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## Habitat Use of Pallid Bats in Coniferous Forests of Northern California

### Abstract

Limited information exists on the ecology and habitat requirements of the pallid bat (*Antrozous pallidus*) inhabiting forested ecosystems at the northern limits of its range. We used mist netting, radiotelemetry, and emergence counts at roosts to identify foraging and roosting habitat of pallid bats on the Plumas National Forest in northern California during summer 2007. Pallid bats used a variety of structures for day and night roosting, including live trees and snags, a rock crevice, and a building. Live trees and snags used for roosting were consistently tall in height, large in diameter, and located in mature stands in micro-sites with low percentages of overstory and mid-story cover. The height of roosting sites used by pallid bats in live trees and snags was low relative to the height of the stems selected for roosting. Size of foraging areas varied among sex and reproductive classes of pallid bats, with lactating females ( $1.56 \text{ km}^2 \pm 0.88 \text{ SE}$ ) exhibiting the smallest foraging areas and post-lactating females ( $5.97 \text{ km}^2 \pm 2.69 \text{ SE}$ ) having the largest foraging areas. Sierran mixed conifer and white fir habitats comprised significantly larger proportions of the available habitat within foraging areas of adult females than other habitats. Long distance movements during nightly foraging,  $> 2 \text{ km}$ , were common for all sex and reproductive classes of pallid bats. These data indicate that pallid bats inhabiting coniferous forests choose alternate habitats in which to forage and roost from those typically used by the species in other regions of its distribution.

### Introduction

The pallid bat (*Antrozous pallidus*) is a species that inhabits arid deserts and xeric ecosystems across a large expanse of western United States, reaching its northernmost distribution in southwestern Canada and its southern limits in central Mexico (Hermanson and O'Shea 1983). Although the species has been recorded at elevations exceeding 2400 m (Black 1974), it is believed to be most prevalent at elevations below 1800 m (Orr 1954, Ports and Bradley 1996, Warman et al. 1998). The pallid bat has been observed using mixed-conifer and evergreen forests (Jones 1965, Rabe et al. 1998, Morrell et al. 1999) and tropical deciduous forests (Van Gelder 1959, Baker 1967); however, limited information exists on the ecology of this species in forested ecosystems.

A variety of structures have been documented as roosting sites of the pallid bat including caves, mines, rock crevices, live trees and snags, and bat houses and human-made structures (Vaughan

and O'Shea 1976; Hermanson and O'Shea 1983; Lewis 1994; Pierson et al. 1996; Rabe et al. 1998; Tatarian 1999, 2001; Rambaldini 2006). Regardless, the overwhelming majority of roosting sites that have been described are in rock crevices (Orr 1954; Vaughan and O'Shea 1976; Hermanson and O'Shea 1983; Lewis 1993, 1994; Rambaldini 2006), particularly for bats living in arid or semi-arid environments. The pallid bat typically day roosts and night roosts in alternate structures (Hermanson and O'Shea 1983, Rambaldini 2006), and exhibits seasonal variation in use of and fidelity to day roosts (Vaughan and O'Shea 1976, O'Shea and Vaughan 1977, Lewis 1996). Although the pallid bat is known to use trees and snags as roosting sites (Davis 1944, Hall 1946, Orr 1954, Brown et al. 1997, Rabe et al. 1998), the relative importance of these structures to the ecology of this species in forested ecosystems remains unclear.

The pallid bat is primarily a gleaner that typically forages close to the ground at distances  $< 3 \text{ km}$  from roosting sites (Barbour and Davis 1969, O'Shea and Vaughan 1977, Bell 1982, Johnston and Fenton 2001). A variety of habitats have been described as suitable foraging space of the pallid

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bat including shrub-steppe grasslands, open pine forest, oak-savannah woodland, rock outcrops, lava flows, and agricultural systems (Jones 1965, Barbour and Davis 1969, Whitaker et al. 1981, Bell 1982, Hermanson and O'Shea 1983). Regardless, a comparison of the relative importance of available habitats to the foraging ecology of this species has not been made. In this paper we describe the roosting and foraging behavior of the pallid bat inhabiting conifer forests of northern California, with an emphasis on use of tree roosts and available foraging habitats.

## Study Area

This study was conducted on the Feather River and Mount Hough ranger districts of the Plumas National Forest located south of Quincy, California, an area encompassing ca. 315,000 ha. Topography is rugged and variable with side slopes approaching 80% in places and relatively flat benches possessing alpine meadows on the top of ridges. The study area covered portions of the North, Middle, and South Forks of the Feather River drainage, typified by deep canyons and side slopes that are difficult to traverse. Elevations range from 1180 to 2250 m. This region of California experiences a Mediterranean climate with hot and dry conditions during the growing season followed by cool, wet winters (Bailey et al. 1994). The distribution of vegetative communities is impacted by topographic relief with western slopes and higher elevations receiving more precipitation than eastern slopes and lower elevations. Annual precipitation averages ca. 980 mm with a mean temperature in July of 20.5 °C (data available at [www.ncdc.noaa.gov/oa/ncdc.html](http://www.ncdc.noaa.gov/oa/ncdc.html)).

Forests on the Plumas National Forest include mixed-fir, mixed conifer, and pine-cedar communities. Dominant tree species are white fir (*Abies concolor*) and Douglas-fir (*Pseudotsuga menziesii*), with ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), sugar pine (*P. lambertiana*) incense cedar (*Calocedrus decurrens*), and red fir (*A. magnifica*) also present. Selective logging is common throughout the region, with clearcut harvesting and fire-related salvage logging having increased in frequency since the 1980s (McKelvey and Johnson 1992). These practices have produced minimal impact on tree species composition but have altered the size class distribution of trees in affected areas (McKelvey and Johnson 1992).

## Methods

All sampling was conducted from June to July 2007. We captured bats using mist nets of various sizes (i.e., 2.6 m in height and 2.6 to 20 m in length) placed across flyways, over open water, and in habitats perceived likely to be used by pallid bats as foraging areas ( $n = 33$  sites). Mist nets were set prior to sunset and monitored for ca. 4 hrs each night. For each pallid bat captured we determined gender and reproductive condition using external secondary sexual characteristics (Racey 1988), assessed age by examining the extent of ossification of epiphyseal cartilage in the finger joints (Anthony 1988), measured length of morphological characteristics, and measured mass using a Pesola spring scale. For adult pallid bats of sufficient mass (Aldridge and Brigham 1988), we used Torbot ostomy appliance adhesive (Torbot Group, Inc., Cranston, Rhode Island) to temporarily attach 0.55g, SOM-2011 transmitters (Wildlife Materials, Inc., Murphysboro, Illinois) to the mid-dorsal surface. Bats were held for 15 min following transmitter attachment to allow the adhesive sufficient time to dry and form a secure bond with the skin surface.

We tracked pallid bats to day and night roosts using hand-held, 3-element Yagi-Uda antennae coupled with TRX 1000S receivers (Wildlife Materials, Inc.). We coordinated searches among personnel using vehicles with radio communications and omni-directional antennae for 'listening' for signals while moving among points high in elevation. When tracking a bat proved unsuccessful for two successive days, we switched to aerial tracking techniques. We performed aerial tracking during daylight hours to detect 'missing' transmitter signals. Once a signal was detected, ground crews attempted to locate the day roost.

Day and night roosts of pallid bats were described by type of structure (i.e., tree, rock crevice, or human-made structure). For tree roosts, we recorded the species, whether the tree was live or dead, whether the top of the stem was broken, bark thickness (i.e., thin vs. thick), diameter at breast height (cm), stem height (m), and canopy height (m). We visually-estimated the bark remaining (%) and the extent of exfoliating bark (%), and in the immediate vicinity of the roost tree we estimated overstory cover (%) and mid-story cover (%). We recorded slope aspect (°), roost aspect (°), and the height of the roost (m). We counted the number

of bats emerging from day roosts at twilight to estimate colony size. To minimize the likelihood of disturbance to the bats, care was taken to count bats from a hidden location at an extended distance from the roost.

To estimate foraging area sizes and assess available habitats within foraging areas of pallid bats, we used nighttime radiotracking to determine direction and relative signal strength of bats during foraging bouts from multiple tracking stations. Points were placed along the bearing line at distances determined by signal strength and then used in calculating 95% minimum convex polygons (95% MCP) with the Home Range Tools extension (Rodgers et al. 2007) for ArcGIS 9.2 (ESRI, Redlands, California). We did not use triangulation methods in locating bats. Instead, bats with transmitters emitting strong signals were presumed to be 200 m away, medium-strength signals 500 m away, and weak signals 1200 m distant; these approximate distances were based on average measures of the strength of signals coming from radiotagged bats in day roosts where the location and distance of the bats were known, and from periodic simultaneous tracking with a mobile unit to ensure that bats were in the vicinity of the estimated location. Availability of habitats within individual foraging areas of pallid bats was determined using GIS data from the Plumas National Forest that was based on habitat associations presented in the California Wildlife Habitat Relationships (CWHHR) system (Mayer and Laudenslayer 1988). For the Plumas National Forest, this GIS data set was comprised of 10 habitats including Sierran mixed conifer (SMC), white fir (WFR), wet meadows (WTM), barrens (BAR), montane chaparral (MCP), montane hardwood (MHW), ponderosa pine (PPN), perennial grassland (PGS), montane riparian (MRI), and urban (URB). We tested for differences in the availability of habitats within foraging areas using a one-way ANOVA, with habitats as the main effect and individual females as random samples (SAS Institute, Inc., Version 9.1, Cary, North Carolina). This test was combined with a Fisher's LSD means separation procedure to determine differences among specific habitats.

## Results

We captured pallid bats at 21.2% (n = 7) of the netting sites totaling 22 individuals. Lactating

females were captured between 27 June and 15 July (n = 7), pregnant females on 1 and 3 July (n = 2), and post-lactating females on 22 and 25 July (n = 3); one female captured on 27 June was non-reproductive. We captured male pallid bats between 15 and 25 July (n = 9), with four individuals exhibiting scrotal testes on 25 July; no juvenile pallid bat was captured.

We radiotracked 12 adult pallid bats, including six lactating, one pregnant, two post-lactating, one non-reproductive female, and two non-reproductive males. We located 14 roosting sites, four of which could not be identified due to terrain with slopes approaching 80% in steeper canyons. The remaining 10 roosts included four live trees, four snags, a rock crevice, and a building. Tree species used as roosts included live and dead incense cedars (n = 5), live and dead ponderosa pines (n = 2), and a live sugar pine. Incense cedars were used as both day and night roosts, and remaining tree species were only used as day roosts. No roost of either male bat was identified due to terrain constraints.

All trees used as roosts by pallid bats were stems possessing thick bark and all roost trees were intact at the top of the bole. In general, live and dead roost trees were large in diameter (> 100 cm dbh), tall in height (> 25 m), and possessed a high percentage of remaining bark (Table 1). Roosting sites were typically located in cavities, mostly basal hollows, as opposed to beneath bark

TABLE 1. Habitat characteristics (mean ± SE) of live and dead trees used as roosting sites by pallid bats on the Plumas National Forest, California, in summer 2007. Data are based on sample sizes of four trees each.

Habitat Characteristic	Live Tree Roosts	Dead Tree Roosts
Diameter (cm)	109 ± 33.2	104 ± 15.8
Height (m)	32 ± 6.65	25 ± 6.7
Bark remaining (%)	96.2 ± 1.25	85 ± 8.4
Exfoliating bark (%)	7.5 ± 3.22	50 ± 20.3
Canopy height (m)	29.2 ± 7.8	23.5 ± 2.63
Overstory cover (%)	26.2 ± 15.4	23.8 ± 9.45
Mid-story cover (%)	16.2 ± 14.6	16.2 ± 6.25
Roost aspect (°)	178 ± 38.3	73.5 ± 4.6
Roost height (m)	5.3 ± 0.7	5.83 ± 1.8
Slope aspect (°)	176 ± 58	204 ± 35.2

or in external crevices. Dead trees used as roosts possessed a higher percentage of exfoliating bark than live roost trees. Roost trees of pallid bats were situated in stands with tall canopies, but were located in micro-sites with low percentages of overstory and mid-story cover, suggesting that solar exposure was likely a factor in roost-site selection by adult females. The height of roosting sites used by pallid bats in trees was low relative to the height of the stems selected for roosting. Roosting sites in dead trees were predominantly oriented to the east, whereas roost sites in live trees exhibited greater variation in orientation with the average toward southerly exposures. Roost trees of pallid bats generally occurred on south-facing slopes.

We conducted 13 emergence counts at known roosts of pallid bats. Six other counts were attempted 100 m upslope from unknown roosts situated in steep canyons without success. The maximum number of bats observed exiting any roost was 58 on 19 July from a live ponderosa pine that was 45 cm in diameter and 29 m in height; the location of the roost was 5 m above ground. The average number of bats recorded during emergence counts at pallid bat roosts was  $15.4 \pm 4.7$  bats.

Size of foraging areas of pallid bats appeared to vary among sex and reproductive classes, with lactating females exhibiting the smallest foraging areas ( $1.56 \text{ km}^2 \pm 0.88 \text{ SE}$ ) and post-lactating females the largest foraging areas ( $5.97 \text{ km}^2 \pm 2.69 \text{ SE}$ ; Table 2). Pallid bats that we radiotracked demonstrated long distance movements on one or more nights of foraging, typically exceeding 2000 m in length. However, except for lactating females, most pallid bats used foraging areas in relatively close proximity to their day roosts. Day

roosts of pallid bats were usually situated within 500-600 m of an available source of water.

Availability of habitats within foraging areas of adult female pallid bats was not equal ( $F = 5.31$ ;  $P < 0.0001$ ), with Sierran mixed conifer and white fir habitats comprising significantly larger proportions of the available habitat than other habitats ( $P < 0.05$ ; Table 3). All of the potential habitats in the CWHR classification system were found in at least one or more foraging areas of adult female pallid bats except for montane riparian habitat. In contrast, foraging areas of the two adult male pallid bats that we radiotracked did not include either wet meadow or urban habitat, respectively.

## Discussion

Pallid bats occupy a diversity of ecosystems, roosting and foraging in a range of habitat conditions throughout their distribution (Hermanson and O'Shea 1983). Regardless, flexibility in choice of roosting habitat has not been reflected in the roosting sites described for the species in most published studies (Orr 1954; Vaughan and O'Shea 1976; Hermanson and O'Shea 1983; Lewis 1993, 1994). Prior to our study, information on the extent to which pallid bats used live trees and snags for roosting had been limited to anecdotal observations (Davis 1944, Hall 1946, Orr 1954, Brown et al. 1997, Rabe et al. 1998). Rock crevices as potential roosting habitat were abundant throughout our study area; however, we found only a single tagged pallid bat roosting in a rock crevice, even though these habitat conditions are generally associated with roosting behavior of the species throughout much of its distribution (Vaughan and O'Shea 1976; Hermanson and O'Shea 1983; Lewis 1993, 1994). Instead, the majority of the roosts we

TABLE 2. Foraging area size ( $\text{km}^2$ ) and distances traveled (m) by pallid bats on the Plumas National Forest, California, in summer 2007. Where appropriate, data are mean  $\pm$  SE. Sample sizes are number of bats and number of roosts, respectively.

Sex and/or reproductive class	Foraging area size	Longest distance moved	Distance to water from roost	Distance to foraging area from roost
Lactating females (n = 6, 6)	$1.56 \pm 0.88$	$3453 \pm 835$	$358 \pm 114$	$2450 \pm 845$
Pregnant female (n = 1, 2)	3.17	4719	$300 \pm 197$	$893 \pm 893$
Post-lactating females (n = 2, 1)	$5.97 \pm 2.69$	$2204 \pm 881$	482	210
Non-reproductive female (n = 1, 2)	2.43	4433	$671 \pm 63$	$180 \pm 180$
Non-reproductive males (n = 2, 1)	$4.12 \pm 3.0$	$2271 \pm 953$	443*	0

\*Based on an approximated location for unknown roost.

TABLE 3. Percentages of foraging areas (mean  $\pm$  SE) of pallid bats in habitats of the California Wildlife Habitat Relationships system (CWHR) on the Plumas National Forest, California, in summer 2007. Data are based on six adult females and two adult males.

Gender	Habitats*									
	SMC	WFR	WTM	BAR	MCP	MHW	PPN	PGS	MRI	URB
Females	38.2(11.0)	30.8(11.3)	1.8 (1.2)	0.7(0.4)	9.9(1.9)	8.4(3.0)	2.6(0.9)	6.0(6.0)	-	1.6(1.6)
Males	47.5(9.0)	20.2(1.8)	—	0.2 (0.2)	2.5(1.5)	17.5(5.5)	0.2(0.2)	11.5 (11.5)	0.5(0.0)	—

\*Habitats are Sierran mixed conifer (SMC), white fir (WFR), wet meadow (WTM), barrens (BAR), montane chaparral (MCP), montane hardwood (MHW), ponderosa pine (PPN), perennial grassland (PGS), montane riparian (MRI), and urban (URB).

discovered were in live trees or snags, suggesting that pallid bats in northern California adapted to changes in the availability of roosting habitats or changes in roost site requirements by switching to alternate structures when in coniferous forests; a pattern consistent with observations for three radiotagged pallid bats in ponderosa pine forests in northern Arizona (Rabe et al. 1998).

Pallid bats in our study selected lived trees and snags for roosting that were large in diameter, tall in height, and located in stands of mature trees, a pattern common for other species of tree-roosting bats in coniferous forests of the Pacific Northwest (Ormsbee and McComb 1998, Waldien et al. 2000, Weller and Zabel 2001, Baker and Lacki 2006). Pallid bats also located their roosts in trees at heights well below the canopy layer, and chose roost trees in stand micro-site conditions with open canopies and minimal mid-story cover, presumably to allow for increased solar exposure resulting in warmer temperatures inside cavities and crevices used for roosting (Bakken and Kunz 1988). Selection of trees and snags surrounded by sparser vegetation has been reported in a number of studies on tree-roosting bats (Betts 1996, Vohnhof 1996, Vohnhof and Barclay 1996, Ormsbee and McComb 1998), so this pattern was not unexpected for pallid bats. Further, the importance of roost microclimate to the ecology and reproductive success of pallid bats has been demonstrated for populations roosting in rock crevices in more arid climates (Vaughan and O’Shea 1976, Lewis 1993).

Studies examining foraging behavior in pallid bats have emphasized populations of bats occupying open habitats, such as grasslands and other semi-arid environments (O’Shea and Vaughan 1977, Bell 1982, Johnston and Fenton 2001). Thus, prior to our study, the extent to which these bats used more cluttered habitats, such as closed-canopy forest, when traveling or foraging

had been relatively unstudied (Van Gelder 1959, Jones 1965, Baker 1967, Morrell et al. 1999). Pallid bats have been described as gleaners that forage in relatively open habitats close to the ground (Bell 1982, Johnston and Fenton 2001). Regardless, examination of habitats in our study area showed that wet meadows, barrens, montane chaparral, and perennial grasslands, habitats with relatively uncluttered foraging conditions, represented only 18.4% and 14.2% of the available space within estimated foraging areas of female and male pallid bats that we radiotracked, respectively. We suggest these data indicate that pallid bats inhabiting coniferous forests in northern California may spend considerable time traveling and foraging in habitats more cluttered than typical for other portions of the distribution of this species.

Pallid bats in northern California frequently traveled considerable distances to reach foraging areas. We documented four bats traveling > 4 km on a single night to reach foraging areas, with a maximum distance of 6.7 km estimated for a lactating female. Travel distances recorded for pallid bats in other geographic locations are normally within 3 km (O’Shea and Vaughan 1977, Bell 1982, Johnston and Fenton 2001), however, distances traveled from roosting sites as far as 11 km (Brown et al. 1997) and 30 km (Davis 1966) have been reported, suggesting that even though this species uses a gleaning foraging strategy it is capable of long-range movements.

Our study presents more detailed information of the habitat use of pallid bats in forested ecosystems than has been previously available. Regardless, we suggest that conclusions drawn in this paper be tempered with caution for the following reasons. The study area we surveyed was extremely large (ca. 315,000 ha), making an exhaustive survey of the area impossible given the time frame we were allotted. Further, the terrain in some valleys

was extremely steep, exceeding 80% slopes, rendering four roosting sites, particularly those of male bats, inaccessible. So it is likely that some behavioral patterns of pallid bats in this region were missed. Second, our telemetry effort was distributed among several sex and reproductive class combinations, resulting in limited inference on variation in foraging behavior and habitat use among these groups. Third, we failed to capture a single juvenile pallid bat in this study despite a sampling effort of 33 netting sites, so no attempt could be made to evaluate habitat use, behavior or timing of volancy in young bats. Lastly, because radiotagged bats were studied across such a large area, no attempt to evaluate 'habitat selection' using distance-based methods was possible (e.g., Menzel et al. 2005, Sparks et al. 2005, Johnson et al. 2007). Thus, we only assessed the availability of habitats within foraging areas and it remains unclear whether more open habitats, which represented < 20% of the available space within foraging areas of both female and male bats, were used more or less than available during foraging bouts. Clearly, more data on habitat use of pallid

bats in forested ecosystems are needed to ensure that long-term management plans adequately address the needs of this species.

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