

BAT ACTIVITY IN THE BOREAL FOREST: IMPORTANCE OF STAND TYPE AND VERTICAL STRATA

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We examined habitat use by bats in the boreal forest of central Saskatchewan during summer 1995 by monitoring echolocation calls across forest types and through the canopy of mature forest. We sampled bat activity in mature aspen (*Populus tremuloides*)-white spruce (*Picea glauca*) mixedwood, aspen, and jack pine (*Pinus banksiana*) stands and recorded passes from little brown (*Myotis lucifugus*), northern long-eared (*M. septentrionalis*), big brown (*Eptesicus fuscus*) or silver-haired bats (*Lasionycteris noctivagans*), and hoary (*Lasiurus cinereus*) bats. There were significantly more bat passes per night in the aspen-white spruce mixedwood forest than in aspen or jack pine forest. There was no difference in the proportion of feeding buzzes recorded from aspen-white spruce mixedwood and aspen forest. In aspen forest, mean number of hoary bat calls per night was higher above than below the canopy, whereas number of *Myotis* calls was higher within and above the canopy than below the canopy. There was no difference in the number of feeding buzzes recorded among the three canopy heights. Bat activity peaked toward sunset below the canopy but was more uniform within and above the canopy. Our results highlight the importance of mature aspen-white spruce mixedwood and aspen forest as habitat for boreal forest-dwelling bats and demonstrate for the first time that insectivorous bats are active both within and above canopy levels of the boreal forest.

Key words: Anabat, bats, bat detector, boreal forest, echolocation, habitat-use, foraging, forest type, forest canopy

Several studies have examined habitat use, in particular foraging activity, by bats in high-latitude temperate forests of North America (Grindal and Brigham, in press; Kalcounis and Brigham, 1995; Thomas, 1988). However, to our knowledge, only one previous study has been conducted on bats in boreal forest (Crampton and Barclay, in press). Those authors determined the relationship between habitat use by bats and stand age in aspen-dominated mixedwood forest and found that foraging activity was most intense in mature stands and bats roosted exclusively in old stands. Crampton

and Barclay (in press) hypothesized that key structural attributes of older stands included presence of old trees and gaps in the canopy, which provided roost sites and foraging locations, respectively. Although evidence that bats prefer older stands is convincing, it is not clear how bats respond to structure and vegetative composition among different types of mature boreal forest stands.

The influence of habitat structure on animals has long interested ecologists (e.g., MacArthur, 1958). Heterogeneity is an intrinsically important and defining attribute

of mature forest. For highly mobile forest-dwelling animals such as bats, forests can be viewed as a volume of potentially usable habitat. Until recently, observer bias and technical constraints have limited our knowledge of how bats use the vertical space. As a consequence, bat use of forest habitat has been studied primarily from the perspective of the forest floor.

To date, no studies have addressed the question of whether bats regularly fly and forage above the canopy of temperate forests. Given that some species of bats fly as high as 3,000 m (McCracken, 1996), it seems likely that the volume of space above the forest canopy represents important habitat for bats. Current information about distribution of vertical foraging activity by bats suggests that vertical space is partitioned, but this is based almost exclusively on studies of frugivorous bats in tropical forests (Francis, 1994; Heideman and Heaney, 1989; Zubaid, 1994).

The presence of well-defined canopies (and often sub-canopies) in mature forest presents bats with differences in structure through the vertical dimension of the forest. Numerous studies have used wing morphology to predict structural complexity of habitats used by foraging bats (Aldridge and Rautenbach, 1987; Brigham et al., 1997; Kalcounis and Brigham, 1995; Saunders and Barclay, 1992). These studies lead to the prediction that highly maneuverable species (i.e., small bats with low wing loading) should be able to exploit habitat containing many obstacles (i.e., clutter; sensu Fenton, 1990), as well as more open habitat. Cluttered habitats should be preferred by bats because this is where insect densities tend to be high (Kalcounis and Brigham, 1995). In contrast, larger, less maneuverable species (large bats with high wing loading) should be more restricted to foraging in open forests, forest gaps, or areas above the canopy.

The southern mixedwood region of the Canadian boreal forest is a diverse mosaic of forest types and ages that is primarily the

result of fire-driven disturbance (Johnson, 1992; Rowe and Scotter, 1972). Diversity of forest types across the southern boreal mixedwood forest and the availability of the Boreal Ecosystem Atmosphere Study (BOREAS) flux towers, which projected above the canopy in several forest types, provided us with an opportunity to quantify how bats use both horizontal and vertical spatial axes in mature forests of different composition.

Our purpose was twofold. First, we wished to evaluate bat activity as measured from the ground in old and mature stands to determine if activity differed among forest types. Secondly, we wanted to measure vertical distribution of bat activity in three forest types in the boreal forest to determine if bat activity differed below, within, and above the canopy and if that activity varied temporally. For both parts of the study, we used ultrasonic detectors to identify species and assess relative activity.

MATERIALS AND METHODS

Our study was conducted during summer 1995 in and near the Prince Albert Model Forest (Bouman et al., 1996) located within the Southern Boreal Ecoregion of Saskatchewan, Canada. We determined bat activity by monitoring echolocation calls using the Anabat system (Titley Electronics, Ballina, Australia; O'Farrell et al., 1999), which is specifically designed to facilitate identification of free-flying bats by producing frequency-time graphs of echolocation calls. The system can be deployed remotely because it runs on batteries and records echolocation calls to audiotapes for later transcription and computer analysis.

Forest types.—We sampled bat activity simultaneously in three forest types: aspen (*Populus tremuloides*)—white spruce (*Picea glauca*) mixedwood (three stands), mature aspen (three stands), and jack pine (*Pinus banksiana*)—two stands. On each of 16 consecutive nights, one stand of each forest type was sampled simultaneously. We randomized the sampling order among stands within each forest type. Because we randomly selected stands for sampling on each night, we did not sample all stands over the 16 nights in exactly the same proportion. We

sampled the three aspen–white spruce mixed-wood stands on 6, 6, and 4 nights; the three aspen stands on 4, 4, and 8 nights; and the two jack pine stands on 9 and 7 nights. Within a stand, we randomly selected locations for bat detector placement on every sampling night. Bat detectors were always >100 m from the nearest road and >50 m from the nearest trail. Sites were selected from Provincial forest inventory maps and cover maps for Prince Albert National Park. All stands were of fire-origin ranging from 80 to 120 years old and were located in $>1,000$ -ha tracts of contiguous forest. Stand size, as estimated from forest inventory maps, was ≥ 30 ha.

At each site, the Anabat system was placed ca. 3–4 m high with the microphone of the detector pointed toward the middle of the stand and directed at an angle of 45° from the ground. The detector system was connected to a timer with a light sensor that turned the system on at dusk and off at dawn. A signal-activated recorder was used so that the system was recording only when incoming echolocation calls were detected. The automated nature of our protocol allowed us to remotely sample three stand types simultaneously on each night of the study. We randomly assigned individual detector systems on any given night to control for any differences in the amount of airspace sampled by individual units.

Vertical dimension.—To assess the effect of vertical forest structure on bat activity, we set Anabat systems below, within, and above the canopy of mature (60–80 years) aspen, old (i.e., >80 -year) black spruce (*Picea mariana*) and mature jack pine forest. To gain access to areas within and above the forest canopy, we used three of the BOREAS flux towers. All three towers were located in the BOREAS southern study area. The “aspen” tower ($55^\circ 35' \text{N}$, $106^\circ 10' \text{W}$; 33-m high) was in 60-year-old, 21-m-high forest dominated by aspen and balsam poplar (*P. balsamifera*) with an understory of hazelnut (*Corylus cornuta*) and wild rose (*Rosa woodsii*). The “black-spruce” tower ($53^\circ 98' \text{N}$, $105^\circ 05' \text{W}$; 25-m high) was in 155-year-old, 10–13-m-high forest dominated by black spruce with some jack pine and tamarack (*Larix laricina*), and with ground cover of feather moss (*Pleurozium schreberi*) and Labrador tea (*Hyloconium splendens*). The “jack-pine” tower ($54^\circ 12' \text{N}$, $104^\circ 43' \text{W}$; 30-m high) was in 60–75-year-old,

12–15-m-high, forest dominated by jack pine with green alder (*Alnus crispa*) understory and ground cover of bearberry (*Arctostaphylos uva-ursi*) and feather moss. No towers were located in aspen–white spruce mixedwood forest.

We sampled bat activity at the aspen tower on 10 nights, black-spruce tower on 6 nights, and jack-pine tower on 7 nights. On a given tower, we placed three detector systems on scaffolds that corresponded to: understory height, ca. 2 m below canopy height, and ca. 2 m lower than the height of the tower but above the canopy. Those three heights are referred to here as below, within, and above canopy, respectively. Each detector system was placed perpendicular to the tower. One unavoidable constraint that may have affected the volume of space sampled by detectors at each level was the difference in the amount of clutter between areas above the canopy (open) and areas within and below the canopy (cluttered relative to above the canopy). Due to differing levels of sound attenuation in open versus cluttered areas, the volume of space being sampled by detectors at each level probably differed to some extent. Detectors were far enough apart that there was no overlap in sampling among detector systems. Detector systems sampled from 2200 h to 0400 h the following morning to include both dusk and dawn in the sampling. We recorded echolocation call sequences in real time to assess nightly temporal patterns of bat activity at each level. Audiotapes were changed every hour, and all sequences recorded by the bat detector were transcribed from audiotape to computer disk.

Echolocation call analysis.—Echolocation calls were analyzed using Anabat5 software (O'Farrell et al., 1999). For each bat species, or species group, we counted number of echolocation passes per night to obtain an index of bat activity. We defined a pass as a sequence of two or more echolocation pulses separated by at least a 1-s pause before the next sequence. For each recorded pass, the following measurements were obtained: number of pulses, maximum and minimum frequencies of pulses, modal frequency of pulses, duration of pulses, and interpulse interval. We also used characteristics of echolocation calls to assess foraging activity. When bats attack insect prey, they increase the repetition rate of their echolocation pulses (referred to as a feeding buzz—Griffin, 1958). For each recorded pass, we noted the presence of a feeding buzz

and referred to those passes as feeding passes, regardless of the number of feeding buzzes per pass.

We categorized all bat passes into three frequency categories, which broadly correspond to species or species groups (Fenton et al., 1983). Sequences with a modal frequency of 20–26 kHz and maximum frequency <30 kHz were classified as hoary bats (*Lasiurus cinereus*), those with a modal frequency of 26–35 kHz and a maximum frequency of 30 kHz–40 kHz were classified as big brown (*Eptesicus fuscus*) or silver-haired (*Lasionycteris noctivagans*) bats, and those with modal frequencies >40 kHz and a maximum frequency >40 kHz were classified as *Myotis* species. To discriminate between passes of *E. fuscus* or *L. noctivagans* from *L. cinereus*, we used duration of pulses and interpulse interval; *L. cinereus* have pulses of longer duration, with more time between each pulse than *E. fuscus* and *L. noctivagans* (Fenton et al., 1983). We did not further subdivide the *Myotis* group into the little brown (*M. lucifugus*) or the northern long-eared (*M. septentrionalis*) bat because of the overlap in the call structure of these species, due to intra-individual and intraspecific variation. We detected no red bats (*Lasiurus borealis*) during our study.

Statistical analyses.—We used JMP IN version 3 software (Sall and Lehman, 1996) for all statistical analyses. We tested number of bat passes recorded per night for homoscedasticity using a Levene's test. When number of bat passes per night were homoscedastic, we used analysis of variance (ANOVA). When number of bat passes per night were heteroscedastic, we used a non-parametric Welch ANOVA, which can be interpreted as a variance-weighted *F*-test in which observations are weighted by an amount inversely proportional to the variance estimates (Sall and Lehman, 1996). We used a nested ANOVA (random-stand effect nested within fixed forest-type effect) to test among forest types for differences in number of bat passes recorded per night, relating to two null hypotheses: there was no difference between number of bat passes recorded in each forest type and there was no effect of stands within each forest type on number of bat passes recorded. To determine if foraging by *Myotis* species was associated with a particular forest type, we calculated the proportion of passes of *Myotis* that contained at least one feeding buzz. Proportions

were calculated for each of the 16 nights in the mixedwood, aspen, and jack-pine forests. We used a Wilcoxon signed-rank test to evaluate differences in the proportion of passes containing at least one feeding buzz recorded among forest types. For the vertical dimension part of our study, we compared data collected from each tower separately because of differences in vertical forest and canopy structure among forest types. We tested for differences between pairs with a Tukey-Kramer HSD test. For all statistical tests we used a 0.05 rejection criterion, and data are presented as mean \pm 1 SE.

RESULTS

Forest types.—During 16 sampling nights, we recorded 3,621 bat passes. Of those, 12% (444 passes) contained at least one feeding buzz. Seventy-six percent of all passes were recorded in aspen–white spruce mixedwood forest, whereas 22% and 2% were recorded from aspen and jack-pine forest, respectively. Ninety percent of all recorded passes were from the two *Myotis* species, whereas 8% and 2% were recorded from *E. fuscus*–*L. noctivagans* and *L. cinereus*, respectively. Because so few calls were recorded from the *E. fuscus*–*L. noctivagans* group, we did not concern ourselves with the distinction between these two species.

Within each forest type there was no difference between stands (mixedwood, $F = 2.90$, $d.f. = 2, 13$, $P > 0.05$; aspen, $F = 5.19$, $d.f. = 2, 5.6$, $P > 0.05$; jack-pine, $F = 3.35$, $d.f. = 1, 8.1$, $P > 0.05$). The whole-model nested ANOVA was significant ($F = 9.46$, $d.f. = 7, 40$, $P < 0.0001$) with the mean number of bat passes per night recorded in aspen–white spruce mixedwood forest being higher than in either aspen or jack pine forests (Fig. 1).

Our analysis of feeding buzzes was restricted to calls of *Myotis* in mixedwood and aspen forest because there were no feeding buzzes recorded in jack-pine forest and because feeding buzzes recorded in aspen–white spruce mixedwood and aspen forest were all made by the two *Myotis* species. The proportion of *Myotis* passes that

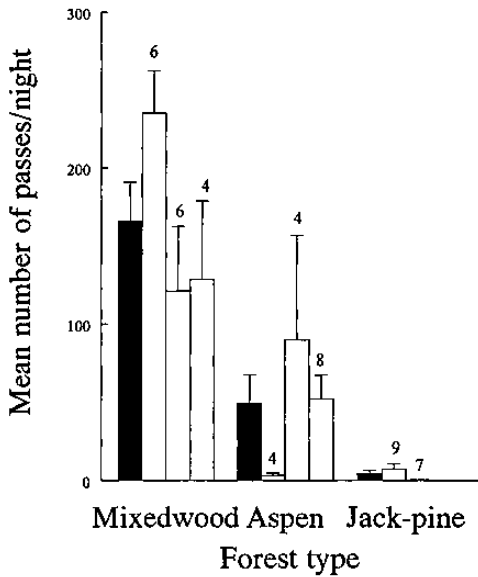


FIG. 1.—Mean ($\pm 1 SE$) numbers of bat passes per night recorded in each of the three forest types (solid bar). The open bars beside each solid bar represent the mean ($\pm 1 SE$) number of bat passes per night recorded in each of the stands within that forest type (three stands of aspen–white spruce mixedwood, three stands of aspen, and two stands of jack-pine forest). Numbers above each bar represent the number of nights that stands were sampled.

contained at least one feeding buzz did not differ between aspen (0.08 ± 0.02) and mixedwood (0.20 ± 0.06) forest ($Z = 1.77$, $d.f. = 15$, $P > 0.05$).

Vertical dimension.—We recorded 1,054 bat passes, of which 62% were from the aspen tower, and 20 and 18% from the spruce and jack-pine towers, respectively. Only 6% of passes contained feeding buzzes, most (59/67) from the aspen tower. Because of the low overall level of feeding, our analysis of feeding was restricted to the aspen tower and absolute numbers of feeding buzzes at each height rather than to proportions of feeding passes. To test for a height effect, we pooled feeding buzzes from all species.

More calls per night of *Myotis* than *E. fuscus*–*L. noctivagans* or *L. cinereus* were

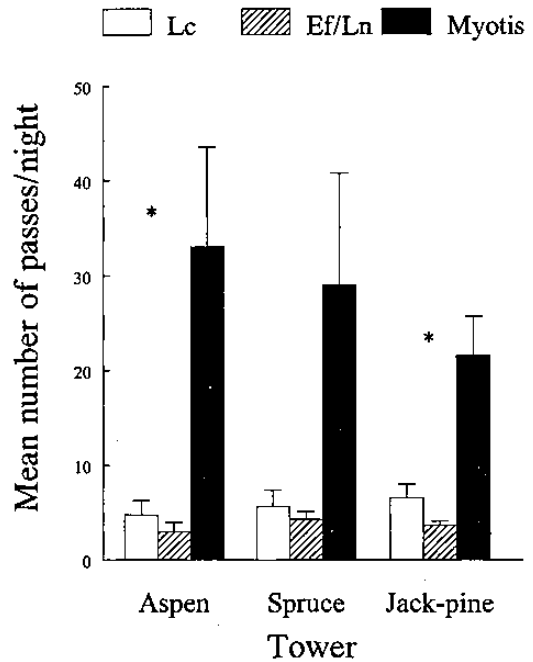


FIG. 2.—Mean ($\pm 1 SE$) numbers of calls per night of *L. cinereus* (Lc), *E. fuscus*–*L. noctivagans* (Ef/Ln), and *Myotis* at the three towers (aspen, spruce, and jack-pine). Asterisks indicate significant differences among species, or species groups, at each tower.

recorded from the aspen ($F = 8.68$, $d.f. = 2, 15.2$, $P < 0.05$) and jack-pine ($F = 10.11$, $d.f. = 2, 8.7$, $P < 0.05$) towers but not from the spruce tower ($F = 2.20$, $d.f. = 2, 7.8$, $P > 0.05$; Fig. 2). At the aspen tower, more passes per evening were recorded within and above the canopy than below the canopy ($F = 6.42$, $d.f. = 2, 13.4$, $P < 0.05$). Within each species, *L. cinereus* and *Myotis* differed among levels at the aspen tower (Table 1). The mean number of calls per night of *L. cinereus* was higher above the canopy than below the canopy, whereas the mean number of calls per night of *Myotis* were higher within and above the canopy than below the canopy at the aspen tower (Fig. 3a). There was no difference in the mean number of bats recorded at the three levels of the spruce ($F = 1.80$, $d.f. = 2, 8.1$, $P > 0.05$) and jack pine ($F = 2.09$,

TABLE 1.—Summary ANOVA results for differences in number of calls recorded for bats at each vertical level (below, within, and above the canopy) according to species or species group and tower location (aspen, spruce, and jack pine). An ANOVA was run for each species, or species group, at each level. There were too few calls of *E. fuscus* recorded in the spruce forest to run an ANOVA.

Tower	Bat species	F	d.f.	P
Aspen tower	<i>L. cinereus</i>	5.29	2, 16	0.02
	<i>E. fuscus</i> - <i>L. noctivagans</i>	0.69	2, 17	0.52
	<i>Myotis</i>	4.95	2, 12	0.03
Spruce tower	<i>L. cinereus</i>	0.25	2, 11	0.78
	<i>Myotis</i>	2.79	2, 9	0.11
Pine tower	<i>L. cinereus</i>	0.91	2, 8	0.44
	<i>E. fuscus</i> - <i>L. noctivagans</i>	0.68	2, 8	0.53
	<i>Myotis</i>	1.65	2, 8	0.25

d.f. = 2, 10.8, $P > 0.05$) towers. Mean number of calls per night of *L. cinereus*, *E. fuscus*-*L. noctivagans*, and *Myotis* did not differ among levels at the spruce and jack-pine towers (Table 1; Fig. 3b and 3c). Although the trend was toward higher levels of feeding above the canopy, there was no difference in number of feeding buzzes recorded among the three heights at the aspen tower ($F = 1.93$, *d.f.* = 2, 6, $P > 0.05$; Fig. 4).

To determine nightly temporal patterns in activity, we used the real time data for each recorded sequence. Because the amount of activity was correlated with sunset time, the time of each recorded sequence was converted to minutes after sunset. We pooled sequences from each level over all forest types. Activity peaked early in the evening below the canopy, but activity was more uniform throughout the night within and above the canopy (Fig. 5).

DISCUSSION

Compared to other studies, our results showed that the level of bat activity in ma-

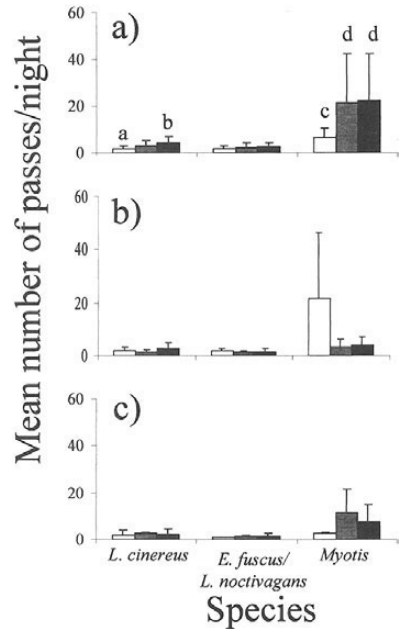


FIG. 3.—Mean (± 1 SE) numbers of calls per night of *L. cinereus*, *E. fuscus*-*L. noctivagans* and *Myotis* at the three levels (open bars—below canopy, hatched bars—within canopy, and closed bars—above the canopy) in a) aspen, b) spruce, and c) jack-pine forests. Bars denoted with different letters are significantly different.

ture boreal mixedwood forest was extremely high. Parker (1996), who examined the ecology and distribution of bats in temperate Alaskan rainforests using the Anabat system, recorded only 150 bat passes over 25 sampling nights in old-growth forest, compared to our 3,621 bat passes over 16 sampling nights. Erickson and West (1996) also recorded a low level of activity during a 2-year study in mature forest in Washington. Despite differences in protocol, the most appropriate comparison to our study is that of Crampton and Barclay (in press), who examined the relationship between habitat use and stand age in aspen-dominated mixedwood boreal forest in Alberta, Canada. In a 2-year study that used QMC (narrowband) bat detectors (Ultra Sound Advice, London, United Kingdom) they recorded only 1,933 bat passes.

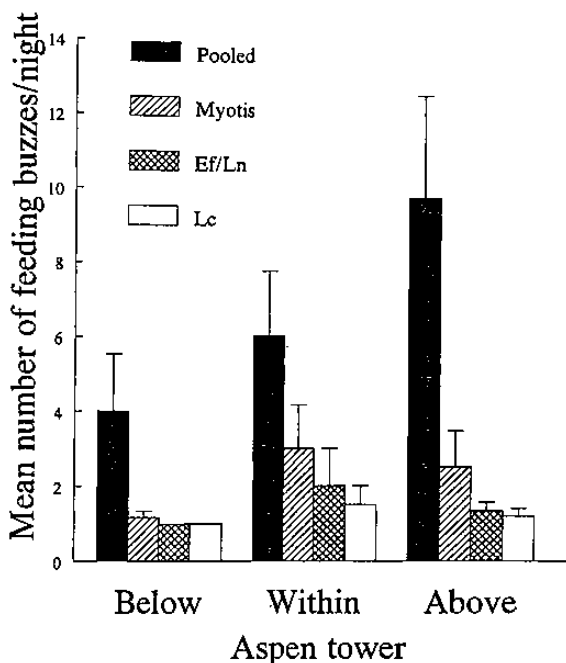


FIG. 4.—Mean ($\pm 1 SE$) numbers of feeding calls per night of *L. cinereus* (Lc), *E. fuscus*–*L. noctivagans* (Ef/Ln), and *Myotis* at each height of the aspen tower. Within each vertical strata, feeding buzzes were pooled across species (solid bars) for statistical analysis.

Our results must be viewed in light of biases inherent in using ultrasonic detectors to assess bat activity and habitat selection. For example, it is impossible to distinguish between recordings of the same individual flying in front of the bat detector a number of times as opposed to several individuals flying in front of the bat detector only once (O'Farrell et al., 1999). However, our protocol does generate an index of relative activity, regardless of the number of individuals being recorded. This method also has been used convincingly by other researchers engaged in the assessment of relative habitat use by bats (Hayes, 1997).

Our results indicate that bats discriminate among types of mature forest, with significantly more activity in aspen-white spruce mixedwood forest than in monotypic aspen or jack-pine forest stands. The two main

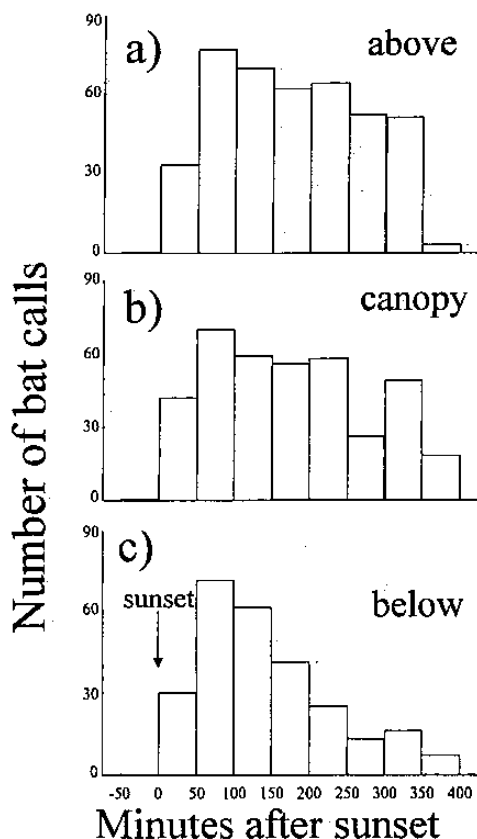


FIG. 5.—Distributions of the temporal pattern of activity by bats a) above the canopy, b) within the canopy and c) below the canopy in the three forests (pooled). The activity peak shortly after sunset (50–100 min) is evident only below the canopy.

factors that determine habitat selection by insectivorous bats are presumed to be prey availability and roost sites (Fenton, 1997). Although bats foraged in both aspen–white spruce mixedwood and aspen stands, there was significantly more activity in mixedwood stands, suggesting that the latter provides both roost sites and foraging opportunities.

We did not record a feeding pass in either jack-pine stand, perhaps due to the low number of bats sampled or to a low number of insects. Although we have no data on insect abundance, we suspect that abundance and diversity of insects were lower

in jack-pine stands because that forest is less complex structurally than aspen-white spruce mixedwood and aspen forest. Different forest types also provide different food and habitat for insects (Molles, 1982). Forest types also may differ in insect diversity and abundance because of the production of resins synthesized by conifers as a defensive secretion against insect attack (Funk and Croteau, 1994).

During spring and summer, bats spend most of their time, apart from commuting and foraging, in the roost. In forests such as those in our study area, where buildings and caves are not abundant, bats depend on trees for roosting sites. Trees have several potential roost sites, including foliage and bark, crevices beneath loose bark, abandoned hollows of woodpeckers, and naturally formed cavities. Forest-dwelling bats in southern British Columbia and Saskatchewan typically roost in abandoned hollows of sapsuckers (*Sphyrapicus*) and woodpeckers (Kalcounis and Brigham, 1998; Vohnhof and Barclay, 1996). Sapsuckers and other woodpeckers are known to excavate nest sites in our study area, predominantly in mixedwood and deciduous forest.

Although most activity occurred in the mature mixedwood forest, we were not able to examine use of the vertical dimension in this forest type because no BOREAS tower was present there. We expect that the highest levels of bat activity occurred in this forest type. Nevertheless, our results clearly showed that insectivorous bats were active both within and above canopy level in all three boreal forest types. A similar pattern also was found for mid- and below-canopy level activity by a variety of bat species in a more diverse community in old-growth forests on Vancouver Island, British Columbia (Bradshaw, 1996, 1997). These results suggest that to gain complete insight into habitat use by bats, sampling must be conducted above and below forest canopies and not just from the forest floor. Francis (1994) reached a similar conclusion of the vertical

distribution of activity by fruit-eating bats in a mist-netting study in Malaysia. In aspen forest, we found stratification of activity by *L. cinereus* and *Myotis* only. That *L. cinereus* was more active above than below the canopy is consistent with the hypothesis that the increased structural clutter associated with vegetation makes interior forest habitats less appealing to large, fast flying, relatively unmaneuverable bats (Brigham et al., 1997). Bradshaw (1997) also found species-specific and forest-type specific patterns in the stratification of both bat-foraging and commuting activity which could not be attributed to morphology alone. Why *L. cinereus* did not respond the same way in all three forest types is unclear, but this could be due to small sample (and low statistical power) because big bats such as *L. cinereus* are less common than smaller *Myotis* (Barclay and Brigham, 1991).

Thomas (1988) found that temperate forest bats commonly roost in old-growth stands but disappear quickly from those areas after dusk. It is possible that instead of moving horizontally to foraging locations, as Thomas (1988) postulated, bats migrate vertically to exploit insects in or above the canopy. Grindal and Brigham (in press) showed that activity by foraging bats was concentrated along forest edges and suggested that the top of the canopy may likewise act as an edge that supports high levels of activity (see also Bradshaw, 1996).

It usually is assumed that maneuverable species tend to use cluttered areas, which are more likely to support higher densities of prey (Kalcounis and Brigham, 1995). Thus, it is not surprising that the smaller *Myotis* were detected commonly within and below canopy levels and that we recorded a relatively high level of activity by *Myotis* throughout the night above the canopy. Bats with morphological characters that allow maneuverable flight close to vegetation are not constrained to flying only in cluttered areas (Brigham et al., 1992). Open habitats that support high densities of prey are ex-

ploited routinely by so-called "clutter-tolerant" bat species (Brigham et al., 1992; Saunders and Barclay, 1992).

Bats may fly above the canopy because flight can be direct and economical while commuting to foraging areas. Bats that are morphologically capable of doing so should forage at and below the level of the canopy where higher densities of insects likely occur. Below-canopy activity likely is associated not only with feeding but also with commuting to and from roost sites. Similar to Thomas (1988), most of the activity we recorded at the below-canopy level occurred early in the evening. This is consistent with the idea that bats leave roost sites (usually below canopy) and move to canopy or above-canopy levels rather than remaining at below-canopy levels. However, our data are not consistent with the idea that bats are simply commuting through the canopy. Although not significantly different, there was a trend along the vertical dimension toward more feeding buzzes in canopy and above-canopy levels by all bats.

Our results show that aspen and aspen-white spruce mixedwood forests supported significantly higher levels of feeding by bats than did jack-pine forest. We recorded few feeding buzzes during our study and most of the feeding buzzes we recorded from the BOREAS towers were in the aspen forest. Data from both parts of our study suggest that pure conifer stands support low levels of foraging activity by bats, whereas the preferential use by bats of some boreal forest types may be the result of differences in quality and quantity of roosting sites or resources that different forest types provide for foraging bats. There is some evidence that general levels of bat activity, as indicated by monitoring echolocation calls, are predictably associated with insect activity (Rautenbach et al., 1996), and it is likely that the jack-pine and spruce forests support relatively low densities of prey.

Our results have implications for forest management. The southern boreal mixed-

wood zone of western Canada, and especially aspen-white spruce mixedwood forest, is currently the target of major harvest (Stelfox 1995). We hope that our results encourage future studies to evaluate factors influencing use of above-canopy habitat by bats. Our data from the southern boreal mixedwood forest clearly indicate the need for future studies that use acoustic sampling to record bat activity at both the canopy and above-canopy levels, in addition to the standard protocol of sampling from near the ground.

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