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ROOST TREE AND HABITAT CHARACTERIZATION OF THE SOUTHWESTERN MYOTIS (*MYOTIS AURICULUS*) AT THE NORTHERN EXTREMITY OF ITS RANGE

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ABSTRACT—Characteristics of potential maternity roosts of the southwestern myotis (*Myotis auriculus*) at the northern extremity of its range are largely unknown. Maternity roosts are key resources for bat populations. An understanding of roost-site selection is critical for effective bat conservation and management. Over the summers of 2008–2011, we tracked 13 reproductive *M. auriculus* females to 21 maternity roost sites in piñon-juniper-dominated woodlands on Kirtland Air Force Base in Albuquerque, New Mexico. Using point-quarter sampling, we compared the habitat characteristics of roost trees to 100 randomly selected control trees. The best predictors of suitable *M. auriculus* roost sites were tree diameter and elevation. Roost trees were commonly one-seeded junipers (*Juniperus monosperma*) with relatively large diameters. Roost stands also contained more ponderosa pines (*Pinus ponderosa*) and Gambel oak (*Quercus gambelii*) than expected by chance but less *J. monosperma* than expected by chance. Roost stands often occurred on flat ground at high elevations and exhibited relatively high solar gain. For effective management of this species, we suggest that habitat supporting large, cavity-containing trees be preserved across the species' range.

RESUMEN—Se desconocen en gran medida las características de los posibles dormitorios de maternidad del myotis orejudo (*Myotis auriculus*) en el extremo norte de su área de distribución. Los dormitorios de maternidad son recursos clave para las poblaciones de murciélagos. Comprender la selección del dormitorio es fundamental para una conservación y gestión eficaz de los murciélagos. Durante los veranos de 2008 a 2011, rastreamos 13 hembras reproductivas de *M. auriculus* hasta 21 dormitorios de maternidad en bosques dominados por piñones y enebros en la base de la Fuerza Aérea de Kirtland en Albuquerque, Nuevo México. Utilizando un muestreo punto-cuarto, comparamos las características del hábitat de los árboles dormitorios con 100 árboles de control seleccionados al azar. Los mejores predictores de los dormitorios adecuados para *M. auriculus* fueron el diámetro del árbol y la elevación. Los árboles dormitorios fueron comúnmente enebros de una sola semilla (*Juniperus monosperma*) con diámetros relativamente grandes. Los rodales también contenían más pinos ponderosa (*Pinus ponderosa*) y roble de Gambel (*Quercus gambelii*) de lo esperado al azar, pero menos *J. monosperma* de lo esperado al azar. Los rodales con dormitorios a menudo ocurrían en terrenos planos a grandes alturas y exhibían una ganancia solar relativamente alta. Para un manejo efectivo de esta especie, sugerimos que se conserve el hábitat que sustenta árboles grandes que contengan cavidades a través del área de distribución de la especie.

Most temperate bats require roost sites that offer protection from the characteristic daily variation in ambient conditions (Kunz, 1982). Importantly, suitable roost sites, especially sites that could act as maternity roosts, in which the development of young occurs, are likely to be an important limiting resource for bat populations (e.g., Tuttle, 1979; West and Swain, 1999). Effective habitat conservation and management for bats therefore require understanding of species-specific roosting requirements. *Myotis auriculus*, the southwestern myotis, has a geographic range extending

from the American Southwest south to Guatemala (Hoffmann et al., 1987), and in the United States occurs only in Arizona and New Mexico. Within New Mexico, populations are commonly found in areas of the southwestern and western mountains (Adams, 2003). The maternity-roosting behavior of the southwestern myotis has been the focus of very few studies (Rabe et al., 1998; Bernardos et al., 2004; Barclay and Kurta, 2007; Tye and Geluso, 2020). Bats such as the southwestern myotis require particular attention because their roosts are essential to the success of current

and future generations of bats, but are under threat due to increasing wildfire severity and frequency, among other stressors exacerbated by the current climate change projections for the southwestern United States (MacDonald, 2010).

Roost selection in bats can be affected by a variety of ecological factors including predation risk, physiological constraints of adults or young, morphology, and social behavior (Findley, 1993). Most tree-roosting bats in temperate regions prefer tall, dead trees (snags) with relatively large diameters that contain cavities or sections of exfoliated bark (Adams, 2003). Individual species also often demonstrate specific habitat requirements in roost-site selection. Although some researchers have observed bats choosing trees within low-density forests (Barclay and Kurta, 2007), other researchers have found that roosts can also be located in high stand-density areas (Rabe et al., 1998; Bernardos et al., 2004). Such variable findings underscore the importance of continued research to fully understand species-specific roost tree selection.

For North American tree-roosting bats, the selection of roosts relies, in general, on environmental features that contribute to pup survival, especially for maternity roosts. Typically, each bat species selects only one or two roost types to inhabit (Adams, 2003; Barclay and Kurta, 2007). However, reproductive females may be further restricted to roosts that possess suitable microclimates (Barclay and Kurta, 2007). To reduce energy requirements, females typically choose roosts on E- or SE-facing slopes that keep the roost warm during the day (Adams, 2003), a behavior that has been observed in maternity roost studies to facilitate pup survival (Schmidly, 1991; Britzke et al., 2003). Also, reproductive females tend to roost at lower elevations than those of male or nonreproductive females, suggesting specific environmental preferences for maternity roosts (Barclay and Kurta, 2007).

The southwestern myotis is a gleaning insectivore that prefers environments consisting of shorter shrubs of mesquite and chaparral habitats or the taller trees of oak (*Quercus*) forests, ponderosa pine (*Pinus ponderosa*) forests, and piñon-juniper (*Pinus edulis-Juniperus*) woodlands (Adams, 2003). During the summer, lactating southwestern myotis females are known to cohabit in maternity roosts (Adams, 2003; Bernardos et al., 2004), whereas males tend to switch frequently between different roost sites (Adams, 2003). *Myotis auriculus* individuals tend to avoid human-made structures as roosting sites (Tye and Geluso, 2020). Instead, tree cavities and exfoliated bark are the preferred roost sites for both males and females (Bernardos et al., 2004; Tye and Geluso, 2020).

Most *M. auriculus* research has focused on their presence or absence in the environment or as part of broader roost-site studies including multiple species (Contreras-Balderas et al., 2007). Some of this research has made predictions regarding general habitat preferences of the species within areas in Arizona and New Mexico, suggesting that the

southwestern myotis may favor pine-oak habitat (Morrell et al., 1999) or piñon-juniper forests over ponderosa pine forests (Chung-MacCoubrey, 2005). Tye and Geluso (2020) tracked female *M. auriculus* to roosts in Fremont's cottonwoods (*Populus fremontii*) along the Mimbres River in New Mexico. However, few studies have quantified the characteristics of both the roost tree and surrounding habitat of female *M. auriculus* roost sites (but see Bernardos et al., 2004), and sample sizes in some of these studies have been low (Rabe et al., 1998; Tye and Geluso, 2020).

There is a documented need for additional information on *M. auriculus* roost-site selection, especially within the northern extremity of its range in New Mexico (Adams, 2003). In 1998, the Western Bat Working Group assigned a medium level of concern to the southwestern myotis in an area including the location of our study (Adams, 2003), indicating the need for more data to reevaluate its conservation status. Some of the crucial life history information needed for *M. auriculus* includes colony size, day roosts, winter range, and hibernacula (Adams, 2003; Harvey et al., 2011).

We examined a population of *M. auriculus* occurring at the northernmost tip of the species range in the Rio Grande Valley, New Mexico. One of our objectives was to develop a meaningful, detailed model for the characterization of maternity roost habitat for the southwestern myotis in the region. In developing this model, we sought to compare roost trees and roost tree stands by comparing these to randomly chosen trees and stands within the study area. We focused on six key parameters: tree diameters, tree species, tree stand densities, slope, elevation, and solar gain.

MATERIALS AND METHODS—Study Area—We conducted fieldwork in woodland areas of the Manzanita Mountains on Kirtland Air Force Base (UTM 13S 353226E 3878693N) SE of Albuquerque, in Bernalillo County, New Mexico. Elevation on the study site ranged between 1,784 and 2,438 m. The location is characterized by piñon-juniper woodlands, ponderosa pine-Gambel oak forests, Chihuahuan desert scrub, and piñon pine-dominated forest.

Capture Methods—We mist netted near water holes on Kirtland Air Force Base during the summers (June–July) of 2008–2011. Mist-netting sites included Sol Se Mete Spring, Coyote Springs, Tijeras Arroyo Golf Course ponds, guzzlers in Sol Se Mete Canyon, Burn Site, Otero Canyon, David Canyon Tank, and Forest Road 321. We placed between one and four mist nets (Avinet Inc., Portland, Maine) varying between 6 and 18 m in length at each site. We monitored nets continuously from sunset to midnight or 1 h after the last bat capture, following published netting techniques (Kunz and Kurta, 1988). For each bat captured, we recorded species, sex, forearm length, weight, capture time, and, when possible, reproductive condition.

Roost Identification—We located roost trees by attaching radio transmitters (models LB-2N and LB-2, Holohil Systems Ltd., Ontario, Canada, and Philip Blackburn, Nacogdoches, TX) to captured, visibly lactating *M. auriculus* females (Bernardos et al., 2004). Transmitters weighed 0.35 g, following weight

recommendations of Aldridge and Brigham (1988). We tracked tagged bats every day beginning the morning after their capture until transmitters fell off or the signal was no longer detectable in the study area. To conduct radio telemetry, we used a three-element Yagi antenna and one of two receivers (R-1000, 148.000–151.999 MHz, Communications Specialists, Inc. (Orange, CA, USA), or LA-12Q, 150.000–153.999 MHz, AVM Instrument Co. (Colfax, CA, USA)). We followed published radio telemetry methods (Wilkinson and Bradbury, 1988). When proximate to the tagged bat, we positioned the receiver near potential trees to identify the roost tree based on signal strength. Using a Garmin eTrex global positioning system unit (Olathe, KS, USA), we recorded the coordinates for each roost tree. We also conducted direct observations at confirmed roost trees, beginning 30 min before sunset and continuing until about 20 min after we observed the last bat to confirm that roosting bats were in the tree. We recorded the total number of bats exiting and the time of their exits.

Tree and Stand Measurements—Upon locating maternity roosts of *M. auriculus*, we recorded the tree height (m), the aspect and slope ($^{\circ}$) of the terrain, the dimensions of the cavity (cm), the diameter at breast height (DBH, cm), and the decay stage, following classifications presented by Vonhof and Barclay (1996). In addition, we located random trees equally distributed according to similar elevation and habitat type by using aerial photographs of the study site. Using this approach, we identified 100 random points that we then visited on foot and used as the central point (origin) for a measured random tree plot. Some points were inaccessible due to their location within hazardous zones or restricted areas on the base. Because we could not continually monitor random trees, we cannot be certain that bats, at some point in time, did not use these randomly selected trees as roosts.

We conducted roost and random tree plot measurements between 7 July 2011 and 28 June 2012 by using a standardized point quarter method (Fig. 1; Cottam and Curtis, 1956). All measured trees had to have a minimum height of 1.3 m and a minimum DBH of 2.54 cm because these are the published minimum requirements for female *M. auriculus* roost-site selection (Rabe et al., 1998; Bernardos et al., 2004). We obtained DBH either by measuring with standard tape and converting the measurement to circumference or by using DBH tape. In each cardinal direction quadrant—NE, SE, SW, and NW—we located the closest tree to the original tree and then recorded its DBH and distance from the center tree. We repeated this procedure of locating quadrants and taking measurements, using four other trees located 10 m N, S, E, or W from the original tree. Throughout these sampling procedures, we recorded, for each tree, its DBH, distance, and species and its associated cardinal direction and quadrant. Thus, for each random and roost plot, we measured 21 total trees.

We used a geographic information system to georeference and map all tree and stand coordinates. We used a 10-m resolution digital elevation model (New Mexico Resource Geographic Information System Program, www.rgis.unm.edu) with spatial analysis to create slope and aspect layers. We created a solar radiation layer by using ArcMap 9.3 (Environmental Systems Research Institute, Redlands, CA, USA), calculating solar gain in watt hours/m² totals for 2011 for each digital elevation model pixel. Solar gain is primarily a function of elevation and aspect; relatively higher, and therefore unshaded, southerly facing

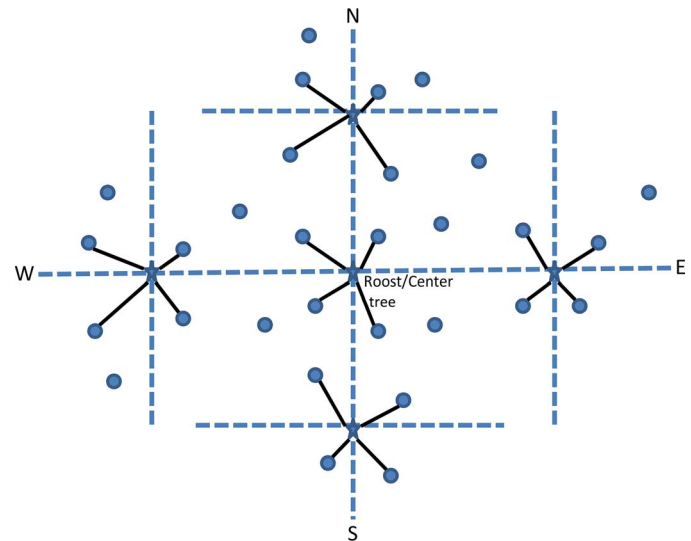


FIG. 1—Diagram of the standardized point-quarter method used to measure random ($n = 100$) and southwestern myotis (*Myotis auriculus*) roost ($n = 21$) tree stand measurements over the 2011 and 2012 summers on Kirtland Air Force Base, Albuquerque, New Mexico. We measured the closest trees to the center tree (roost or random tree) falling in NE, SE, SW, and NW quadrants and repeated measurements around trees 10 m N, W, S, and E of the center tree. For each tree measured, we recorded diameter at breast height, tree species, and distance (represented by solid lines) from its center tree.

slopes receive the most sunlight. We implemented Hawth's Tools point intersect tool (Environmental Systems Research Institute, Redlands, CA, USA) to obtain the elevation, slope, aspect, and solar gain for each plot point.

Statistical Methods—We performed all statistical analyses using R version 2.15.0 (R Development Core Team, 2012). We produced back-to-back histograms using the Hmisc package in R software. We conducted nonparametric Wilcoxon tests to examine DBH differences between roost trees and all other measured trees. We also performed an additional Wilcoxon test to compare DBH of roost trees with all other trees measured in roost stands. To determine whether bats selected specific tree species as roost sites, we used a chi-squared test of independence to compare expected frequencies of roost tree species to corresponding observed frequencies.

We used an unbalanced nested analyses of variance with log-transformed distances to evaluate density differences between roost and random stands. We used a Welch's t test to compare the densities of roost center points (including trees most adjacent to the roost tree) and other points (to the N, S, E, and W) within the roost stand. To differentiate the tree species compositions of roost and random stands, we conducted a chi-squared test of independence. Finally, we implemented three Wilcoxon tests to compare differences in slope, elevation, and solar gain between roost and random tree stands.

We used a multiple logistic regression to develop a roost characterization model (i.e., potential drivers of roost-site selection) including solar gain, elevation, slope, and DBH (Bernardos et al., 2004; Tye and Geluso, 2020). All variables except for solar gain showed a normal distribution, so we performed a square root transformation to normalize the solar gain data before analysis.

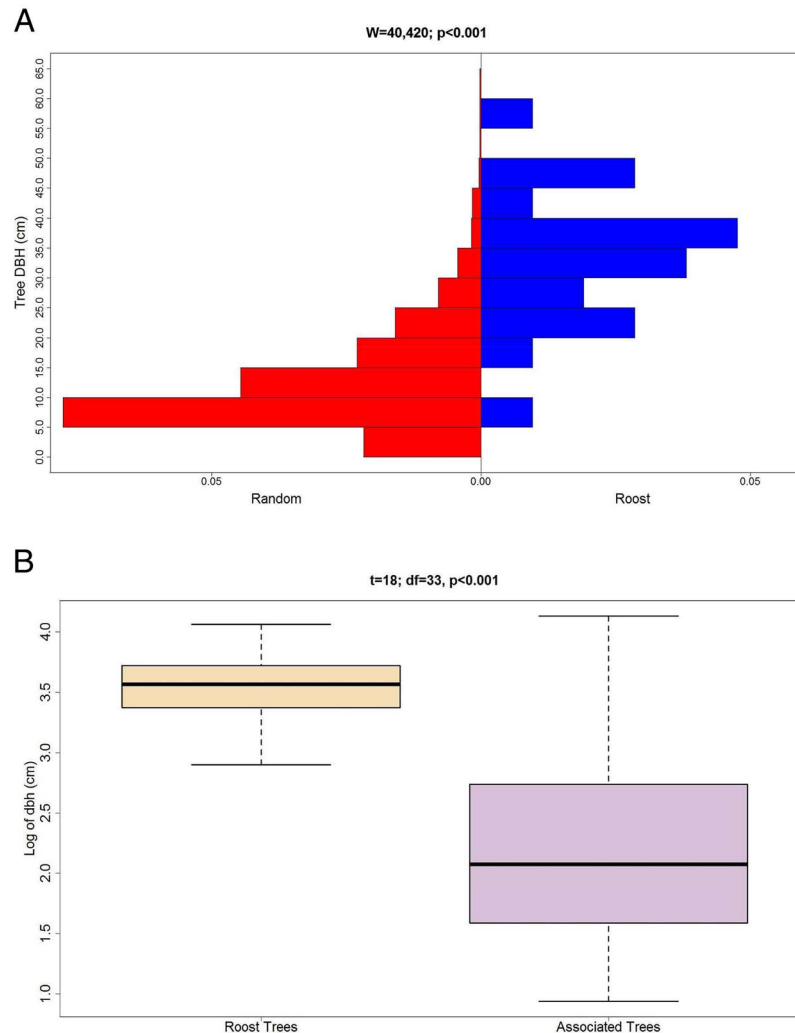


FIG. 2—(A) Back-to-back histogram of diameter at breast height measurements (DBH, y axis) from southwestern myotis (*Myotis auriculus*) roost trees ($n = 21$; on the right) and randomly selected trees ($n = 2466$; on the left) on Kirtland Air Force Base. (B) Standard box plots of the logarithm of diameter at breast height (DBH, cm; y axis) of southwestern myotis (*Myotis auriculus*) roost trees ($n = 21$) and trees ($n = 420$) measured within roost tree stands (x axis) on Kirtland Air Force Base. Roost trees had significantly larger DBH values, and the statistical values are shown at the top of the figure.

Next, we assessed the collinearity matrix by examining variance inflation values. We checked the fit and appropriation of the regression model with goodness-of-fit tests and then confirmed linearity between the log odds ratio of stand category (roost or random) and the predictor variables with a component residual plot. We compared the predictive value of models containing different combinations of variables to select the simplest model and estimate the relative contribution of each predictor variable based on Akaike's Information Criterion corrected for sample size values (Burnham and Anderson, 1998).

RESULTS—We radio-tagged 13 lactating female *M. auriculus* over summers 2008–2011. We successfully tracked 12 females to what we believe were maternity roost sites because all of these bats were lactating females. In 2010, we tagged one female twice, both in June and July. In 2009 and 2010, bats reused roosts that had been used the previous year. We tracked six of the tagged *M. auriculus*

to multiple roost sites (range, 1–6), and all presumed to switch roosts frequently, because 14 of the 20 roosts with known residence times had a bat occupant for only one night and no roost had a bat occupant for more than four consecutive nights. All roosts occurred within tree cavities. Direct observations at roost trees were generally small and ranged from 1 to 23 individuals (mean, 7.1 ± 7.4). Overall, nonroost tree DBH ranged from 2.55 to 62.39 cm, whereas roost tree DBH ranged from 7.13 to 58.22 cm (Fig. 1). We collected data from 21 roost trees (16 *J. monosperma*, 3 *P. edulis*, and 2 *Q. gambelii*) and roost tree stands and 100 random nonroost trees and nonroost tree stands.

Roost Trees—Roost trees had significantly larger DBH than randomly selected trees within the study area ($W = 40,420$, $P < 0.0001$; Fig. 2A). Also, roost trees were significantly larger than trees within their own stands ($t = 18$, $df = 33$, $P < 0.001$; Fig. 2B). A chi-squared test of independence

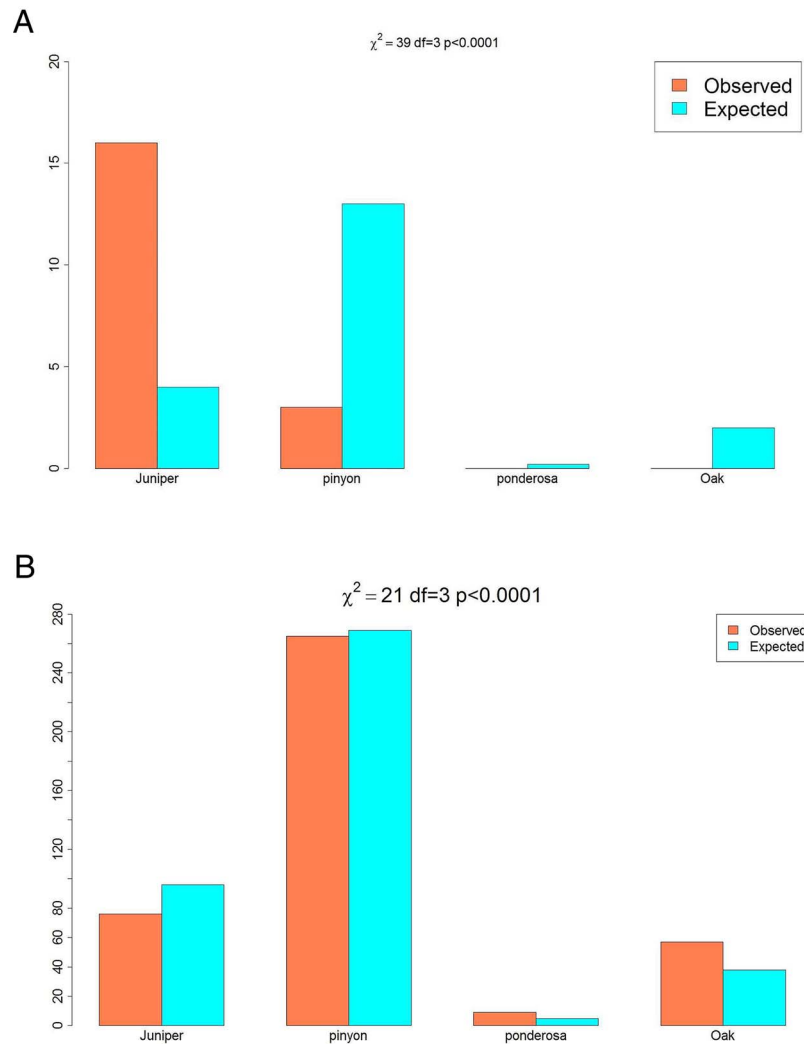


FIG. 3—(A) Comparison between tree species frequency in southwestern myotis (*Myotis auriculus*) roost trees and expected frequencies obtained from a chi-squared test of independence with tree species composition from random tree stands. We measured 21 roost trees over summer 2011 on Kirtland Air Force Base. (B) Frequency distribution of observed and expected tree species occurring within southwestern myotis (*Myotis auriculus*) roost tree stands. We generated expected frequencies by a chi-squared test of independence comparing tree species within roost and random tree plots (see text for details). Stands measured over summer 2011 on Kirtland Air Force Base.

showed that roost trees are *J. monosperma* more often than expected ($\chi^2 = 39$, $df = 3$, $P < 0.0001$; Fig. 3A).

Roost Stands—A chi-squared test of independence ($\chi^2 = 21$, $df = 3$, $P < 0.0001$) revealed that roost stands contained more *P. ponderosa* and *Q. gambelii* than expected (Fig. 3B). Tree density was significantly higher in roost stands ($F = 74.9$, $df = 105$, $P < 0.001$; Supplementary Material Fig. S1). Furthermore, the density of trees around the center point was higher than the density of trees around the other four points (N, S, E, and W) in roost plots ($t = -4$, $df = 123$, $P < 0.001$; Supplementary Material Fig. S2). Roost plots had lower slopes ($W = 1,751$, $P < 0.0001$; Supplementary Material Fig. S3), higher elevations ($W = 1,751$, $P < 0.0001$; Supplementary Material Fig. S4), and higher solar gain than random plots ($W = 531$, $P < 0.001$; Supplementary Material Fig. S5). Our logistic regression model demonstrated

that log (DBH) and elevation were two significant predictors of whether a tree was a suitable roost ($P < 0.001$ and $P = 0.02$, respectively). Data passed preliminary tests of multicollinearity (greatest variance = 2) and goodness of fit. Removing either solar gain or slope from our model did not significantly reduce the fit of the model ($P = 0.50$ and $P = 0.14$, respectively), but removing either DBH or elevation did ($P < 0.00001$ and $P = 0.01$, respectively). We obtained four essentially equivalent logistic regression models (Δ Akaike's Information Criterion corrected for sample size values < 2). Our fully saturated model was $\ln(\text{odds}(\text{roost type})) = -49.9 - 0.049 \text{ slope} + 0.017 \text{ elevation} + 2.84 \log(\text{DBH}) + 0.0015 \text{ solar gain}$.

DISCUSSION—We found that maternity roosts of *M. auriculus* were commonly in large-diameter *J. monosperma* within

high-density tree stands, occurring on relatively flat ground at higher elevations with relatively high solar gain. Roost stands contained more *P. ponderosa* and *Q. gambelii* and less *J. monosperma* than randomly selected stands. We distinguished roost trees from random trees primarily by the former having a larger DBH and growing at a higher elevation.

Bernardos et al. (2004) conducted an extensive study of roost trees of *M. auriculus* and surrounding stand characteristics in the Coconino National Forest of Arizona. This study also found that tree size and stand density were important features of *M. auriculus* roost trees and the surrounding forest (Bernardos et al., 2004). Specifically, they found that relatively large, tall Gambel oak trees served as roosts and that the density of large oak trees in the surrounding stands was higher than in areas around randomly selected trees (Bernardos et al., 2004). Similarly, Rabe et al. (1998) concluded that larger trees in Coconino National Forest, especially those with exfoliating bark, were important for eight species of bats, including the southwestern myotis. More recently, Tye and Geluso (2020) further confirmed the importance of large trees for *M. auriculus* roosts by showing that female bats only used large cottonwoods (*P. fremontii*) for their roosts. However, the researchers conducted all three of these previous studies at sites with very different habitats compared with our study site. In Cococino National Forest, ponderosa pine–Gambel oak habitats dominate (Rabe et al., 1998; Bernardos et al., 2004), whereas riparian vegetation prevails along the Mimbres River in southwestern New Mexico (Tye and Geluso, 2020). Thus, it is unsurprising that, in contrast to our results, these previous studies have reported that either Gambel oak (Rabe et al., 1998; Bernardos et al., 2004) or cottonwoods were the preferred roost sites for *M. auriculus* (Tye and Geluso, 2020). We found that 76% of *M. auriculus* roosts on Kirtland Air Force Base occurred in *J. monosperma*.

In general, snags suitable for tree-roosting bats typically have large diameters and loose exfoliating bark (Rabe et al., 1998; Kalcounis-Ruppell et al., 2005; Rancourt et al., 2007; Perry and Thill, 2008). At our study area, we found that *M. auriculus* significantly preferred *J. monosperma* cavities over large-diameter pines with exfoliating bark. We also observed that these *J. monosperma* roost tree stands had higher solar gains because of their aspect and elevation. We also observed more large *P. ponderosa* snags in more heavily shaded canyon bottoms. It is possible that despite the higher elevation of these *J. monosperma* roosts, the solar gain advantages that they possess make them more suitable thermally than the large *P. ponderosa* snags, which the bats often preferred in other studies.

Our study adds to the limited available information about the southwestern myotis and further expands the habitats the species is known to use to include woodlands dominated by piñon pine and one-seed juniper, which are widespread in the American Southwest. Furthermore, our study

highlights that an investigation of roost microclimate for *M. auriculus* across its range would be a particularly productive approach for characterizing suitable roost sites and perhaps directing artificial roost construction for this species. In addition, examining *M. auriculus* roost use during seasons other than the maternity or summer season could also inform future conservation approaches (Britzke et al., 2006; Hein et al., 2008). Finally, our results highlight that conservation-focused research must be conducted across the diversity of habitats across the range of a species to generate location-specific roost tree models to preserve potential roost sites, especially as temperatures warm in the western United States (MacDonald, 2010) in response to climate change.

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