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Cover Photograph: A Little Brown Myotis (*Myotis lucifugus*) affixed with a radio transmitter and forearm band at the Tahoma Woods study area in Mount Rainier National Park. © S. Mitchell, National Park Service, October 2021.

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Differences in Fall Roost Use by Little Brown Myotis (*Myotis lucifugus*) and California Myotis (*Myotis californicus*) in the Washington Cascade Region

Michael E. Hansen[1,*], Dana M. Sanchez[1], Tara Chestnut[2]

Abstract - Little is known about the fall and winter ecology of *Myotis* in western North America. We radio-tracked Little Brown Myotis (*Myotis lucifugus*) and California Myotis (*Myotis californicus*) from August to December in Mount Rainier National Park, WA, USA. We identified 24 roosts used by Little Brown Myotis, 11 by California Myotis, and 3 used by both species. We observed movements up to 13.2 km for Little Brown Myotis and 1.4 km for California Myotis. Little Brown Myotis left study areas between October and December, likely moving to winter roosts. Bats left an all-male roost weeks later than bats from a maternity colony. California Myotis remained through mid-December, suggesting they over-wintered locally. California Myotis alternated between short (2–6 days) and long (12–20 days) durations of roost use and continued to use buildings and snags as roosts through the end of telemetry in mid-December.

Introduction

Little is known about the fall and winter ecology of *Myotis* populations in the United States in regions from the Rocky Mountains westward (hereafter referred to as western *Myotis*) (Jung et al. 2014; Weller et al. 2009, 2018). Most of our knowledge of winter roost structures and seasonal patterns of habitat use are based on observations of *Myotis* in eastern North America (Weller et al. 2018). Many eastern *Myotis* hibernate in caves and mines in massive aggregations of hundreds or thousands of individuals, and often migrate great distances to reach hibernation sites (Davis and Hitchcock 1965, Weller et al. 2018). In contrast, western *Myotis* appear to hibernate closer to their summer grounds, either alone or in small groups, and in smaller, more discrete structures, such as crevices in rock and soil (Blejwas et al. 2021, 2023; Johnson et al. 2017; Neubaum 2018; Weller et al. 2018). These dispersed hibernacula are very difficult to locate, so our knowledge of western *Myotis* outside the summer season is based on very few studies and almost exclusively focused on *Myotis lucifugus* (Le Conte) (Little Brown Myotis) (Blejwas et al. 2021, Johnson et al. 2017, Neubaum 2018). Locating fall and winter roosting habitat and documenting movement are essential to building a foundational understanding of life history and management needs for populations of western *Myotis*.

Fall and winter bat ecology in the West has become a conservation priority due to the spread of white-nose syndrome (WNS), a cutaneous fungal infection that has killed millions of bats across North America since its discovery in 2006 (Cheng et al. 2021). WNS is caused by a cold-adapted fungus, *Pseudogymnoascus destructans* (Blehert and Gargas) Minnis and D.L. Lindner (Pd), that can infect the tissues of torpid bats when their body temperature is low (Verant et al. 2012, 2014). Detections of WNS were restricted to eastern North America until 2016, when it was found in a Little Brown Myotis in King County, Washington, 48 km

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north of Mount Rainier National Park (hereafter Mt. Rainier) (Lorch et al. 2016). The fungus was first discovered within Mt. Rainier in 2017 and has since been detected at other locations across the park, as well as several Washington counties and other western states (WDFW 2020).

Mt. Rainier has accessible study populations of Little Brown Myotis and *Myotis californicus* (Audubon and Bachman) (California Myotis) that have been the focus of ongoing disease surveillance and mark-recapture efforts since 2017. *Myotis* is the genus most impacted by WNS (USFWS 2022). Eastern populations of Little Brown Myotis have suffered major declines due to WNS, and documenting the species' overwintering ecology is vital to disease management, as WNS spreads in the West (Cheng et al. 2021, Jung et al. 2014). California Myotis, on the other hand, are among the only 2 *Myotis* in the Pacific Northwest with no detections of clinical signs of WNS, along with *Myotis ciliolabrum* (Merriam) (Western Small-footed Myotis) (USFWS 2022). Little Brown Myotis and California Myotis appear to have different overwintering tactics, which may be relevant to species-specific vulnerability to Pd. Fall and winter movements and roost use of Little Brown Myotis in the West have been tracked in a small number of studies, which all show a distinct transition from transient fall habitat to hibernacula, followed by cessation of activity through the winter (Blejwas et al. 2021, Johnson et al. 2017, Neubaum 2018). In contrast, active California Myotis are frequently observed over winter, more so than any other *Myotis* in the Pacific Northwest, yet very little is known about their winter natural history (Burles et al. 2014, Falxa 2007, Geluso 2007, Krutzsch 1954, Maser 1981, Nagorsen and Brigham 1993, Young and Scudday 1975). *Myotis* populations in western Washington represent the leading edge of WNS spread in the western United States. Expanding our knowledge of roost use and species-specific behaviors within this disease frontier is vital for understanding basic life history and potential differences in WNS susceptibility, and informing disease management actions as the outbreak progresses.

Our first objective was to document the phenology of the autumn transitional period from summer roosts to fall habitat and then to overwintering habitat for California Myotis and Little Brown Myotis. Next, we sought to describe the types of roost structures used in the fall and winter, and the distance and frequency of movement between successive day roosts. Finally, we compared differences in phenology, habitat use, and movement between species and study areas. Based on observations of Little Brown Myotis in other western states, we predicted that Little Brown Myotis would eventually transition from transient fall roosts in buildings and snags to hibernacula in rock or soil, and then cease activity. In contrast, because of the frequent observations of winter activity in California Myotis, we expected that California Myotis in our study would not transition away from their autumn grounds as the season progressed and would instead transition locally to roost structures that provide more stable temperatures to facilitate longer bouts of torpor while remaining intermittently active.

Field-site Description

We studied fall movements and roosts of Little Brown Myotis and California Myotis in and around Mt. Rainier, which lies approximately 100 km southeast of Seattle, in Washington State, on the western slope of the Cascade Range. We selected capture sites based on the presence of bat roosts that had been previously discovered and monitored by National Park Service (NPS) staff. We worked in 2 study areas: the Ohanapecosh River drainage (hereafter Ohana) on the southeast side of Mt. Rainier, and the Tahoma Woods administrative area (hereafter T-Woods), which lies outside and west of the main body of the park (Fig. 1). The

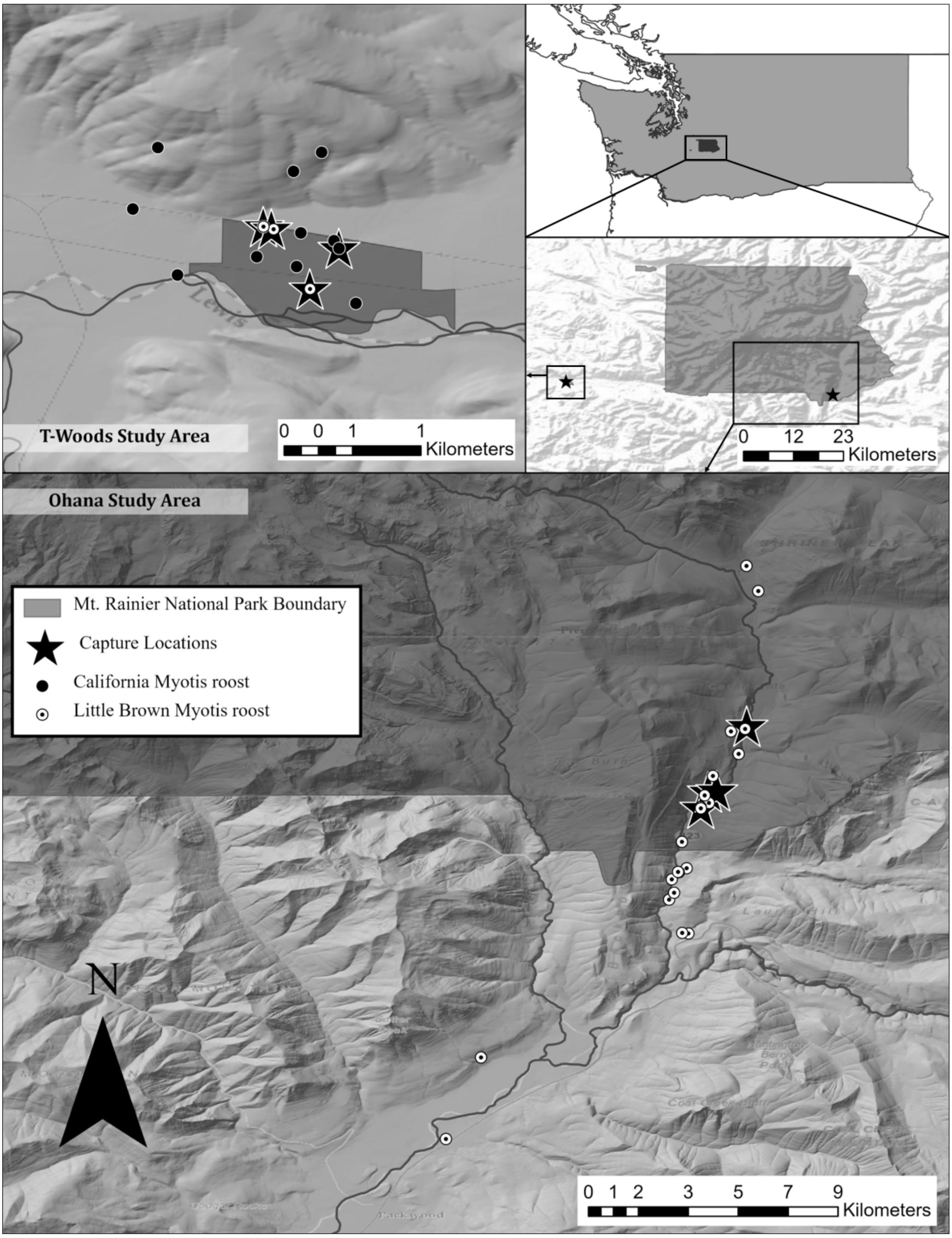

Figure 1. Maps of the T-Woods and Ohana study areas, including all capture and roost locations used by telemetered California Myotis (*Myotis californicus*) and Little Brown Myotis (*Myotis lucifugus*) from 21 September through 15 December 2021, and 22 August through 14 December 2022. Maps in the upper right indicate study area locations relative to Mount Rainier National Park boundaries and within western Washington State.

climate at both study areas is typical of the Pacific Northwest, with long, cool wet seasons and relatively dry summers.

The Ohana study area is in a steep river valley that is extensively forested with old growth *Tsuga heterophylla* (Raf.) Sarg. (Western Hemlock) and *Pseudotsuga menziesii* (Mirb.) Franco. (Douglas-fir) (Hemstrom and Franklin 1982). Telemetry at this study area took place between 340 m and 740 m in elevation, mostly inside Mt. Rainier National Park and Gifford Pinchot National Forest. This area is almost entirely undeveloped except for a small NPS housing area and a few campgrounds. The Ohana housing area has 2 bat boxes which house a maternity colony of Little Brown Myotis every summer. The Ohana colony is part of long-term WNS monitoring efforts at the park, and the first detection of Pd within Mt Rainier was made at this site in the spring of 2017 (Tara Chestnut, National Park Service, Ashford, WA, pers. obs.).

The other study area, T-Woods, is a 108-ha NPS property at 425 m elevation and is located roughly 15 km from the western boundary of Mt. Rainier. The property has a mix of administrative and employee housing buildings, surrounded by state forest, comprised mostly of Douglas-fir and Western Hemlock of varying age, as well as farmland and rural residential properties. A bat box and shed in this study area have been part of the ongoing WNS monitoring effort, where bats have been captured and banded intermittently since 2019. Populations of Little Brown Myotis and California Myotis have both been observed roosting in the bat box, in the exterior eve of the shed that the box is attached to, and in a nearby series of 4 connected heavy-duty tarp storage tents, as well as the eaves and attic vents of some adjacent buildings during the spring and fall. Little Brown Myotis and California Myotis appear to be largely absent from these roosts in the summer. A small number of *Myotis evotis* (Allen) (Long-eared Myotis) use the interior of the shed that the bat box is attached to during summer, as well as the storage tents, but have not been observed using the bat box.

Methods

The Little Brown Myotis maternity colony in the bat box at Ohana was intended to be our primary focus when we began field work in fall 2021. We began capture attempts in late September but were only able to tag 2 bats from Ohana during the first year. Due to this difficulty in tagging at Ohana, we focused the remainder of our tagging effort in 2021 in T-Woods, because we knew bats were still present there. Based on our experience in 2021, we began tagging earlier at the Ohana bat box in 2022. Bats began to vacate the box in late August, so we switched from capturing at the bat box to mist netting over nearby sections of the Ohanapecosh River in September. When mist netting at Ohana was no longer successful, we again moved our efforts to T-Woods. A summary of the capture timeline can be found in Table 1.

We captured bats roosting in bat boxes and buildings using homemade funnel traps and by hand, and we captured bats on the landscape with mist nets (polyester, 38-mm mesh for bats; Avinet, Dryden, NY). We recorded species, sex, age class (when possible), and body mass of each bat. We determined species in the field with a combination of morphology and analysis of release calls. We viewed release calls live using Echometer Touch Pro detectors (Wildlife Acoustics, Inc., Concord, MA) and recorded release calls using Pettersson D500X acoustic recorders (Pettersson Elektronik, Uppsala, Sweden). Recorded calls were then analyzed in Sonobat (v.4.4.1, SonoBat, Arcata, CA). We determined age by the degree of epiphyseal fusion in the 3rd and 4th finger joints for bats captured in summer. This technique is only useful for identifying juveniles for about 29 days after birth (Brunet-Rossinni and Wilkinson 2009, Kunz and Anthony 1982); therefore, bats captured from September to November were listed as unknown age, except for previously banded bats whose age could be determined from NPS banding records.

We tracked bats using radio tags that transmit on a single frequency with coded pulses for individual identification (VHF Nanotags, models NTQB2-1 [0.26 g] and NTQB2-2 [0.32 g]; Lotek Engineering Inc., Newmarket, ON, Canada). Tag weights did not exceed the recommended 5% of the individual's body weight (Aldridge and Brigham 1988), which set the minimum weight for tagging at 5.2 g for NTQB2-1 tags and 6.4 g for NTQB2-2 tags. Additionally, bats with any obvious signs of injury or ill health were excluded from tagging. The NTQB2-1 tags were set to burst intervals of 3, 7, or 13 sec; tags with these burst intervals had estimated battery lives of 19, 39, and 63 days, respectively. To attach tags to bats, we located the space between the scapulae and clipped the fur short with scissors, then applied a thin coat of latex ostomy adhesive (Liquid Bonding Cement, Torbot Group, Inc., Cranston, RI) to both the clipped area and the tag and pressed the glued portions together for about 30 seconds. We then rolled the bat up in a small piece of nylon for 15 min, to hold the tag against the bat while the adhesive dried. We also applied aluminum lipped forearm bands (2.9 mm; Porzana, BTO Services Ltd., Norfolk, United Kingdom) to each radio-tagged bat, so recaptured individuals could be identified after tags had detached. We tracked bats on foot, from vehicles, and from fixed-wing aircraft. All animal handling for this project followed standard operating procedures and methods approved for field research of bats by the National Park Service Institutional Animal Care and Use Committee (NPS IACUC) (https://www.nps.gov/orgs/1103/upload/NPS-IACUC-Bat-SOP-Final-1.pdf).

We conducted ground telemetry at least once a week, but generally 3–4 times per week in Ohana and 4–6 days per week in T-Woods, depending on personnel availability. We attempted to identify the exact roost structure whenever possible, but when we were unable to access an area during ground tracking due to time constraints or private land access issues, we took bearings from multiple points to triangulate and estimate location. Ground surveys were supplemented with 3 fixed-wing flights in 2021, and another 3 flights in 2022.

Aerial telemetry flights began about an hour before sunset and continued for at least an hour after sunset to locate emerging bats whose signal might otherwise be blocked while inside a roost. Prior to the first telemetry flight, we placed activated tags in trees, on the ground, and up to 0.5 m under piles of rocks to assess tag detectability from the air.

Table 1. Capture date range, number (n) and sex (F: female, M: male) of California Myotis (*Myotis californicus*) and Little Brown Myotis (*Myotis lucifugus*) captured and radio-tagged at 2 study areas at Mount Rainier National Park,WA, during 2021–2022, to determine fall and overwintering movements and roost use.

Study Area	Species	Date range of capture by year	*n* (sex F, M)
Ohana	Little Brown Myotis	21 September 2021–04 October 2021	2 (1, 1)
		22 August 2022–15 October 2022	11 (7, 4)
T-Woods	Little Brown Myotis	05 October 2021–10 November 2021	9 (0, 9)
		01 November 2022	1 (0, 1)
	California Myotis	06 October 2021 and 17 October 2021	2 (2, 0)
		08 November 2021–17 November 2022	3 (1, 2)

We obtained temperature data (Fig. 2) from Remote Automated Weather Stations at Ohana (National Environmental Satellite, Data, and Information Service, ID FA65211A; 50 m from bat box) and T-Woods (FA6184D8; 1 km from bat box but at the same elevation).

We used ArcGIS Pro 2.2.9 (ESRI, Redlands, CA) and referenced satellite imagery to determine presence of human structures in the vicinity of triangulated telemetry locations for bats, and to measure distances between roost locations and capture sites. We calculated roost occupancy duration (days) using the span between the first and last observation of a bat in a roost, provided there were no intervening detections elsewhere or signal loss from that roost. For example, if a bat was found in the same roost on a given day and again 2 days later, but there was no telemetry done between those days, we assumed that the bat continued to use that roost during the intervening day(s) and included those days in the count. We calculated medians and interquartile ranges (IQR) for all continuous variables, including the total days tracked, days detected, duration of roost occupancy, the number of different roosts used, distance from capture location, distance between sequential roosts, cumulative distance traveled, and distance traveled per day. We performed summary calculations in RStudio 2022.7.2.576 (Posit Software, Boston, MA).

Results

We captured a total of 193 bats and radio-tagged 28 individuals: 23 Little Brown Myotis (8 females, 15 males) and 5 California Myotis (3 females, 2 males) (Table 1). All bats captured at Ohana were Little Brown Myotis, while T-Woods captures included both Little

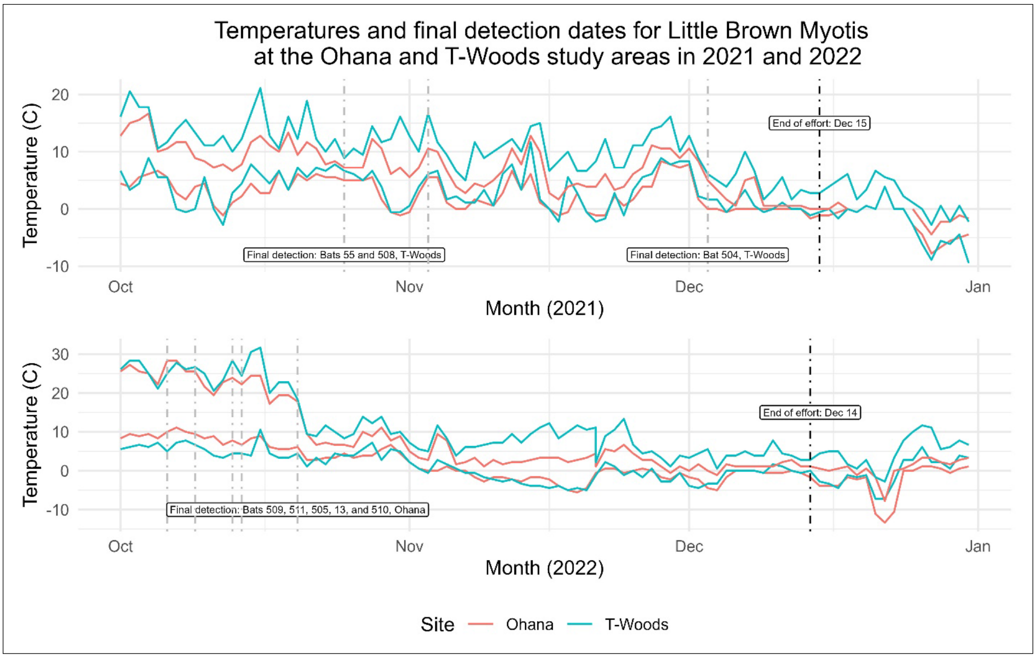

Figure 2. Minimum and maximum daily temperatures for the Ohana and T-Woods study areas at Mount Rainier National Park, WA, and final detection dates (gray dashed lines) for Little Brown Myotis that were tracked for >24 h after the capture night and had functional tags on the final detection date. For all Little Brown Myotis (*Myotis lucifugus*), final detection date represents an estimated date of emigration from fall habitat. All California Myotis (*Myotis californicus*) with functional tags were still roosting in the T-Woods study area at the end of the telemetry effort (black dashed line).

Brown Myotis and California Myotis. Little Brown Myotis at Ohana were captured by funnel trap from a bat box (n = 5), as well as by mist netting on the landscape (n = 8). At T-Woods, we captured bats by hand extraction or funnel trap from roosts. All Little Brown Myotis from T-Woods were captured at the bat box (n = 3), the exterior eve of the shed the box is attached to (n = 1), or from tarp storage tents located 30 m away from the box and shed (n = 6). Two California Myotis captured at T-Woods were from the bat box, and the remaining 3 were captured from roost locations in the eves of 2 other buildings, which we located through tracking other tagged bats.

Little Brown Myotis captured from the maternity bat box at Ohana in August 2022 exhibited an even ratio of juveniles and adults (50.6% juveniles, n = 162). Of the Little Brown Myotis captured in Ohana in September and October whose age could be determined, 6 were juveniles and 1 was an adult. At Ohana, the sex ratio was female skewed (80%, n = 162) during August, but more males (60%, n = 15) were captured in September and October. All Little Brown Myotis captured in T-Woods were male, and California Myotis were evenly split between sexes (Table 1).

We tracked 5 California Myotis and 15 Little Brown Myotis for 1–58 days following tagging (median [IQR] = 15 [6–31]) but never located the remaining 8 Little Brown Myotis. We tracked bats over a total of 113 days, with 47 telemetry days in 2021 and 66 days in 2022. We tracked 5 California Myotis and 13 Little Brown Myotis bats for >1 day and tracked 4 California Myotis and 9 Little Brown Myotis bats to >1 roost. We also conducted aerial surveys on 6 occasions. Five of the 6 flights were >610 m above ground level (AGL) and included a search radius of approximately 10 km around the T-Woods study area and approximately 30 km around the Ohana study area. One daytime flight in 2022 went as low as 152 m AGL over an approximately 10-km radius of the Ohana capture location to search for attenuated signals from bats underground. Test tags that were located aboveground or buried beneath <0.5 m of rock cover were detected from the air during the >610m AGL flights, while deeper tags were not detected. No test tags were deployed during the lower AGL flight.

Across both study areas, 9 (39%) of the 23 tagged Little Brown Myotis were never relocated after the capture night or the following night. Only 1 of these individuals (Bat 226) was subsequently relocated during telemetry efforts, including aerial searches that covered a 10–30 km radius around the capture site. Bat 226, a Little Brown Myotis from Ohana, was relocated by air approximately 10 km from the capture site, and was never relocated during ground searches. This was the only detection of a tagged bat from aerial surveys that was not already located during ground surveys.

We identified a total of 38 different roost locations (16 at T-Woods, 22 at Ohana). We were able to identify the specific structure used for 23 of these locations. We could not identify structures for the remaining 15 locations due to land access issues or an inability to pinpoint the specific structure through telemetry. Of these 15 locations with unidentified structures, we were able to categorize all but 4 as either natural or building roost structures based on the presence or absence of human structures in the area (Table 2). We defined building roosts as any human-made structure, including the bat boxes and storage tents. Both species and sexes used natural and building roosts across study areas, but we detected a greater proportion of males in human structures compared to females of the same species and study area. All the identified natural roosts across species and study areas were in snags, and bats generally roosted high up in snags (upper 1/3), based on emergence observations or signal strength.

Little Brown Myotis

Number and type of roost. We categorized 25 roosts used by Little Brown Myotis across both study areas, 7 in human structures and 18 in natural structures. We identified the specific roost structure for 15 of these, including 7 buildings and 8 snags (Table 2). California Myotis also roosted in 3 of these buildings, though we did not observe the 2 species grouped together within the roost. All snags were Douglas-fir or Western Hemlock. Little Brown Myotis used both bare (n = 2) and barked (n = 6) snags. Use of natural roosts by Little Brown Myotis was almost completely restricted to the Ohana study area; at T-Woods only 1 Little Brown Myotis used a natural roost (Table 2). Little Brown Myotis occupied 1–5 roosts, although most used 1–3 (Table 3). We tracked 9 Little Brown Myotis to more than 1 roost, and of those, 6 returned to a previously occupied roost at least once. Three returns were to buildings, 2 were to snags, and 1 was to an unknown structure on private property.

Distances between roosts. Roosts were located 0–12.73 km from the bats' original capture locations at Ohana and 0–0.58 km at T-Woods. Minimum values of 0 in this case refer to instances when bats returned to the roost where they were initially captured on subsequent days. Movement between sequential roosts ranged from 0.26 to 13.16 km in Ohana and from 0.08 to 0.62 km in T-Woods (Table 4). Cumulative total distance of observed movements between day roosts for individual Little Brown Myotis ranged from 0.2 to 41.4 km.

Duration of roost occupancy. Little Brown Myotis at T-Woods (n = 4) remained at individual roosts for 1–23 consecutive days. Little Brown Myotis at Ohana (n = 11) occupied roosts for 1–10 consecutive days, although occupancy was not always confirmed daily. The longest observed roost occupancy was by a Little Brown Myotis at T-Woods, which was detected in the same bat box for 23 days (10 November–2 December 2021), with 18 days of visual confirmation that the bat was still in the same location.

Table 2. The number and types of roost structures used, and the percent of total detections and cumulative number of days bats were detected in each roost type for California Myotis (*Myotis californicus*) and Little Brown Myotis (*Myotis lucifugus*) that were tracked for >24 hours in Mount Rainier National Park, WA, September–December 2021, and August–December 2022. Populations are divided by study area, species, and sex (F: female, M: male). Roost categories are the detected roost locations divided into human-made, natural, or unidentified roost structures. For roost structures that were not directly observed, roost type is based on the presence or absence of human structures near the detected locations. Note that 1 building in T-Woods was used as roosts by both species. Only 1 individual Little Brown Myotis at T-Woods used a natural roost (same individual used 2 different natural roosts) and was only detected at each of those locations for a single day. The cumulative number of days is the sum of days each individual bat was detected in each structure, with the percent of total detections that represents in parentheses.

Study Area	Species	Sex	*n*	Number of human structures	Number of natural structures	Number of unknown structures	Days detected in human structures	Days detected in natural structures	Days detected in unknown structures
Ohana	Little Brown Myotis	F	6	1	11	1	1 (03%)	30 (79%)	7 (18%)
		M	3	2	2	0	3 (38%)	5 (63%)	0 (0%)
T-Woods	Little Brown Myotis	M	4	3	2 (1 individual)	0	61 (97%)	2 (03%)	0 (0%)
	California Myotis	F	3	5	4	0	33 (46%)	39 (54%)	0 (0%)
		M	2	2	2	2	26 (65%)	8 (20%)	6 (15%)

Timing of departure from study area. Of the 23 tagged Little Brown Myotis, 6 had batteries die or tags detach during telemetry. Seventeen Little Brown Myotis with working tags eventually left the study area from which they were captured. Eight of these Little Brown Myotis were tracked for >1 day, and the timing of their departures differed between the study areas (Table 5, Fig. 2). At T-Woods, Little Brown Myotis (n = 3, all males) left the study area between late October and early December. At Ohana, each Little Brown Myotis (n = 5, 2 females and 3 males) left on a different night within a 2-week period in mid-October. Two of the bats departing Ohana were recaptures of banded juveniles from the nearby maternity colony, and their final detection dates were 52 and 53 days after the maternity colony emptied (<10 bats observed in box) on 22 August. The other 3 bats were unmarked individuals from mist-netting, and their association with the maternity colony was not known.

California Myotis

Number and type of roost. We located 11 roosts used by California Myotis—6 in natural structures and 5 in buildings. Both sexes used both roost types, with females using slightly more natural roosts (51% of female detections were in natural roosts) and males favoring buildings (65% of male detections were in buildings) (Table 2). We identified specific structures for 10 of the California Myotis roost locations; 5 in snags and 5 in buildings. Bats used Douglas-fir or Western Hemlock snags, except for 1 female California Myotis that roosted in 2 different *Acer macrophyllum* Pursh. (Bigleaf Maple) snags in addition to a Western Hemlock. California Myotis only roosted in snags with some remaining bark. California Myotis used 2–7 roosts; most used 2–3 (Table 3). We tracked all 5 California Myotis to more than 1 roost, and 3 California Myotis used the same roost more than once; 2 bats returned to previously used roosts in buildings and 1 bat returned to the same snag (Fig. 3).

Distances between roosts. Roosts were located 0–1.43 km from the capture location. Movement between sequential roosts ranged from 0.46 to 1.43 km. Cumulative total distance of observed movements between day-roosts for individual California Myotis ranged from 0.3 to 4.5 km.

Table 3. The number of roosts used by an individual bat and the number of consecutive occupancy-days each bat spent in a single roost for California Myotis (*Myotis californicus*) and Little Brown Myotis (*Myotis lucifugus*) tracked for >24 hours, in Mount Rainier National Park, WA. Data are presented by study area, sex (F: female, M: male), and species during fall 2021 and 2022. Reported are the median values of the total number of roosts used by each individual bat and the average number of consecutive tracking days each bat was detected at a single roost, with the interquartile range (IQR) in parentheses.

Study Area	Species	Sex	*n*	Median number of roosts	Average consecutive roost occupancy-days
Ohana	Little Brown Myotis	F	6	3 (2 - 4)	1.6 (1.1 - 2.1)
		M	3	1 (1 - 1.5)	3.0 (2.3 - 3.5)
T-Woods	Little Brown Myotis	M	4	3 (2.5 - 3.3)	4.4 (3.5 - 6.3)
	California Myotis	F	3	2 (2 - 4.5)	11.7 (9.3 - 15.8)
		M	2	3 (3 - 3)	5.9 (5.4 - 6.3)

Late-season persistence in study area. All tagged California Myotis (n = 5) remained in the study area until tag failure through battery death (n = 1, female, battery died on 7 November), tag detachment (n = 1, male, tag found on 11 December), or the end of effort in mid-December (n = 3, 2 females and 1 male, Table 5). California Myotis remained at individual roosts for 1–20 consecutive days. Roost occupancy by California Myotis that were tracked into December (n = 4) appeared to be in 2 categories of duration, with short-term roost use of 2–6 days, and long-term occupancy of 12–20 days. There were no instances of bats using roosts for the intermediate length of 7–11 days (Fig. 3), although we did not confirm locations for bats on most weekend days during this period. Both buildings and snags were used by California Myotis for both short- and long-term roosts until the end of telemetry effort in mid-December (Fig. 3).

Discussion

We documented roost structures, durations of use, and movement distances, which have rarely been described in fall and winter for western *Myotis*. We observed differences in movement and phenology between California Myotis and Little Brown Myotis at 2 study areas within and near Mt. Rainier. We found that all tagged California Myotis remained detectable in the study area throughout the telemetry effort (October–mid-December), while Little Brown Myotis eventually disappeared from both study areas. We found that individuals from the population of Little Brown Myotis from the T-Woods were detected until later in the fall than those from the Ohana population. We observed a bimodal distribution of roost-use durations in California Myotis, with either short-term or long-term use, and that California Myotis continued to use snag and building roosts into December.

There was a distinct difference in our observations of the 2 species. All Little Brown Myotis signals were lost during periods when the radio tags would have still been active, meaning they either left the area or transitioned to a roost that blocked the transmitter signal, but California Myotis provided no evidence of movement away from the capture area.

Table 4. Distances in km between consecutive roosts of California Myotis (*Myotis californicus*) and Little Brown Myotis (*Myotis lucifugus*) tracked to >1 roost in fall 2021 and 2022. Reported are the median values of the average distance bats between sequential roosts and sum of all the sequential distances between roost locations for each bat divided by the number of days that bat was located with the interquartile ranges in parentheses, except when n = 1. Data are reported by species, sex (F: female, M: male), and study area within Mount Rainier National Park. The sequential distance does not include the distance from the capture location to the first located roost to avoid any disruption in usual movement distances due to capture stress.

Study Area	Species	Sex	*n*	Average distance between sequential roosts (km)	Distance traveled (km) / detection days
Ohana	Little Brown Myotis	F	5	1.9 (1.2 - 2.7)	1.12 (0.67 - 1.82)
		M	1	4.4	5.42
T-Woods	Little Brown Myotis	M	3	0.1 (0.1 - 0.3)	0.01 (0.01 - 0.10)
	California Myotis	F	3	0.3 (0.3 - 0.4)	0.03 (0.02 - 0.05)
		M	2	0.5 (0.1 - 0.6)	0.13 (0.09 - 0.17)

This aligns with our expectation that Little Brown Myotis would move to subterranean hibernacula followed by minimal winter activity, and that California Myotis would remain in the area and continue to be intermittently active into the winter, as suggested by previous acoustic studies (Falxa 2007, Burles et al. 2014). Sample sizes were small, but the complete separation in this behavior between the 2 species was notable.

We expected to see California Myotis transition to rock crevices or subterranean roosts sometime in late fall, but they continued to use buildings and snags throughout the tracking period. They did, however, exhibit periods of longer occupancy at individual roosts in late fall than have been observed in other studies during summer (Brigham et al. 1997). We observed short-term occupancy duration of 2–6 days, which is comparable to summer observations of California Myotis using roosts for 3–6 days (Brigham et al. 1997), but we also observed longer-term use of roosts for 12–20 days (Fig. 3). We observed California Myotis making at least occasional flights through to the end of telemetry effort in mid-December. Our observations were consistent with previous studies of regular winter activity (Burles et al. 2014, Falxa 2007, Geluso 2007, Krutzsch 1954, Maser 1981, Nagorsen and Brigham 1993, Young and Scudday 1975).

We had expected California Myotis to move to subterranean roosts, like those used by other *Myotis* over winter (Blejwas 2023, Blejwas et al. 2021, Johnson et al. 2017, Neubaum

Table 5. Study area, species of bat, bat identification number, sex (F: female, M: male), age class (J: juvenile, A: adult, U: unknown), and final detection date. Data presented are for all bats telemetered at Mount Rainier National Park, WA, that were tracked for >24 h after the capture night and had functional tags on the final detection date. For all Little Brown Myotis (*Myotis lucifugus*), final detection date represents an estimated date of emigration from fall habitat. All California Myotis (*Myotis californicus*) were still roosting in the T-Woods study area at the end of the telemetry effort, so the final detection date for California Myotis is the final day that telemetry was performed that year (2021 or 2022).

Study Area	Species	Bat ID # (Sex, age class)	Tag date	Final detection
T-Woods	California Myotis	506 (F, U)	17 October 2021	15 December 2021 (end of effort)
		17 (F, U)	8 November 2022	14 December 2022 (end of effort)
		322 (M, U)	17 November 2022	14 December 2022 (end of effort)
	Little Brown Myotis	55 (M, U)	19 October 2021	25 October 2021
		508 (M, U)	19 October 2021	3 November 2021
		504 (M, A)	11 October 2021	3 December 2021
Ohana	Little Brown Myotis	509 (M, U)	3 October 2022	6 October 2022
		511 (M, U)	3 October 2022	9 October 2022
		505 (F, J)	3 October 2022	13 October 2022
		13 (M, J)	11 October 2022	14 October 2022
		510 (F, U)	3 October 2022	20 October 2022

2018, Weller et al. 2018), but we did not observe such a shift. Snags and buildings were used by California Myotis through the telemetry effort ending in mid-December. Cave and mine hibernacula are frequently mentioned as winter habitat for California Myotis (Barbour and Davis 1969, Perkins et al. 1990, Reeder 1949, Schmidly and Bradley 2016), but we did not observe any rock or subterranean roosts. One individual was still visible under the eve of a roof in mid-December, in a crevice that would have provided little buffering from external temperatures. Winter records of California Myotis roost sites are limited, but our observations are consistent with records in Oregon and Washington, which report most winter observations in buildings (70.4%, n = 27), though there was no indication if these were active or torpid bats (Perkins et al. 1990). We found no published records confirming trees or snags as winter roosts for California Myotis, though several studies have suggested this likely to be the case (e.g., Burles et al. 2014, Falxa 2007). Our detection of California Myotis in snags in December appears to be a novel observation for the species. Telemetry through winter

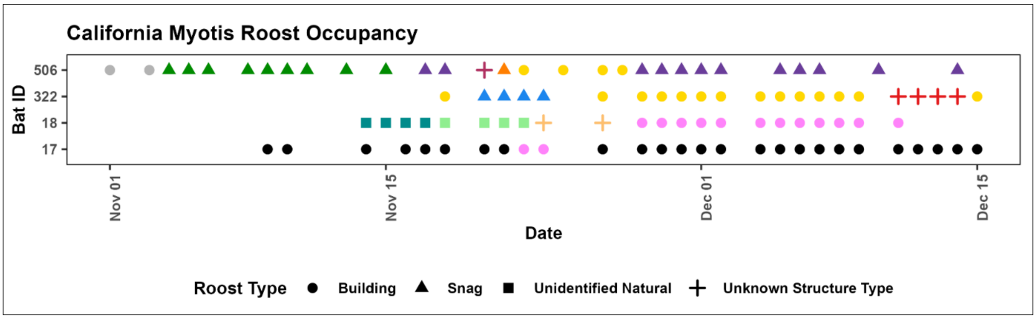

Figure 3. Roost occupancy* by individual telemetered California Myotis (*Myotis californicus*) in late fall 2021 and 2022 in the T-Woods study area in Mount Rainier National Park, WA. Bat ID on the Y-axis represents the tag numbers of 4 individual California Myotis. The X-axis indicates the calendar date of the observation from 1 November through 15 December. Roost data for each bat begin the day after capture and gaps between detections are days when bats were not tracked. Differences in color indicate different individual roost locations. For example, the yellow circle was a building roost that bats 506 and 322 both used. The shape of the symbol indicates if the bat was roosting in snag, unidentified natural (signal detected in an area without buildings, but the roost structure was not identified), building, or unknown structure type. Unknown structures resulted from either signals detected on inaccessible private property or indicate a series of days when that bat was not detected during telemetry; therefore, it must have been using 1 or more unknown roosts for a series of days before returning to its previous roost.

*A note about potential tag detachments: In instances where we detect a tag but cannot confirm that it is still attached to a bat visually or through detected movement, it is possible that we are detecting the signal of a detached tag inside a roost. Bat 322 moved on the final night before telemetry effort ended and Bat 18 was visible in its roost up until the day its tag fell off on 11 December, so we are certain that those tags were still attached to those bats throughout the period reported in this table. The last visual confirmations for bat 506 were on 28 and 29 November, when it was seen exiting its snag roost at dusk. Bat 506 did not exit at dusk during our last emergence survey attempt on 5 December, so we cannot confirm its tag was still attached after 30 November. We also cannot confirm attachment for Bat 18 following its final detected movement, which occurred sometime between 23 and 25 November, when it switched between roosts. It did not emerge from its roost during night surveys on 9 or December. We did leave a data-logging receiver by its roost for 3 nights earlier in the season (10–13 November) prior to its final move, which recorded continuous and stable signal strength from its tag, suggesting that this bat remained in place for multiple nights during a time when we know its tag was still attached.

would be necessary to determine whether this species continues to use buildings and snags year-round or if bats switch to subterranean hibernacula in colder conditions.

Our observations suggest some potential avenues for future studies to explore California Myotis winter natural history and Pd susceptibility. We cannot make any statements about torpor and arousal states from location data alone, but it is interesting to note that the longer periods between roost switching that we observed (12–20 days) overlap with the average winter torpor bouts observed in other hibernating *Myotis* (Brack and Twente 1985, Hope and Jones 2012, Jonasson and Willis 2012), leaving open the possibility that California Myotis could undergo torpor bouts of a similar duration. If periodic roost switching continues throughout winter, the associated time spent at normothermic temperatures could provide the opportunity to mount an immune response and combat fungal infection at regular intervals (Bouma et al. 2010, Meteyer et al. 2011). If the types of roost structures we observed are less conducive to fungal growth than subterranean hibernacula, that could also have implications for Pd infection in California Myotis and the potential for persistence of the fungus in their winter roosts from year to year. Exploring these possibilities would require quantification throughout winter of the duration and frequency of arousals, as well as the environmental conditions within winter roosts.

As expected, Little Brown Myotis eventually moved out of the study areas and presumably transitioned to either new locations or to substrates that blocked detection. In Ohana, Little Brown Myotis telemetry signals disappeared in mid-October (7–20 October 2022), which aligns with timing of hibernation observed in other studies of Little Brown Myotis in the Pacific Northwest. Blejwas et al. (2021), for example, found that Little Brown Myotis in southeast Alaska entered hibernation by late October (1 September–24 October), whereas Burles et al. (2014) noted that Little Brown Myotis disappeared from acoustic monitoring sites after 25 October in British Columbia, Canada. The timing of hibernation in these other studies in similar climates suggest that the disappearance of telemetry signals in our study area represented the transition from fall habitat to overwintering habitat. Bats may have traveled farther than the 30-km search radius of our aerial telemetry to their hibernation sites. However, other studies have documented short distances travelled to hibernacula (<30 km; Blejwas et al. 2021, Johnson et al. 2017, Neubaum 2018) and shifts from roosts in buildings and snags to subterranean structures, so it is possible that, on the observed disappearance dates, bats transitioned into ground-level hibernacula, which blocked detection of the radio signal from the air. Test tags buried beneath >0.5 m of large, loose rocks were not detected during flights, so if tagged bats entered an underground roost that was deeper than this or in a denser material, like solid rock or soil, it is likely that we would have lost their signal.

Little Brown Myotis at T-Woods disappeared from the study area later in the fall than Little Brown Myotis at Ohana (Table 5, Fig. 2). There are several factors that could potentially influence this difference in timing. It should be noted that final detection dates for the 2 study areas were based on data from different years and sample sizes were very small. Additionally, all captures and telemetry at the T-Woods location started significantly later than those at Ohana, so sampling bias could have contributed to the differences observed between these study areas. However, Little Brown Myotis were still present at T-Woods as late as 3 December, which was later in the fall than in previous studies of hibernation phenology in the Northwest (Blejwas et al. 2021, Burles et al. 2014).

All Little Brown Myotis trapped in T-Woods for this project, as well as those trapped for regular spring WNS monitoring since 2019 (n = 17) have been males. Therefore, the Little Brown Bats that use this complex of roosts (the shed exterior, bat box, and adjacent tarp tents) in the spring and fall appear to be a male-specific group, or bachelor colony. Male bats appear to remain active longer than females in the autumn, potentially to maximize mating opportunities (Burns and Broders 2015, Cope and Humphrey 1977).

Differences in environmental factors between the 2 study areas could contribute to phenological differences. The mix of state forest and agriculture surrounding T-Woods likely provides different foraging opportunities from the dense old-growth forest of Ohana. Slightly higher temperatures in T-Woods (Fig. 2) in the fall could facilitate insect activity, or at least aid in passive rewarming from daily torpor, allowing for lower energy costs for activity later into the winter months (Bernard et al. 2021, Geiser and Drury 2003, Hope and Jones 2012). Unfortunately, comparing emigration dates in relation to weather conditions between the Ohana and T-Woods populations is limited by the lack of concurrent-year data for the 2 study areas, due to the failure to track any bats from Ohana successfully in 2021 (Fig. 2).

Detections of Little Brown Myotis in T-Woods were limited to just 5 roost locations and most those detections were in the 2 most frequently used roosts: the bat box and the adjacent tarp storage tents. Little Brown Myotis mostly moved back and forth between these 2 roosts, with a couple bats moving to other locations briefly, and then returning. Little Brown Myotis at Ohana, on the other hand, used both a variety of snags and building roosts, as did California Myotis that shared the bat box and tarp tents with the T-Woods Little Brown Myotis (Table 2). While our study cannot explain the higher level of roost fidelity and later timing of emigration by the T-Woods Little Brown Myotis, these would both be interesting aspects to consider in future studies that address differences between populations in the fall, particularly regarding roost use specific to bachelor colonies, which remain understudied (Weller et al. 2009). Documenting the state of sperm storage would be important in future studies to add context for timing of mating.

Our observations of variation in fall habitat use between Little Brown Myotis populations and demographic groups, and the initial documentation of California Myotis over the fall-winter transition period provide a foundation to inform future studies that explore the ecological underpinnings of these behaviors. The findings of this study were limited in scope and sample size, and more effort will be needed to confirm our conclusions. Much remains to be discovered about fall transition behavior of hibernating bats in western North America. Here, we have expanded knowledge of habitat use for 2 species in a season that has received little research attention. Additional research is needed to fill remaining knowledge gaps of bat habitat requirements pre-hibernation, in light of the spread of WNS in the West.

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Literature Cited

Aldridge, H.D.J.N., and R.M. Brigham. 1988. Load carrying and maneuverability in an insectivorous bat: A test of the 5% "rule" of radio-telemetry. Journal of Mammalogy 69:379–382.

Barbour, R.W., and W.H. Davis. 1969. Bats of America. University Press of Kentucky, Lexington, KY. 286 pp.

Bernard, R.F., E.V. Willcox, R.T. Jackson, V.A. Brown, and G.F. McCracken. 2021. Feasting, not fasting: Winter diets of cave hibernating bats in the United States. Frontiers in Zoology 18:48.

Blejwas, K.M. 2023. Movements of Little Brown Myotis from autumn transition roosts to hibernacula near Juneau, Alaska. Northwestern Naturalist 104:266–271.

Blejwas, K.M., G.W. Pendleton, M.L. Kohan, and L.O. Beard. 2021. The Milieu Souterrain Superficiel as hibernation habitat for bats: Implications for white-nose syndrome. Journal of Mammalogy 102:1110–1127.

Bouma, H.R., H.V. Carey, and F.G.M. Kroese. 2010. Hibernation: The immune system at rest? Journal of Leukocyte Biology 88:619–624.

Brack, V., Jr., and J.W. Twente. 1985. The duration of the period of hibernation of three species of vespertilionid bats. I. Field studies. Canadian Journal of Zoology 63:2952–2954.

Brigham, R.M., M.J. Vonhof, R.M.R. Barclay, and J.C. Gwilliam. 1997. Roosting behavior and roost-site preferences of forest-dwelling California Bats (*Myotis californicus*). Journal of Mammalogy 78:1231–1239.

Brunet-Rossinni, A.K., and G. Wilkinson. 2009. Methods for age estimation and the study of senescence in bats. Pp. 315–325, *In* T.H. Kunz and S. Parsons (Eds.). Ecological and Behavioral Methods for the Study of Bats. John Hopkins University Press, Baltimore, MD. 901 pp.

Burles, D.W., M.B Fenton, R.M.R. Barclay, R.M. Brigham, and D. Volkers. 2014. Aspects of the winter ecology of bats on Haida Gwaii, British Columbia. Northwestern Naturalist 95:289–299.

Burns, L.E., and H.G. Broders. 2015. Maximizing mating opportunities: Higher autumn swarming activity in male versus female *Myotis* bats. Journal of Mammalogy 96:1326–1336.

Cheng, T.L., J.D. Reichard, J.T.H Coleman, T.J. Weller, W.E. Thogmartin, B.E. Reichert, A.B. Bennett, H.G. Broders, J. Campbell, K. Etchison, D.J. Feller, R. Geboy, T. Hemberger, C. Herzog, A.C. Hicks, S. Houghton, J. Humber, J.A. Kath, R.A. King, S.C. Loeb, A.Masse, K.M. Morris, H. Niederriter, G. Nordquist, R.W. Perry, R.J. Reynolds, D.B. Sasse, M.R. Scafini, R.C. Stark, C.W. Stihler, S.C. Thomas, G.G. Turner, S. Webb, B.J. Westrich, and W.F. Frick. 2021. The scope and severity of white-nose syndrome on hibernating bats in North America. Conservation Biology 35:1586–1597.

Cope, J.B., and S.R. Humphrey. 1977. Spring and autumn swarming behavior in the Indiana Bat, *Myotis sodalis*. Journal of Mammalogy 58:93–95.

Davis, W.H., and H.B. Hitchcock. 1965. Biology and migration of the bat, *Myotis lucifugu*s, in New England. Journal of Mammalogy 46:296–313.

Falxa, G. 2007. Winter foraging of Silver-Haired and California Myotis bats in western Washington. Northwestern Naturalist 88:98–100.

Geiser, F., and R.L. Drury. 2003. Radiant heat affects thermoregulation and energy expenditure during rewarming from torpor. Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology 173:55–60.

Geluso, K. 2007. Winter activity of bats over water and along flyways in New Mexico. Southwestern Naturalist 52:482–492.

Hemstrom, M.A., and J.F. Franklin. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. Quaternary Research 18:32–51.

Hope, P.R., and G. Jones. 2012. Warming up for dinner: Torpor and arousal in hibernating Natterer's Bats (*Myotis nattereri*) studied by radio telemetry. Journal of Comparative Physiology B. Biochemical, Systems, and Environmental Physiology 182:569–578.

Johnson, J.S., J.J. Treanor, M.J. Lacki, M.D. Baker, G.A. Falxa, L.E. Dodd, A.G. Waag, and E.H. Lee. 2017. Migratory and winter activity of bats in Yellowstone National Park. Journal of Mammalogy 98:211–221.

Jonasson, K.A., and C.K.R. Willis. 2012. Hibernation energetics of free-ranging Little Brown Bats. Journal of Experimental Biology 215:2141–2149.

Jung, T.S., K.M. Blejwas, C.L. Lausen, J.M. Wilson, and L.E. Olson. 2014. Concluding remarks: What do we need to know about bats in northwestern North America? Northwestern Naturalist 95:318–330.

Krutzsch, P.H. 1954. Notes on the habits of the bat, *Myotis californicus*. Journal of Mammalogy 35:539–545.

Kunz, T.H., and E.L.P. Anthony. 1982. Age estimation and post-natal growth in the bat *Myotis lucifugus*. Journal of Mammalogy 63:23–32.

Lorch, J.M., J.M. Palmer, D.L. Lindner, A.E. Ballmann, K.G. George, K. Griffin, S. Knowles, J.R. Huckabee, K.H. Haman, C.D. Anderson, and P.A. Becker. 2016. First detection of bat white-nose syndrome in western North America. mSphere 1:e00148-16.

Maser, C. 1981. Natural History of Oregon Coast Mammals. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR. 496 pp.

Meteyer, C.U., M. Valent, J. Kashmer, E.L. Buckles, J.M. Lorch, D.S. Blehert, A. Lollar, D. Berndt, E. Wheeler, C.L. White, and A.E. Ballmann. 2011. Recovery of Little Brown Bats (*Myotis lucifugus*) from natural infection with Geomyces destructans, white-nose syndrome. Journal of Wildlife Diseases 47:618–626.

Nagorsen, D.W., and R.M. Brigham. 1993. Bats of British Columbia. UBC Press, Vancouver, BC, Canada. 164 pp.

Neubaum, D.J. 2018. Unsuspected retreats: Autumn transitional roosts and presumed winter hibernacula of Little Brown Myotis in Colorado. Journal of Mammalogy 99:1294–1306.

Perkins, J.M., J.M. Barss, and J. Peterson. 1990. Winter records of bats in Oregon and Washington. Northwestern Naturalist 71:59–62.

Reeder, W.G. 1949. Hibernating temperature of the bat, *Myotis californicus pallidus*. Journal of Mammalogy 30:51–53.

Schmidly, D.J., and R.D. Bradley. 2016. The Mammals of Texas. University of Texas Press, Austin, TX. 720 pp.

U.S. Fish and Wildlife Service (USFWS). 2022. Bats affected by WNS. Available online at https://www.whitenosesyndrome.org/static-page/bats-affected-by-wns. Accessed 14 March 2022.

Verant, M.L., J.G. Boyles, W. Waldrep, Jr., G. Wibbelt, and D.S. Blehert. 2012. Temperature-dependent growth of *Geomyces destructans*, the fungus that causes bat white-nose syndrome. PLoS One 7:e46280.

Verant, M.L., C.U. Meteyer, J.R. Speakman, P.M. Cryan, J.M. Lorch, and D.S. Blehert. 2014. White-nose syndrome initiates a cascade of physiologic disturbances in the hibernating bat host. BMC Physiology 14:10.

Washington Department of Fish and Wildlife (WDFW). 2020. Fungus that causes bat-killing disease confirmed in Chelan and Snohomish counties. Available online at https://wdfw.wa.gov/news-room/news-release/fungus-causes-bat-killing-diseaseconfirmed-chelan-and-snohomish-counties. Accessed 14 March 2022.

Weller, T.J., P.M. Cryan, and T.J. O'Shea. 2009. Broadening the focus of bat conservation and research in the USA for the 21st century. Endangered Species Research 8:129–145.

Weller, T.J., T.J. Rodhouse, D.J. Neubaum, P.C. Ormsbee, R.D. Dixon, D.L. Popp, J.A Williams, S.D Osborn, B.W. Rogers, L.O. Beard, and A.M. McIntire. 2018. A review of bat hibernacula across the western United States: Implications for white-nose syndrome surveillance and managemen PLoS One 13:e0205647.

Young, D.B., and J.F. Scudday. 1975. An incidence of winter activity in *Myotis californicus*. Southwestern Naturalist 19:452–452.