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Vertical Stratification of Bat Activity in an Old-Growth Forest in Western Washington

Abstract

We examined the amount and temporal patterns of bat activity at four different heights in an old-growth conifer forest at the Wind River Canopy Crane Research Facility in south-central Washington. Analysis of 2,304 bat passes showed that amount of activity differed among vertical strata. For *Myotis* bats, activity was greatest in the lower canopy, followed by the ground-level and upper canopy, respectively. We did not detect activity of *Myotis* above the canopy. Non-*Myotis* bats used lower and upper canopies more frequently than ground-level and above the canopy. Temporal patterns of activity generally exhibited a bimodal distribution, but the extent of bimodality and the time and relative size of peaks differed with species group and among heights. Activity was greatest at ground-level early in the night and later shifted to higher strata. Patterns of use of old-growth forests by bats may reflect the complex vertical structure of the vegetation in those forests. Exclusive use of ground-based equipment can result in an incomplete picture of the activity of bats in complex forest stands.

Introduction

The vertical and horizontal spatial patterns of trees and other vegetation in forests (forest structure; Oliver and Larson 1996) influence patterns of bat activity. In the Pacific Northwest, Thomas (1988) found old-growth forests supported higher levels of bat activity than did young stands, and hypothesized that differences in levels of activity resulted from increased availability of roosts (large diameter snags) in older forests. Humes et al. (1999) reported similar results, and also found that levels of activity differed among young forests in relation to tree density; amount of bat activity in young stands with low densities of trees was intermediate between young dense stands and old-growth forests. Erikson (1998) found that amount of bat activity differed among age-classes of young managed forests. Hayes and Adam (1996) reported that activity of bats in riparian areas in the Oregon Coast Range was influenced by vegetation, with dramatically lower levels of activity of myotis bats (*Myotis* sp.) in areas that had been clearcut and more activity of larger bats (primarily silver-haired bats, *Lasionycteris noctivagans*) in logged areas. Similarly, in other regions, activity of bats has been shown to be influenced by forest structure (e.g., Fenton et al. 1992, Grindal and Brigham 1998, Kalcounis et al. 1999, Kavanagh and Bamkin 1995, Krusic et al. 1996, Zubaid 1993).

In addition to the influences of forest structure on activity of bats among forest stands, forest structure may also influence patterns of use within forest stands. Because bats use space three-dimensionally, forest structure may influence vertical patterns of bat activity as well as horizontal patterns of use. Kalcounis et al. (1999) examined vertical patterns of use of bats in aspen (*Populus tremuloides*), black spruce (*Picea mariana*), and jack-pine (*Pinus banksiana*) forests in the boreal forest of central Saskatchewan. In aspen forests, they found that *Myotis* were most active within and above the canopy of aspen stands and that there was more activity of hoary bats (*Lasiurus cinereus*) above than below the canopy. However, activity did not significantly differ among heights in spruce or jack-pine forests. Vertical patterns of bat activity in coniferous forests of the Pacific Northwest have not previously been reported.

We examined amounts and patterns of activity of bats in different vertical strata of an old-growth coniferous forest in western Washington. Because old-growth forests in the region are structurally complex (Franklin and Spies 1991), we hypothesized that use by bats would differ among vertical strata. In addition, we hypothesized that patterns of activity would differ among species.

Methods

This study was conducted at the Wind River Canopy Crane Facility, located in the Thornton T. Munger Research Natural Area and the Wind River Experimental Forest in the Gifford Pinchot National Forest. The site is in the southern Wash-

ington Cascade Mountains, near Carson, Washington, at an elevation of 355 m. The area receives approximately 250 cm of precipitation per year, mostly occurring as rain falling between October and May. The study site is an old-growth forest with an overstory dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), with western redcedar (*Thuja plicata*), Pacific silver fir (*Abies amabilis*), grand fir (*A. grandis*), and western white pine (*Pinus monticola*) being less abundant. Overstory trees range from 200 to 400 years old with maximum heights of 65 m. Understory trees include Pacific yew (*Taxus brevifolia*) and Pacific dogwood (*Cornus nuttallii*). The most abundant understory shrubs are vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), and California hazelnut (*Corylus cornuta* var. *californica*). The canopy structure of the site has been described as "bottom-heavy," indicating that the majority of the vegetation occurs within the lower one quarter of the height of the stand (Parker 1997). The study area is centered on the Wind River canopy crane, a construction crane measuring 74.5 m in height at the jib. The jib of the crane extends 85 m with a counterweight jib extending 35 m in the opposite direction. Bat species that are likely to use the site include Townsend's big-eared bat (*Corynorhynus townsendii*), big brown bat (*Eptesicus fuscus*), silver-haired bat, hoary bat, California myotis (*Myotis californicus*), long-eared myotis (*M. evotis*), little brown myotis (*M. lucifugus*), fringed myotis (*M. thysanodes*), long-legged myotis (*M. volans*), and Yuma myotis (*M. yumanensis*).

We used Anabat II bat detectors (Titley Electronics, Ballina, NSW, Australia), automated with delay switches, to record echolocation calls of bats onto audio tapes (Hayes and Hounihan 1994). To account for potential differences in sensitivity of detectors (Larson and Hayes in press), we calibrated detectors using a Transonix IX pest repeller (Ryans by Mail, Laguna Hills, CA).

We established echolocation monitoring stations at two points for each of four heights: ground-level, the lower canopy (17 to 25 m above the ground), the upper canopy (35 to 40 m above the ground), and above the canopy (75 m above the ground). Locations of echolocation monitoring stations above the canopy were constrained by the structure of the canopy crane; stations were positioned at the end of the jib and counterweight jib (85 m and 35 m from the crane's center, respectively). Because the crane was allowed to freely spin, or "weathervane," during the night to prevent damage when an operator was not present, location of stations above the canopy could vary both within and among nights. We used the distances to the ends of the jib and counterweight jib to describe two concentric circles surrounding the base of the crane. We located one monitoring station at randomly generated compass bearings along each circle on the ground, lower canopy, and upper canopy. Stations on the ground were placed under plywood shelters to protect the equipment from rain (Hayes and Hounihan 1994). Stations in the lower and upper canopy were placed in plywood shelters suspended between two trees by rope. Stations could not always be placed precisely at the randomly generated points because of the position of trees but each station was positioned within 10 m of the randomly generated point. Detectors on the ground and in the lower and upper canopy were oriented with microphones facing toward the area with the greatest opening. Those above the canopy were oriented with microphones facing perpendicular to the axis of the crane boom. All detectors were tilted upward at a 30-degree angle.

We conducted our study during nine nights between 8 July and 14 August 1996. Generally two, but at least one station at each height was operational each night. Simultaneous sampling at each height allowed us to account for temporal variability among nights (Hayes 1997).

We downloaded and digitized all calls using the ZCAIM Interface and ANABAT 5 software package (Titley Electronics, Ballina, NSW, Australia). Time and location were recorded in file headers created for each call. We examined each pass and noted the minimum and maximum frequency and the duration of calls. Calls were grouped into three broad categories for analysis: 1) calls identified as having characteristics similar to most species of bats in the genus *Myotis* (typically high frequency, short duration calls) were placed in the *Myotis* group (O'Farrell 1997), 2) calls with characteristics similar to the big brown bat, silver-haired bat, hoary bat, and fringed myotis (all with typically low-frequency, long duration calls) were placed into the non-*Myotis* group, and 3) fragmentary calls that did not yield sufficient

information regarding frequency and duration were classified as undetermined. Further taxonomic refinement was not possible because a high percentage of calls were fragmentary.

We examined differences in log-transformed number of passes by vertical stratum using a two-way ANOVA using SAS PROC GLM. We generated least squares estimates of log-transformed means for number of passes in each vertical stratum and conducted multiple comparisons for number of passes among strata using Fisher's protected LSD. To assess temporal patterns of activity, we partitioned the period between sunset and sunrise into 20 equal-length periods (mean = 27.1 min., range 25.5 to 29.6 min.) to account for differences in length of nights during the study period. We then determined the number of passes occurring in each 5-percentile period (Hayes 1997). We used the Kolmogorov-Smirnov Two-Sample Test (Sokal and Rohlf 1995) to examine differences in temporal patterns of use by bats among vertical strata. P-values for the Kolmogorov-Smirnov Test were taken from tables provided by Rohlf and Sokal (1981).

Results

We recorded 2,304 bat passes. Of these, 1,207 (52.4%) were classified as *Myotis*, 154 (6.7%) as non-*Myotis*, and 943 (40.9%) as undetermined.

Significantly different numbers of passes by *Myotis* were detected at each vertical stratum (Table 1). The greatest number of passes were recorded in the lower canopy, followed by the ground-level and upper canopy, respectively. No calls recorded above the canopy were classified as *Myotis*, although it is possible that some of the calls recorded above the canopy and classified as undetermined may have been produced by *Myotis* bats. The patterns observed for undetermined passes

and for total passes were similar to that for *Myotis*, as would be expected given the predominance of use by *Myotis* bats in the study area.

The largest number of passes for non-*Myotis* bats were recorded in the upper canopy, followed by the lower canopy, ground-level, and above the canopy (Table 1). Number of passes of non-*Myotis* bats at the ground-level was not significantly different than number of passes recorded above the canopy, and number of passes recorded in the lower canopy did not differ from that recorded in the upper canopy.

Over all vertical strata combined, activity of *Myotis* exhibited a bimodal distribution with peaks during the fifth and ninetieth percentile of the night. However, temporal pattern of activity for *Myotis* at the ground-level differed significantly from that in the lower ($P < 0.005$) and upper ($P < 0.001$) canopy. There was a strong peak in activity of *Myotis* at the ground-level in the first fifth percentile of the night with a smaller and less pronounced peak during the last 15% of the night (Figure 1); 49.7% of all *Myotis* calls recorded at the ground-level were recorded during the first 5% of the night. In contrast, the largest peak in activity in the lower canopy occurred during the last 25% (roughly 2-1/2 hours) of the night; with 53.4% of all *Myotis* passes recorded in the lower canopy during this period (Figure 1). Relative to the pattern observed at ground-level, the early evening peak in activity in the lower canopy was much smaller and was shifted later by roughly one-half hour (one 5-percent interval). The pattern of activity for *Myotis* in the upper canopy showed a slight bimodal tendency, with somewhat more calls recorded during the latter portion of the night than in the earlier portion of the night. Temporal patterns of activity in the lower and upper canopy were not significantly differ-

TABLE 1. Median number of passes across all nights. Confidence intervals (in parentheses) were calculated for log-transformed numbers and back-transformed for ease of interpretation. Median values for number of passes having the same superscript within a column are not significantly different ($P > 0.05$) from one another. Total passes are the sum of passes categorized as *Myotis*, non-*Myotis*, and undetermined.

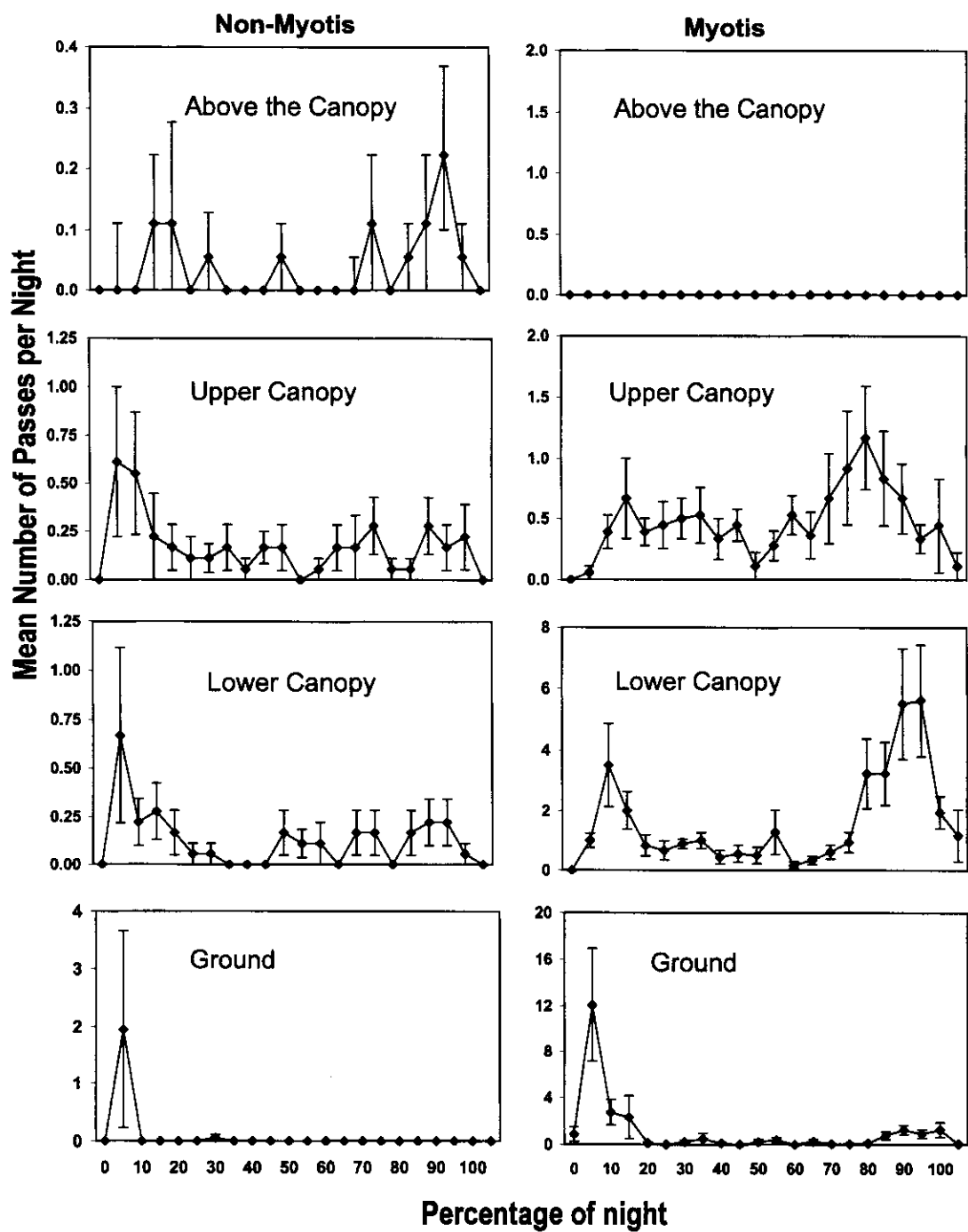| Vertical stratum	Category of passes		
	Myotis	Non-*Myotis*	Total passes
Above canopy	0	0.6 (0.2-1.2)[a]	0.9 (0.4-1.6)[a]
Upper canopy	8.8 (6.5-11.8)[a]	1.8 (1.1-2.7)[b]	22.6 (16.4-30.9)[b]
Lower canopy	27.1 (19.7-37.1)[b]	1.7 (1.0-2.7)[b]	46.5 (32.6-65.7)[c]
Ground-level	15.0 (10.8-20.7)[c]	0.5 (0.1-1.0)[a]	33.8 (23.7-48.1)[bc]

Figure 1. Temporal distribution of activity for passes classified as *Myotis* or as non-*Myotis* for each vertical stratum. Level of activity is scaled differently for each stratum and taxonomic group to illustrate temporal patterns. Passes at 0 and 105% of the night represent all passes recorded prior to sunset and after sunrise, respectively.

ent ($P > 0.10$). Differences in patterns of activity among levels reflect a shift in use of the area over the course of the night. During the initial 5% of the night, over 90% of the *Myotis* passes were recorded at ground-level (Figure 2). Activity then shifted to higher vertical strata with most of the activity occurring in the lower canopy during most of the rest of the night; the predominance of activity in the lower canopy was most pronounced during the last 20% of the night.
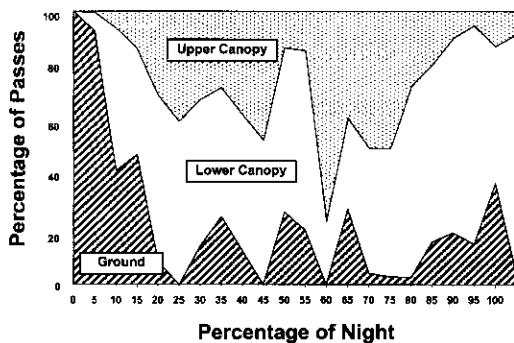

Figure 2. Temporal pattern of relative amount of *Myotis* activity recorded at ground-level, the lower canopy, and the upper canopy. Passes at 0 and 105% of the night represent all passes recorded prior to sunset and after sunrise, respectively.

Non-*Myotis* bats also showed a strong peak in activity during the first 5% of the night, although a second peak later in the night was not evident. The early evening peak was most pronounced at the ground-level (Figure 1); only one pass of non-*Myotis* bats was recorded at ground-level after the first 5% of the night. Less pronounced peaks in non-*Myotis* activity were observed during the first 5% of the night in the lower and upper canopy, and a low, but relatively consistent, amount of activity was recorded throughout the rest of the night. Activity was consistently low throughout the night above the canopy and no distinct modality was evident, although patterns may have been obscured by the extremely small number of calls recorded at that level. The pattern of activity at ground-level for non-*Myotis* bats was significantly different than that observed at each of the other three levels ($P < 0.001$); temporal patterns of activity for non-*Myotis* at the lower canopy, upper canopy, and above the canopy were not significantly different ($P > 0.10$).

Discussion

Studies that monitor echolocation calls to assess activity of bats typically are conducted using bat detectors placed on or very near to the ground. We found patterns of use differed substantially among vertical strata, and that these patterns differed between species groups. Thus, exclusive use of ground-based equipment may result in an incomplete picture of the activity of bats in complex forest stands. Results of echolocation-monitoring studies conducted in forested environments using only ground-based equipment should thus be interpreted with recognition of potential limitations in inference that result from sampling only one vertical stratum (Hayes in press).

The bimodal pattern of activity observed at ground-level for *Myotis* bats is consistent with patterns observed in other studies (Erkert 1982, Hayes 1997, Kunz 1973, Maier 1992, Taylor and O'Neill 1988, Thomas 1988), although the relative magnitude of the peak observed during the early portion of the night in this study exceeds that typically observed. The bimodal pattern of activity of bats in old-growth forests of the Pacific Northwest has been interpreted to result from an initial pulse of activity as bats leave their roost sites, followed by decreased activity in the middle of the night as bats forage in other areas, and a second peak of activity resulting as bats return to their roost sites during early morning hours (Thomas 1988). Others (Hayes 1997, Kunz 1974, Kunz et al. 1975) have attributed the bimodal pattern of activity of bats to an initial period of foraging and roosting after emergence from day roosts, reduced activity in the middle of the night when bats are at night roosts, and a final bout of foraging and commuting before returning to day roosts.

Kalcounis et al. (1999) suggested that vertical shifts in activity may account for temporal patterns of activity observed at ground-level. We observed a shift in activity from ground-level to higher vertical strata through the night (Figure 2), consistent with this hypothesis. The mechanisms responsible for these vertical shifts in activity are not clear, but may be related to vertical shifts in abundance or availability of insects through the night. Shifts in height of activity do not, however, account for all of the observed bimodality in activity, as a bimodal pattern is evident even when all vertical strata are combined. Night-roosting probably accounts for some of this bimodality,

as night-roosting comprises a substantial portion of the activity budget of some species (Anthony et al. 1981, Barclay 1982, Perlmeter 1996) and periods of night-roosting generally overlap with periods when recorded activity is lowest (Adam and Hayes in press, Kunz 1974, Perlmeter 1996). Movement from day-roosts to foraging habitat undoubtedly occurs as well (Waldien 1998), and may account for a portion of the pattern in some habitats.

Myotis and non-*Myotis* bats exhibited different patterns of use of vertical strata. Differences in use of vertical strata between *Myotis* and non-*Myotis* bats in our study may have resulted from a number of factors. Differences in use of habitat among species of bats have been postulated to be related, in part, to differences in abilities to exploit resources with more maneuverable species concentrating use in more cluttered habitats and less maneuverable species predominantly using less cluttered environments (Aldridge and Rautenbach 1987, Brigham et al. 1997, Crome and Richards 1988, Kalcounis and Brigham 1995, Kalcounis et al. 1999, McKenzie and Rolfe 1986, and Norberg and Rayner 1987); this may account for the different patterns of use we observed for *Myotis* and non-*Myotis* species.

The complex vertical structure of old-growth forests in the Pacific Northwest (Franklin and Spies 1991) provides the opportunity for partitioning and exploitation of diverse niches by aerial insectivores, such as bats. Other taxa, including epiphytes (McCune et al. 1997) and birds (Shaw and Flick in press), differ in presence, abundance, or use of habitat at different heights in old-growth coniferous forests. Forests with simple vertical structure, such as young conifer plantations, may not provide a diversity of foraging niches for bats; this may, in part, account for differences in activity of bats in older and younger forests (Thomas 1988, Humes et al. 1999). We were unable to test this hypothesis because our work was limited to a single site, and we could not compare patterns of activity among forests differing in structural complexity. Comparative studies to evaluate this hypothesis through examination of differences in activity of bats at different heights among forests in the Pacific Northwest differing in vertical complexity would be valuable.

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