BAT ACTIVITY ACROSS THE VERTICAL GRADIENT OF AN OLD-GROWTH REDWOOD FOREST

By

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A Thesis

Presented to

The Faculty of Humboldt State University

In Partial Fulfillment

Of the Requirements for the Degree

Masters of Arts

In Biological Sciences

May, 2011
BAT ACTIVITY ACROSS THE VERTICAL GRADIENT OF AND OLD-GROWTH REDWOOD FOREST

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ABSTRACT

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Throughout their global distribution, bats vary in their use of microhabitats along the vertical strata of forests. Ground-based detection techniques typically cannot sample canopy strata in taller forests as it falls beyond detection and netting range. High-flying bats, those that exploit the canopy and above-canopy edge, may avoid capture or be under-represented in assessments using these methods. To improve our understanding of how bats use forests, I assessed bat activity and species stratification along the vertical gradient near Bull Creek in Humboldt Redwoods State Park, Humboldt County, northern California. Humboldt Redwoods State Park is the tallest forest in the world, containing 70 percent of known trees over 107 m. Two coast redwood, *Sequoia sempervirens*, trees were equipped with full spectrum automated bat detector units at treetop (108 m), middle crown (50 m), and ground level (5 m) from April 2008 to November 2009, excluding December and January. I sampled 1,365 detector nights and recorded 3,796 echolocation sequences containing one or more calls. I identified the presence of 12 species: *Corynorhinus townsendii, Eptesicus fuscus, Lasionycteris noctivagans, Lasiurus blossevillii, L. cinereus, Myotis californicus, M. evotis, M. lucifugus, M. volans, M. thysanodes, M. yumanensis, and Tadarida brasiliensis*. Two species, *L. blossevillii*, and *T. brasiliensis*, were undocumented in previously published surveys from redwood
forests. I recorded the highest amount of activity at the treetop and least at the middle
crown for both trees (65% and 43% at treetop, 7% and 23% at middle crown and 28%
and 33% at ground level). I observed a greater number of species present at ground level
compared to middle crown and treetop detectors at both trees. However, the data revealed
a difference in the species composition of calls recorded at each level. Non-\textit{Myotis}
species composed 95% of the calls at the treetop, 87.5% at middle crown, and 21% at
ground level. Calls from all \textit{Myotis} species averaged 71% of all calls recorded from the
ground level compared to less than 4% at both middle crown and treetop detectors. There
was a marked decline, but not an absence of activity, during late fall through early spring.
The combination of a temperate climate and observations of larger, migratory species
during November, February, and March suggests the potential for resident populations or
inland migrants overwintering in these forests. My findings illustrate the need to consider
the full vertical habitat when designing bat habitat use studies, as species composition
varies across the vertical gradient in forests.
AKNOWLEDGEMENTS

This study would not have been possible without the support of many people. I would like to thank my advisor, Joseph M. Szewczak, for making this research possible and giving me the opportunity to grow and to learn. I’d like to thank all the members of my committee including Dr. Brian Arbogast, Dr. Stephen Sillett, and Dr. William Zielinski for their advise and editing support. This work was a long time in the making and I appreciate their commitment to helping me through the process. I am deeply grateful to Dr. Stephen Sillett, Jim Spickler, and Marie Antoine for deploying and retrieving heavy steel boxes and hundreds of meters of cable into these magnificent trees. Without their effort, this research would not be possible. Thanks to Jay Harris of California State Parks, North Coast Redwoods District for providing access to Humboldt Redwoods State Park and Sandpiper Technologies for help with fuel cell set up and design. Thanks to Heather Perry for countless hours of discussion, edits, and for her continual support. Thanks to Lewis McCrigler for assistance constructing recording units. I would especially like to thank everyone else who offered encouragement and support through the process of doing this study including Ryan Byrnes, Aaron Corcoran, Linda Dean, Dave Franklin, Zachary Loman, and Gabe Rayes. This project was partially funded by grant support from the Strategic Environmental Research and Development Program (SERDP).
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INTRODUCTION

Previous investigations document clear variation in habitat use among vertical forest strata by bats worldwide (Bernard, 2001; Bradshaw, 1996; Francis, 1994; Hayes & Gruver, 2000; Henry et al., 2004; Kalcounis et al., 1999; Menzel et al., 2005). Ground based detection techniques preclude sampling canopy strata in taller forests as they are outside the range of bat detectors and higher than can be sampled by mist-nets. High-flying bats, those that exploit the canopy and above-canopy edge, may avoid capture or be under-represented in assessments using these methods. This bias could limit our understanding of bat-forest ecology and lead to incorrect assessments of habitat use. This in turn could lead to inappropriate land use management decisions.

Adaptation of true flight in bats bestows distinct advantages in exploiting habitat. However, flight is a method of locomotion that is sensitive to variations in habitat spatial structural complexity (McKenzie & Rolfe, 1986). Structural complexity, also termed clutter, is defined here as a measure of the number of different physical attributes present and the relative abundance of each of these attributes in an area (McElhinny et al., 2005). Some examples of physical attributes include foliage, branches, rocks, trunks, snags, and other vegetation. A high degree of structural complexity would be described as an area containing many physical obstacles. The degree of clutter in an area dictates what areas are physically and perceptually accessible to a flying bat.

Not all bats exploit habitat to the same extent. Morphological and physiological differences among bat species confer specialization advantages to foraging in particular
habitats (Aldridge & Rautenbach, 1987; Bradshaw, 1996; Crome & Richards, 1988; McKenzie & Rolfe, 1986; Norberg & Rayner, 1987). Small changes in physical space can have significant influence on a bat’s ability to maneuver or navigate. Additionally, within species preferences for foraging in spatially complex environments vary with age and the presence of conspecifics (Adams, 1997). Therefore, habitat heterogeneity may be a key component in promoting bat species diversity (Hodgkison et al., 2004).

A forest can be seen as vertically stratified layers that extend horizontally throughout the habitat (Bradshaw, 1996). The interface of each layer (edge habitat) is a highly utilized portion of the forest by bats (Vaughan et al., 1997) and exists both below and above the cluttered canopy region. The continuum of variation in clutter as one moves vertically from ground level provides a great diversity in available habitat where not all habitat is used equally. Bat activity also exhibits substantial temporal (e.g., day to day, week to week and seasonal) variability (Hayes, 1997). Thus a comprehensive and accurate accounting of bat species composition and distribution necessitates long-term sampling regimes to account for temporal variations along with sampling the full vertical gradient beyond that reached by ground-based detection. Nowhere may these considerations have more impact on bat species assemblages than in the tallest forest in the world, the old-growth coast redwood, *Sequoia sempervirens* forest of Humboldt Redwoods State Park (hereafter ‘HRSP’), Humboldt County, California.

As a habitat of special concern and the tallest forests on Earth, the old-growth redwood forest offers a unique opportunity to study bat species diversity and activity relating to habitat vertical stratification at an extreme vertical scale. Rich with suitable
roosting habitat, a temperate climate, and spatial complexity, these forests may provide refuge for a greater number of bat species than previously recognized. Unfortunately, due to historic logging practices, less than five percent of these original old growth redwood forests remain and our understanding of how bats use these forests provides insufficient support for management decisions. Forest management decisions directly influence forest components important to bats such as characteristics and abundance of roost sites, amount of clutter, availability of prey and availability of water (Hayes & Loeb, 2007). Obtaining baseline data on bat species presence, distribution and activity is a critical step in properly implementing forest management decisions that will minimize negative direct and indirect impacts to bats.

Monitoring bat activity and species richness along the complete vertical habitat can be difficult and resource-intensive, often requiring a great deal of ingenuity to overcome logistical challenges that invariably arise. Acoustic sampling techniques are an appropriate tool for studying bats along the vertical habitat as they provide an automated, non-invasive and reliable survey. Acoustic sampling entails passively recording and then analyzing the echolocation calls produced by passing bats. Acoustic sampling enables surveys of large regions as well as detection of species that fly outside the range of, or otherwise avoid capture in, mist nets (O'Farrell et al., 1999).

The use of acoustic sampling for use in bat monitoring research has become more widespread as advancements in hardware and software continue to make the acquisition and analysis of acoustic data easier, less expensive, and more automated. Acoustic monitoring has limitations as a sampling technique, however, as bat echolocation calls
vary between environments (Obrist, 1995) and exhibit significant intra-species variability (Kalko & Schnitzer, 1993) and inter-species overlap in call characteristics among sympatric species (Parsons & Szewczak, 2009).

Analysis of acoustic data entails a two-step process. First, recordings need to be digitized and call time amplitude and frequency amplitude information extracted. Second, call parameters are compared to previously recorded calls of known origin. Acoustic analysis requires a large reference call library of high quality calls to compare unknown calls to and a high degree of specialized training to determine accurate identification of calls (Parsons & Szewczak, 2009). Recent advances utilizing complex algorithms such as ensembles of neural networks and hierarchical decision trees have demonstrated call identification utilities robust enough to handle the complex task of analytically comparing call characteristics (Jennings et al., 2008; Redgwell et al., 2009).

Redwood Forests

The old-growth coast redwood *Sequoia sempervirens* forest provides an extreme example of a vertically stratified environment. Redwood, a member of Cupressaceae, is found only in a narrow, non-continuous 724-km strip along the Pacific Coast of California, from San Louise Obispo to the southwestern tip of Oregon State. Individuals can live for over two thousand years and reach heights of 115.6 m (S. C. Sillett, personal communication). Stands documented with a wood volume of more than 10,000 m³ ha⁻¹ make them the most massive forests on earth (Sawyer et al., 1999). Redwood is
extremely resistant to rot, inedible to most herbivores and develops thick, fire-resistant bark. In the few remaining old-growth forests, large trunks support dense, interweaving crowns that restrict most sunlight from reaching the under story, creating an occlusive layer with sparse vegetative growth below it. Large trees often have lower trunks that are free of branches for the first 50 m or more (Sillett et al., 2010). Where light can penetrate the canopy, younger trees of differing ages form layers of successive growth, increasing spatial complexity near ground level. Such variation in structure creates a vertical stratification of habitats that influences use by bats through effects on a variety of environmental conditions including air temperature (Anthony et al., 1981; Avery, 1985; Lacki, 1984; Vaughan et al., 1997), humidity (Lacki, 1984), wind speed (Avery, 1985; O'Farrell & Bradley, 1970), rain intensity (Fenton, 1970), moonlight (Hecker & Brigham, 1999), and insect abundance (Anthony et al., 1981; Avery, 1985; Kunz, 1973; Lacki, 1984; Rydell, 1989).

Along its range redwood is found with a suite of associated plant species in various densities, ages, and in various stages of spatial complexity. Forest stands with a substantial component of redwood trees vary widely in their structure, species composition, environmental conditions, and ecosystem processes (Noss, 2000). Due to the great degree of variability in redwood forest composition, Noss (2000) divides redwood forests into three zones (Northern, Central and Southern) along its range; each zone is shaped by the substrate, topography, and environment (Figure 1). These differences have been quantified in previous bat research where fewer species and different species proportions have been identified from guano samples taken from
redwood hollows in Mendocino County located in the Central zone compared to those obtained in Del Norte County located in the Northern zone (Zielinski et al., 2007).

The limited available research on the association between bats and redwoods shows that bats routinely use basal crevices and burn scars, cavities created from repeated fires, of redwood trees for night and day roosts throughout the year (Gellman & Zielinski, 1996; Mazurek & Zielinski, 2004; Purdy, 2002; Roberts, 2008; Zielinski & Gellman, 1999). These cavities are seasonally used as maternity roosts by several species, including use by a State of California species of special concern and known cave roosting species, Townsend’s big-eared bat (*Corynorhinus townsendii*) (Mazurek, 2004). Research has also documented basal hollows as mating sites (Rainey et al., 1992). Using terrestrial acoustic, netting, and roost surveys from these studies and that of Mazurek (2002) indicate a high degree of overall bat activity associated with redwoods. However, these sampling techniques only sampled the lowest 10% of the available vertical habitat leaving our understanding of how bats use redwood habitat incomplete.

Cumulatively, studies have documented the presence of *Corynorhinus townsendii, Eptesicus fuscus, Lasionycteris noctivagans, Lasiurus cinereus, Myotis californicus, Myotis evotis, Myotis lucifugus, Myotis thysanodes, Myotis volans, and Myotis yumanensis* in forests containing redwoods. Despite the paucity of studies investigating bats in the redwood forest Noss (2000) has proposed that bats may be the most closely tied of all mammals to late-serial redwood forests.

This study was the first to utilize continuous full-spectrum acoustic sampling along the full vertical gradient of a redwood forest for an annual cycle. Goals were 1) to
observe bat species richness in an old-growth redwood forest, 2) to quantify how bat activity and species presence vary across the vertical forest gradient, and 3) to investigate how seasonal changes affect bat species presence within an old-growth redwood forest.
MATERIALS and METHODS

Study Site

This study was conducted from April 16th 2008 to November 19th 2009 (excluding December and January due to technical issues) at Humboldt Redwoods State Park in southern Humboldt County California (40.3° N, 124.0° W). The park is located in the Eel river watershed roughly 50 km south of Eureka and 24 kilometers east of the Pacific Ocean. The park consists of over 20,000 ha, half of which are old-growth forest making it the largest remaining old-growth redwood forest. The old-growth forest on the alluvial flats along Bull Creek (45-65 m elevation), a tributary of the Eel River, is overwhelmingly dominated by redwood; redwood accounts for 99 percent of the trees while California bay Laurel (*Umbellularia californica*), Douglas fir (*Psuedotsuga menziesii*) and tanoak (*Lithocarpus densiflorus*) make up the remaining 1 percent (Sawyer et al. 2000). This is the tallest forest in the world, containing more than seventy percent of known living trees over 107 m in height (S. C. Sillett personal communication). This area has a temperate climate known for dry summers and wet winters. Temperature ranges from 10-30°C in the summer to 0-10°C in the winter with an annual rainfall of 165-200 cm, occurring mostly from November to May (Humboldt Redwoods Interpretive Center, n.p.). During the time of peak rainfall, seasonal creeks swell and interweave their way along the flats saturating the ground.
Equipment and Deployment

Bat detector units were installed at three height intervals, treetop (~108 m), mid-crown (~50 m) and ground level (~5 m) in two redwood trees, which were 111 and 109 m tall. Trees were 3 km from each other and both located along the alluvial terraces of Bull Creek at least 50 m from the water. Bat detector units consisted of a Weigmann type 1 3R enclosure fitted with an up facing PVC elbow attached through the front that cradled a Pettersson D240X full spectrum ultrasonic bat detectors (Pettersson Elektronik AB, Uppsala, Sweden) within the enclosure. This arrangement channeled sound from an upward direction down then up again to the detector so as to protect it from inclement weather and moisture. Each detector was connected to an iriver H320 digital recording unit (iriver.com) with Rockbox firmware version r12246m 070210 (Rockbox.org). All three iriver units for each tree were housed in a Pelican case at the base of each tree. Also housed in the pelican case was an Energy For You 600, 25-watt fuel cell (SFC, Brunnthal-Nord, Germany) connected to three 12 volt, 12 amp hour batteries and Morningstar SunSaver-6 (Morningstar Corporation, Newton, PA) charge controller. Power was supplied to the detector units via a 14-gauge twin wire lamp cord and a ground cable connected to a ground rod running the length of the tree along the trunk. Ground level detectors were connected to their corresponding recording device using an RCA cable with ¼ inch stereo adapters attached to each end. To minimize signal degradation over the long distances to the upper two units, the upper and middle crown bat detectors were connected to an AVO-A2MINI-WP-F balun (Intelix, Middletown, WI)
via a stereo ¼ inch audio cable (as per recommendation by Mike Balisteri of Avian Consulting Services). Each balun was connected to an identical unit on the ground using a Cat5 cable.

Pettersson D240X bat detectors were set on auto, 1.7- second automatic recording period. Any high frequency sound of sufficient intensity would trigger the detector to produce a 17 second time expansion signal. The detector was unable to record any new signals during the time expanded 17-second playback to the recorder. The recorders running under Rockbox firmware labeled each file with a time and date stamp. Bat detectors were calibrated prior to installation using a Victor Sonic Rodent Repellent device. This unit broadcasted a high frequency tone that I used to standardize the trigger sensitivity of each bat detector.

Detector units and associated wiring were installed using nylon cord and small fencing nails where needed. Detector units were oriented outward into the most open area available. Orienting the detectors toward open space rather than highly cluttered areas produces a greater number of detections (Weller & Zabel, 2002). For this reason, the mid-crown detectors likely had an inherently different “view” from one another depending on tree morphology and spatial complexity at that level. The detection range of each unit consisted of the area straight out and above due to the orientation of the PVC elbow. Therefore the treetop detector sampled the space at and above the forest’s highest foliage. To ensure detectors were not recording the same bat at multiple vertical strata at the same time, recording units were synchronized and later verified by comparing time of recordings. Further, detector units at each tree were located approximately 50 vertical
meters from one another, more 3 times the distance used in similar studies in other forest
types (Kalcounis et al., 1999; Menzel et al., 2005).

File Processing and Data Management

I counted a detector operating from 1600 to 0830 hours the next day as one
detector night. To record the Pettersson bat detector-triggered events, the recording units
were set on Trigger mode where the unit would begin recording after the input signal
from the bat detector was greater than 25 decibels and remained recording until the signal
dropped below 40 decibels for at least two seconds. This setting provided the best results
for this configuration in obtaining calls while minimizing overloading the microphone or
missing passing bats during. Each recording was stored as a separate .mp3 file with a
corresponding time and date stamp. Data were retrieved from the recording units in the
field via a laptop computer as often as possible, ranging from every few days up to
several weeks. Due to equipment failure and disturbance (human and animal) not all the
detectors were active at the same time all the time. Files were then converted to .wav
format in the laboratory for analysis.
Species Identification Protocol

Bat detectors would trigger a recording event from any high frequency sound of sufficient intensity that reached the microphone. Recordings of non-target organisms, weather, or other environmental events required removal prior to analysis of bat echolocation recordings. Bat echolocation recordings were separated from recordings containing spurious noise using SonoBat 3 (SonoBat, Arcata CA) Scrubbing Utility. This Utility searches each recording and isolates those files that contain non-random sound trends that indicate a bat echolocation call. However the scrubber utility did not effectively discriminate between low frequency bat calls and those of birds and insect. Bird and insect noise recordings were subsequently discarded manually based on call structure. Insects produce very rapid, broadband pulses of sound that appear nearly continuous and last several seconds. Birds produce a wide array of vocalizations that can contain many different sound types including frequency-modulated calls, broadband and constant frequency components dissimilar from bat vocalization sequences. Low frequency bat calls are typically low bandwidth and can have a slight frequency-modulated component at the beginning or end of the call depending on the species and environment. Pulses in a call sequence are separated by an inter pulse period where no sound is produced. The inter-pulse period can range from a few milliseconds to several seconds.

Echolocation calls can be characterized as belonging to one of three categories as bats pursue aerial prey; search, approach and feeding phase calls (Griffin et al., 1960).
Calls become shorter, more frequency modulated and more frequent in time as bats hone in on a target. The modification of call characteristics provides a pursuing bat greater detail on the targets position and trajectory. However, call characteristics from different bat species become more similar in approach and feeding pulses. All call types (search, approach, feeding and social) were included, however, only search phase call types were identified to species. Call sequences were identified to species where call characteristics were sufficient to provide conclusive species identification. Approach and feeding pulse calls were placed in species groups whose calls of those types overlap.

A single trained individual classified each echolocation call (containing one or more echolocation pulses) using SonoBat 3 Automated Call Identification software. SonoBat uses a decision engine based on the quantitative analysis of approximately 10,000 species-known recordings from across North America. It automatically recognizes and sorts calls, then processes the calls to extract six-dozen parameters that describe the time-frequency and time-amplitude trends of a call. SonoBat classifies calls using an ensemble consensus of hierarchical decision algorithms and reports a single species decision if the result exceeds the user-defined discriminant probability threshold. If a classification decision does not exceed the threshold at any step in the hierarchy, then SonoBat reports the species or hierarchical groups that sum to the threshold and does not proceed past that point in the decision hierarchy. Final classification follows a number of redundant secondary checks that the classification decisions fall within known expectations for each species, and within ranges that provide robust and confident results (Szewczak J.M. and A.J. Corcoran, In Preparation).
All call identifications were confirmed manually using quantitative parameters and qualitative visual comparisons with known species call types. This was done using conservative criteria for species identification based on established parameter criteria for each species. Parameters included bandwidth (frequency range), frequency with the greatest power kHz \( f_{\text{max}} \), highest apparent frequency \( f_{\text{hi}} \), lowest apparent frequency \( f_{\text{lo}} \), characteristic frequency \( f_c \), amplitude distribution (Power), call duration (dur), slope of call at both the upper and lower end of the call, inter pulse interval, and repetition rate. In instances where call characteristics or quality did not facilitate the identification to species level, calls were identified to the lowest tier species group that contained species with similar call characteristics. For example, species group \textit{M. californicus} / \textit{M. yumanensis} contained calls with the diagnostic \textit{Myotis} downturn at the end of each call and characteristic frequencies at or above 46kHz.

Species accumulation curves were constructed to compare bat species use among vertical strata and between trees as it related to sampling effort. Species accumulation curves are a means to assess inventory completeness and standardize the comparisons of different inventories (Soberon & Llorente B, 1993). Not all the detectors in this study were operational at the same time. Therefore, use of species accumulation curves provides a means of comparing the number of species observed and the amount of time that is necessary to observe those species at each of the six detector locations. This serves two purposes, (i) standardize the sampling effort to allow comparison among height levels and (ii) provide an estimate for the amount of sampling effort required to account for all species observed in this study for use in future surveys of this area.
I used custom software program developed by Dr. Joseph M. Szewczak based on methods described in Moreno and Halffter (2000). The linear dependence model was implemented and assumes the number of species collected will decrease linearly as the sampling effort increases; \( S(t) = \frac{a}{b}[1 - \exp(-bt)] \). \( S(t) \) is the species observed at time \( t \), \( a \) represents the rate of increase at the beginning of the sampling and \( b \) is the species accumulation. I used the number of nights as the sampling effort. Data from each night were subsequently added to the analysis until the asymptote in species richness was reached. The model randomized the sampling over two thousand times to smooth out the curve in order to eliminate the influence of order in which the nights were added.

In an effort to fully explore the data, two species accumulation curves for each detector were constructed. One curve included all calls recorded, including those identified to species and those placed in species groups. The second included only those calls that were identified to species. The ability to identify a call or not could bias results if only calls identified to species were included. However, including calls only from species groups and removing calls identified to species within those groups could be too broad an observation.

Activity

I determined mean monthly activity for each detector by dividing the total number of calls recorded in each month by the number of days each detector was operational in that month. This standardized the detectors for comparison, as not every detector was
operational at the same time. This also facilitated the observation of temporal changes in activity within and among species and species groups.

Model and Assumptions

Traditional occupancy and habitat use models use multi-point or randomized sampling as an approach to elucidate bat habitat use (Hayes & Gruver, 2000; Kalcounis et al., 1999). Moving detectors between randomized plots was not a feasible option in this forest due to the shear height of these trees and the difficulty of rigging equipment in them. Additionally, a moratorium on redwood tree climbing from March to September prevented access during one half of the year. This coincides with the breeding season of the Marbled Murrelet (Brachyramphus marmoratus), a federally listed species of primarily pelagic seabird who rely on these old-growth forests for nesting habitat (Ralph, 1997). In an effort to obtain a richer understanding of the use of this forest by bats we chose an observational method and decided to permanently attach detector units in two trees to continually monitor bat activity remotely for an annual cycle.

With the use of any acoustic tool in the acquisition of bat data and inference to habitat use, it is necessary to clearly articulate the limitations and assumptions inherent in the study design a priori in order to limit erroneous conclusions. Such errors could ultimately result in inappropriate conclusions (Gannon et al., 2003). For the purpose of this study, the following assumptions about interpreting echolocation call data were made as established by Gannon et al. (2003). Calls were interpreted as species or species
groups. Each capture (recorded echolocation sequence containing one or more calls) was treated as an independent incident. A capture was defined as a single recorded sequence containing at least one echolocation pulse. Differences in habitat were described as vertical layers (ground, mid-crown, and treetop) in the forest at fixed designated locations. The sample area was spatially sampled by having two trees each sampling three vertical layers, sampling along the vertical spectrum. Temporal variability is accounted for by continuously sampling as often as equipment was functional for 18 months. This research was a preliminary exploration of variance in bat distribution and community composition by canopy height in this specific section of old-growth redwood forest of HRSP.
RESULTS

Species Identification and Stratification

The six detectors deployed during this study recorded for 1,365 detector nights. A total of 3,769 bat vocalizations were recorded and isolated from the nearly 236,000 raw signals captured. A total of 1,775 (47.1%) recorded calls were positively identified to species (Table 1). A total of 12 species of two families were identified. In family Vespertilionidae, Corynorhinus townsendii, Eptesicus fuscus, Lasionycteris noctivagans, Lasiurus blossevillii, L. cinereus, Myotis californicus, M. evotis, M. lucifugus, M. volans, M. thysanodes, and M. yumanensis were detected. In family Molossidae, Tadarida brasiliensis was detected. Two species, L. blossevillii and T. brasiliensis, were undocumented in previously published research from any redwood forests. Additionally, L. cinereus was not recorded in previously published research from HRSP. The remaining 1,994 (52.9%) vocalizations were placed in species groups where overlapping call characteristics of similar call types or poor recording quality did not allow for confident identification to species level (Table 1). Calls recorded from L. blossevillii, M. evotis, and M. thysanodes each represent less than one half percent of the number of calls recorded. Lasiurus blossevillii produce frequency-modulated calls with a distinct inflection point (knee) often with an upturn at the end with $f_c$ around 40 kHz. Completely flat, constant frequency calls, and call sequences with pulses varying a few kHz in $f_c$ (typical of Lasiuran bats) around 40 kHz have also been observed from this species. Calls
of *L. blossevillii* of poor quality (due to being out of range or other disturbance) can appear similar to *M. lucifugus* or *M. volans* calls of similar quality that lack the discriminating *Myotis* downturn at the end of the call. Therefore, these calls were identified very conservatively and were only identified to species where call quality ensured confident and unambiguous identification.

Vocalizations from *L. noctivagans*, *L. cinereus*, and *T. brasiliensis* become very similar in cluttered habitat where bats shift to shorter, more frequency modulated calls for foraging and navigation. Characteristics of these call types often overlap, reducing the accuracy at which calls can be identified to species. Poor recording quality can confound attempts at species identification. Therefore, unless I could confidently discriminate these species, these calls were grouped into a Laci / Lano /Tabr category.

Call quality proved to be insufficient for confident species identification for many of the high frequency (\( f_c > 40 \text{ kHz} \)) *Myotis* bats. Therefore, those calls that were identified to species were placed in either of the two *Myotis* bat groups that were formed during classification based on call similarities. Those *Myotis* groups include *M. lucifugus / M. volans* group (\( f_c \text{ 39-45 kHz} \)) and *M. californicus / M. yumanensis* group (\( f_c > 46 \text{ kHz} \)). This allowed the use of species identified calls with the larger group of calls that were placed in species groups for analysis.

There was dramatic separation of species distribution among the three vertical strata (treetop, mid-crown, and ground) sampled (Figure 2 and 3). Total number of calls of each species recorded at different strata (Figure 2) indicates differential use of habitat. *Lasiurus cinereus* and *T. brasiliensis* calls identified to species indicate preference for
treetop over mid-crown and ground level. *Lasionycteris noctivagans* calls identified to species showed less separation among vertical levels though they were detected more at treetop level than at mid-crown and ground level. Reducing both the species identified and group identified calls from these three aforementioned bats into a single group reduces our precision while providing greater accuracy in determining height preference of these bats (Figure 2). Calls from this group were recorded nearly three times as often at the middle crown and nine times as often at the treetop compared to the ground detector. *Myotis* bats from both groups were recorded more often at ground level compared to both higher detectors.

Comparing the breakdown of calls from each species / group recorded at each detector we see that there is relative consistency between both trees (Figure 3). Combining results from both trees we see that *L. noctivagans, L. cinereus* and *T. brasiliensis* collectively account for 96 percent of calls recorded at the treetop detector, 90 percent at the mid-crown detector and 23 percent at ground level. Both *Myotis* species collectively averaged 71 percent of all calls recorded from the ground level compared to less than 4 percent at both mid-crown and treetop detectors. The *M. lucifugus / M. evotis* group was recorded 295 times at ground level and 25 times at the mid-crown detector. There were no accounts of this group at the treetop detectors. *M. californicus* and *M. yumanensis* comprised 49 percent of all calls a ground level, and only 3 percent at the mid-crown and treetop level detectors, respectively.

The linear dependence model for the species accumulation curves appropriately matches our observed data for most detectors (Fig. 3). The middle crown detector at tree
2, including both species-only curve and species-with-species-group curve, recorded all species at that site in 64 days. The model for that same detector did not reach asymptote until 215 days of sampling (Table 2). Both species-only curves and species-with-species-group curves for all detectors behaved similarly in the time it took to reach asymptote at each level, with one exception: the ground detector at tree 2 species-with-species-group curve. The observed species-with-species-group data for the ground level detector at tree 2 recorded all species nearly 100 days before the asymptote reached the same value. However, the observed data for the species-only curve at the same detector took 168 days to account for all species, matching the asymptote of the model curve. The discrepancy between observed data and model predictions indicate the potential influence of low species evenness, or surveys being conducted during times of low seasonal activity.

The ground detector at tree 1 recorded the greatest number of species (11) of all detectors in 179 days. The mid-crown detectors at the two trees were different in that tree 1 detector recorded twice the number of species, but it took four times as long as the mid-crown detector at tree 2. The total amount of time necessary to observe all species and species-groups varied among detector location ranging from 180-257 days of sampling. More species were observed at each level at tree 1 compared to tree 2.
Activity

Activity was not consistent between trees (Table 3). There is a differential stratification in activity between them. Sixty-five percent of calls per night at tree 2 were at treetop level, while 7 percent were at mid-crown, and 28 percent were at ground level. Comparatively, tree 1 exhibited less stratification with 43 percent of calls per night at treetop level, 23 percent at mid-crown level, and 33 percent at ground level. There is considerable variation in activity among months and between years at each strata sampled (Table 4, Figure 4a-b). There was a bimodal increase in activity for most species coinciding with spring and fall (Appendix 1). Reduced activity was observed during winter for all species and species groups (Figs. 5a-b). Detections of most bat species during winter demonstrates that some bats remain active and in the area throughout the year.
DISCUSSION

Tall forests, such as old-growth redwood, present difficult environments in which to assess bat use as up to 90% of the available habitat is outside the detectable and netting range of ground-based survey methods. However, to fully assess how bats use a forest, it is imperative to sample the complete vertical habitat because bats do not use all forest strata equally. Results of this study show that even the treetops of the tallest trees on earth are used by bats. In fact, the majority of activity occurred at the treetop. Relying solely on ground-based survey methods clearly imparts an incomplete understanding of habitat use obtained by such methods in tall forests.

Twelve species were identified through analysis of echolocation calls recorded at different vertical strata. Three of the twelve identified species are not accounted for in previously published research using ground-based methods conducted in this forest; *Lasiurus cinereus, L. blossevillii, and Tadarida brasiliensis*. Additionally, *L. blossevillii* and *T. brasiliensis* have not been documented in published research conducted in any coast redwood forest. *Lasiurus cinereus, T. brasiliensis, and Lasionycteris noctivagans* are long distance flyers more often observed foraging in open areas. This study observed few accounts of these bats at ground level. Thus, the treetop sampling revealed the presences of species that were not – and perhaps could not – be detected from the ground. Comparatively, these species comprised more than 93% of calls from the treetop and more than 87% of calls from the mid-crown detector at both trees. As most observed activity occurred at the mid-crown and treetop (72% tree 1 and 66% tree 2), ground-
based detection regiments would underestimate the presence of these bats substantially. This further exemplifies how taller forests exceed the ability of ground-based detection techniques to provide an accurate survey for bats.

The constructed species accumulation curves show the greatest species richness observed at ground level for both species-only and species-with-species-group curves. However, the proportion of species found at ground level is extremely biased toward *Myotis* bats, which account for as much as 75% of all samples recorded at that level (Fig. 3). We see similarity in the lack of *Myotis* calls in the treetop and middle crown detectors of both trees indicating a high degree of stratification that begins at least at the middle crown area.

The length of time required to account for all species observed at each detector provides us some insight into the general evenness of the species in the environment. Reaching species saturation in a low amount of time indicates that species are abundant and present in equivalent amounts relative to one another. Habitats containing one or more species with low abundance, or species that are acoustically elusive or difficult to account for will extend the effort needed to observe all species. The mid-crown and ground detectors at tree two show the observed data reaching saturation before the expected value reached asymptote. The remaining detector locations have the observed and expected curve in closer congruity. The expected survey effort needed to fully account for all species at each of the detector locations indicated by the exponential model ranged from 180 to 267 days (Fig. 3). The actual sampling effort ranged from 52 to 231 days. The discrepancy between the observed and model predictions could be
explained by (i) detectors were operational during times of expected low activity (inclement weather) and (ii) the long duration of the study included sampling nights during times with low seasonal activity. However, seasonal effects on the ground detector at tree 1 were limited as it was not operational during February through May of 2009, due to site disturbance. This coincides with the period of lowest observed annual bat activity. The asymptote was not reached at this detector until 179 days of sampling. Highest annual temperatures coincide with lowest annual rainfall, May through October (Appendix 1). Bats are most active during these environmental conditions. We can thus assume that a negative weather influence of bat activity is minimal during these months.

The linear dependence model in this study predicts an average of 202 sampling days (ranging from 180-226 depending on detector) required to sample 100% of species and species groups. The sampling effort necessary to observe 80% of the species and species groups ranges from 40-121 days of sampling depending on detector location (Table 2). This is an important consideration for future bat research protocol in this area as bat surveys conducted in North America can range from as little as few days to a few weeks of sampling during months of peak seasonal activity (Hayes, 1997; Hayes & Gruver, 2000; Kalcounis et al., 1999). Sampling at this reduced rate would dramatically reduce the number of species accounted for and underestimate species richness.

Despite 18 months of nearly continual survey, only two *L. blossevillii* echolocation calls were identified. *Lasiurus blossevillii* is thought to be a migratory, predominantly solitary, tree roosting species (Barbour & Davis, 1969; Griffin, 1970).
Both recordings were from tree 1, one at the treetop and one at ground level. Both calls were recorded in the fall (August and September) during their peak migration period.

Little is known of *L. blossevillii* in California, however, there are suspected to be migratory and resident members in the state (Cryan, 2003). Coast redwood forests are not a likely location to observe these bats. *Lasiurus blossevillii* prefers cottonwood and sycamore groves from California’s central valley and costal Mendocino County south into Mexico as primary roosting habitat (Pierson et al., 2004). Humboldt Redwoods State Park lies approximately 50 km north of the expected northern coastal summer range of *L. blossevillii* in California (Szewczak & Pierson, 1997). It is unclear whether so few calls were recorded due to detector placement, low annual numbers, or local rarity. This species is of particular conservation concern due to high levels of mortality at wind-energy sites across North America (Arnett et al., 2008), and because our ability to accurately monitor their numbers is confounded by their solitary, migratory behavior. Though the result of this study includes very few recordings from this species, it is evident that in tall forests, monitoring the full vertical strata provides a more accurate account of habitat use by high flying migratory species than those obtained from ground-based detection systems alone. Conducting more studies of this kind in a network of forest ecosystems both locally and regionally should provide new insights into the ecology of this and other elusive migratory species.

The State of California Department of Fish and Game describes *T. brasiliensis* as common in California and locally abundant. Though *T. brasiliensis* roosts have been observed in buildings located in Arcata, CA approximately 65 km to the north of the
study area, this species is categorized as uncommon along the north coast region of California, including HRSP (Harris, 2005). My findings suggest otherwise, as over 13% of all calls recorded in this study were identified as *T. brasiliensis*. This discrepancy could be a direct result of reliance on ground-based detection methods, which have not documented this species in any coast redwood. *Tadarida brasiliensis* is a high altitude, high speed flyer (Vaughan, 1966) and thus likely been undetected during previous ground based sampling. This is supported by the fact that only 3% of the recordings from ground detectors in this study were identified as *T. brasiliensis*.

There are differences in design and approach to studying vertical stratification of bats in different forest ecosystems. Each habitat is structurally different, requiring unique approaches to monitoring vertical strata. Given the great differences among habitats thus surveyed, there is consistency in observed differences in use and species stratification along the vertical gradient. The closest comparison to this study is one conducted in an old-growth mixed conifer forest in Washington State, where *Myotis* species were reported to be more abundant below the canopy and non-*Myotis* species more abundant near the treetop (Hayes & Gruver, 2000). That study involved randomized moveable plots among three height intervals in a 75-m-tall forest. However, surveys were only conducted between early July and mid August 1996. Through continuous monitoring at static locations I observed dynamic fluctuations in the amount of activity and presence of different species at each level throughout the year and even between years. One example was a shift in the amount of activity observed at treetop and ground level between August and September 2008 compared to the same months in 2009 (Fig. 4a).
Myotis species are known to occupy higher canopy strata while being nearly absent at ground levels in boreal aspen forest stands (Kalkounis et al. 1999). However, species of Myotis in this redwood forest were abundant at ground level, and nearly absent higher above the ground. Investigations of bat activity with respect to foraging height in the coastal plains of South Carolina revealed differential foraging activity (Menzel et al. 2005). Non-Myotis bats showed a three-fold increase in the amount of activity above the canopy than within or below it. They observed a more even distribution of bat species above the canopy compared to the two lower levels. Though results are similar in HRSP regarding non-Myotis vertical stratification, these data do not allow such habitat wide inferences into vertical strata evenness given the limited number of sampling points available. However, it is evident by the presence of open foraging bats such as L. cinereus, L. noctivagans and, to a lesser extent T. brasiliensis at the ground level that these bats are not just flying over the habitat but through it as well. The open structure below tall tree crowns like those around the two trees sampled in this redwood forest is suitable for clutter-adapted species. However, it is likely that open foragers are not occluded from this area due to the open structure created from having crowns beginning so high on the trunk.

An important assumption used in this, and many previous studies utilizing acoustic techniques, is that all bats have the same likelihood of detection (Gannon et al., 2003). There are two facets to this assumption; likelihood of detection is equal among bat species and equal among detectors. In reality not all bat species have the same probability of detection due to the great variability of vocalizations among species, the plasticity of
calls due to spatial and environmental conditions, as well as behavioral differences. The distance at which a bat vocalization will be recorded by a detector is dependent on call intensity (amplitude), frequency, orientation and direction, angle of incidence to the detector, and to some extent, air temperature and humidity. Different bat species vocalize at different amplitudes (Parsons and Szewczak 2009). Low frequency vocalizations attenuate more slowly as they travel through the air compared to high frequency sounds of the same intensity. This creates a bias of detection among bat species. Bats that produce louder and lower frequency vocalizations are detected at a greater distance than quieter bats or those utilizing higher frequencies. Habitat structure can also have significant influence on the detectability of sound (Patriquin et al., 2003). This study assumed that all bats had an equal chance of being detected. This study also assumed that bats did not alter their call types in response to their proximity to clutter and therefore each detector has the same overall detection probability.

A limitation of relying solely on acoustic sampling techniques to determine bat abundance is the inability of such techniques to distinguish between vocalizations from a multitude of individual bats or the continued presence of the same individual. However, acoustic sampling has been successfully used to determine habitat use and areas of importance at various spatial scales that can then be further tested with other techniques (Gannon et al., 2003; Sherwin et al., 2000). Overall, the results of this research show relatively low bat activity in HRSP relative to similar studies in other western North American forest habitats (Hayes & Gruver, 2000; Kalcounis et al., 1999). Over 2,300 bat passes were recorded during a nine-night survey (54 detector nights maximum) in a
southern Washington state Douglas-fir (*Pseudotsuga menaiesii*) and western hemlock (*Tsuga heterophylla*) dominated old-growth forest (Hayes & Gruver, 2000). Additionally, records of >100 calls/night have been observed in aspen (*Populus tremuloides*) and white pine (*Picea glauca*) mixed stand forest in Saskatchewan, Canada (Kalcounis et al., 1999). Comparing these results to the roughly 3,700 bat passes recorded from over 1,300 detector nights at HRSP suggests a paucity of bats using this area. Adjusting for the fact that this survey includes nights with expected low activity (e.g. cold and or inclement weather) there were only 12 nights where activity exceeded more than 20 calls/night (maximum 35 calls/night).

The comparatively low level of bat activity found at HRSP could be explained by a scarcity of insect prey, potentially due to redwood being extremely resistant to insect herbivory and there being little else available to sustain large insect populations. This might explain the very reduced number of feeding buzzes recorded from detectors in this study. Previous research shows bat activity is not consistent throughout forests. In a temperate old-growth forest in British Columbia, Canada, activity was found to be significantly higher up to 30 m from waters edge compared to forest interior sites, >100 m from waters edge (van den Driessche et al., 1999). The two trees surveyed in this study lie >50 m from Bull Creek and these results may therefore under-represent foraging behavior and overall bat activity that exists along the riparian corridor. Riparian areas are important to bats as a source of drinking water and food (Racey, 1998). The lack of terrestrial insect prey may concentrate bat foraging to aquatic insect prey. This could make aquatic insects an extremely important food source for bats in this forest and
potentially focus activity in those areas to a greater extent than in non-redwood
dominated forests. Considering the influential role bats have in distributing nutrients from
riparian areas to forest interiors (Power & Rainey, 2000) further investigation is needed
to determine if the low activity level observed in this study is consistent throughout this
forest and how it relates to activity and feeding behavior closer to riparian areas.

Weather can have significant influence on the activity of bats (Anthony et al.,
1981; Avery, 1985; Fenton, 1970; Lacki, 1984). Bats are known to remain inactive when
temperatures are low, rain is falling, or wind speeds are too severe. Some variation in the
bat activity observed at different strata might be explained by climate influences or
differences in cover at each detector (e.g. exposed treetop compared to sheltered ground).
Variation in bat activity could also be due to differential sampling effort between
detectors. In temperate latitudes most bat monitoring efforts have occurred primarily in
the summer and fall, coinciding with the peak in activity for resident and migrating bats.
This study encompassed 18 months of nearly continuous monitoring, providing for direct
observation of seasonal variances and/or interseasonal changes. Many North American
bat species are migratory, yet we still possess only a cursory understanding of where they
go during certain times of the year (Cryan, 2003). In this study, overall activity peaked in
August, September, and October corresponding with fall migration. Increases in activity
during April and May were consistent with spring migration. *Lasiurus cinereus* displayed
a very strong annual bimodal activity consistent with spring and fall migration patterns in
this species (Cryan, 2003). Overall, there was a marked decline, but not an absence of
activity during late fall through early spring.
Observations of larger bodied, migratory species such as *L. cinereus*, *L. noctivagans* and *T. brasiliensis*, during November, February and March, suggests there may be resident populations or inland migrants overwintering in these forests. This could be due to the temperate climate being favorable year-round. There is a precipitous decline in the activity of both *Myotis* groups in late fall and again very little activity from *Myotis* species in early spring. Another limitation of relying solely on acoustic sampling techniques is that bats are only detected if they are active. It is not possible to tell whether bats have migrated out of the area to overwintering habitat or are holding over within the sampling area until conditions are suitable for foraging. Roost surveys provide direct evidence as to the presence or absence of bats and there have been some observations of substantial amounts of guano collected during winter months in some redwood hollows (Gellman & Zielinski, 1996) indicating that bats may indeed be overwintering in coast redwoods. My findings remain inconclusive to support whether these small-bodied bats are remaining to overwinter here or migrating inland to cooler hibernacula.
CONCLUSION

The magnitude of the trees in this forest and the open structure above, within and below the canopy region pose many logistical difficulties to studying bat-forest interactions. Given the assumptions and the stated limitations of acoustic sampling techniques the results of this study expand our understanding of bat presence and stratification at these sites. This was an observational study designed to provide a novel glimpse into a highly complex ecological system. The cost and availability of equipment and logistical challenge of deploying the equipment did not permit more sample sites or randomized plot locations. As such, it is important to recognize the limitations of the approach of this study. Because I was unable to sample more than two trees in this forest, the data did not permit a statistical comparison of use between trees and among vertical strata. However, this does not reduce the usefulness of such an endeavor. This was the first long term survey that monitored across the vertical height of this forest. Through direct comparison, we see that not all vertical strata are used the same by bats. Direct evaluation among the treetop, mid-crown, and ground level detectors and comparisons to research conducted previously using ground-based methods provide evidence of greater species use than obtainable though ground based methods alone. These results can provide a foundation to develop a long-term monitoring program designed to study more of the forest than possible in this study.
Additionally, there are a number of other old-growth redwood forests containing different assemblages of plant and animal species that would benefit from sampling the full vertical habitat. The common thread to the collection of research on bats and vertical stratification in many habitats is that not all bat species use vertical habitat equally. Therefore every bat survey, especially those conducted in tall forests, should include sampling the vertical strata when possible in order to accurately assess habitat use. Given that redwoods are reduced to their present low numbers and exist nowhere else on the planet our understanding of their ecological processes and organismal interactions have global importance in implementing forest management practices as well as species conservation.
Figure 1. Map of the natural distribution of coast redwood, showing three major and twenty-five minor ecological sections, from Noss (2000) Chapter 3, pg. 42, figure 3.1 Location of Humboldt Redwoods State Park added.
Table 1. List of identified species and the associated number of identified calls recorded by each. Also listed are the species groups that were used to classify vocalizations where call characteristics overlapped between species or call quality was insufficient to determine species identification. * denotes species that have not been accounted for by published redwood studies. † denotes species that has not been accounted for by published redwood studies in Humboldt county.

<table>
<thead>
<tr>
<th>Species</th>
<th>Total # Calls Identified</th>
<th>Percent of Total Recordings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corynorhinus townsendii</td>
<td>9</td>
<td>0.24%</td>
</tr>
<tr>
<td>Eptesicus fuscus</td>
<td>3</td>
<td>0.08%</td>
</tr>
<tr>
<td>Lasionycteris noctivagans</td>
<td>308</td>
<td>8.17%</td>
</tr>
<tr>
<td>Lasiurus blossevillii *</td>
<td>2</td>
<td>0.05%</td>
</tr>
<tr>
<td>Lasiurus cinereus †</td>
<td>823</td>
<td>21.84%</td>
</tr>
<tr>
<td>Myotis californicus</td>
<td>66</td>
<td>1.75%</td>
</tr>
<tr>
<td>Myotis evotis</td>
<td>17</td>
<td>0.45%</td>
</tr>
<tr>
<td>Myotis lucifugus</td>
<td>20</td>
<td>0.53%</td>
</tr>
<tr>
<td>Myotis thysanodes</td>
<td>11</td>
<td>0.29%</td>
</tr>
<tr>
<td>Myotis volans</td>
<td>2</td>
<td>0.05%</td>
</tr>
<tr>
<td>Myotis yumanensis</td>
<td>6</td>
<td>0.16%</td>
</tr>
<tr>
<td>Tadarida brasiliensis *</td>
<td>506</td>
<td>13.43%</td>
</tr>
<tr>
<td>Total</td>
<td>1,773</td>
<td>47.04%</td>
</tr>
</tbody>
</table>

Species Groups

| Antrozous pallidus, Eptesicus fuscus | 14 | 0.37%          |
| Lasionycteris noctivagans, Eptesicus fuscus | 127 | 3.37% |
| Lasionycteris noctivagans, Lasiurus cinereus, Tadarida brasiliensis | 937 | 24.86% |
| Myotis californicus, Myotis yumanensis | 603 | 16.00% |
| Myotis lucifugus and Myotis volans | 298 | 7.91% |
| Lasiurus blossevillii, Myotis lucifugus, Myotis volans | 2 | 0.05% |
| Social calls                          | 15 | 0.40%          |
| Total                                 | 1,996 | 52.96%        |
Figure 2. Total number of calls recorded for each species / species group at each of the three height levels (blue bars - treetop, red bars - middle crown, green bars - ground level) combining results from both trees.
Figure 3. Fraction of calls recorded by species / species group and corresponding species accumulation curves (SAC) for the six detectors. Two SAC for each detector plot 1) data for species and group identified calls and 2) data for species identified calls only. See appendix for name abbreviations.
Table 2. Total number of species and species-groups observed at each detector including linear dependence model predictions for the number of sampling days necessary to account for 100% and 80% of species and species-groups.

<table>
<thead>
<tr>
<th>Detector</th>
<th>Total # of species and species groups observed</th>
<th>Linear dependence model based prediction</th>
<th>Days required to detect 100%</th>
<th>Days required to detect 80%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treetop</td>
<td>11</td>
<td></td>
<td>257</td>
<td>121</td>
</tr>
<tr>
<td>Mid-crown</td>
<td>12</td>
<td></td>
<td>226</td>
<td>66</td>
</tr>
<tr>
<td>Ground</td>
<td>16</td>
<td></td>
<td>198</td>
<td>54</td>
</tr>
<tr>
<td>Tree 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treetop</td>
<td>8</td>
<td></td>
<td>187</td>
<td>40</td>
</tr>
<tr>
<td>Mid-crown</td>
<td>6</td>
<td></td>
<td>215</td>
<td>90</td>
</tr>
<tr>
<td>Ground</td>
<td>13</td>
<td></td>
<td>180</td>
<td>58</td>
</tr>
</tbody>
</table>
Table 3. Bat activity represented as number of recordings from both redwood trees. Calls per night are derived by dividing the total number of recorded calls by the total number of operational nights at each detector. Percent of calls at tree represents the proportion of calls at that height out of total calls at tree.

<table>
<thead>
<tr>
<th></th>
<th>Tree 1</th>
<th>Tree 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Treetop</td>
<td>Mid-crown</td>
</tr>
<tr>
<td>Total number of recordings</td>
<td>1208</td>
<td>645</td>
</tr>
<tr>
<td>Total number of nights operational</td>
<td>254</td>
<td>267</td>
</tr>
<tr>
<td>Calls per night</td>
<td>4.8</td>
<td>2.4</td>
</tr>
<tr>
<td>Percent of calls at tree</td>
<td>43.4</td>
<td>23.2</td>
</tr>
</tbody>
</table>
Table 4. Mean number of calls per month. Number in parenthesis is days detector was operational. Mean was calculated by dividing total number of calls per month by the number of days detector was operational, weighted by the number of days in that month. Used to standardize values to compare between trees and among height intervals.

** Denotes months where detector was not operational. Highlighted fields represent months with fewer than 7 sampling nights.

<table>
<thead>
<tr>
<th>Month</th>
<th>Treetop</th>
<th></th>
<th></th>
<th>Mid-crown</th>
<th></th>
<th></th>
<th>Ground</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Tree 1</td>
<td>Tree 2</td>
<td>Tree 1</td>
<td>Tree 2</td>
<td>Tree 1</td>
<td>Tree 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>April-08</td>
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Figure 4. Overall activity measured in average number of calls per night (total number of calls per month divided by the number of days detector was operational) at each of the three height levels (blue bars-treetop, red bars-middle crown, green bars-ground level). ● Indicates months where no data was collected. Arrow’s indicates months where one or more detector sampled less than seven days in that month (see Table 3).
Figure 5 Averaged number of calls per month (total number of calls per month divided by the number of days detector was operational in that month) for *L. noctivagans*, *L. cinereus*, and *T. brasiliensis*. Left column of graphs are from tree 1 and right column is from tree 2 (blue bars = treetop, red bars = middle crown, green bars = ground level). ● Indicates months where no data were collected. Scales for species differ.
Figure 6. Average number of calls per month (total number of calls per month divided by the number of days detector was operational in that month) for *M. lucifugus / M. evotis* group and *M. californicus / M. yumanensis*. Left column of graphs are from tree 1 and right column is from tree 2 (blue bars = treetop, red bars = middle crown, green bars = ground level). ● Indicates months where no data were collected. Scales for species differ.
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Norberg, U. and J. Rayner. 1987. Ecological morphology and flight in bats (mammalia; chiroptera): Wing adaptations, flight performance, foraging strategy and


Roberts, A.L. 2008. Bat use of old growth redwood basal hollows with increasing isolation in contiguous, remnant, and legacy forest stands. Humboldt State University, Arcata, California.


List of recorded species with associated four-letter abbreviation.

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Temperature and precipitation data for April 2008 to November 2009 as recorded from the Burlington Ranger Station, Humboldt Redwoods State Park, Humboldt County, California (high temperature – red bars, low temperature – black bars)