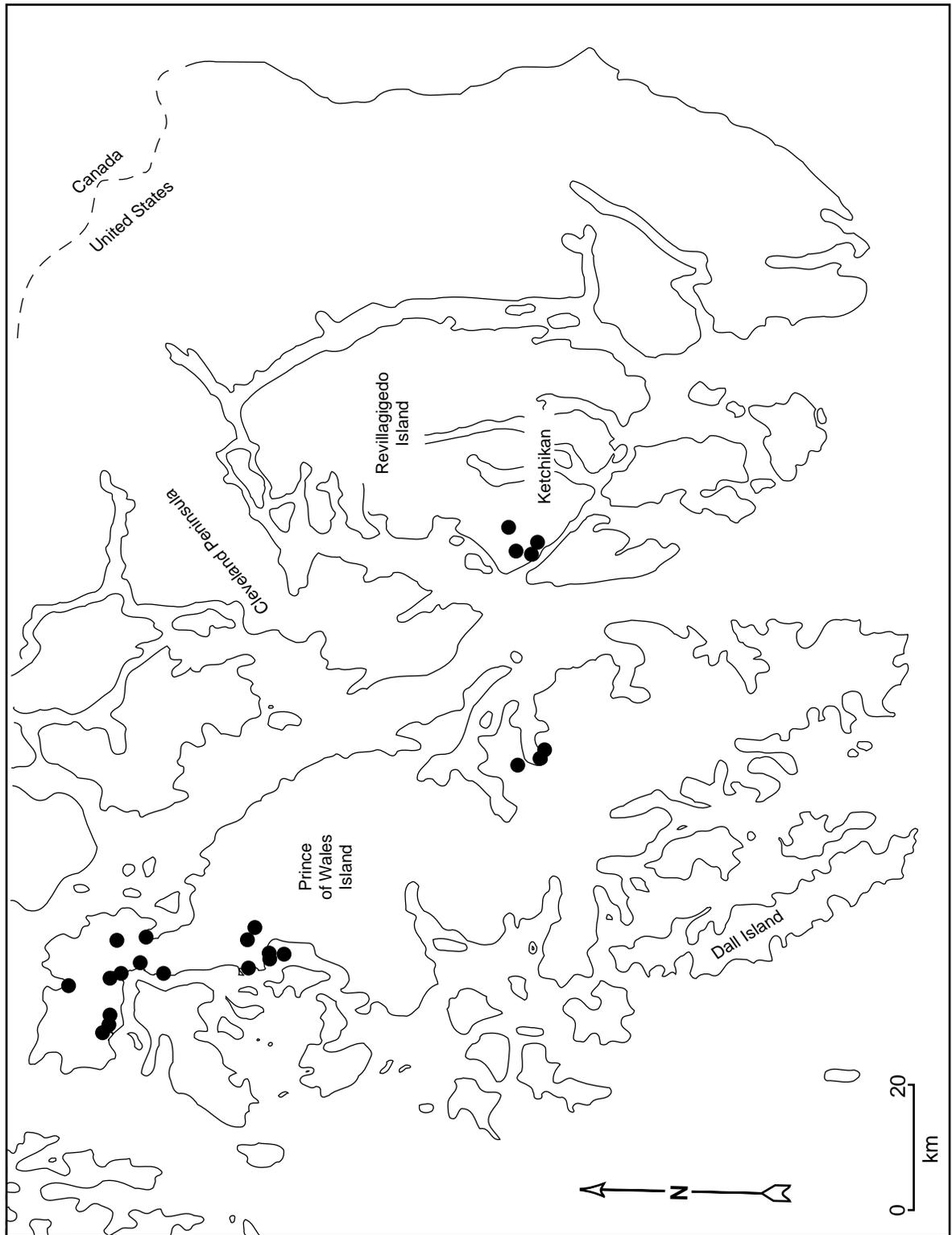
FIGURE 1   *Southeastern Alaska.*

FIGURE 2   *Study area on Prince of Wales and Revillagigedo islands in southeastern Alaska.* ● *represent study sites.*

TABLE 1   *Vegetation characteristics and karst occurrence of 20 × 40 m plot at study sites*

Site name	Karst	Dominant overstorey species[1]	Dominant understorey species[1]	Canopy height[2]	Number trees[3]	Number snags[4]	Stream width	Stream grad
Riparian sites								
Red Creek	no	WH/SS	Vacc/DC	24 m	28	7	20 m	2%
Turn Creek	yes	WH/SS	Vacc	27 m	26	2	10 m	2%
108 Creek	no	WH/SS	Vacc/SC	34 m	7	6	18 m	2%
Yatuk Creek	yes	WH/SS	DC/SB	37 m	12	1	10 m	2%
Polk Creek	no	WH/RC	Vacc/SL	31 m	23	14	25 m	4%
Frog Pond	no	SP	CB	7 m	10	0	15 m	0%
Old-growth sites								
Calder	yes	WH/RC	Vacc/SF	31 m	34	9		
Beaver Falls	yes	WH/SS	Vacc/DC	33 m	33	5		
River's End	yes	WH	Vacc/DC	34 m	15	7		
Sarkar	no	WH	Vacc	34 m	18	2		
Polk	no	WH	Vacc/DC	31 m	28	7		
Perseverance	no	WH/RC	Vacc/SC	30 m	31	6		
Clear-cut sites								
Calder	yes	WH/SS[5]	Vacc	5 m	0	0		
Roaring Road	yes	WH[5]	Vacc/DC	2 m	0	0		
Naukati	yes	WH/SS[5]	Vacc	1 m	0	0		
Yatuk	no	WH[5]	Vacc	3 m	0	0		
Polk	no	WH[5]	Vacc	2 m	0	0		
Ketchikan	no	WH[5]	Vacc/SC	2 m	0	0		
Second-growth sites								
Calder	yes	WH/SS	Vacc	18 m	86	1		
Starlight	yes	WH/SS	Vacc/DC	10 m	37[6]	1		
Naukati-1	yes	WH/SS	Vacc	18 m	110	2		
Naukati-2	yes	WH/SS	Vacc	18 m	104	2		
Polk	no	WH/SS	Vacc/DC	17 m	52	0		
Pipeline	no	WH	Vacc/DC	12 m	60	1		

[1] WH = *Tsuga heterophylla* (western hemlock), SS = *Picea sitchensis* (Sitka spruce), RC = *Thuja plicata* (red cedar), SP = *Pinus contorta* (shore pine), Vacc = *Vaccinium alaskaense/ovalifolium* (blueberry species), DC = *Oplopanax horridum* (devil's club), SC = *Lysichitum americanum* (skunk cabbage), SL = *Gaultheria shallon* (salal), SF = *Polysticum munitum* (swordfern), SB = *Rubus spectabilis* (salmonberry), CB = *Empetrum nigrum* (crowberry).

[2] Average canopy height of overstorey trees in riparian, old-growth, and second growth. Average height of young trees in clearcuts.

[3] Number of trees ≥ 12 cm DBH (diameter at breast height).

[4] Number of dead trees ≥ 12 cm DBH and ≥ 2 m tall.

[5] Tree species before harvest.

[6] Site thinned in mid-1980s.

and herb) species at each study site (Table 1; DeMeo et al. 1992) were described. To ensure within-habitat uniformity, we estimated overstorey height with a clinometer and tape, and quantified trees and snags within a 20×40 m area at each site. Multiway analysis of variance determined that there were significant structural differences among the four habitat types ($p < 0.05$; Zar 1984). Tukey pairwise comparisons determined that average stand height, number of trees per plot, and number of snags per plot differed between habitats (Table 2; $p < 0.05$; Zar 1984). Sample size was too small to determine within-habitat differences between karst and non-karst sites.

Activity Levels and Types of Calls

To determine relative levels of bat activity among habitat types, echolocation calls were recorded with countdown-mode bat detectors and delay switches (Anabat II, Titley Electronics, Ballina, N.S.W., Australia) attached to voice-activated, cassette tape-recorders (Radio Shack Realistic Minisette 20). A single bat call was defined as ≥ 2 ultrasonic pulses (Griffin 1958) detected from the time the bat detector began recording calls until the calls were no longer audible. The time of each call was recorded automatically. The electronic equipment was placed in a plastic box with a hole for the microphone and a 3-cm roof to shelter the microphone from rain. A light sensor turned the system on at dusk and off at dawn. One bat detector was placed in each site at least 90 m inside the habitat and approximately 2 m above the ground. To reduce the effect of weather, all habitat types were monitored every night. All 24 sites were monitored ultrasonically for 1 to 9 nights (average 4.6).

Bat calls were transcribed from the recordings and grouped in 5-minute intervals. Anabat II Bat Call Analysis software version 1.1 (Titley Electronics, Ballina, N.S.W., Australia) was used to display call sonagrams to determine whether questionable sounds were bat calls or extraneous noise (e.g., raindrops). We could not unequivocally differentiate species of *Myotis* by their calls because the vespertilionid species inhabiting southeastern Alaska are difficult to differentiate by their call characteristics (Thomas et al. 1987; Thomas 1988). A feeding buzz was defined as an increased pulse repetition rate that blended the calls together into a buzz (Griffin 1958). To test for differences in the proportion of nights with bat activity and the proportion of calls containing feeding buzzes, we used χ^2 tests (Zar 1984). Because bat calls were not normally distributed and variances were not equal, Kruskal-Wallis one-way analysis of variance was used to compare average calls per night among habitat types.

TABLE 2   *Tukey pairwise comparisons of habitat characteristic means ($p \leq 0.05$)*

Habitat type	Stand height	Number of trees	Number of snags
Riparian	A	B	AB
Old growth	A	B	A
Clearcut	B	C	CB
Second growth	C	A	C

Means with the same letter are not significantly different.

Activity Patterns

To test whether nightly activity patterns differed between habitat types or temporally, we compared nightly patterns of call activity in the periods 14–21 July and 17–28 August. Only old-growth and riparian sites had adequate activity for comparison. To remove the bias of fewer calls at the end of the night due to rain noise running the tape out or battery failure, we calculated a weighted average of calls-per-5-minute-interval in which equipment was working. To remove autocorrelation, we used a moving average of 5 intervals. Time from sunset to sunrise increased from 7 hours 6 minutes to 9 hours 58 minutes between 14 July and 28 August. Length of twilight decreased from 48 minutes (13% of the night) to 18 minutes (3% of the night). Therefore, we compared intervals beginning 30 minutes before sunset, rather than using clock time. Activity that occurred later than 7 hours 9 minutes after sunset (i.e., sunrise on 14 July) was excluded from comparison. Resulting patterns were compared using Kolmogorov-Smirnov goodness of fit tests for cumulative data (Zar 1984). Because of the small data set, we tested only whether overall patterns differed, and did not statistically compare portions of the night.

RESULTS

Activity Levels and Call Type

One-hundred and fifteen nights of sampling yielded 2716 bat calls. There were 2508 bat calls detected in riparian habitat during 31 nights sampled; 150 calls in old growth during 25 nights; one call in second growth during 30 nights; and 57 calls in clearcuts during 29 nights (Table 3). In addition to calls listed above, bats were detected on two additional nights in riparian sites, but the number of calls could not be determined. These nights were only used to compare the proportion of nights with bat activity. Proportion of nights with bat activity (≥ 1 call per night) differed significantly between the four habitats ($\chi^2 = 33.04$, $p \leq 0.05$). Pairwise comparisons showed no significant difference in number of nights with activity in riparian versus old growth ($\chi^2 = 0.71$, $p \leq 0.05$). There were significantly more nights with activity in old growth than in clearcuts ($\chi^2 = 6.29$, $p \leq 0.05$), and in clearcuts than second growth ($\chi^2 = 5.70$, $p \leq 0.05$).

T A B L E 3 *Bat activity in forest habitats*

Habitat type	Total number of calls	Number of nights sampled	Average calls per night[a]	Percentage of nights with bat activity[a]	Percentage of calls with feeding buzz[a]
Riparian	2508	31 + 2[b]	81 A	97 A	15 A
Old growth	150	25	6 B	76 B	4 B
Clearcuts	57	29	2 B	28 C	10 B
Second growth	1	30	0.03 C	3 D	0
Total	2716	115			

[a] Items with the same letter are not significantly different (p ≤ 0.05).

[b] 31 nights were used to calculate percentage of total calls and average calls per night, 33 nights were used to calculate percentage nights with bat activity. See text for explanation.

Average number of calls per night among the four habitats was significantly different (H = 68.27, $p \leq 0.001$). Multiple comparisons showed significant differences between riparian and old growth (H = 3.40, $p \leq 0.05$), old growth and second growth (H = 3.82, $p \leq 0.05$). Differences between average calls per night in old growth and clearcuts were not significant (H = 2.48, $p \leq 0.05$). However, 47 of the 57 calls in clearcuts occurred during the night of 5 July. There was no significant difference in average calls per night between clearcuts and second growth (H = 1.40, $p \leq 0.05$). In riparian sites, a sample of 731 calls revealed that 110 contained feeding buzzes, while in old growth 6 of 150 calls contained feeding buzzes. In clearcuts, 6 of 57 calls contained feeding buzzes; 5 of these were among the 47 calls detected on 5 July. The single call in second growth did not contain a feeding buzz. There was a significant difference in proportion of calls that contained feeding buzzes among riparian, old growth, and clearcut habitats ($\chi^2 = 11.97$, $p \leq 0.05$). Pairwise comparisons showed significant differences between riparian and old growth ($\chi^2 = 11.57$, $p \leq 0.05$), but not between clearcuts and riparian ($\chi^2 = 0.734$, $p \leq 0.05$), or between clearcuts and old growth ($\chi^2 = 3.05$, $p \leq 0.05$).

Activity Patterns

Calls were not detected before sunset or after sunrise in any habitat during the study period (Figure 3). Activity patterns differed significantly between old-growth and riparian habitats in July (df = 88, $p \leq 0.001$, D = 0.205); in August between old-growth and riparian habitats (df = 126, $p \leq 0.001$, D = 0.172); and in riparian habitat between July and August (df = 88, $p \leq 0.001$, D = 0.205). There was no significant difference between July and August activity patterns in old growth (df = 94, $p > 0.05$, D = 0.138). Both July and August activity in riparian areas began 15–20 minutes after sunset. In July there were two additional activity peaks within 4 hours of sunset, and almost no activity during the next 3 hours before sunrise. In August, activity was low throughout the remainder of the night, even though the night was longer and twilight was shorter.

DISCUSSION

Riparian Areas

Riparian habitat had the highest proportion of nights in which bats were detected, the highest number of bat calls per night, and the highest proportion of calls containing feeding buzzes. Among the four habitats sampled, riparian areas were the most important foraging sites for bats. The importance of riparian areas as feeding habitat has been frequently noted at lower latitudes and in drier climates (Buchler 1976; Fenton and Bell 1979; Bell 1980; Nagorsen and Brigham 1993). *Myotis lucifugus*, the most commonly encountered species in southeastern Alaska (Parker et al. unpublished data), tends to circle when foraging (Fenton and Bell 1979; Fenton et al. 1980). The higher number of bats detected per night may have been influenced by individual bats being detected multiple times as they foraged. Nevertheless, the higher proportion of nights that bats were detected in riparian habitat, and the high proportion of calls containing feeding buzzes in these sites support the conclusion that riparian areas are important bat habitat.
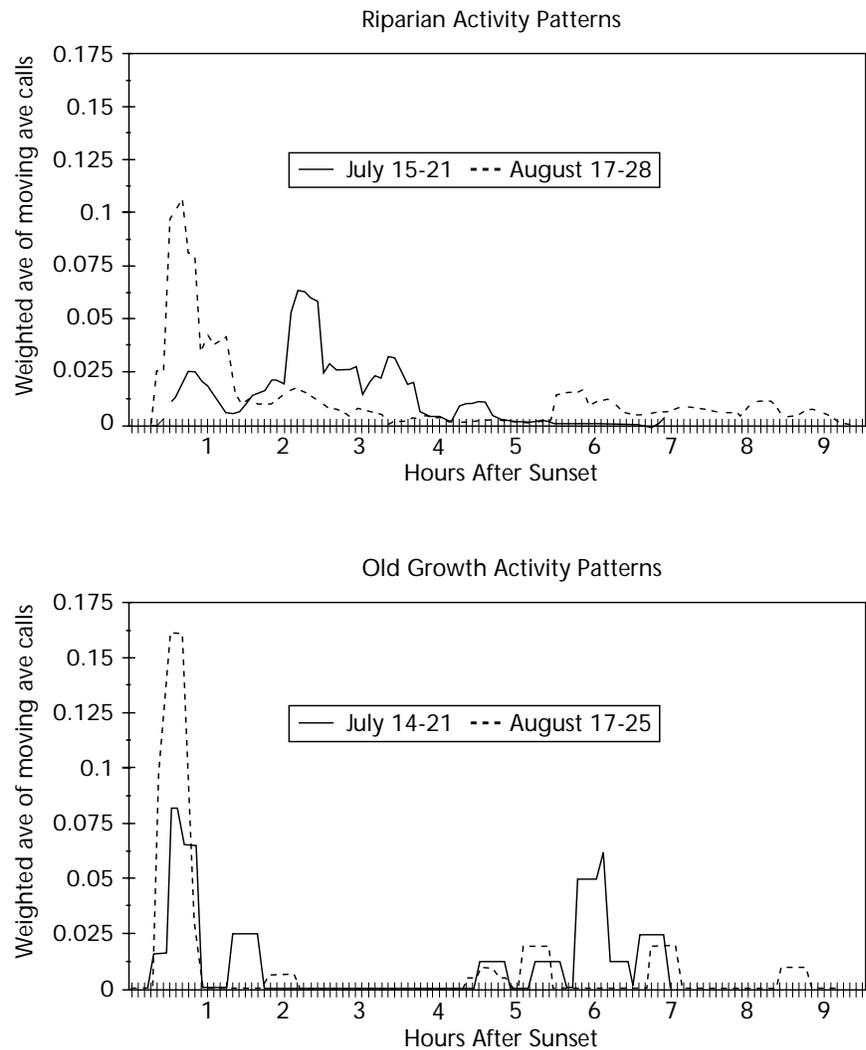
FIGURE 3   *Activity patterns during 14–21 July and 17–28 August in riparian and old-growth sites.*

The temporal change in activity patterns in riparian areas likely reflects seasonal changes in energy needs at this high latitude. We suggest that the prolonged foraging activity in July is in response to the high energy demand of lactation and the subsequent need to forage longer. This corroborates other studies that found that female *M. lucifugus* forage up to 4 hours per night during late pregnancy and lactation (Kurta et al. 1989), and forage several times per night, returning to the maternity roost to nurse their young between foraging bouts (Anthony and Kunz 1977; Anthony et al. 1981). By mid-August, females no longer have the high-energy demand of lactation (Kurta et al. 1987), and can meet energy needs in a shorter period of time (Anthony and Kunz 1977). This is reflected by the August activity pattern, in which most activity occurred within 2 hours of sunset. Insect availability is low during the latter part of the night (Anthony and Kunz 1977; Barclay 1991), and probably makes foraging less efficient than conserving energy (Pulliam 1981) by roosting. Foraging juveniles may account for the low-activity level during the remaining

8 hours before sunrise in August. Juveniles are less adept at capturing insects, and must forage longer to meet energy needs (Anthony and Kunz 1977). A similar change in foraging patterns was noted for *Pipistrellus pipistrellus* at 57°N latitude in Scotland. During lactation these bats foraged just after sunset and again prior to sunrise. During pregnancy and post-lactation they foraged only once, immediately following sunset (Swift 1980). In contrast to our study, Anthony et al. (1981) found that *M. lucifugus* in New Hampshire had a bi-modal pattern of foraging activity throughout the summer. Differences in study methods may be responsible for differences observed between this study and *M. lucifugus* in New Hampshire. We monitored echolocation calls in riparian habitat, whereas Anthony et al. (1981) monitored bats leaving and entering night roosts.

Old-Growth Forests

Old-growth was the habitat with the second-highest bat activity. Even though old-growth sites had fewer average calls per night, calls were heard during 76% of nights monitored. This regular occurrence of bats suggests that it is important for summer roosts. Southeastern Alaska's temperate rainforests contain abundant live trees, snags, and fallen logs in a variety of sizes (Alaback 1991). Such structural diversity provides suitable sites for cavity-roosting species (Bunnell and Allaye-Chan 1984), such as bats (Barclay and Cash 1985; Christy and West 1993). Use of old-growth forests by bats for roosting and foraging has been documented in British Columbia, Washington, and Oregon (Barclay and Cash 1985; Lunde and Harestad 1986; Thomas 1988; Christy and West 1993). Bat roosts and foraging sites are likely to occur throughout old-growth forests, dispersing bats and decreasing the likelihood of a bat passing by an ultrasonic detector placed randomly in the forest. In addition, because bats in old-growth sites were primarily commuting, they were not likely to pass the detector more than once. The six calls with feeding buzzes in old growth indicate that foraging also occurred in old growth. It is likely that all bat species in southeastern Alaska forage in old-growth forests (Saunders and Barclay 1992; Nagorsen and Brigham 1993; van Zyll de Jong and Nagorsen 1994), especially *M. keenii* (Parker and Cook, in review). Nightly activity patterns in old growth remained the same in July and August. This predominantly commuting activity was highest immediately following sunset when bats left their roosts to travel to foraging sites. A few bats were detected at different intervals throughout the rest of the night, and may have been bats returning to day roosts.

Old-growth forests in southeastern Alaska may be important to bats primarily for roosting sites. However, too little is known about the ecology of bats in these temperate rainforests to be sure that they are not equally important as foraging areas for species, such as *M. keenii* (Parker and Cook, in review). Availability of roost structure is thought to be an important factor limiting bat distribution and abundance in temperate climates (Humphrey 1975; Kunz 1982). In other portions of their range, *M. lucifugus, M. volans, M. californicus, M. keenii*, and *L. noctivagans* roost under loose bark, in snags, and hollow trees (Barclay and Cash 1985; Thomas 1988; Christy and West 1993). In addition, extensive karst formations in southeastern Alaska (Buddington and Chapin 1929; Aley et al. 1993; Baichtal, 1995) provide numerous caves and crevices where hibernating bats have been observed (Parker et al. unpublished data).

Clear-cut Forests

The smaller proportion of nights in which bats were detected in clearcuts rather than in old growth indicates that bat activity in old growth was more consistent. This is likely due to the lack of roost structure in clearcuts. Clear-cut harvest of timber eliminates snags, decaying trees, and large trees with loose bark (Cline et al. 1980), thereby eliminating roost sites.

Insectivorous bats exploit patches of insects (Belwood and Fenton 1976; Bell 1980), and this is apparently what at least one bat was doing in the clearcut that showed unusually high bat activity on 5 July. Activity on that night also influenced the lack of statistical significance in the average calls per night between clearcuts and old-growth or riparian habitats. Clearcuts in southeastern Alaska may be used occasionally by *L. noctivagans* and *M. volans*, which sometimes forage in open areas (Fenton and Bell 1979; Nagorsen and Brigham 1993).

Second-Growth Forests

The high density of even-sized, closely spaced trees, and the lack of snags and decaying trees in second growth (Alaback 1984a; Bunnell and Allaye-Chan 1984) are likely reasons for the low activity of bats in this habitat. In southeastern Alaska, old-growth characteristics, including the structural diversity needed for roosts, begin to develop 150–200 years after harvest (Alaback 1984b). It is possible that bats commonly foraged above the second-growth canopy and were not detected because the dense canopy blocked echolocation calls. However, the single echolocation call recorded in second growth indicates that it is possible to detect calls in this habitat. More calls should have been recorded if bats foraged above the second-growth canopy. In a similar study in the Pacific Northwest, bats were detected three to ten times less often in second-growth than in old-growth forests, even when bat detectors were placed in the tree canopy as well as on the ground (Thomas 1988). Our study indicates that little bat activity occurs in second-growth forests of southeastern Alaska.

Ecology of *Myotis lucifugus*

Reproduction in *M. lucifugus* also appears to differ between southeastern Alaska and lower latitudes. At lower latitudes, in areas of high summer rainfall and low ambient temperature, *M. lucifugus* has a low female:male ratio, and females are non-reproductive (Thomas 1988; Barclay 1991). Inclement weather may not allow sufficient time during the night for females to meet energy demands of pregnancy and lactation (Thomas 1988; Barclay 1991; Grindal et al. 1992). In southeastern Alaska, however, the female:male ratio is equal, and reproductive females have been captured (Parker et al. unpublished data). This suggests that female *M. lucifugus* are able to meet the energy demands of pregnancy and lactation in southeastern Alaska rainforests, even though prolonged rainstorms are common. Changes in activity patterns between lactation and post-lactation support this conclusion. Consumption of over 15% non-volant prey, such as spiders (Parker, unpublished data; Whitaker and Lawhead 1992), may enable these bats to maintain a positive energy balance.

Federal law in the United States requires public land managers to inventory and maintain viable populations of wildlife affected by land-management practices, such as timber harvesting (United States Congress 1976). Our study suggests that old-growth forests and riparian areas provide roosting and foraging habitat for the five bat species in southeastern Alaska. Extensive past and future harvesting in southeastern Alaska (United States Department of Agriculture 1991, 1993) suggests a significant impact on these species. Our data also indicate that clearcuts are not important bat habitat, perhaps because clearcuts do not provide roosting structure. However, bats occasionally fed on insect swarms in clearcuts. Closed-canopy second growth is not used by bats in southeastern Alaska. Old-growth characteristics that provide suitable roost sites for bats do not develop until at least 150 years after harvesting. Current plans for the Tongass National Forest project a 150-year harvest rotation (United States Department of Agriculture 1991). Planning and environmental assessment processes for public lands should include this information when considering the effects of land-management practices.

Southeastern Alaska is unique among high-latitude archipelagos because of its large number and high diversity of caves (Aley et al. 1993; Baichtal, 1995). Over 1,769 km² of southeastern Alaska's 26,305 km² Tongass National Forest are on karst terrain (United States Department of Agriculture, in press). Caves and crevices are also important bat habitat (Hill and Smith 1984). Personal observations (Parker and Cook) suggest that bats occupy caves during cold spells in the winter, but leave these caves during warmer spells. Guano and skeletal remains have been observed in several caves. However, during eight summers of intensive mapping and exploration of more than 340 significant caves, no bats have been observed (Lewis and Allred, unpublished data). Future studies should examine seasonal changes in roost selection to determine when bats in southeastern Alaska occupy forest and cave roosts. Studies should also assess what aspects of cave morphology create microclimates suitable for hibernating bats. Because some of the most productive forests in southeastern Alaska are on karst (Baichtal, 1995), this component of southeastern Alaska's rainforest ecosystem should be especially important bat habitat, providing forest and cave roosts, as well as foraging habitat. Documentation of winter activity patterns and foraging strategies in relation to weather patterns and habitat type will be important in determining the effects of timber harvesting on bats.

Our study provides evidence that the ecology of *M. lucifugus* in southeastern Alaska cannot be extrapolated from studies of this species at lower latitudes. Reproduction appears to differ between *M. lucifugus* in southeastern Alaska and conspecifics at lower latitudes. Ecology of *M. volans* and *M. keenii*, *M. californicus*, and *Lasionycteris noctivagans* in southeastern Alaska has not been established because no data are available for these species (Parker et al., unpublished data). Foraging strategies, prey availability, and reproductive success of these species should be assessed in southeastern Alaska.

Although questions remain about how habitat modification in south-

eastern Alaska affects bat populations, this study strongly suggests that present levels of timber harvesting will have a detrimental effect on these bat populations. We provide strong evidence that neither clearcuts, nor second-growth forests provide habitat characteristics essential to most southeastern Alaska bats during the summer. We also provide evidence that unharvested, old-growth forests and riparian zones provide habitat characteristics essential to bats.

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