

Bat activity across the vertical gradient of an old-growth *Sequoia sempervirens* forest

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We investigated how bats use habitat structure along the vertical gradient of an old-growth *Sequoia sempervirens* (redwood) forest. Ground-based detection methods would underrepresent bats that use the canopy and above-canopy airspace in this forest as they reach far beyond practical netting and acoustic detection range. We equipped two tall trees with full spectrum automated bat detectors at treetop (108 m), lower crown (55 m), and ground level (5 m) from April 2008 to November 2009, excluding December and January. We sampled 1,365 detector nights, recorded 3,769 echolocation sequences (bat passes), and found 12 species, two of which, *Lasiurus blossevillei* and *Tadarida brasiliensis*, that had no prior documented presence in redwood forests. The maximum proportion of bat activity occurred at treetop, although ground level species diversity exceeded that of the lower crown and treetop, and species composition differed among locations. Non-*Myotis* species composed 95% of the calls at the treetop, 88% at lower crown, and 21% at ground level. Calls from *Myotis* species averaged 71% of all calls recorded at ground level compared to less than 4% at both lower crown and treetop. Activity declined markedly, but did continue, during the winter months we sampled. The combination of a temperate climate and observations of larger, migratory species during November, February, and March suggested the potential for resident populations or inland migrants overwintering in this forest. These findings emphasize the importance of sampling throughout the calendar year and including the full reach of the vertical habitat when quantifying bat activity in forests.

Key words: acoustic monitoring, vertical stratification, bat activity, habitat use, old-growth redwood, *Sequoia sempervirens*

INTRODUCTION

Sampling in forests across the world has revealed clear variation in bat use across the height gradient from ground level, up through the canopy, and above the tallest trees (Francis, 1994; Bradshaw, 1996; Kalcounis *et al.*, 1999; Hayes and Gruver, 2000; Bernard, 2001; Henry *et al.*, 2004; Menzel *et al.*, 2005; Pereira *et al.*, 2010). The ways bats distribute their activities along this vertical gradient differs among forests (Kalcounis *et al.*, 1999). Diversity of foraging strategies and flight specializations among bat species confer advantages to differentially exploit forest canopy structures. Old-growth forests have higher structural complexity than younger forests and consequently exhibit higher levels of bat activity and species diversity (Hayes and Gruver, 2000). Ground-based capture and acoustic techniques have insufficient range to sample forest canopies and will miss or underrepresent high-flying open-air foraging bats that exploit the canopy and above-canopy airspace. In tall

forests, ground-based methods will also underrepresent bats using the understory and lower canopy.

The western North American coniferous forest canopy has only received limited sampling of bat use. Bats in the tallest of these forests, which are dominated by *Sequoia sempervirens* (hereafter redwood), have been studied exclusively from ground level, revealing that bats routinely use basal crevices and fire cavities of redwood trees for night and day roosts throughout the year (Gellman and Zielinski, 1996; Zielinski and Gellman, 1999; Purdy, 2002; Mazurek and Zielinski, 2004; Roberts, 2008). Several species use these cavities as maternity roosts, including a State of California species of special concern and known cave roosting species, Townsend's big-eared bat (*Corynorhinus townsendii*) (Mazurek, 2004). Terrestrial based acoustic, netting, and roost surveys indicate a high degree of overall bat activity associated with redwoods, but the canopy remains virtually unexplored for bats.

Rich with suitable roosting habitat and a temperate climate (S. C. Sillett and R. Van Pelt, personal

communication), old-growth redwood forests may provide resources for a greater number of bat species than previously recognized. Here we report on the first long-term, full-spectrum acoustic sampling of bat activity across the vertical gradient of a tall redwood forest. We quantified bat species richness and how habitat use by species differed among three vertical strata of two trees over a 20-month period.

MATERIALS AND METHODS

Study Site

Redwood trees occur in a narrow, discontinuous, 724-km-long strip along the Pacific coast of California, from San Luis Obispo to the southwestern tip of Oregon. Our study occurred in Humboldt County, where trees reach over 2,500 years old and 115 m tall (S. C. Sillett, R. Van Pelt, A. L. Carroll, and R. D. Kramer, unpublished data), forming massive forests with above-ground masses exceeding 4 Gg and a leaf area index > 15 (S. C. Sillett and R. Van Pelt, personal communication). These dense canopies are deep with emergent trees having giant trunks free of branches for 50 m or more and redwood foliage on suppressed trees extending nearly to ground level (Sillett *et al.*, 2010). Large spaces above understory vegetation and between redwoods are thus available for aerial foraging by bats across much of the forest, although limited by the density of trunks.

Sampling occurred from 16 April 2008 to 19 November 2009 at Humboldt Redwoods State Park (HRSP, 40.3°N, 124.0°W). Half of the 20,000-ha park protects the most extensive remaining old-growth redwood forest, which occurs along Bull Creek (45–65 m elevation), a tributary of the Eel River. In

the alluvial portion of this forest, redwood accounts for the vast majority of tree biomass with *Notholithocarpus densiflorus*, *Umbellularia californica*, and *Pseudotsuga menziesii* making up the remainder (Sawyer *et al.*, 2000). The climate is Mediterranean with warm, dry summers and cool, wet winters. Maximum monthly temperatures reached 26°C during summer, minimum monthly temperatures reached 3°C during winter, and there was an average monthly rainfall of 64 mm during the sampling (PRISM Climate Group, 2013). Both summers (June to September) received < 10 mm of precipitation per month, and 74% of total rainfall occurred from October to May (Fig. 1).

Equipment and Deployment

To assess bat species presence and activity patterns across the vertical gradient, we installed bat detector units using rope-based climbing methods at treetop (108 m), lower crown (50 m), and ground level (5 m) strata in two redwood trees, 111 and 109 m tall. Both these trees stand on the alluvium of Bull Creek about 50 m from the water, with at least two km of redwood forest on either side of the drainage. A separation of about three km between the trees prevented simultaneous sampling of the same bats. Bat detectors consisted of a weatherproof enclosure fitted with an upward facing PVC elbow attached through the front that cradled a Pettersson D240X full spectrum ultrasonic detector (Pettersson Elektronik AB, Uppsala, Sweden) within the enclosure. Each detector connected to a digital recorder housed in a Pelican case at the base of each tree along with an Energy For You 600, 25-watt fuel cell (SFC, Brunthal-Nord, Germany) connected to three 12-volt batteries and Morningstar SunSaver-6 (Morningstar Corporation, Newton, PA) charge controller. Power reached detectors via lamp cord and a ground cable connected to a ground rod running the length of the trunk. We used an AVO-A2MINI-WP-F balun (Intelix, Middletown, WI)

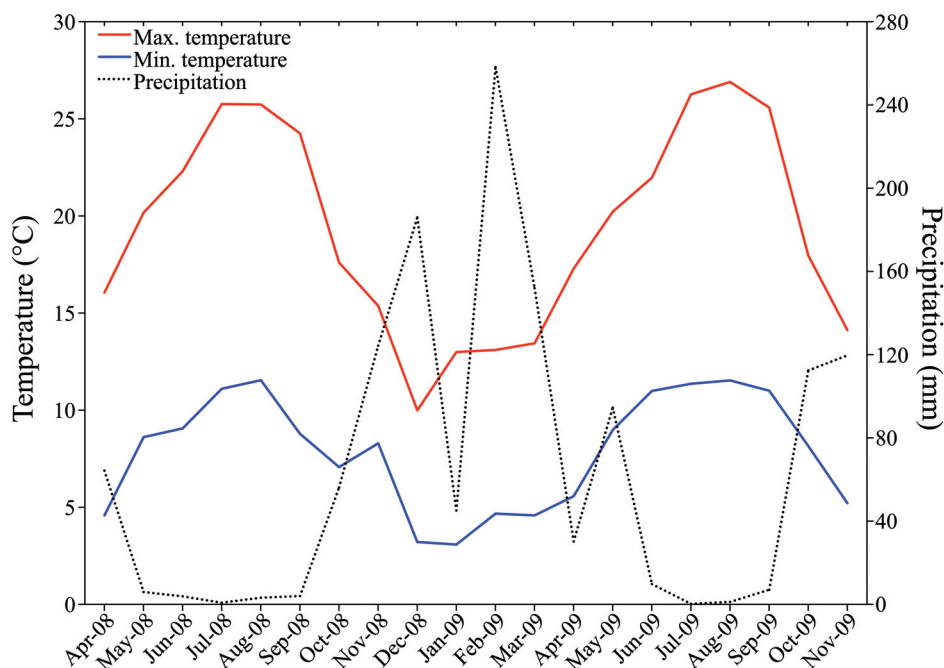


FIG. 1. Estimated monthly air temperatures (maximum, minimum) and precipitation for Humboldt Redwoods State Park, California, during 20-month sampling period (PRISM Climate Group, 2013)

to minimize signal degradation over long distances (M. Basteri, personal communication).

We secured equipment to the trees by lashing detectors and wiring to branches with nylon cord and tacking wires to trunk bark with small fencing nails. We oriented microphone coverage outward into the most open airspace available to maximize detections (Weller and Zabel, 2002). Orientation of the PVC elbow ensured that the range of each unit encompassed the area straight out and above the detector. Ground-level detectors sampled gaps in understory vegetation and the uncluttered space outward from lofty main trunks free of branches. Lower crown detectors faced gaps between adjacent trees just above the base of each tree's live crown. Treeline detectors sampled the space around and above the tree's highest foliage. To ensure that detectors did not record the same bat at multiple locations simultaneously, we synchronized recording units and later verified different bats by different recording times. The distance of the bat from the detector to acquire a detectable and identifiable recording varies with the orientation of the bat, species, and structural clutter (Parsons, 1996; Ahlén and Baagøe, 1999; O'Farrell and Gannon, 1999; Patriquin *et al.*, 2003). This can range from about 30 m for loud bats in open air flying toward the detector to less than 10 m for quiet bats flying away from the detector and within vegetation clutter. Thus, the physical separation of the detectors also prevented simultaneous detections of the same bats and enabled spatial resolution.

Sampling proceeded until depletion of a power supply, malfunction, or damage caused by black bears (*Ursus americanus*) and humans that prevented all detectors from operating simultaneously during the sampling period, and resulted in missing data for all of December and January. We defined a detector operating from 16:00 to 08:30 hours the next day as one detector night. Recordings were stored as separate .mp3 files with a corresponding date and time stamp. We retrieved data from recorders via laptop computer at intervals ranging from every few days to several weeks. All field-acquired .mp3 files were converted to .wav format in the laboratory for analysis. Mean monthly activity for each detector was computed as total number of bat passes recorded in a month divided by number of nights each detector operated that month.

Species Identification

Detectors automatically triggered a recording event from any high frequency sound of sufficient intensity. We removed most non-target signals from other ambient sounds with the SonoBat Scrubber Utility prior to analyzing bat echolocation recordings using SonoBat 3 software (SonoBat, Arcata, CA). All recognizable bat echolocation call types (search, approach, feeding and social) were used to count bat activity, but only search phase call types were used to identify species. The number of pulses captured per recorded sequence varied because of intra-specific and extra-specific differences in call duration and repetition rate between clutter and open air foraging. Multiple pulse recordings can benefit identification confidence as they provide more information and variation for analysis. However, even a single pulse with sufficient call quality can enable identification for an acoustically distinct call type for some species (Parsons and Jones, 2000). After automated processing with SonoBat 3 running default settings, followed by manual vetting and confirmation of species identifications using known call characteristics (Szewczak *et al.*, 2011). We defined a bat pass, or sequence, as per Fenton (1970) as having two or more

echolocation calls, with each sequence separated by one second or more. Many recorded sequences exhibited ambiguous call types that prevented confident identification to species, and we only used those call types exhibiting unique characteristics for establishing species presence at each recording station (Szewczak *et al.*, 2011).

For recordings with insufficient call characteristics or quality to permit confident species identification (Szewczak *et al.*, 2011), we classified bat pass sequences to the lowest acoustic group having overlapping call characteristics. For example, the species *Myotis californicus*/*Myotis yumanensis* (Myca/Myyu) both present downward sweeping calls with diagnostic *Myotis* downturn at the end of each call and characteristic frequencies at or above 46 kHz. Although longer duration calls from each species of high quality (e.g., from a bat passing close to the microphone, free from distortion, and providing complete call characteristics) can enable confident disambiguation of this species pair, when we could not separate them we combined them into the Myca/Myyu group. Indistinct features and call quality also proved insufficient for confident identification of other high frequency ($F_c > 40$ kHz) *Myotis* species. As a result, we allocated many of these calls in either of the two *Myotis* based on call similarities: a *Myotis lucifugus*/*Myotis volans* (Mylu/Myvo) group (F_c 39–45 kHz) as with the *M. californicus*/*M. yumanensis* group ($F_c > 46$ kHz). This allowed the use of species identified calls with the larger group of calls that were classified as groups for analysis.

The western red bat, *Lasiurus blossevillei*, makes frequency-modulated calls with a smooth curvature, often end with an upturn in frequency, and have a characteristic frequency (F_c) around 40 kHz (De Oliveira, 1998; Parsons and Jones, 2000; Szewczak, 2002; Parsons and Szewczak, 2009). This species also makes completely flat, constant-frequency calls, and call sequences (bat passes) with pulses varying a few kHz in F_c (typical of Lasiurine bats) of around 40 kHz. Indistinct, poor quality calls of *M. lucifugus*, often the result of greater distance from the detector microphone, can leave fragments missing the lower amplitude call components such as the *Myotis*-discriminating downturn at the end of the call and can leave signal fragments similar to *L. blossevillei* calls. We thus identified *L. blossevillei* conservatively and only noted this species when call quality ensured confident identification using characteristics unique to this species, i.e., U-shaped calls varying in characteristic frequency, call duration, and call repetition rate across a sequence (Szewczak, 2011). Three other species (*Lasionycteris noctivagans*, *Lasiurus cinereus*, and *Tadarida brasiliensis*) produce similar calls. Ambiguity of these call types reduced the number of species identifications, particularly with samples having poor recording quality. When we could not confidently discriminate sequences with overlapping characteristics to these species, we grouped them as Laci/Lano/Tabr.

Analyses

We generated species accumulation curves (SAC) to compare bat activity among strata and between trees as a function of sampling effort. These curves enable assessment of inventory completeness and standardize comparisons of different inventories (Soberon and Llorente, 1993). Because not all detectors in this study remained operational simultaneously, SAC also provided a means to compare the number of species observed and time necessary to detect those species at each location. SAC were generated via methods described in Moreno and Halffter

(2000). The linear dependence model, which assumes the number of species collected will decrease linearly as sampling effort increases, was implemented as

$$S(t) = a/b[1 - \exp(-bt)]$$

where $S(t)$ denotes the species observed at time t , a represents the rate of increase at the beginning of sampling, and b is species accumulation. A detector night was the sampling unit. Data were randomly accumulated by nights until reaching the asymptote in species number. The model considered each unit independent and randomized sampling for over 2,000 iterations to generate a smooth curve. The resulting equation eliminated the influence of sampling order in construction of SAC and allowed for an adequate fit to the cumulative model.

Two SAC were generated for each detector location. One curve encompassed all calls recorded, including those identified to species and those placed in groups. The second curve considered only calls identified to species. As only a subset of recordings enabled confident species identification, results could be biased. However, including calls only from groups and removing calls identified to species within those groups could provide too broad an observation, so we applied both analyses to complement each other.

Assumptions

Traditional occupancy models employ multi-point or randomized sampling to elucidate bat habitat use (Kalcounis *et al.*, 1999; Hayes and Gruver, 2000). We did not move detectors between randomized plots in the forest, and our study was limited to six detectors (i.e., three fixed strata on two trees). Thus,

each detection was treated as an independent observation, and temporal variability was assessed over periods of continuous sampling whenever possible. 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 moratorium protects the federally listed marbled murrelet (*Brachyramphus marmoratus*), during its breeding season. Primarily a pelagic seabird, marbled murrelets rely on these old-growth forests for nesting habitat (Ralph *et al.*, 1995; Ralph, 1997).

RESULTS

The six detectors deployed during this study operated for 1,365 days and recorded 236,000 events that yielded 3,769 recognized bat vocalization sequences. Of those, 47% had sufficient features that enabled positive identification of 12 species (Table 1). All but one species detected belonged to the family Vespertilionidae, except for *T. brasiliensis* which is a member of the family Molossidae. Calls of *L. blossevillei*, *M. evotis*, and *M. thysanodes* each represented less than 0.5% of species detections. The remaining 53% of vocalizations had ambiguous call characteristics, similar call types, or poor

TABLE 1. Summary of bat species and groups identified via acoustic sampling along the vertical gradient of an old-growth redwood forest at Humboldt Redwoods State Park, California, 2008–2009. Four-letter species abbreviations given in parentheses excluding *Antrozous pallidus* (Anpa). Groups used to classify vocalizations where recordings lacked sufficient information for confident species identification

Species/Species groups	Total calls identified	Total detections (%)
Species		
<i>Corynorhinus townsendii</i> (Coto)	9	0.24
<i>Eptesicus fuscus</i> (Epfu)	3	0.08
<i>Lasionycteris noctivagans</i> (Lano)	308	8.17
<i>Lasiurus blossevillei</i> (Labl)	2	0.05
<i>L. cinereus</i> (Laci)	823	21.84
<i>Myotis californicus</i> (Myca)	66	1.75
<i>M. evotis</i> (Myev)	17	0.45
<i>M. lucifugus</i> (Mylu)	20	0.53
<i>M. thysanodes</i> (Myth)	11	0.29
<i>M. volans</i> (Myvo)	2	0.05
<i>M. yumanensis</i> (Myyu)	6	0.16
<i>Tadarida brasiliensis</i> (Tabr)	506	13.43
Total	1,773	47.04
Species groups		
Anpa, Epfu	14	0.37
Lano, Epfu	127	3.37
Lano, Laci, Tabr	937	24.86
Myca, Myyu	603	16.00
Mylu, Myvo	398	7.91
Labl, Mylu, Myvo	2	0.05
Social calls	15	0.40
Total	1,996	52.96

recording quality that prevented confident species identification but enabled allocation into seven groups (Table 1).

Bat activity exhibited clear stratification from ground to treetop (Fig. 2). Two species, *L. cinereus* and *T. brasiliensis*, were much more frequent at treetop than other strata. Another species, *L. noctivagans*, showed less separation among locations but also had more detections at the treetop than at lower crown and ground level. Combining data from these three species and the Laci/Lano/Tabr group revealed a clear canopy preference for these bats, which collectively accounted for 96% of detections at treetop, 90% at lower crown, and 23% at ground level (Figs. 2 and 3). In contrast, *Myotis* species and groups had far more detections at ground level than in the canopy (Figs. 2 and 3). Bats in this genus comprised 71% of all detections at ground level. Two species, *M. californicus* and *M. yumanensis*, comprised 49% of all detections at ground level and only 3% at other locations.

Species accumulation curves revealed effects of low species evenness and highlighted that sampling occurred during periods of low bat activity (Fig. 3). The total amount of time necessary to observe all species and groups varied among detector locations and ranged from 180–257 nights of sampling. Both SO and SG curves for all detectors required a similar time to reach maximum at each location, except ground level near Tree 2. At this location, 13 species and groups were detected in 55 nights, but the final species was not detected for another 133 nights. Maximum species richness occurred at ground level near Tree 1, where 16 species groups and 11 individual species were detected in 179 days.

Trends in overall bat activity varied between trees, with Tree 1 having more species detections at each level compared to Tree 2 (Table 2 and Fig. 3). Tree 2 had 65% of detections at the treetop, 7% at lower crown, and 28% at ground level, whereas Tree 1 exhibited less vertical stratification with 43%

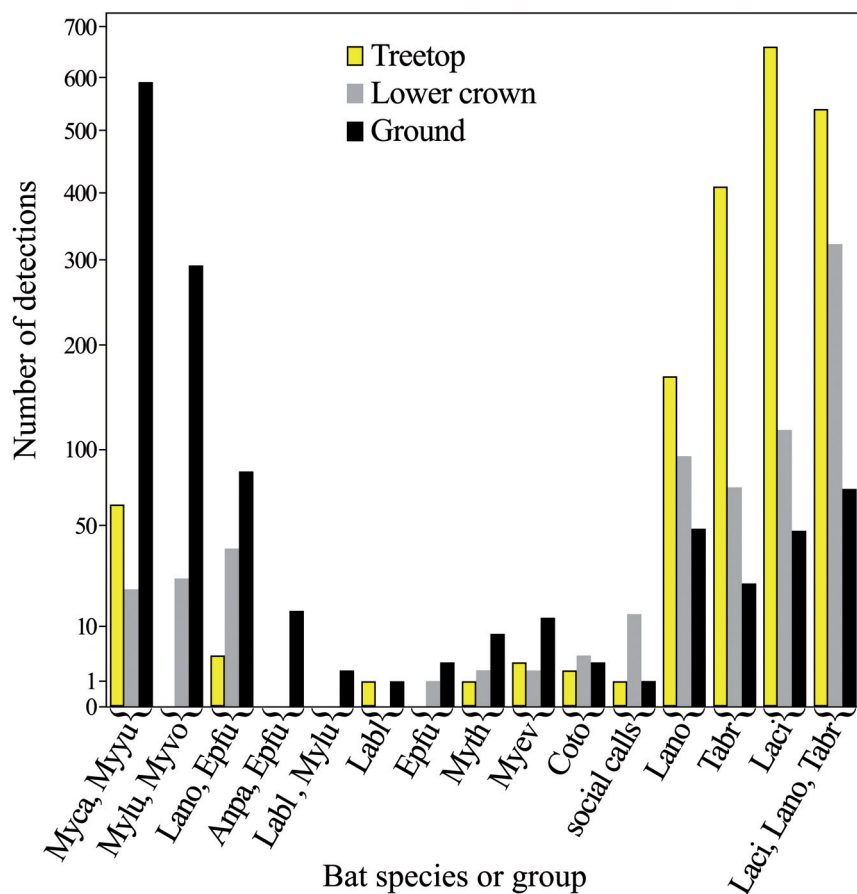


FIG. 2. Total number of bat detections for species and groups at treetop, lower crown, and ground locations, combining results from two trees at Humboldt Redwoods State Park, California, 2008–2009. Note that number of detections is square root transformed. Social calls not assigned to species or groups also indicated

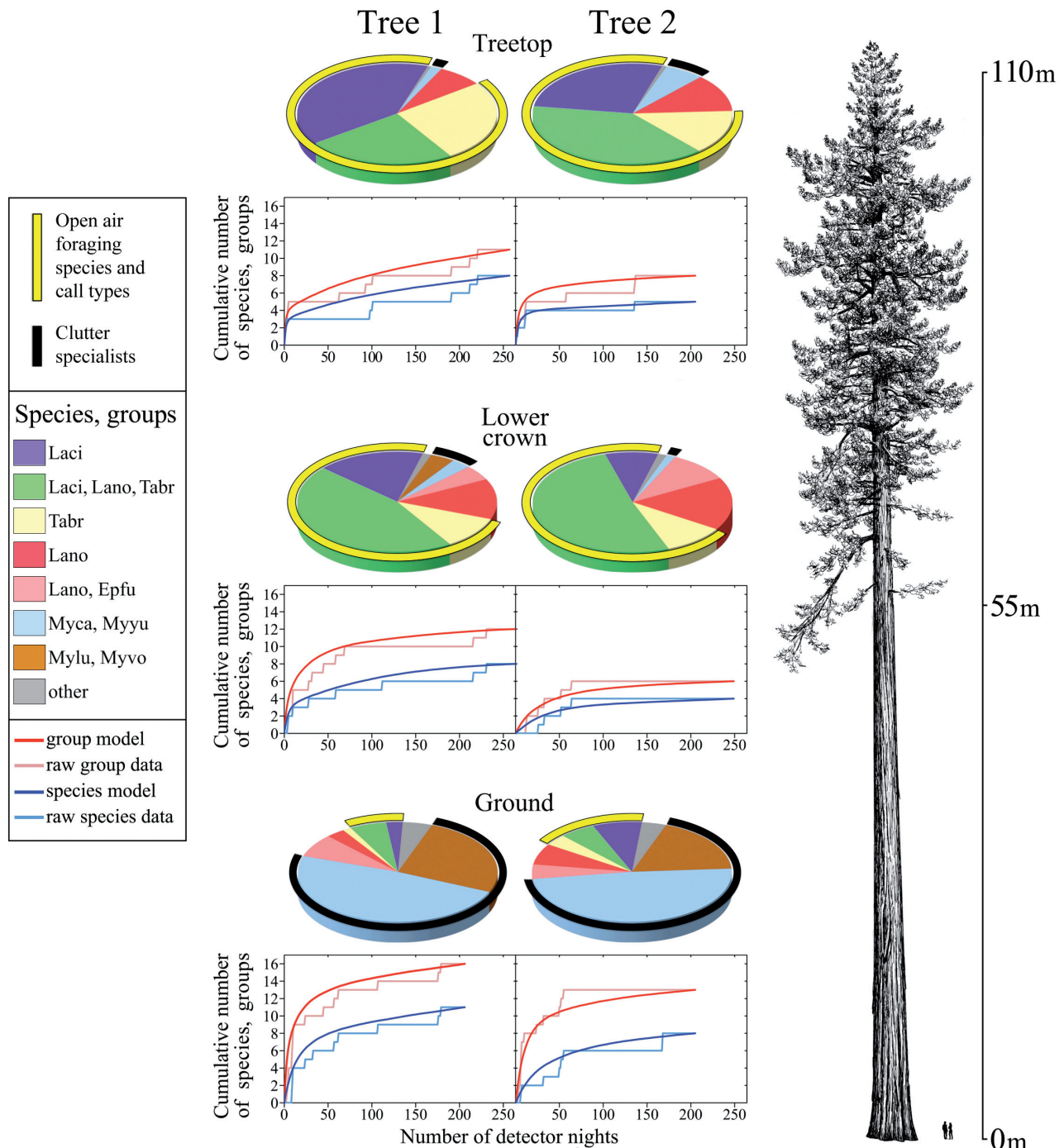


FIG. 3. Distribution of bat detections by species and group along with corresponding accumulation curves for 6 detector locations sampled in an old-growth redwood forest at Humboldt Redwoods State Park, California, 2008–2009. Outer rings of pie charts designate proportional groupings of open air foraging bats and clutter specialists with undesigned proportion representing generalists (Barbour and Davis, 1969; Brigham, 1991). Proportion ring for open air foraging bats includes open air foraging call type from silver-haired bats (Lano) that fall into the ambiguous grouping Laci, Lano, Tabr (Fenton, 2003). Raw group and species data shown along with linear dependence models. Tree drawing courtesy of Dr. Robert Van Pelt

of detections at the treetop, 23% at lower crown, and 33% at ground level.

Trees showed considerable monthly variation in bat activity across strata (Table 3, Fig. 4). Equipment

failure prevented a complete assessment of seasonal variation, but overall bat activity was highest in summer and lowest in February, the only complete winter month we sampled (Fig. 4). These data

TABLE 2. Bat activity at Humboldt Redwoods State Park, California, 2008–2009, represented as number of bat passes (detections) and expressed as the proportion of total detections at each detector location and normalized to detections per night for two tall redwood trees

Character	Tree 1			Tree 2		
	Treetop	Mid-crown	Ground	Treetop	Mid-crown	Ground
Total number of bat passes	1208	645	928	642	69	277
Total detector operational nights	254	267	206	183	247	208
Bat passes per detector night	4.8	2.4	4.5	3.5	0.3	1.3
Percent of passes at sampled level	43.4	23.2	33.4	65.0	7.0	28.0
Number of species identified at sampled level	9	9	12	6	4	9

demonstrate bats remain active in this forest throughout the year, and most species were detected at least once during a winter month.

DISCUSSION

Tall forests present logistical challenges for quantification of bat activity as the majority of habitat available to bats lies beyond the detection of ground-based sampling. Extreme tree heights allowed us to position detectors at ≈ 50 m intervals, more than three times the distance used in similar studies of shorter forests (Kalcounis *et al.*, 1999; Menzel *et al.*, 2005). At least two-thirds of our bat detections occurred above detection range of ground equipment. Reliance on ground-based sampling would ignore a majority of usable habitat in this old-growth redwood forest.

We identified 12 bat species through identification of vocalizations. Two species, *T. brasiliensis* and *L. blossevillii*, had no previous documented occurrence in redwood forests, and *L. cinereus* had no previous reported occurrence in HRSP. These bats had few detections at ground level, consistent with the known behavior of these species as long distance flyers and open air foragers (Vaughan, 1966; Barbour and Davis, 1969). Compared to ground level, these three species comprised $> 93\%$ of detections at the treetop and $> 87\%$ of detections from the lower crown. Ground-based sampling alone would have grossly underestimated their activity in this forest.

The highest bat species richness in the forest occurred near ground level and was biased toward *Myotis*, which accounted for over 66% of all detections at that location, and consistent with their foraging behavior as clutter specialists, i.e., highly

TABLE 3. Mean number of bat passes (detections) at Humboldt Redwoods State Park, California, 2008–2009, per month normalized to detections per night. Months with fewer than seven operational nights are denoted with ‘?’ symbol

Month-year	Tree 1			Tree 2		
	Treetop	Lower crown	Ground	Treetop	Lower crown	Ground
Apr-08	1	0	0	2	< 1	0
May-08	5	2	4	3	< 1	2
Jun-08	5	4	5	0	0	0
Jul-08	4	4	5	4	1	1
Aug-08	7	4	5	5	1	3
Sep-08	4	2	11	?	?	?
Oct-08	3	?	6	?	?	?
Nov-08	?	?	?	1	0	< 1
Dec-08	?	?	?	?	?	?
Jan-09	?	?	?	?	?	?
Feb-09	1	1	?	< 1	< 1	0
Mar-09	3	< 1	?	2	0	0
Apr-09	4	2	?	2	0	< 1
May-09	?	?	?	2	0	3
Jun-09	2	3	2	3	< 1	2
Jul-09	4	2	1	4	< 1	2
Aug-09	16	2	2	4	0	2
Sep-09	7	4	5	7	< 1	3
Oct-09	2	1	< 1	4	< 1	< 1
Nov-09	0	0	0	?	?	?

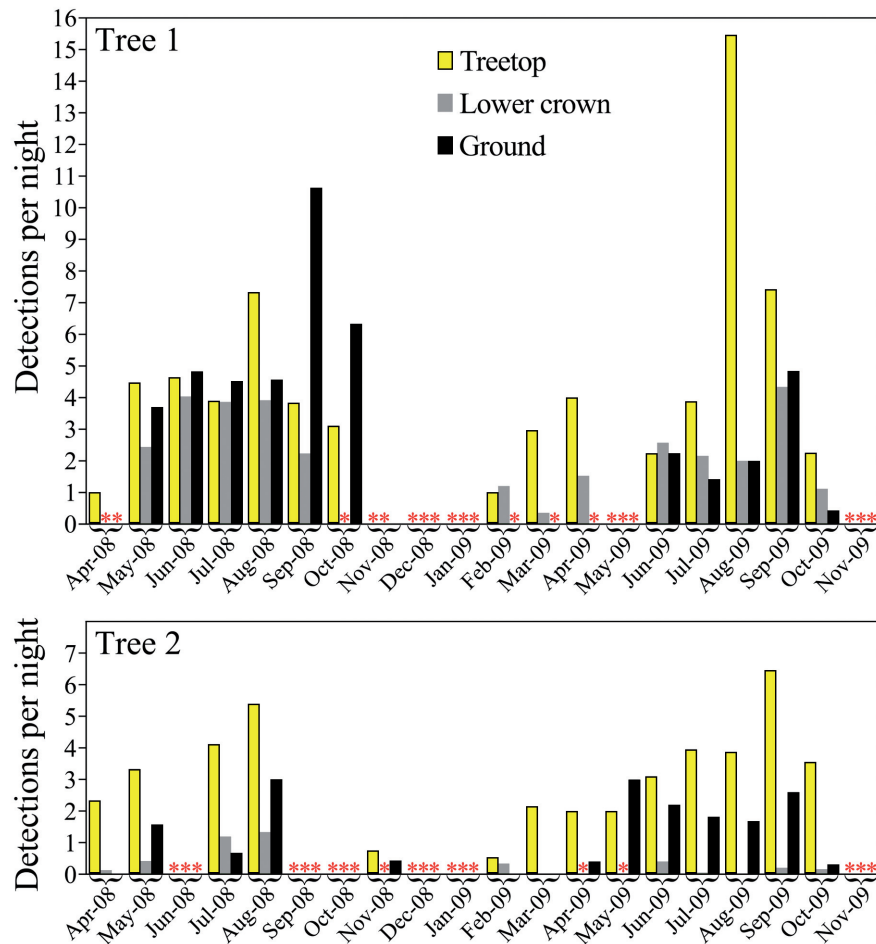


FIG. 4. Monthly bat activity measured as mean number of detections per night (i.e., total number of calls per month divided by number of days detector was operational that month) at three strata in two old-growth redwood trees at Humboldt Redwoods State Park, California, 2008–2009. Red asterisks (*) indicate detectors with < seven operational nights per month

maneuverable flight in and around vegetation and other obstacles (Barbour and Davis, 1969; Broders *et al.*, 2004). The corresponding lack of *Myotis* detections at treetop and lower crown locations of both trees indicates vertical stratification of the redwood forest bat community, with some species foraging mostly near the ground and others foraging more frequently in and above the canopy. A similar vertical stratification of bats was observed in a 75-m-tall *Pseudotsuga-Tsuga* forest in Washington State, with *Myotis* species more abundant near ground level and non-*Myotis* species more abundant in the canopy (Hayes and Gruver, 2000). A much shorter coastal forest of South Carolina exhibited a similar stratification of bats, but had a more homogeneous distribution of species above compared to within and below the canopy (Menzel *et al.*, 2005). The occasional detection of open-foraging bats such as *L. cinereus*, *L. noctivagans*, and *T. brasiliensis* at

ground level demonstrate that these species do pass through the redwood forest near ground level as well as within and above the canopy. The large, relatively clutter-free spaces of this tall forest clearly provide suitable habitat for open-air foragers.

The State of California Department of Fish and Wildlife describes *T. brasiliensis* as common in California and locally abundant. Though *T. brasiliensis* roosts in buildings around Arcata, California, which is 65 km north of the study area, some reports categorize this species as uncommon along the north coast of California, including HRSP (Harris, 2005). Our findings indicated this species occurs more commonly than recognized by ground-based sampling, as it accounted for > 13% of all species-classified detections. This species flies high and fast in open air (Vaughan, 1966) and has thus likely avoided detection during previous studies. Even so, long-term ground-based sampling can still detect

T. brasiliensis, which comprised 3% of our ground level detections.

Although many bat acoustic sampling studies assume equal likelihood of detection among species and between detectors, unequal detection probabilities does limit the resolution of acoustic sampling (Gannon *et al.*, 2003). In reality, not all bat species have the same probability of detection due to the great variability of vocalizations among species (both in time-frequency structure and amplitude of calls) and plasticity of calls in response to variation in habitat structure and foraging strategy (Obrist, 1995; Patriquin *et al.*, 2003). Bat echolocation calls also exhibit significant intra-species variability (Kalko and Schnitzler, 1993) and demonstrate overlap in call characteristics among sympatric species (Parsons and Szewczak, 2009). Moreover, the distance at which a bat detector may record vocalizations depends on call intensity (amplitude), frequency, orientation, and direction of the bat relative to the microphone, angle of incidence to the detector, physical obstructions between source and detector, and to some extent, air temperature and humidity (Parsons and Szewczak, 2009). All of these factors create some bias of detection among bat species. Species that produce louder and lower frequency vocalizations will gain detection at a greater distance than quieter bats or those utilizing higher frequencies such as *Myotis*. For example, our infrequent detection of *C. townsendii* was likely, in part, an artifact of this species' low intensity calls (Weller, 2007). Despite these limitations, acoustic sampling provides a powerful tool for studying bats in tall forests by providing an automated, non-invasive means to conduct long-term surveys. Further, acoustic sampling permits detection of species that fly outside the range of, or otherwise avoid capture by, mist nets (O'Farrell *et al.*, 1999).

Overall, the redwood forest we studied exhibited relatively low bat activity compared to other forests in other western North American forests (Kalcounis *et al.*, 1999; Hayes and Gruver, 2000). A 9-night survey in a *Pseudotsuga-Tsuga* forest recorded more than 2,300 bat passes (Hayes and Gruver, 2000), and > 100 passes per night were observed in boreal *Populus-Picea* forest in Saskatchewan (Kalcounis *et al.*, 1999). The 3,769 bat passes recorded over 1,365 nights at HRSP (i.e., a mean of 2.8 passes per night) indicates a paucity of bat use in this forest. There were only 12 nights during our sampling when bat activity exceeded more than 20 passes per night (and a maximum 35 passes per night). As the predominant biomass in this forest, redwood's resistance to

insect herbivory and toxicity to pathogens (Olsen *et al.*, 1990) may reduce overall insect prey abundance and this could account for the relatively low bat activity compared to other forests. However, confirmation of this correlation must remain speculative and await direct investigation.

Weather influences the activity of bats, which reduce activity during periods of low temperatures, heavy rainfall, and strong winds (Fenton, 1970; Anthony *et al.*, 1981; Lacki, 1984; Avery, 1985). Some of the differences we observed in bat activity across the forest canopy likely reflected a response to weather, although our long sampling period enabled detection of bats during favorable conditions at each detector location. Though hibernating bats have been documented foraging during warm nights in winter (Avery, 1985), most bat habitat use monitoring in temperate latitudes occurs during peak activity austral months for resident and migrating bats. Regrettably, we still have only a cursory understanding of most North American bat migrations (Cryan, 2003). Overall activity in the redwood forest peaked during fall migration, and we also observed increased activity during April and May consistent with spring migration. One species, *L. cinereus*, displayed strongly bimodal activity coincident with previously documented spring and fall migrations (Cryan, 2003). While bat activity slowed, it did not cease during winter months in the redwood forest we studied. Our observations for large-bodied, migratory species such as *L. cinereus*, *L. noctivagans*, and *T. brasiliensis* during November, February, and March, suggest resident populations or inland migrants overwintering in the redwood forest. The mild coastal climate may provide refuge from harsher winters further inland. At least one banding recovery from an inland *T. brasiliensis* supports this conjecture (P. Leitner, personal communication). A decline in activity during winter may indicate either seasonal movement out of the area to cooler inland hibernaculae or increased use of torpor while at local roosts. Our few *Myotis* detections in February support the latter hypothesis. Roost surveys of basal hollows with observations of guano deposition provide further evidence of bat presence during winter in redwood forests (Gellman and Zielinski, 1996).

This initial long-term survey of bats across the vertical gradient of the world's tallest forest revealed that bat species partition their resource utilization across the microhabitats of the redwood strata, and vary it across the year. A more complete appraisal of this partitioning and patterns of usage will await

more extensive survey initiatives in this logistically challenging vertical bioscape. Elucidating what drives bat distribution and usage in redwood forests will require parallel assessments of additional ecologically relevant cofactors. These include insect distribution and abundance, microclimate, proximity to water resources, and physical and age structure of the redwood stands.

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