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The Milieu Souterrain Superficiel (MSS) as hibernation habitat for bats: implications for white-nose syndrome

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Recent studies have revealed that western populations of little brown bats (*Myotis lucifugus*) in North America exhibit different hibernation behavior than their eastern counterparts. Understanding these differences is essential for assessing the risk white-nose syndrome (WNS) poses to western bat populations. We used acoustic monitoring and radiotelemetry to study the overwintering behavior of little brown bats near Juneau, Alaska during 2011–2014. Our objectives were to identify the structures they use for hibernation, measure the microclimates within those structures, and determine the timing of immergence and emergence and the length of the hibernation season. We radiotracked 10 little brown bats to underground hibernacula dispersed along two ridge systems. All hibernacula were ≤ 24.2 km from where the bats were captured. Eight bats hibernated in the "Milieu Souterrain Superficiel" (MSS), a network of air-filled underground voids between the rock fragments found in scree (talus) deposits. Two bats hibernated in holes in the soil beneath the root system of a tree or stump (rootball). At least two hibernacula in the MSS were reused in subsequent years. Average MSS and rootball temperatures were warmer and more stable than ambient temperature and were well below the optimal growth range of the fungus that causes WNS. Temperatures in the MSS dropped below freezing, but MSS temperatures increased with depth, indicating bats could avoid subfreezing temperatures by moving deeper into the MSS. Relative humidity (RH) approached 100% in the MSS and under rootballs and was more stable than ambient RH, which also was high, but dropped substantially during periods of extreme cold. Acoustic monitoring revealed that bats hibernated by late October and began emerging by the second week of April; estimates of minimum length of the hibernation season ranged from 156 to 190 days. The cold temperatures, dispersed nature of the hibernacula, and close proximity of hibernacula to summering areas may slow the spread and reduce the impacts of WNS on local populations of little brown bats.

Key words: hibernacula, little brown bat, microclimate, Milieu Souterrain Superficiel, Mesovoid Shallow Stratum, *Myotis lucifugus*, radiotelemetry, rock scree, white-nose syndrome

The little brown bat (*Myotis lucifugus*) is one of the most widespread bats in North America, ranging from Alaska and northern Canada south to Mexico (Fenton and Barclay 1980). In the eastern portion of its range, little brown bats are regarded as a cave-obligate hibernator, typically aggregating in large numbers (Barbour and Davis 1969) and constituting up to 90% of the hibernating bat community (Wilder et al. 2011). Caves and mines are a limited resource and little brown bats in the East travel tens to hundreds of kilometers between their summering grounds and winter hibernacula (Davis and Hitchcock 1965; Humphrey and Cope 1976; Norquay et al. 2013). Several lines of evidence suggest that the hibernation behavior of little brown bats changes as one moves westward. Other than Townsend's big-eared bat (*Corynorhinus townsendii*), western bat species, including little brown bats, rarely hibernate in caves or mines, and if they do, the numbers involved are small (Weller et al. 2018). In Colorado, radiotagged little brown bats roost in high-elevation talus fields in autumn, where they presumably hibernate; winter surveys of nearby caves and mines found hibernating *Myotis* in only 35% of surveys, and numbers were small (Neubaum 2018). Although bats have been observed using a few caves in southern Southeast Alaska in winter, typically only 1–2 bats are present (15 was the maximum) and only during periods of extreme cold (J. Baichtal, USFS, pers. comm.). Despite the presence of numerous mines in the Juneau area, extensive surveys found no evidence of bats using them for hibernation (B. Weed, Juneau/Alaska's Hidden History, pers. comm.).

Genetic studies also support the idea that western little brown bats exhibit different hibernation behavior than their eastern counterparts. Range-wide genetic analyses using mitochondrial and nuclear markers show that little brown bats form one large panmictic population in eastern North America, but they exhibit greater genetic structure west of the Great Plains (Vonhof et al. 2015; Wilder et al. 2015). Frequent long-range movements of bats from multiple summering sites to the same hibernacula, combined with visits to other hibernacula during swarming, likely contribute to high levels of gene flow in the East (Norquay et al. 2013). In contrast, given that the high levels of genetic structure among summer sampling sites in the West mirror the geography of those sites, western little brown bats likely are swarming and hibernating close to their summering grounds (Wilder et al. 2015).

There is a growing body of evidence that rock crevices are a particularly important alternative to caves and mines for hibernating bats. Acoustic studies have found that winter bat activity in areas without caves or mines is associated with rock features such as outcrops and boulder fields (Lemen et al. 2016; Hammesfahr and Ohms 2018; MDIFW 2018). Radiotelemetry and observational studies have documented bats hibernating in a variety of rock crevice types, including erosion holes (Lausen and Barclay 2006), narrow cracks (Lausen and Barclay 2006; Klug-Baerwald et al. 2017), wider crevices (Neubaum et al. 2006; White et al. 2020), and scree (Michaelsen et al. 2013; Neubaum 2018). Scree (also known as talus or colluvium) is a loose or unconsolidated deposit of rock fragments. The terms scree, talus, and colluvium often are used interchangeably, although some authors reserve the term talus for deposits having an uphill rockfall source such as a cliff (Neuendorf et al. 2005). The size of the rock fragments can vary from small chips to large boulders, but the convoluted nature of the interstitial spaces means hibernating bats are not visible from openings at the surface.

European entomologists have adopted the term “Milieu Souterrain Superficiel” (MSS), most commonly translated as “mesovoid shallow substratum,” to refer to the subterranean habitat created by the network of air-filled underground voids and cracks between accumulations of rock fragments that make up scree deposits (Mammola et al. 2016). The MSS has many similarities to caves, including a stable microclimate, permanent darkness, and the presence of subterranean invertebrates; the chief distinction is the size of the voids, which are too small to allow human access (Mammola et al. 2016). Colluvial MSS occurs on steep mountain slopes and is insulated from surface conditions by a layer of soil and possibly vegetation; the thickness of this layer is the most important determinant of microclimate within the MSS (Mammola et al. 2016). Bare colluvial MSS is considered an early stage of colluvial MSS and lacks a covering soil layer, although the inner zone may achieve a stable microclimate in other ways (Mammola et al. 2016). Bats have been found hibernating in both colluvial MSS (Michaelsen et al. 2013) and bare colluvial MSS (Neubaum 2018).

The unexpected detection of white-nose syndrome (WNS) in a little brown bat in western Washington in March 2016 (Lorch et al. 2016) highlights the lack of information on the overwintering behavior of western bats. WNS is caused by a fungus, *Pseudogymnoascus destructans* (Pd), that invades the tissues of the ears, muzzles, and wings, of hibernating bats, causing extensive physiological disruption and eventually death (Warnecke et al. 2012; Verant et al. 2014). In caves and mines in eastern North America, transmission occurs primarily within hibernacula during the hibernation season (Langwig et al. 2015a, Hoyt et al. 2018), although summer activity at hibernacula likely contributes to spreading the fungus to new sites (Ballmann et al. 2017). Transmission routes for bat populations occupying noncavernous hibernacula such as rock crevices remain largely unconfirmed. Once infected, caves and mines act as environmental reservoirs for the fungus (Lorch et al. 2013; Hoyt et al. 2014), contributing to high prevalence of infection in little brown bats by late hibernation during the first winter the fungus is present (Langwig et al. 2015b), and by early hibernation thereafter (Langwig et al. 2015a, 2015b). Due in part to the bats’ clustering behavior during hibernation, WNS has severely impacted the little brown bat (Langwig et al. 2012) and this species is considered a primary driver of the spread of the disease in eastern North America (Wilder et al. 2011, 2015). Given its continental distribution, susceptibility to WNS, and role in spreading the disease, understanding the hibernation behavior of little brown bats in the western portion of their range is essential for assessing the risk WNS poses to western bat populations and the potential for developing an effective, western North American-specific response.

Hibernating behaviors of bats affect almost every aspect of the WNS disease cycle. A bat’s choice of a hibernaculum determines the available microclimates that in turn affect the growth rate of the fungus, and the length of the hibernation season determines how long the fungus can grow. In laboratories, Pd grows optimally between 12.5°C and 15.8°C, with little growth at temperatures approaching 0°C (Verant et al. 2012), and results of laboratory and field studies support the hypothesis that hibernating at cooler temperatures can improve bat survival. Captive little brown bats infected with Pd have higher survival when they hibernate at 4°C than at 10°C (Johnson et al. 2014; Grieneisen et al. 2015); population declines are lower in cooler hibernacula (Langwig et al. 2012); and higher fungal loads are correlated with higher roosting temperatures and greater WNS impacts (Langwig et al. 2016). However, fungal loads of several palearctic bat species in the wild peak at much lower temperatures (5–6°C) than in laboratories, suggesting that factors other than temperature can influence fungal growth rates (Martínková et al. 2018).

Humidity is another factor that can affect fungal growth rates although few studies have examined its effects. Hibernating bats are susceptible to dehydration and smaller-bodied bats appear to select hibernacula with higher humidity to reduce evaporative water loss (Boyles et al. 2017). However, Pd presumably grows better at higher humidity, potentially offsetting the benefit of hibernating at colder temperatures and altering the optimal hibernation conditions for bats in the presence of WNS (Hayman et al. 2016). Population declines of Indiana bats (*Myotis sodalis*) following WNS infection are higher at hibernacula with higher relative humidity (RH—Langwig et al. 2012). For Pd grown at 13°C in the lab, fungal growth increases with increasing RH up to 81.5%, above which there is no further increase in growth (Marroquin et al. 2017). However, most bats hibernate at temperatures well below 13°C and it is unknown whether the relationship between humidity and fungal growth rates holds at lower temperatures.

To better understand how WNS might affect little brown bats in Southeast Alaska, we used acoustic monitoring, radiotelemetry, and trail cameras, to study their overwintering behavior in Juneau, Alaska. We aimed to identify the structures little brown bats use for hibernation, measure the microclimates within those structures, determine the timing of immergence and emergence, and the length of the hibernation season. We also wanted to determine whether little brown bats exhibited the same fidelity to noncavernous hibernacula that they do to caves and mines. We hypothesized that little brown bats would hibernate locally, either singly or in small groups, in noncavernous hibernacula rather than migrating to karst areas elsewhere in Southeast Alaska and hibernating in large aggregations. We also hypothesized that little brown bats in this mild, coastal temperate rainforest environment would have a shorter hibernation season than those at inland sites at comparable latitudes.

Materials and Methods

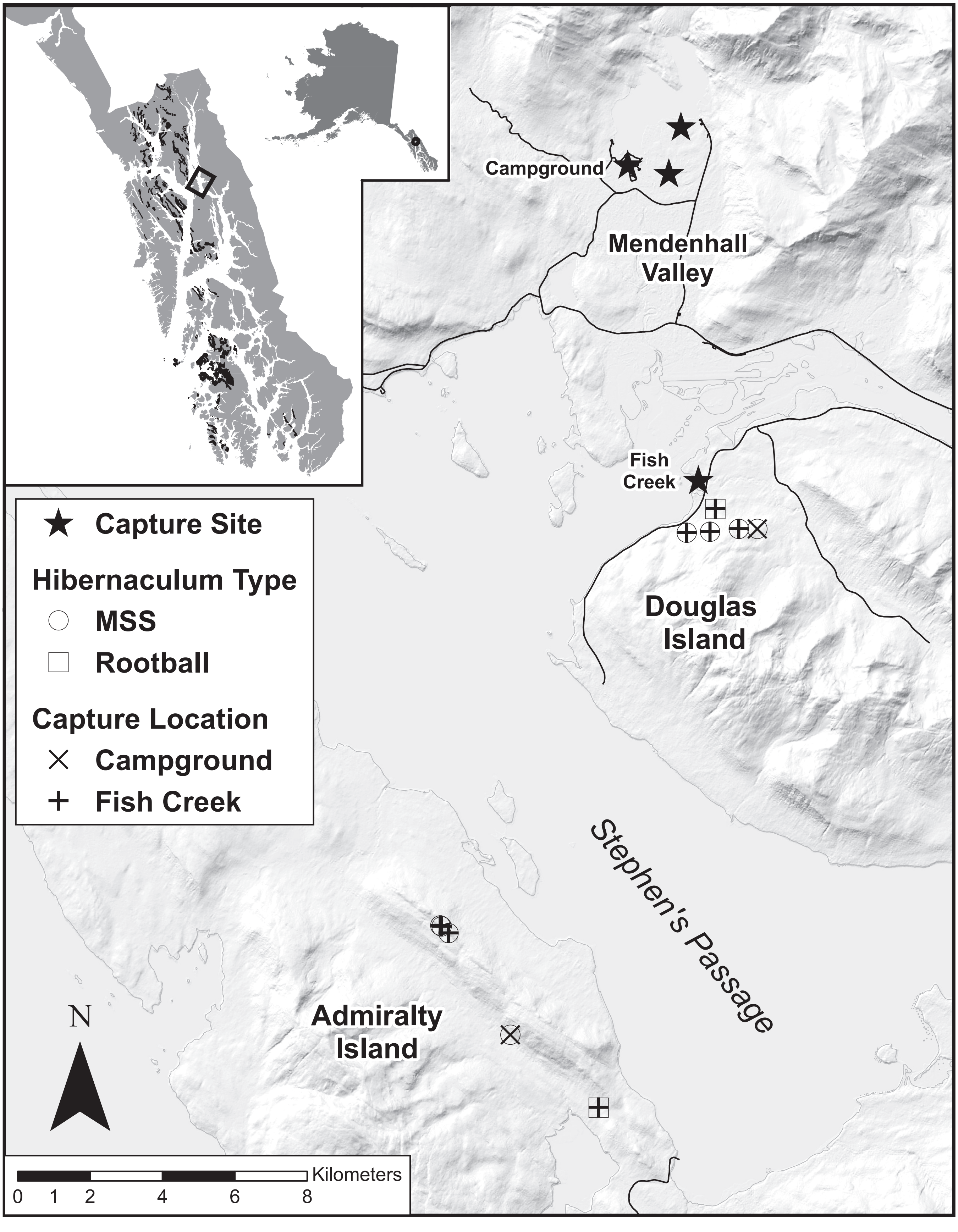
Study area.—We carried out the study in the coastal southeastern region of Alaska, in and around Juneau (Fig. 1). The area is dominated by the rugged mainland Coast Range Mountains and Juneau Icefield that form the border with British Columbia, Canada. Mountainous islands to the west separate the mainland from the open Pacific Ocean by ~125 km. The mountains interact with the warm currents of the Pacific Ocean to create a maritime climate with cool, wet summers and mild, wet winters. Average annual temperature on the Juneau mainland is 5.6°C; winter (December – February) temperatures average −1.4°C, with a diurnal temperature range of 5.1°C (National Climatic Data Center 2013). Monthly precipitation averages 9.4 cm during the driest months (February – July) and almost doubles during the wettest months (August – January—National Climatic Data Center 2013). The habitat is coastal temperate rainforest dominated by Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and mountain hemlock (*Tsuga mertensiana*), with shore pine (*Pinus contorta*) present in wetter muskeg (bog) areas.

The mountains in the Juneau area are constituted by uplifted layers of greenstone, graywacke, slate, greenschist, and metavolcanic flow breccia, which are prone to mechanical and chemical weathering (Miller 1972). In addition to natural geologic weakness, glacial erosion, isostatic rebound, and environmental conditions (e.g., frequent heavy rainfall, freeze-thaw cycles, high-elevation snowfall, and high winds that topple trees), jointly result in mass wasting deposits that dominate the mountain slopes and their bases (Miller 1972; Swanston 1972). These deposits are covered with a thin layer of soil, organic debris, and vegetation, and therefore are classified as colluvial MSS (Mammola et al. 2016).

Capture and radiotelemetry.—We focused our capture and radiotelemetry efforts at two Juneau area sites. Our main capture site was a small pond at Fish Creek that is separated from the Fish Creek estuary by a series of dikes (Fig. 1); it is the only coastal freshwater pond on the northern end of Douglas Island and is a foraging location for local bats. We also captured bats at three mainland sites located in the northern Mendenhall Valley, near Mendenhall Lake (Fig. 1). The Mendenhall Valley is the largest expanse of flat land in Juneau. Freshwater is abundant in the lakes, creeks, and numerous kettle and dredge ponds that dot the valley. Summer bat activity is high and most known little brown bat maternity roosts in the Juneau area are located there.

We captured bats between late August and early October 2011 – 2014 in mist nets suspended over ponds, across gaps in the vegetation, and across trails. We recorded body mass, identified bats to species, and classified them as adults or juveniles by backlighting the wing and examining the degree of epiphyseal fusion in the phalanges (Anthony 1988). Body mass was measured to the nearest 0.1 g with a portable digital scale (Ohaus SP-401 Scout Pro Balance, 400 g × 0.1 g, Ohaus Corporation, Parsippany, New Jersey). We fitted a subset of adult little brown bats with radiotransmitters: 0.30 g (A2414; Advanced Telemetry Systems, Isanti, Minnesota) or 0.31 g (LB-2X; Holohil Systems Ltd., Carp, Ontario, Canada). We radiotagged animals weighing > 6.0 g so that transmitters were < 5% of body mass to reduce the chances of adverse effects on behavior or survival of bats (Aldridge and Brigham 1988; Neubaum et al. 2005). We attached transmitters by trimming the fur between the scapulae and gluing the transmitters with nontoxic surgical glue (Skin-Bond Cement, Smith and Nephew United, Inc., Largo, Florida). We wrapped the bats in nylon stockings for 5 min to allow the glue to dry before releasing them. Our capture and handling protocols followed ASM guidelines (Sikes et al. 2016) and were approved by the Alaska Department of Fish and Game Animal Care and Use Committee (2011-022, 2014-13).

We located day roosts of bats daily using a combination of ground-based and aerial telemetry. We located bats on the ground using a handheld telemetry receiver (R410; Advanced Telemetry Systems, Isanti, Minnesota) and 3-element Yagi antenna, initially from a vehicle, then on foot. When bats could not be located on the ground, we undertook aerial telemetry using a Piper Super Cub (Piper Aircraft, Inc., Vero Beach,


Campground
Mendenhall Valley
Fish Creek
Douglas Island
Stephen's Passage
Admiralty Island
★ Capture Site
Hibernaculum Type
○ MSS
□ Rootball
Capture Location
× Campground
+ Fish Creek
N
Kilometers
0 1 2 4 6 8

Florida) fitted with 4-prong antennas mounted halfway out on each wing strut and pointed down at a 45° angle. A U52 cable with BNC connectors connected each antenna to a switchbox and a TR-5 programmable scanning telemetry receiver (Telonics, Mesa, Arizona). The airplane was equipped with a Sigtronics (San Dimas, California) intercom, allowing both the pilot and biologist to hear the radio signal from the bat and communicate without interrupting the signal. We varied radiotag pulse rates over the course of the study to determine the optimal trade-off between ease of locating a bat and battery life. Pulse rates ranged from 40 to 13 pulses per minute, with a corresponding battery life of 18 – 54 days. We successfully located bats (including at hibernacula) at all pulse rates.

During 2011 we conducted aerial telemetry during the day only; we located a few transient bats, but no hibernacula. In subsequent years, we flew at night when weather permitted and attempted to follow bats as they flew to their hibernacula. We began night flights at sunset. We circled the areas where bats had roosted during the day and continuously scanned frequencies until we detected movement away from the area. Once a bat departed, we followed that individual and circled it continuously until the bat stopped moving, the signal disappeared, or we ended our search due to unsafe conditions. We recorded GPS points along the path of the bat and at its last known location and tracked it on the ground later to locate the roost. We classified the roost as a hibernaculum if it was underground and the bat remained there until its tag died. We probed potential hibernacula entrances using an industrial endoscope with a 2-m cable (G series, Environmental Management Services, Canton, Georgia), but were unable to maneuver the camera head deeper than 1 m and did not observe any bats. Therefore, at each site, we selected the most probable entrance based on signal strength and recorded its dimensions. We also recorded GPS coordinates, elevation, slope, and aspect for each site.

We monitored hibernacula with a combination of acoustic detectors and trail cameras during the winter of 2013 – 2014. In autumn 2013, we deployed SM2Bat+ detectors with omnidirectional SMX-US microphones (Wildlife Acoustics, Maynard, Massachusetts) facing three hibernacula entrances to detect bats if they left during winter and to determine the potential date of emergence. We programmed detectors to record in zero-cross mode to conserve battery life and collected them in the spring or summer of 2014. Call quality in these highly cluttered environments was poor, so we manually screened all files to remove noise, but did not attempt to identify calls to species. In autumn 2014, we set up an infrared Moultrie A-5 trail camera (Moultrie Feeders, Birmingham, Alabama) at the entrance to a hibernaculum we found the previous year to determine if it was reused. In 2015 and 2016 we deployed Moultrie A-5 or D-333 trail cameras in late August or early September, at four and five hibernacula, respectively, and collected them the following spring or summer. Cameras were set to automatically record a 10 s (A-5) or 30 s (D-333) video at 30 frames per second whenever the camera detected motion.

Microclimate monitoring and statistical analyses.—In 2013 and 2014 we deployed iButton DS-1923 hygrochron dataloggers (Maxim Integrated, San Jose, California) to measure temperature and RH inside and outside of presumed hibernacula. In 2015 and 2016 we deployed iButtons at random openings in the MSS or under rootballs within 20 m of presumed hibernacula entrances. Due to the difficulty of maneuvering the dataloggers underground, we placed most only 1 m deep, with the average being slightly deeper for the MSS ($\bar{X} = 0.93$ m, $SD = 44.6$ m, range = 0.15 – 2.45 m) than the rootballs ($\bar{X} = 0.84$ m, $SD = 25.6$ m, range = 0.37 – 1.00 m). The dataloggers were programmed to record temperature and RH at 2-h intervals. At each site, an iButton was attached to the north side of a tree near the entrance, approximately 1.5 m aboveground, to measure ambient conditions. Ambient dataloggers at two sites in 2014 – 2015 failed, so we used ambient data from the nearest site that was at a similar elevation. In 2015 and 2016 we attached iButtons to sticks to prevent squirrels and other animals from pulling them out of the MSS; in 2015 our method of attaching dataloggers to sticks interfered with the humidity sensors, so only temperature data were available for that winter. The winters of 2013 – 2014 and 2016 – 2017 were colder than the intervening years, consequently, we summarized temperature and RH data as being from "cold" (2013 – 2014, 2016 – 2017) or "warm" (2014 – 2015, 2015 – 2016) winters. Compared to the average winter temperature for Juneau during 1981 – 2010 (1.17°C), the cold winters were similar (2013 – 2014) or colder (2016 – 2017) than average and the warm winters were warmer than average.

For each hibernaculum, we recorded several qualitative characteristics describing the interior of the cavity: the matrix material (rock, soil, or mixed), the slope of the cavity floor (down or horizontal), angle (whether the cavity ran parallel or perpendicular to the hillside surface), and shape (whether the cavity remained a constant size, widened or narrowed beyond the entrance). Because these qualitative characteristics were not independent, sample sizes were small, and some combinations lacked data, we analyzed each predictor separately. We also recorded the distance of the iButton from the entrance (depth) and entrance size; entrance size was calculated assuming an ellipse based on the measured height and width of the opening.

For comparison with other studies, we computed average winter (December – February) temperatures for MSS and rootball cavities and ambient conditions. Due to the small sample size, we excluded rootball cavities from all other analyses. We also computed average daily temperature and RH by year and study area for both winter and full seasons (October – April) for MSS

Fig. 1.—Map of Juneau, Alaska study area showing sites at which little brown bats were captured and radiotagged during autumn 2011–2014 and locations of 10 hibernacula identified by radiotelemetry. Stars indicate sites where bats were captured, circles indicate hibernacula in the Milieu Souterrain Superficiel (MSS), and squares indicate hibernacula in holes under the rootball of a tree or stump (Rootball). A cross inside the hibernacula symbol indicates the bat was captured at Fish Creek and an × inside indicates the bat was captured at Campground. Karst areas of Southeast Alaska are indicated by dark shading on inset map.

cavities. To calculate these averages, we first calculated daily averages for each cavity, then the means of the daily averages for the entire winter, and finally the winter averages across cavities. This procedure preserves the cavity as the primary sample unit. For RH, in addition to the winter average, we also computed the 10th percentile of the daily winter values. When RH remains high for an extended period, iButton readings may exceed 100%; these values were truncated to 100% prior to analysis.

Although bats can tolerate short bouts of subzero temperatures, they cannot hibernate at temperatures that remain below freezing and Pd cannot grow at subfreezing temperatures. We used a generalized linear model (binomial error, logit link function—Littell et al. 2006) with individual MSS cavities within winters as random effects to estimate the average proportion of time MSS temperatures were below 0°C. We used these models, which included no fixed-effect predictors, to estimate average proportions only, with random effects included to obtain appropriate variances that incorporated repeated measures within cavities. In a similar manner, we computed the proportion of time that MSS temperatures were above 0°C when ambient temperatures were below 0°C (MSS warmer than ambient) and the reverse (MSS colder than ambient).

Temperature regimes varied among years and study areas, which complicated comparisons of MSS microclimates to ambient conditions. To remove variation due to these differences, we calculated the difference between the daily-average MSS temperature and the daily-average ambient temperature (T_{diff}). Positive differences indicate MSS temperatures were higher than ambient. We then estimated average T_{diff} using a general linear model with MSS cavity as a random effect. We used these models, which included no fixed-effect predictors, to estimate average T_{diff} only, with random effects included to obtain appropriate variances that incorporated repeated measures within MSS cavities. Based on similar logic, we computed the daily temperature variance for both ambient and MSS dataloggers and computed the ratio of ambient variance to MSS variance (T_{vr}). A ratio of 1 would indicate ambient and MSS temperatures were equally variable, whereas ratios > 1 would indicate MSS temperatures were more stable. We also calculated ambient–MSS differences for RH for both means (RH_{diff}) and 10th percentiles ($\text{RH}_{\text{diff10}}$) and computed the ratio of ambient RH variance to MSS RH variance (RH_{vr}). We estimated average RH_{diff}, $\text{RH}_{\text{diff10}}$, and RH_{vr} using the same type of general linear models as used for temperature.

We used mixed effects linear models to determine the relationship between depth and entrance size and temperature, T_{diff}, T_{vr}, RH_{diff}, and $\text{RH}_{\text{diff10}}$. We used temperature and RH summaries as responses, depth and entrance size as predictors, and MSS cavity as a random effect. To augment interpretation of the resulting estimates, we calculated AICc weights, which are based on small-sample-corrected AIC scores, and measured the relative support for the compared models, with an AICc weight > 0.5 indicating support for the predictor relative to an intercept-only model (Burnham and Anderson 2002). All analyses were carried out using SAS v. 9.4 (SAS Institute, Cary, North Carolina).

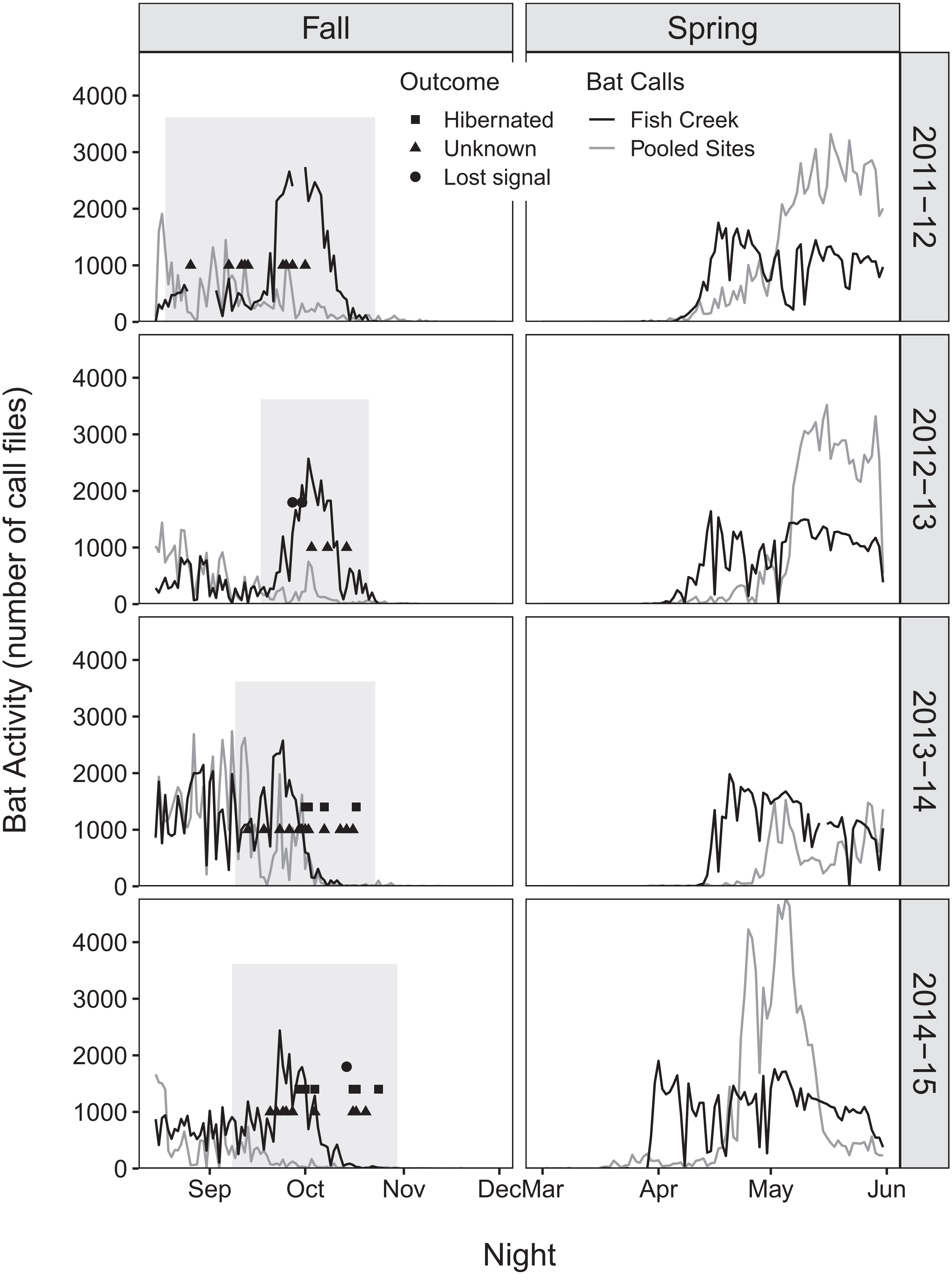
Timing of hibernation and emergence.—We used seasonal patterns of bat acoustic activity on the landscape to determine the timing of hibernation and emergence in the Juneau area. We deployed SM2Bat or SM2Bat+ bat detectors with SMX-US omnidirectional microphones (Wildlife Acoustics, Maynard, Massachusetts) at sites along the Juneau road system that were known to have high bat activity. We monitored a total of 14 sites, but only a subset of those sites was monitored in any given season. During autumn (September – November), we monitored nine sites in 2011, 10 sites in 2012, 11 sites in 2013, and five sites in 2014. During spring (March – May), we monitored 10 sites in 2012, nine sites in 2013, four sites in 2014, and three sites in 2015. Detectors were programmed to record nightly from sunset to sunrise. Calls were recorded in full spectrum, then converted to zero-cross files using Kaleidoscope Pro software (Wildlife Acoustics, Maynard, Massachusetts). We used our own custom-built filter in AnalookW (4.2n, 16 March 2017, copyright C. Corben, Columbia, Missouri) to screen files for *Myotis* calls.

We adapted the methods of Meyer et al. (2016) to estimate the timing of hibernation. We first summed the total number of calls each night across all sites by year and season (autumn and spring), then calculated the overall total for each year–season combination. We defined the end of immergence (start of hibernation) as the date when cumulative autumn activity across all sites declined to 1% of the autumn total and the start of emergence as the date when cumulative spring activity reached 1% of the spring total. We then used those dates to estimate the minimum duration of the hibernation season. We chose a 1% cutoff rather than the 5% used by Meyer et al. (2016), because we were monitoring bats on the landscape, not at hibernacula, and it better captured the final downturn in bat activity in autumn and the initial upswing in spring. Following Humphries et al. (2006), we also estimated the minimum duration of hibernation as the period when average ambient minimum temperatures were below 0°C and compared that to our estimates from bat acoustic activity. Given that immergence and emergence occur over protracted (6 – 8 weeks) periods in the autumn and spring (Norquay and Willis 2014; Meyer et al. 2016), we also estimated the length of the hibernation season based on the dates that cumulative activity reached 50% of the fall and spring totals, to better capture when most bats were transitioning.

The seasonal activity pattern at the Fish Creek site, located at the base of a ridge where we found bats hibernating, was different than at the other sites we monitored. To examine this difference and its relationship to the timing of hibernation, we summed nightly activity totals for all acoustic sites except Fish Creek (pooled sites) and graphed nightly *Myotis* activity for Fish Creek versus pooled sites (Fig. 2).

RESULTS

Radiotelemetry and roost characteristics.—We radiotagged 74 adult little brown bats (46 males and 28 females; 14 in 2011; eight in 2012; 29 in 2013; and 23 in 2014). We successfully tracked 10 of those bats (seven male and three female) to


Fall
Spring
Outcome
■ Hibernated
▲ Unknown
● Lost signal
Bat Calls
Fish Creek
Pooled Sites
2011–12
2012–13
2013–14
2014–15
Bat Activity (number of call files)
0
1000
2000
3000
4000
Sep
Oct
Nov
Dec
Mar
Apr
May
Jun
Night

underground hibernacula; three of those bats were tracked in real time as they transited. Most of the transient roosts ($n = 22$) those bats used before moving underground were in buildings or snags, but two males roosted overnight in live trees (Table 1). Four of the males used ≥ 1 roost structure that we could not locate on the ground due to distance or terrain. There were no anthropogenic structures in the area, so we classified those roosts as "natural" (Table 1). We did not locate any transient roosts for one male that was tracked only by air, but he remained in the same general area before moving underground. The other six males used an average of 2.8 transient roosts (*SD* = 1.2) prior to moving underground, switching roosts on average every 3.4 days (*SD* = 2.5, range = 1–13 days). In contrast, only one of three females switched roosts prior to moving underground; she spent 1 day in the first roost and 18 days in the second (Table 1). We tracked bats aerially at their hibernacula (mostly after sunset) for an average of 22 days (*SD* = 8.0, range = 10 – 38 days) before their tags died; five bats were tracked through late October (22 – 27 October) and four were tracked through mid-November (Table 1).

All 10 hibernacula were located along two ridge systems. Fish Creek is a north-facing ridge located above the main capture site at Fish Creek Pond. The Admiralty ridge is a southwest-facing ridge on Admiralty Island, located 12 km to the southwest of Fish Creek (Fig. 1). Both males and females hibernated on both ridges and bats captured in 2013 and 2014 and at Fish Creek and the Mendenhall Valley also hibernated on both ridges. Bats captured at Fish Creek Pond moved upslope an average of 1.4 km (*SD* = 0.38) to hibernacula on the ridge above and 15.1 km (*SD* = 0.38) to hibernacula on Admiralty. The two bats captured in the Mendenhall Valley traveled 10.7 km to Fish Creek and 24.2 km to Admiralty.

Of the 10 bats that were successfully tracked to hibernacula, eight bats hibernated in the MSS and two bats hibernated in holes beneath the root system of a tree or stump ("rootball"). The four MSS hibernacula at Fish Creek were dispersed along the length of the ridge, whereas at Admiralty three of the four MSS hibernacula were located within 400 m of each other at the north end of the ridge (Fig. 1). This area was a short, steep slope that dropped approximately 200 m from the top of the ridge into a narrow lake running along a muskeg bench at its base (Supplementary Data SD1). The ridge was dotted with numerous sheer cliffs and multilevel, stepped rock outcrops (Supplementary Data SD1). Outcrops on the Fish Creek ridge were smaller and more dispersed than those on Admiralty (Supplementary Data SD1). Admiralty was mostly snow-covered during winter, whereas Fish Creek was only intermittently snow-covered.

The eight MSS hibernacula were located on convex stretches of steep ($\bar{X} = 43°$, $SD = 4.6$), forested slopes with a shallow layer of moss, forbs, duff, soil, and coarse woody debris covering the underlying rock fragments. The combined soil and litter layers near the hibernacula entrances averaged 9.9 cm (*SD* = 2.3) on Admiralty and 14.4 cm (*SD* = 6.4) on Fish Creek. Elevations of MSS hibernacula were 107 – 433 m on Admiralty and 134 – 318 m on Fish Creek. Hibernacula were located in even-aged hemlock or hemlock-dominated stands; most trees had the characteristic J-shape at the base that signifies a creeping hillside (Supplementary Data SD1). Interiors of MSS hibernacula consisted of a jumble of rocks of varying shapes and sizes, creating multiple interstitial pathways into which the bats could crawl. Substrates within those interiors varied from exclusively rock to a mix of rock, soil or organic debris, and roots. The dominant rock type was graywacke, a type of sandstone. Four of the MSS hibernacula were in emergent rock outcrops, two were in the ground but within 20 m above or below an emergent outcrop, and two were in the ground with no obvious outcrop nearby. The hibernacula in rootballs were located on flat terrain (slope ≤ 12.5°) at low elevations (≤ 65 m). The rootball hibernaculum at Fish Creek was in hemlock forest, and the one on Admiralty was on the edge of a forested wetland area (muskeg) dominated by shore pine. Interiors of hibernacula in rootballs were a mix of soil, organic debris, and roots.

Acoustic and video monitoring at hibernacula.—Detectors at hibernacula recorded no activity during winter. In autumn of 2013, we detected 10 bat calls at two MSS hibernacula; eight calls were recorded on the same night at the same hibernaculum. The last call was on 15 November. The first spring detections at the rootball hibernaculum were on 29 March 2014, 1 day after the start of consistent nightly activity at the Fish Creek detector. Activity at the two MSS hibernacula began 2 weeks later, on 12 April and 14 April, when activity at the Fish Creek detector first reached double and triple digits, respectively (Fig. 2). Calls were recorded almost nightly at the rootball hibernaculum between 12 and 20 April 2014, when that detector was removed from the site. Calls were recorded every night except two at one or both MSS hibernacula between 24 April and 18 May 2014; most nights had ≤ 10 calls, but there were seven nights with ≥ 18 calls each, including 99 calls during a 3-day stretch in mid-May and 63 calls on 29 May. Activity at the MSS hibernaculum monitored throughout the active season in 2014 showed multiple spikes in May and early June, sporadic and minimal activity between 5 June and 2 August and increasing activity thereafter, consistent with the timing of swarming (Fig. 3). The detector was not operational for the last 3 weeks of September, but calls were recorded on six nights in October, with a high of 26 calls on 4 October and the last call on 17 October (Fig. 3).

Over three autumns, we recorded 11 videos of bats in September and October during 894 camera-nights of monitoring. We recorded bats at two MSS hibernacula, one on each ridge. In one video a bat entered a hibernaculum on 18 October 2014; the remaining videos showed bats flying by or circling

Fig. 2.—Radiotracking outcomes for little brown bats in Juneau, Alaska relative to seasonal acoustic activity at the base of a ridge used for hibernation (Fish Creek) and all other Juneau area detector sites combined (pooled sites), by season and year. Squares indicate dates on which bats hibernated, triangles indicate the last date a signal was detected when the fate of the bat was unknown, and circles indicate dates when we lost radio signals while actively tracking bats near known hibernation areas. The shaded areas represent the span of time during which radiotags were active.

Table 1.—Dates of hibernation and first and last radiotelemetry locations for 10 bats radiotracked to hibernacula in Juneau, Alaska during 2013–2014. First letter of the bat ID column indicates sex. The number and types of transient roosts used prior to hibernation are followed by the total number of days the bat was tracked to that roost type (in parentheses). When distance or topography prevented us from locating the exact roost, but there were no anthropogenic structures in the area, we classified the roost as "Natural." The last column is the type of roost used for hibernation and the number of days the bat was tracked at that hibernaculum before its tag died. Bats hibernated either in the Milieu Souterrain Superficiel (MSS) or in holes in the soil beneath the root system of a tree or stump (Rootball).

Year	Bat ID	First location	Hibernated	Last location	# of transient roosts (# of days)				Hibernaculum
					Building	Snag	Tree	Natural	Type (# of days)
2013	F14	13 September	1 October	11 October	0	1 (19)	0	0	MSS (10)
2013	F27	29 September	17 October	27 October	1 (18)	1 (1)	0	0	MSS (10)
2013	M19	28 September	6 October	25 October	0	1 (1)	0	2 (3)	Rootball (19)
2013	M28	1 October	6 October	13 November	0	0	1 (1)	2 (5)	MSS (38)
2014	F09	10 September	1 October	22 October	1 (22)	0	0	0	MSS (21)
2014	M04	12 September	30 September	23 October	0	0	0	1 (10)	MSS (23)
2014	M10	11 September	4 October	27 October	1 (16)	0	0	1 (8)	MSS (23)
2014	M18	3 October	24 October	14 November	2 (14)	3 (5)	1 (1)	0	MSS (21)
2014	M22	2 October	17 October	14 November	1 (13)	1 (3)	0	0	Rootball (28)
2014	M23	2 October	16 October	14 November	2 (6)	1 (8)	0	0	MSS (38)

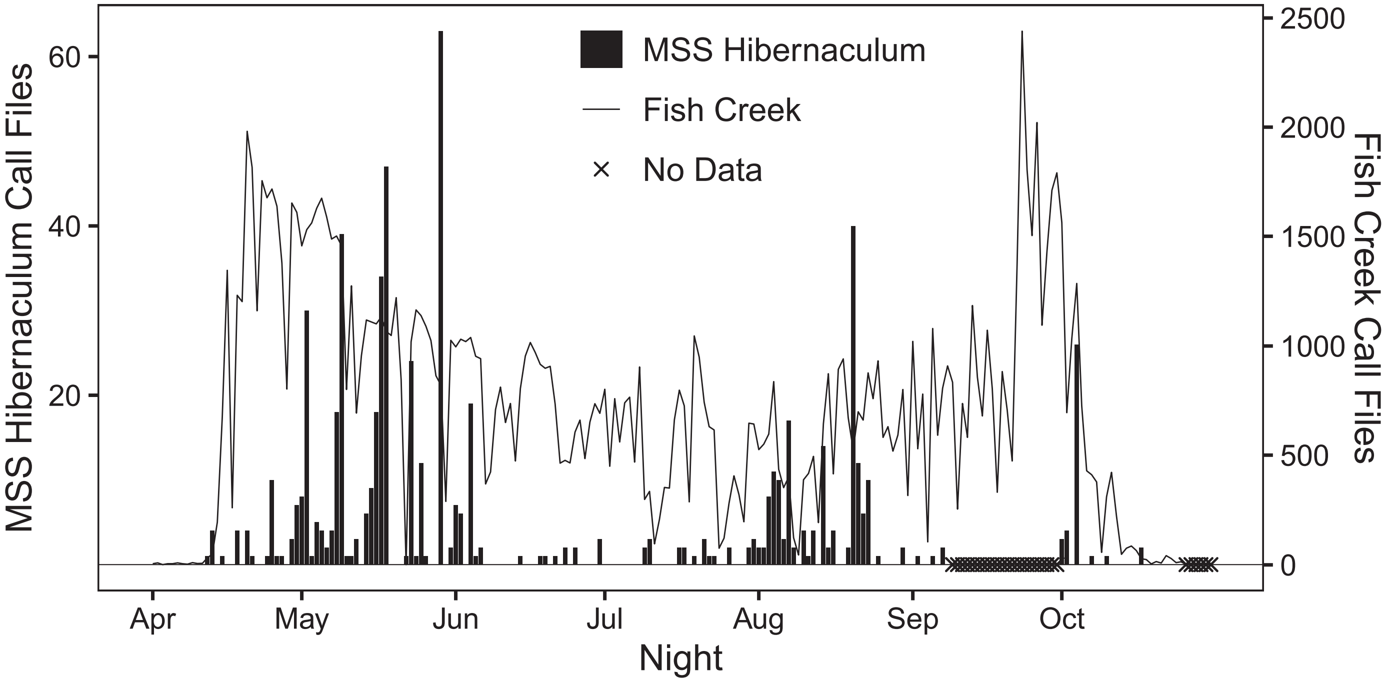


Fig. 3.—Bat acoustic activity during the 2014 active season (April–October) at two sites in Juneau, Alaska. The black bars indicate activity at a hibernaculum in the Milieu Souterrain Superficiel (MSS) used by a radiotagged little brown bat the previous winter; crosshatching denotes that the detector was not operational. The black line depicts activity at a long-term acoustic monitoring site (Fish Creek) located at a pond at the base of the ridge where the bat hibernated.

the entrances of hibernacula. Two of those videos showed a bat flying outside one of the hibernacula (on Fish Creek ridge) on 28 December 2016, the day after several inches of snow fell.

Hibernacula microclimate.—We deployed 83 dataloggers over four winters; 23 ambient (85%), 23 MSS (53%), and nine rootball (69%) dataloggers recorded data and the remainder failed or were pulled out of the cavities by squirrels or other animals.

Across all winters, average temperatures in the MSS ($\bar{X} = 0.3$°C, $CI = -0.20$°C to 0.69°C) and rootballs ($\bar{X} = 0.8$°C, $CI = 0.26$°C to 1.39°C) were warmer than ambient ($\bar{X} = -0.5$°C, $CI = -1.13$°C to 0.06°C; Fig. 4), with slightly overlapping confidence intervals for MSS and ambient temperatures. Although confidence intervals were large and overlapped, there was some suggestion that temperature regimes differed between the two study sites (Table 2). On Admiralty, average ambient temperatures were < 0°C during both cold and warm winters, but average MSS temperatures were > 0°C during cold winters and < 0°C during warm winters (Table 2). In contrast, at Fish Creek both ambient and MSS temperatures were < 0°C during cold winters and > 0°C during warm winters (Table 2). Overall, average daily MSS temperatures were warmer

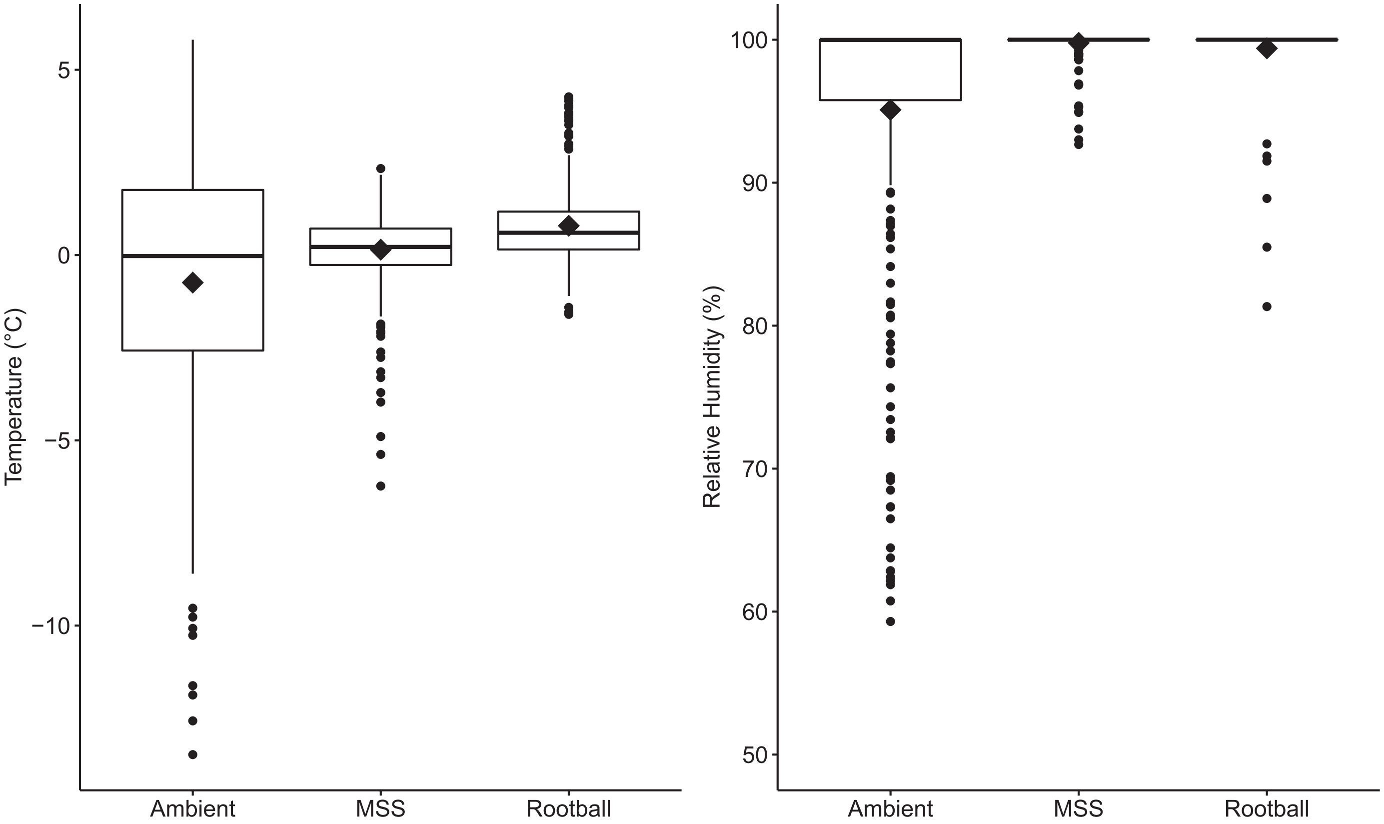


Fig. 4.—Boxplot of temperature and relative humidity for ambient conditions and little brown bat hibernacula in the Milieu Souterrain Superficiel (MSS) or in holes under the rootball of a tree or stump (Rootball) near Juneau, Alaska during the winters (December–February) 2013–2016. Bold bars represent the median, diamonds are the mean, upper and lower box limits are the 75th and 25th quartiles, whiskers indicate the minimum and maximum values, and circles are possible outliers. Sample sizes were 23, 23, and 9 for temperature and 13, 12, and 2 for relative humidity for ambient, MSS, and rootball, respectively.

Table 2.—Average winter (December–February) temperature, relative humidity (RH), and 10th percentile RH (95% *CI*) for ambient conditions and in the Milieu Souterrain Superficiel (MSS) used for hibernation by little brown bats on two ridges in Juneau, Alaska. Values were summarized separately for cold (2013–2014 and 2016–2017) and warm (2014–2015 and 2015–2016) winters.

		Ambient		MSS	
Ridge	Winter	*n*	$\bar{X}$ (95% *CI*)	*n*	$\bar{X}$ (95% *CI*)
Temperature					
Admiralty	Cold	2	−3.0 (−8.7, 2.6)	3	0.5 (−2.0, 3.0)
	Warm	5	−0.6 (−1.1, 0.5)	7	−0.5 (−1.1, 0.1)
Fish Creek	Cold	3	−1.3 (−1.6, -1.1)	6	−0.3 (−1.0, 0.5)
	Warm	7	0.6 (0.0, 1.2)	7	1.3 (0.8, 1.9)
RH (mean)					
Admiralty	Cold	2	95.5 (92.0, 98.9)	3	100 (--, --)
	Warm	1	96.3 (--, --)	3	99.2 (96.4,100)
Fish Creek	Cold	3	93.9 (91.7, 95.4)	4	100 (99.9, 100)
	Warm	4	94.2 (92.9, 96.2)	2	100 (--, --)
RH (10th percentile)					
Admiralty	Cold	2	78.8 (53.2, 100)	3	100 (--, --)
	Warm	1	82.6 (--, --)	3	97.0 (83.8, 100)
Fish Creek	Cold	3	72.3 (62.6, 77.3)	5	100 (--, --)
	Warm	4	74.7 (70.2, 82.8)	3	100 (--, --)

than ambient temperatures during cold winters ($T_{\text{diff}} = 1.87$, $CI = 0.71$°C to 3.03°C). They were slightly warmer during warm winters ($T_{\text{diff}} = 0.31$, $CI = -0.12$°C to 0.74 °C; Table 3) although, confidence intervals overlapped. Across all winters, MSS temperatures were below freezing on average 23% of the time (*CI* = 14–73%) versus 41% of the time for ambient temperatures (*CI* = 34–48%). MSS temperatures remained above freezing 59% of the time (*CI* = 45–73%) that ambient temperatures were below freezing. Following extended periods of below-freezing ambient temperatures, there was typically a lag

Table 3.—Mean differences and variance ratios (95% *CI*) for winter (December–February) microclimate measures of ambient conditions and in the Milieu Souterrain Superficiel (MSS) used by little brown bats for hibernation in Juneau, Alaska. Differences are MSS–ambient and variance ratios are the variance of the ambient measure divided by the variance of the MSS measure; values > 1 indicate ambient measures are more variable than MSS measures. Values were summarized separately for cold (2013–2014 and 2016–2017) and warm (2014–2015 and 2015–2016) winters.

Variable	Winter	*n*	Mean difference (MSS–ambient)	Variance ratio (ambient/MSS)
Temperature (T_{diff}, T_{vr})	Cold	9	1.9 (0.7, 3.0)	26.6 (10.4, 42.7)[a]
	Warm	14	0.3 (−0.1, 0.7)	13.1 (0.7, 25.5)
Mean RH (RH_{diff}, RH_{vr})	Cold	7	5.3 (4.0, 6.5))	131.6 (96.5, 166.8)
	Warm	5	4.3 (1.7, 7.0)	97.3 (0, 207.3)
10th percentile RH (RH_{diff10})	Cold	7	23.9 (18.2, 29.7)	
	Warm	5	19.5 (9.5, 29.4)	

[a] One outlier data point removed from this analysis.

period when ambient temperatures rose back above freezing, while MSS temperatures remained below freezing, a situation that occurred 12% of the time that ambient temperatures were > 0°C (*CI* = 4–20%; Fig. 5). This pattern was even more pronounced later in the hibernation season, when repeated or prolonged bouts of below-freezing weather in late February or March resulted in the MSS remaining below freezing for a sizable proportion of the time in March or April, even as ambient temperatures rose and remained > 0°C (Fig. 5).

MSS temperatures also were more stable than ambient temperatures. On average, the daily variance in ambient temperatures was approximately 26 times greater than the daily variance in MSS temperatures during cold winters (T_{vr} = 26.6, *CI* = 10.4 – 42.7) and 13 times greater during warm winters (T_{vr} = 13.4, *CI* = 0.7 – 25.5; Table 3). MSS temperatures were the most stable during the coldest winter of 2016 – 2017, but rose and fell with ambient temperatures during the unusually warm winter of 2015 – 2016 (Fig. 6). There was a strong seasonality to the differences between MSS and ambient temperatures. In early autumn, the MSS remained warmer than ambient until the first extended below-freezing period, except for brief periods of unusually high ambient temperatures (Fig. 6). Thereafter MSS temperatures generally were much warmer (3 – 9°C) than ambient when ambient temperatures fell below freezing, with the converse being true when ambient temperatures were above freezing (Fig. 6). By spring, when ambient temperatures usually remained above freezing, MSS temperatures almost always were colder than ambient. During the unusually warm winter of 2015 – 2016, temperature differences were much smaller (usually < 2°C) than other years; ambient temperatures remained mostly above freezing (and the MSS was therefore colder) beginning in early January (Fig. 6).

RH across all winters approached 100% in the MSS ($\bar{X}$ = 100%, *CI* = 99.4 – 100%) and rootballs ($\bar{X}$ = 99%, *CI* = 79.9 – 100%), whereas average ambient RH was slightly lower ($\bar{X}$ = 95%, *CI* = 93.9 – 95.8%; Table 2; Fig. 4). Although ambient RH was only somewhat lower than MSS RH, the mean 10th percentile RH values were substantially lower than corresponding estimates for the MSS (Table 2), demonstrating that ambient RH could drop substantially during periods of extreme

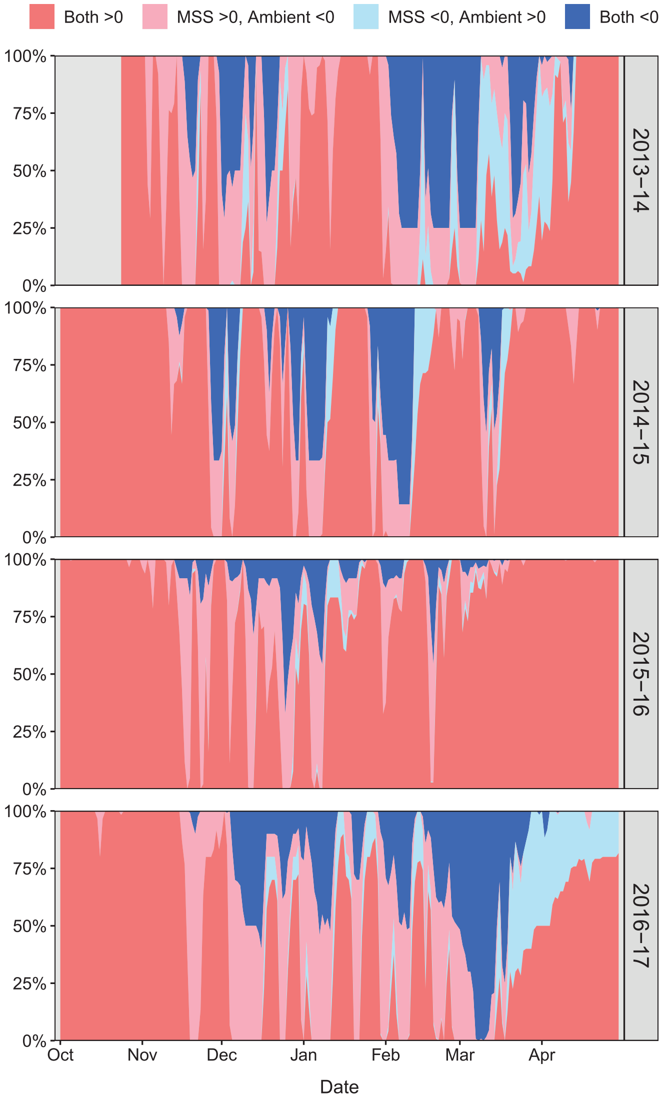


Fig. 5.—Proportion of time temperatures were above or below 0°C for ambient conditions and in little brown bat hibernacula in the Milieu Souterrain Superficiel (MSS) near Juneau, Alaska. Data collection in the MSS did not begin until 24 October during the winter of 2013–2014.

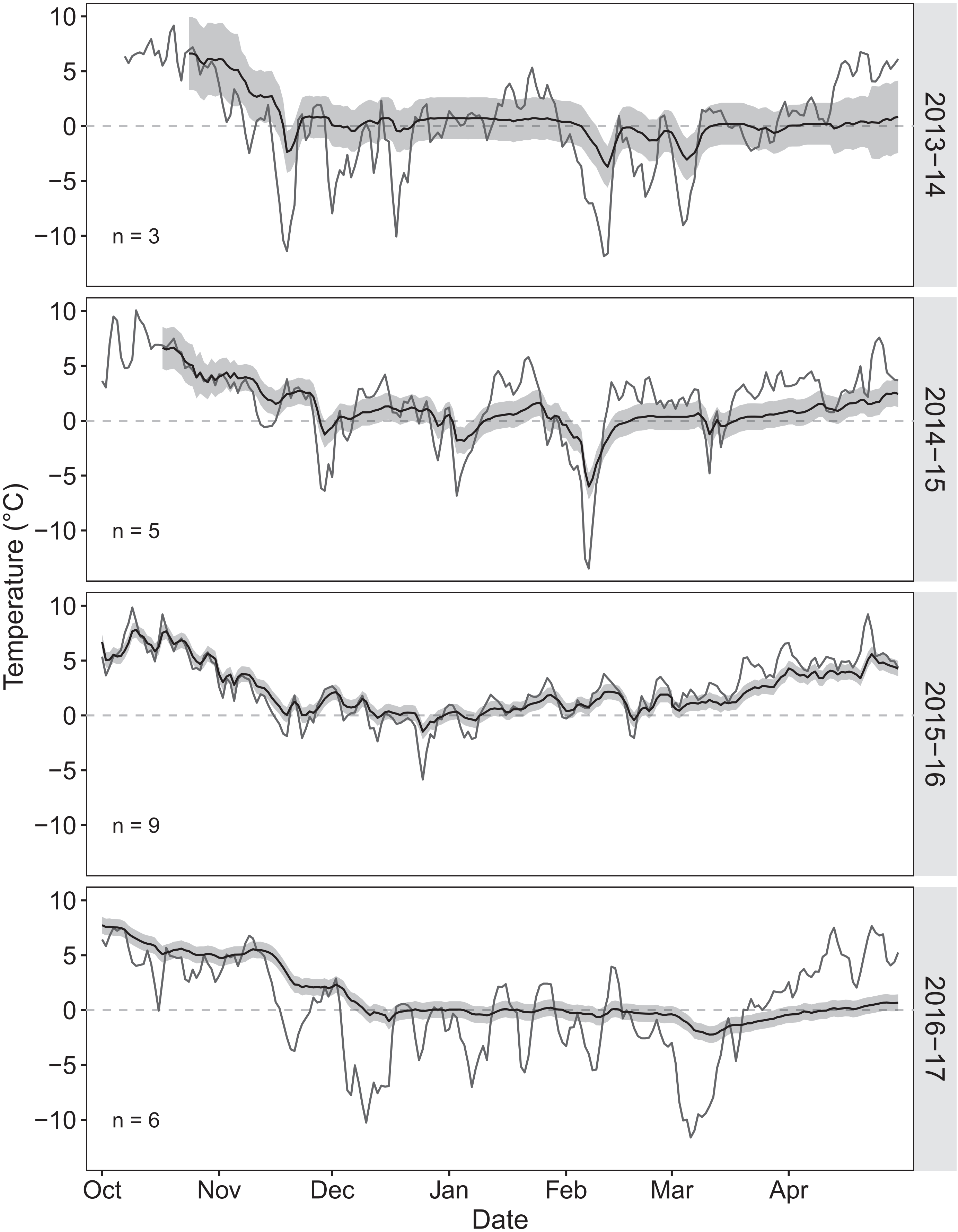


Fig. 6.—Daily-average temperatures for ambient conditions (gray line) and in little brown bat hibernacula in the Milieu Souterrain Superficiel (MSS; black line) with 95% *CI* (gray shading) near Juneau, Alaska, by winter. Light dashed line indicates 0°C. Sample sizes are for the MSS.

cold. In contrast to temperature, there was no evidence that $\mathrm{RH}_{\mathrm{diff}}$, $\mathrm{RH}_{\mathrm{diff10}}$, or $\mathrm{RH}_{\mathrm{vr}}$ were larger in cold winters compared to the warm winter (2014 – 2015) for which we had humidity data (Table 3).

We found no evidence that T_{diff}, T_{vr}, $\mathrm{RH}_{\mathrm{diff}}$, $\mathrm{RH}_{\mathrm{diff10}}$, or $\mathrm{RH}_{\mathrm{vr}}$ were associated with hibernacula characteristics (substrate, slope, angle, interior), aspect, or elevation. The relationships between these measures and entrance size were also weak, although there was moderate support for a relationship between entrance size and T_{vr} (Table 4). There was more support for a relationship between MSS depth and both average temperature and T_{diff}, with temperature increasing 1.1°C and T_{diff} increasing 1.7°C for each meter of depth (Table 4). There was weaker evidence that the proportion of time the MSS temperature was above zero, when the ambient temp was below zero, was positively related to MSS depth (Table 4).

Timing of hibernation and emergence.—The timing of hibernation was relatively consistent among years, despite year-to-year changes in the number of acoustic sites monitored. Immergence ended by 20 or 21 October except for the autumn of 2013, when it ended on 6 October (Fig. 2). The start of emergence ranged from 6 April to 14 April during the first 3 years but began > 1 week earlier (26 March) following the relatively warm winter of 2014 – 2015 (Fig. 2). The minimum length of the hibernation season ranged from 156 to 190 days and the average duration (171 days) was close to the predicted minimum of 168 days from temperature data. Bats entered hibernation 8 – 23 days earlier than the predicted date of 29 October (Fig. 2). Emergence for the first 3 years occurred within 3 days of the predicted date of 11 April, although emergence was 13 days earlier than predicted following the warm winter of 2014 – 2015 (Fig. 2). Using the difference between the estimated midpoints of immergence and emergence, the length of hibernation was 221 – 234 days, 6 – 9 weeks longer than the minimum estimates.

Activity at Fish Creek, a pond at the base of a ridge where bats were confirmed to hibernate, exhibited a strong September or October peak during all 4 years (Fig. 2). In contrast, activity at the pooled sites dramatically decreased from August to October. During years with an October peak, activity at Fish Creek constituted ≥ 87% of the total number of calls for that month. There was a similar pattern at Fish Creek in the spring; activity in April exceeded that of the pooled sites during all 4 years. Early spring activity at Fish Creek peaked 15 – 20 April during the first 3 years and on 1 April during the warmer winter of 2014 – 2015, well before activity picked up at the pooled sites (Fig. 2).

Discussion

Little brown bats hibernated in two types of structures: the MSS and rootballs. Other studies have found bats hibernating in the MSS (Michaelsen et al. 2013; Neubaum 2018), but our study is the first to confirm bats hibernating in rootballs. Although we tracked only two bats to this habitat, they constituted 20% of the total. A resident in Sitka, Alaska, uncovered a live, torpid bat in January while digging soil beneath a rootball for a garden (ADFG 2004), suggesting this behavior may be relatively common in coastal temperate rainforests, where rootballs are an abundant feature. An evening bat (*Nycticeius humeralis*) briefly took refuge in a rootball during a winter cold spell in Missouri (Boyles et al. 2005), and a silver-haired bat (*Lasionycteris noctivigans*) was found either roosting or hibernating in a rodent burrow in the soil in Indiana (Brack and Carter 1985), raising the possibility that bats elsewhere in North America also hibernate in rootballs or soil. Most of the bats in this study hibernated in the MSS, a specific type of rocky subterranean habitat that shares many similarities to caves. Although all types of noncavernous rock roosts or hibernacula often are lumped together as "rock crevices," we argue that the more appropriate generic term should be simply "rock roosts" and the term rock crevice be reserved for those roosts meeting the definition of crevice as "a narrow opening or fissure." Although the term MSS has not previously been used in reference to bat roosts or hibernacula, we prefer it to scree

Table 4.—Effects of depth (m) and entrance area (100 cm^2) on winter (December–February) temperature and relative humidity (RH) in the Milieu Souterrain Superficiel (MSS) used for hibernation by little brown bats in Juneau, Alaska. Average differences are MSS–ambient. Variance ratio is the variance of the ambient measure divided by the variance of the MSS measure; values > 1 indicate ambient measures are more variable than MSS measures. T_{MSS} = MSS temperature and T_{A} = ambient temperature.

Predictor	Response variable	Slope (95% *CI*)	AIC_c weight
MSS depth (m)	Proportion time $T_{\mathrm{MSS}} > 0°\mathrm{C} \mid T_{\mathrm{A}} < 0°\mathrm{C}$	0.4 (0.1, 0. 6)	0.69
	Mean temperature	1.3 (0.4, 2.2)	0.91
	Mean temperature difference	1.6 (0.4, 2.7)	0.90
	Ratio of temperature variances	28.0 (11.7, 44.4)	1.00[a]
	Mean RH difference	0.1 (−2.0, 2.2)	0.19
	Difference in 10th percentile of RH	0.5 (−8.0, 9.0)	0.50
Entrance area (100 cm^2)	Proportion time $T_{\mathrm{MSS}} > 0°\mathrm{C} \mid T_{\mathrm{A}} < 0°\mathrm{C}$	0.0 (−0.0, 0.1)	0.04
	Mean temperature	0.1 (−0.1, 0.4)	0.12
	Mean temperature difference	−0.2 (−0.6, 0.2)	0.18
	Ratio of temperature variances	−2.9 (−9.3, 3.4)	0.73[a]
	Mean RH difference	0.4 (−0.5, 1.3)	0.16
	Difference in 10th percentile of RH	1.3 (−2.5, 5.1)	0.37

[a] One outlier data point removed from this analysis.

or talus, because it emphasizes both its physical structure as the network of interstitial spaces between rocks and its nature as a distinct subterranean habitat. The physical structure of the MSS is quite different from that of a narrow crack or fissure in solid rock and this difference has implications for both the biotic and abiotic environment within it. We encourage future studies to describe rock roosts in sufficient detail that a taxonomy of rock roosts can be developed and the microclimates, distribution, abundance, seasonality of use, and species-specific preferences of the different types compared.

Multiple lines of evidence lead us to conclude that the underground roosts to which we tracked the radiotagged bats were hibernacula, as opposed to autumnal transition roosts. In addition to switching to a new type of roost, the move underground also involved a change in location, with bats aggregating along the same two ridge systems. Bats moved underground in late September or October, which coincided with the disappearance of the remaining radiotagged bats and declining rates of activity at all acoustic monitoring sites. Furthermore, we tracked four of the 10 radiotagged bats through mid-November, by which time activity at all acoustic monitoring sites had ceased. Although male bats switched roosts frequently prior to moving underground, none of the bats changed roosts after moving underground while their radiotags remained active (≥ 3 weeks for seven of 10 bats). Limited battery life prevented us from tracking the bats into winter, but a trail camera recorded a bat circling at the entrance to one of the MSS roosts in late December, supporting the hypothesis that it was a hibernaculum. Finally, the seasonal pattern of activity we observed at the MSS hibernaculum monitored during the active season in 2014 was consistent with that observed at cave hibernacula, with pulses of activity in spring consistent with emergence, minimal and sporadic activity in June and early July, and an increase in activity starting in late July, when swarming commences (Fig. 3; Norquay and Willis 2014; Reimer et al. 2014).

Microclimates in the MSS were warmer than ambient conditions, which agrees with other studies of MSS microclimates in winter (reviewed by Mammola et al. 2016). Average MSS temperatures during winter were nonetheless cold, ranging from −0.5°C to 1.3°C depending on the ridge and whether it was a warm or cold winter. These temperatures fall within the range documented for little brown bat cave hibernacula (−4°C to 13°C—Webb et al. 1996) but are well below average temperatures of eastern little brown bat hibernacula (7.2°C to 8.8°C—Perry 2013). Cold temperatures may be typical of rock hibernacula in western North America; big brown bats (*Eptesicus fuscus*) use rock hibernacula with average winter temperatures of 1.5°C in Colorado (Neubaum et al. 2006) and 0.8°C in Alberta (Klug-Baerwald et al. 2017). Temperatures in the MSS dropped below 0°C fairly frequently, especially during prolonged cold spells; overall, MSS temperatures were < 0°C 23% of the time during winter. This may also be typical for rock hibernacula, because both studies cited above also reported temperatures < 0°C. The cold temperatures we observed, which are below the thermal optimum of 2°C for hibernating little brown bats, would incur greater energetic costs than those above the optimum (Humphries et al. 2006; Boyles and McKechnie 2010), but they also would result in minimal growth of Pd. The strong positive correlation between fungal growth rates, fungal loads, and WNS impacts (Langwig et al. 2016) suggests that low and intermittently freezing temperatures in the MSS should not only reduce fungal growth, but also fungal loads and mortality, thereby reducing population impacts from WNS. Western Washington is part of the same coastal temperate rainforest as Southeast Alaska and bats are likely to hibernate in similar habitats. The first WNS+ little brown bat in Washington was found in March 2016, but the first mass mortality event (> 40 bats) was not detected until spring 2020 (A. Tobin, Washington Dept. of Fish and Wildlife, pers. comm.), providing some support for this hypothesis.

As in Colorado (Neubaum et al. 2006; Neubaum 2018), hibernating bats in this study were not visible and the depths at which they hibernated are unknown, although they were almost certainly at greater depths than the dataloggers. However, given that radio signals are quickly attenuated by rock, the fact we were able to detect a radio signal from the air indicates bats we successfully radiotracked were not very deeply situated. Temperatures in the MSS increased with depth, suggesting that bats in our study experienced warmer temperatures than those we measured and that they could avoid repeated or prolonged exposure to subfreezing temperatures by moving deeper within the MSS. The signal at one hibernaculum appeared to move downhill ~2 m between visits, suggesting that bats move within the MSS; similar movement was observed in a northern bat (*Eptesicus nilssonii*) in Norway (Michaelsen et al. 2013). Depth, likely due to its effect on temperature, appears to be the most important variable influencing the suitability of rock roosts for hibernation. Big brown bats in Alberta, Canada hibernate in rock crevices 1.5 – 1.8 m deep, which are deeper and warmer than random crevices (Klug-Baerwald et al. 2017) and presumed hibernacula of big brown bats in Colorado also are deeper than random crevices, with more stable temperatures (Neubaum et al. 2006).

Temperatures in the MSS were more stable than external air temperatures but were more variable than those reported for rock crevice hibernacula in Alberta, where hibernacula temperatures remain within a narrow range (−1.6°C to 2.7°C), despite external temperatures dropping as low as −40.8°C (Klug-Baerwald et al. 2017). The greater stability in temperatures can be attributed in part to the deeper depth of the dataloggers in Alberta, but it also reflects an important difference between crevice and MSS hibernacula. Narrow, bounded rock crevices more closely approximate solid ground than the MSS, where the voids can vary in shape, size, and number, and often are connected to the surface via multiple pathways. For solid ground, daily fluctuations in air temperatures penetrate to depths of approximately 1 m (for soil) or 1.1 m (for rock), with seasonal fluctuations influencing ground temperatures at depths of 1 – 20 m, depending on the substrate (Pouloupatis et al. 2011). Penetration is deeper in the MSS, where the flux of air within the interstitial spaces must be taken into account; this flux is determined largely by the depth of the covering soil layer, size of the interstices, humidity, and the presence of water (Mammola et al. 2016). Due to the difficulty of maneuvering the dataloggers within the MSS, the openings we sampled had entrances and interiors that were large enough to fit a hand or arm inside. There was moderate support for larger entrance size being associated with greater temperature variability, suggesting larger entrance size contributes to greater flux within the interstitial spaces. If bats hibernating in the MSS are selecting for smaller or narrower openings than the ones we sampled, similar to their winter use of rock crevices (Klug-Baerwald et al. 2017; Moosman et al. 2017), those narrower openings could provide more of a buffer from ambient conditions, particularly if they were associated with correspondingly smaller interstitial spaces.

Snow cover is another variable that potentially influences temperature. Although we lacked detailed data on snow depth and coverage throughout the winter, the ridge on Admiralty had more snow than the ridge at Fish Creek, which most likely explains why hibernacula temperatures in the MSS on Admiralty remained above freezing during cold winters. Ground surface temperatures beneath an insulating layer of snow are close to 0°C and at least one species of bat has been documented hibernating beneath snow directly on the forest floor (Hirakawa and Nagasaka 2018). Although entrances to hibernacula in or beneath rock outcrops likely remained snow-free, snow cover on the surrounding MSS would add to the insulation provided by soil and vegetation and further dampen the effect of ambient conditions on temperatures within the MSS. The most stable temperatures we recorded were at a hibernaculum in the MSS on Admiralty; the temperature varied by only 1°C between late November (following the first significant snowfall), and mid-April, when the datalogger was retrieved from under 1 m of snow.

Aspect and solar insolation are important factors in roost selection during the autumn transition period when bats make use of passive rewarming to alternate between daily torpor bouts and activity (Neubaum 2018). The two ridges in this study had different aspects, with Fish Creek facing almost due north and Admiralty facing southwest; individual hibernacula on each ridge had similar aspects. However, due to the low angle of the sun, short days, dense canopy cover, and heavy cloud cover, solar insolation in this area during winter is low regardless of aspect. The maritime environment likely has a greater influence along the coast in this region than either aspect or solar insolation. Admiralty was colder and snowier than Fish Creek despite having a more southerly exposure, but it faced inland, whereas Fish Creek ridge was exposed to the moderating influence of the ocean.

RH approached 100% during winter in both MSS and rootball cavities. Although this is higher than reported for other studies of MSS microclimates in winter (Mammola et al. 2016), ambient RH in our area also was very high, dropping only during periods of extended cold. It is unknown whether high RH would accelerate growth of Pd at such low temperatures, especially with periodic bouts of below-freezing temperatures (Neubaum et al. 2006; Klug-Baerwald et al. 2017). More research on the effects of humidity on fungal growth is needed, especially at low winter temperatures characteristic of the rock hibernacula studied to date.

We found little brown bats using hibernacula in the MSS, despite the presence of caves and mines in the area, as did Neubaum (2018). There are several large areas of karst in Southeast Alaska (Fig. 1), including on Chichagof Island (46 km away) and Prince of Wales Island (100 km away), both well within the distances that eastern little brown bats are known to travel between summer ranges and winter hibernacula in eastern North America (Norquay et al. 2013). The limited use of caves and mines for hibernation across the West (Weller et al. 2018) suggests that underground structures such as colluvial and bare colluvial MSS and rock crevices are the preferred hibernation habitat for little brown bats where available. Big brown bats and eastern small-footed bats (*Myotis leibii*) use rock crevices in winter in Virginia (Moosman et al. 2017) and winter acoustic detections of *Myotis* spp. near talus in Maine (MDIFW 2018) suggest that eastern bats likely also hibernate in a wider variety of underground structures than previously realized.

The small size of the voids in the MSS in our study precludes large groups of bats from hibernating together in the same cavity. Two MSS hibernacula on Admiralty Ridge were located within 50 m of each other and pulses of acoustic activity at hibernacula in early spring suggest multiple bats were emerging from hibernation in the same general area, if not from the exact same cavities. From the standpoint of WNS transmission, what constitutes a winter colony depends on whether bats hibernating in different cavities interact, which in turn depends on whether the MSS is continuous or patchy, the distance between entrances, and the size of the interstitial spaces. Due to the surface soil layer, we were unable to determine the boundaries or spatial extent of the MSS surrounding each hibernaculum. However, the interstitial spaces were small, requiring bats to crawl rather than fly when traveling underground, and pathways were numerous and frequently dead ended. Therefore, even if the MSS were continuous, bats hibernating in different cavities likely did not interact unless the entrances were very close. Small colony size means that the rate of spread among hibernacula, rather than transmission among bats within hibernacula, will drive WNS impacts on bats hibernating in the MSS. Bats could potentially spread WNS by switching hibernacula aboveground, although we recorded no acoustic activity and only two videos of bats at hibernacula entrances during winter. Swarming is another mechanism by which WNS might spread among hibernacula. The increase in late summer acoustic activity at one of the MSS roosts is consistent with swarming (Fig. 3), raising the possibility that little brown bats hibernating in the MSS swarm where they hibernate. If so, the smaller size and dispersed nature of MSS hibernacula should slow the spread of WNS within an area once it has arrived. If some swarming and mating occurs away from hibernacula, at sites such as the pond at Fish Creek, that could further reduce the importance of hibernacula as environmental reservoirs and help slow the spread of the fungus. More research on swarming in western bats is needed to assess the role it might play in spreading WNS.

All the radiotagged bats hibernated on the same two ridge systems. Given the abundance of steep forested ridges in the study area, this suggests they were selecting for specific conditions at the landscape scale. The ridges are geologically similar; both run parallel to faults and have steep slopes covered with colluvial MSS. Three out of 10 bats hibernated within 400 m of each other on the north end of the ~6.5 km long Admiralty ridge, suggesting a relatively high density of bats hibernating there. In areas where bats hibernate in discrete outcrops, the density of such outcrops likely serves as a good proxy for the density of hibernating bats. Acoustic detectors and trail cameras provided evidence that at least two MSS hibernacula associated with rock outcrops were used in multiple years. Klug-Baerwald et al. (2017) also found fidelity of big brown bats to specific rock crevices. Although Neubaum et al. (2006) did not document big brown bats reusing the same crevice, two bats radiotagged in consecutive years returned either to the same hillside or the same drainage. We did not detect bats returning to the rootball hibernacula or MSS hibernacula not associated with outcrops, which is consistent with previous findings that bats exhibit higher fidelity to more permanent roost structures, such as buildings, caves, and rock crevices (Lewis 1995). More overwintering areas and hibernacula need to be identified to understand what factors are influencing winter roost selection at both landscape and microhabitat scales.

Most of the tagged bats we monitored remained in the immediate vicinity of the capture site until their signals disappeared or we found them hibernating locally. Twice while we were aerially tracking bats, we suddenly lost the signal when we reached Admiralty ridge, supporting the idea that missing bats were hibernating locally in the MSS, but the scree had blocked their radio signals. Furthermore, bats migrating long distances would presumably choose to travel during good weather and begin their journey early in the night. Most bats that disappeared did so later in the night after we stopped tracking or when the weather was too poor for us to fly, suggesting they did not travel far. If most western little brown bats are hibernating locally, as this study and Neubaum (2018) suggest, that could explain both the greater degree of genetic structure found in western populations (Wilder et al. 2015) and the slower spread of WNS in Washington relative to the East and Midwest (White-Nose Syndrome Response Team 2019; WDFW 2020).

By October, *Myotis* acoustic activity declined dramatically, coinciding with the timing of hibernation or disappearance (likely hibernation) of radiotagged bats. Most of that activity was confined to the pond at Fish Creek. There was a similar concordance between the onset of acoustic activity at hibernacula and early spring increases in acoustic activity at the pond. Fish Creek Pond may serve as an important foraging or staging site for bats preparing to enter or newly emerged from hibernation, a swarming site, or some combination of the above. Regardless, the peaks in activity during late autumn and early spring, which we did not observe at any other acoustic site in the Juneau area, can serve as an indicator that bats are hibernating nearby, as well as provide good estimates of the timing of hibernation and emergence. Estimates of hibernation timing from other acoustic monitoring sites varied substantially from site-to-site, although pooled estimates closely approximated those from Fish Creek Pond. We expected bats in the Juneau area to hibernate for a shorter period of time than bats at more interior locations due to the mild coastal winters, but the timing of hibernation (mid-October to early April) was similar or only slightly shorter than that reported for *Myotis* spp. across much of western North America (Olson et al. 2011; Hendricks 2012; Reimer et al. 2014; Hammesfahr and Ohms 2018). Bats completed immergence 1 – 3 weeks earlier than predicted based on when temperatures typically drop below freezing. September and October are the wettest months of the year and the wet and windy weather, in combination with falling, although not necessarily freezing, temperatures likely spurred bats to enter hibernation.

The MSS hibernacula in this study differed from caves and mines in several important ways that should reduce the impacts of WNS on little brown bats in Southeast Alaska, at least in the near term. The potential wider availability of suitable hibernacula, smaller colony size, reduced commuting distances, and colder temperatures should help to slow the spread of WNS to new areas, limit transmission during the hibernation season, reduce fungal growth and therefore fungal loads, and increase overwinter survival. However, if the fungus persists within the MSS, as it does within caves and mine hibernacula, the cumulative effects of repeated exposure over multiple winters may result in increasing impacts over time. Research on MSS microclimates, the seasonality and routes of transmission, and the role of swarming in spreading the fungus is needed in WNS-affected areas in western North America to fully understand the risk WNS poses to little brown bat populations not hibernating in caves or mines.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Photos (from top to bottom) of ridge, rock outcrops, and entrance areas to hibernacula used by radiotagged little brown bats (*Myotis lucifugus*) near Juneau, Alaska, 2013–2014, at (A) Admiralty and (B) Fish Creek study areas. Red arrows indicate presumed hibernacula entrances. Hibernacula were located in the "Milieu Souterrain Superficiel" (MSS), a network of air-filled underground voids and cracks between the rock fragments found in scree (talus) deposits.

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