EFFECTS OF PONDEROSA PINE FOREST RESTORATION ON HABITAT FOR BATS

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ABSTRACT.—Ponderosa pine (*Pinus ponderosa*) forests in the southwestern United States, used by 16 species of bats, are managed with thinning and prescribed fire to restore tree densities and fire regimes to conditions that existed prior to Euro-American settlement. Using 2 approaches (roosting and foraging) to categorize forest habitat for bats, we evaluated how restoration treatments may affect habitat use. We hypothesized that more foraging activity would occur in thinned stands because more species are adapted to open forest, but that more roosts would occur in unthinned stands where snags were unaffected by mechanical treatments and prescribed fire. During the summers of 2006 and 2007, we used acoustic detectors to record call rates of bats as a measure of activity level and compared activity levels among stands that had undergone 3 thinning treatments (light, moderate, and heavy, with 245, 172, or 142 trees per hectare postthinning, respectively) and an unthinned stand as a control (1201 trees per hectare). With radiotelemetry, we located roosts used by reproductive females of 2 common species of forest-associated bats (long-eared myotis, *Myotis evotis*, and Arizona myotis, *Myotis occultus*) during summer 2007. We measured roost characteristics at 3 spatial scales (roost, microplot, and surrounding landscape) to contrast between roosts used by *Myotis* species and randomly selected comparison snags, microplots, and study area landscape. Among thinned and unthinned stands we did not detect a difference in activity levels for all bats ($P = 0.2$), nor a difference in call rates for *Myotis* spp. ($P = 0.1$). However, there was lower activity ($P = 0.01$) for non-*Myotis* bats in unthinned compared to thinned stands. This is probably because most non-*Myotis* species are better adapted to foraging in open forests. Of 24 roosts for long-eared myotis and Arizona myotis, only 31% and 25%, respectively, occurred in thinned stands. Bats selected large-diameter (>68 cm diameter at breast height) ponderosa pine snags with exfoliating bark. Roosts for Arizona myotis were in areas with elements of old-growth structure, whereas roosts for long-eared myotis occurred in areas similar to stratified, midsuccessional, even-aged forest. Managing for large-diameter ponderosa pine snags and a variety of tree densities and age classes will provide roosting and foraging habitat for bats. We found no distinct “best” treatment to recommend overall, likely because of species differences, with some bats better adapted to open-canopy and some to closed-canopy forest. Maintaining diverse habitat will support a diverse bat assemblage.

RESUMEN.—Los bosques de pino ponderosa (*Pinus ponderosa*) en el suroeste de los Estados Unidos, utilizados por 16 especies de murciélagos, son manejados mediante incendios forestales prescritos y controlados para restaurar la densidad de árboles y los regímenes de incendios que existían con anterioridad al asentamiento euroamericano. Empleando dos estrategias (descanso y forrajeo) para clasificar el hábitat forestal de los murciélagos, evaluamos cómo los tratamientos de restauración afectan el uso del hábitat. Planteamos la hipótesis de que la actividad de forrajeo de los murciélagos sería mayor en sitios poco espesos, ya que más especies están adaptadas a bosques abiertos, mientras que la mayoría de los sitios de descanso se asentarían en sitios más espesos, donde los árboles muertos no fuesen afectados por tratamientos mecánicos ni por incendios prescritos. Durante el verano del 2006 y del 2007, utilizamos detectores acústicos para registrar las tasas de llamados de los murciélagos como medida del nivel de actividad y comparamos los niveles de actividad entre tres tratamientos de raleo (suave, moderado e intenso con 245, 172 o 142 árboles por hectárea [aph] post-raleo, respectivamente) y un control sin raleo (1201 aph). Durante el verano del 2007 localizamos, con la ayuda de radio telemetría, las áreas de descanso utilizadas por hembras reproductoras de dos especies comunes de murciélagos asociados al bosque (myotis de oreja larga, *Myotis evotis* y myotis de Arizona, *Myotis occultus*). Medimos las características de los sitios de descanso en tres escalas espaciales (descanso, microparcela y paisaje circundante) para contrastar entre las especies y los árboles muertos, las microparcelas y el paisaje, todos ellos elegidos aleatoriamente (comparación). No detectamos diferencias en los niveles de actividad de ningún murciélago entre los sitios espesos o no espesos ($P = 0.2$), ni diferencia alguna en las tasas de llamadas de los *Myotis* ($P = 0.1$). Sin embargo, detectamos menor actividad ($P = 0.01$) de los no-*Myotis* en los sitios espesos en comparación con los sitios no espesos. Ello se debe, probablemente, a que la mayoría de las especies no *Myotis* se adaptan mejor a forrajear en bosques abiertos. De 24 sitios de descanso de los myotis de orejas largas y de los myotis de Arizona, sólo el 31% y el 25% respectivamente, se encontraron en sitios poco espesos. Los murciélagos eligieron árboles longevos (pino ponderosa) de corteza exfoliante de gran diámetro (>68 cm de diámetro a la altura del pecho). Los sitios de descanso de los myotis de Arizona fueron en áreas con estructuras de crecimiento antiguas, mientras que los sitios de descanso de los myotis de oreja larga se hallaron en áreas similares a las de una sucesión intermedia estratificada, en bosques de igual edad. El óptimo control de los pinos ponderosa longevos de gran diámetro, usados como estructuras de reposo, y de la variedad de densidades de los árboles de diferentes edades, proporcionarán hábitats de reposo y forrajeo para los murciélagos. No encontramos un tratamiento distintivo “ideal” que recomendar en general, probablemente debido a las diferencias en las

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especies de murciélagos, donde algunos se adaptan mejor a los bosques de follajes abiertos y otros a los bosques de follajes cerrados. El mantener un hábitat diverso ayudará al ensamblaje de una gran diversidad de murciélagos.

Ponderosa pine (*Pinus ponderosa*) forests of the southwestern United States are adapted to a frequent fire regime that maintains a relatively open, uneven age structure (Cooper 1960, Minnich et al. 1995). With the exclusion of fire following Euro-American settlement in the late 1800s, these forests are now densely overgrown, fuel heavy, and vulnerable to catastrophic wildfires (Covington and Moore 1994, Covington et al. 1997, Fulé et al. 2012). To reduce fuel loads and the threat of wildfire, many areas are being restored to open, low-density (e.g., <150 trees per hectare [tph]) conditions similar to those that existed prior to Euro-American settlement, by use of thinning and prescribed fire (Cooper 1960, Covington and Moore 1994, Fulé et al. 1997, 2001). These forest management treatments can have substantial and immediate impacts on habitat for bats (e.g., changes in prey availability and accessibility through change in forest density and composition [Aldridge and Rautenbach 1987, Dodd et al. 2012], as well as loss of potential roosting structures through removal or change in surrounding forest structure [Ganey and Vojta 2005]).

Roosts and foraging habitat are key resources for bats (Barclay 1991, Lewis 1995, Vaughan 1997, Kunz and Lumsden 2003, Kusch and Schmitz 2013) that are especially important during reproductive periods when females give birth to and raise young. Maternity roosts are critical for reproduction because a suitable microclimate increases survival and development of young (Racey 1982, Kunz 1987, Zahn 1999). In northern Arizona, females of 16 species use ponderosa pine forests as roosting and foraging habitat (Table 1), wherein they give birth and raise pups during summer (Rabe et al. 1998, Solvesky and Chambers 2009, Saunders 2015). At least 7 of these species use cracks or exfoliating bark of large-diameter ponderosa pine snags as maternity roosts (Rabe et al. 1998, Morrell et al. 1999, Bernardos et al. 2004, Solvesky and Chambers 2009, Saunders 2015). Close proximity of maternity roosts to foraging areas allows reproductive females to conserve energy, since they are limited in the distance they can travel while tending pups (Lewis 1995, Henry et al. 2002).

All bats found in northern Arizona are insectivorous and acquire prey using strategies such as aerial pursuit or hover-gleaning (Hinman and Snow 2003; Table 1). Although bats can be variable in their use of these strategies, aerial pursuit is typically used by less maneuverable species (e.g., hoary bat, *Lasiurus cinereus*) and in areas of low clutter, such as open forests or clearings. Hover-gleaning is used by more maneuverable species and in areas of high clutter, such as closed-canopy forests with dense vegetation (Aldridge and Rautenbach 1987, Norberg and Rayner 1987, Fenton 1990, Mancina et al. 2012). Forest management treatments (thinning and prescribed fire) change the amount of clutter by removing trees and snags (Thomas et al. 1979, Horton and Mannan 1988, McHugh and Kolb 2003), thereby altering foraging habitat and roosts for bats.

Because relatively little is known about the response of bats to forest management, we examined activity levels and located maternity roosts of bats in forests managed using restoration approaches. Our objectives were to determine differences in nightly bat activity (based on call rates) between thinned and unthinned stands during the summer reproductive season, and to describe characteristics of snag roosts selected by bats in this area. We expected higher levels of bat activity in thinned stands because tree densities in these stands were similar to pre-Euro-American settlement (Cooper 1960, Covington and Moore 1994, Covington et al. 1997). We predicted that density of large-diameter snags used as roosts would be higher in unthinned forest because the lack of disturbance from management operations would protect large snags. To evaluate the diversity of roost characteristics, we selected 2 focal species that represented different foraging strategies and the range of roost types in ponderosa pine forests, namely the Arizona myotis (*Myotis occultus*) and the long-eared myotis (*Myotis evotis*). Arizona myotis form large maternity colonies (up to 800 individuals), forage in lower-clutter environments over water and tree canopies, and select large-diameter snags as roosts (M.J. Rabe, Arizona Game and Fish Department,

TABLE 1. Bat species that use ponderosa pine (*Pinus ponderosa*) forests in northern Arizona for roosting or foraging by characteristic call frequency (F_c), U.S. Fish and Wildlife Service species of concern (SC) status, foraging strategy (G = glean, A = aerial pursuit), and clutter adaptation (associated levels of clutter in foraging habitat). In cases where 2 characteristics are defined within one category, the most common is listed first. Call category (M = *Myotis*, n = non-*Myotis*) is listed for those species captured during the 2007 field study.

Scientific name	Common name	F_c (range) (kHz) ^a	Call category	USFWS status	Foraging strategy	Clutter adaptation
<i>Antrozous pallidus</i>	Pallid bat	28.0 (55–26)			G	high
<i>Corynorhinus townsendii</i>	Townsend's big-eared bat	23.4 (43–21)		SC	G/A	high/low
<i>Eptesicus fuscus</i> ^{b,c}	Big brown bat	28.2 (57–27)	n		A/G	low/high
<i>Idionycteris phyllotis</i> ^{b,c}	Allen's lappet-browed bat	27 (24–12)	n	SC	G	high
<i>Lasiurus blossevillii</i>	Western red bat	38.9 (55–39)			A	low
<i>Lasiurus cinereus</i> ^b	Hoary bat	20.1 (26–20)	n		A	low
<i>Lasionycteris noctivagans</i> ^b	Silver-haired bat	26.5 (42–25)	n		A	low
<i>Myotis auricolus</i> ^{b,c}	Southwestern myotis	33–45 (120–25)	M		G	high
<i>Myotis californicus</i>	California myotis	49.1 (100–45)			A	low
<i>Myotis ciliolabrum</i>	Western small-footed myotis	44.3 (95–41)		SC	A	low
<i>Myotis evotis</i> ^{b,c}	Long-eared myotis	34.3 (79–28)	M	SC	G	high
<i>Myotis occultus</i> ^{b,c}	Arizona myotis	40.8 (75–38)	M	SC	A	low
<i>Myotis thysanodes</i> ^{b,c}	Fringed myotis	24.5 (72–20)	M	SC	G	high
<i>Myotis volans</i> ^{b,c}	Long-legged myotis	41.6 (90–37)	M	SC	A	low
<i>Nyctinomops macrotis</i>	Big free-tailed bat	17 (30–17)		SC	A	low
<i>Tadarida brasiliensis</i> ^b	Mexican free-tailed bat	25.5 (32–21)	n		A	low

^aFrom Hayes et al. 2009 and J.M. Szwedzak, Humboldt State University Bat Lab (personal communication).

^bBat species captured during 2007 field study.

^cBat species known to roost in ponderosa pine snags (Rabe et al. 1998, Solvesky and Chambers 2009).

unpublished data; Saunders 2015). Long-eared myotis are hovering gleaners adept at foraging in high clutter; they use a wider variety of roosts (e.g., snags, stumps, caves, sinkholes) but form smaller colony sizes (<50 individuals; Findley and Wilson 1982, Hill and Smith 1984, Hinman and Snow 2003).

METHODS

Study Area

We investigated habitat use by bats in a 6000-ha study area centered on Fort Valley Experimental Forest (FVEF) on the Coconino National Forest in northern Arizona (35°22' N, 111°44' W). The area was dominated by ponderosa pine trees approximately 90 years old with a diameter at breast height (dbh) <30 cm but also included small numbers (≤5%) of Gambel oak (*Quercus gambelii*) below 2250 m and conifers (*Abies* spp. and *Picea* spp.) above 2400 m; few cliffs or rock crevices existed in the area. Elevation ranged from 2160 to 2790 m, slope from 0% to 29%, and the dominant aspect was southwest. The area had a bimodal precipitation pattern with winter snowfall and summer monsoon rains. Mean summer temperature and precipitation was 17.5 °C and 8.9 cm in 2006, and 17.2 °C and 6.5 cm in 2007, respectively (Huebner 2006). Because fire (natural surface, prescribed, and wild) was excluded from 1876 to 2000, tree densities were unusually high prior to forest restoration treatments.

Nightly activity was sampled within twelve 15-ha stands within the FVEF that had received forest restoration treatments (Fig. 1). Nine of the 12 FVEF stands were thinned between December 1998 and September 1999, and broadcast burns were conducted between winter 2000 and spring 2001 (Fulé et al. 2001, Skov et al. 2005). Three replicates of each thinning treatment were implemented by retaining either 1.5 to 3 (heavily thinned), 2 to 4 (moderately thinned), or 3 to 6 (lightly thinned) replacement trees for each evidence of a tree, stump, or snag that existed prior to Euro-American settlement. Because large dead presettlement trees must sometimes be replaced with small postsettlement trees, the number of replacement trees required per presettlement remnant varied depending on the size of suitable replacements >40 cm dbh, and this variation resulted in a small degree of

overlap between tree densities in some stands. Tree density was reduced from an average of 1195 tph (Skov et al. 2005) to 142 tph (SE = 27, range 115–169), 172 tph (SE = 12, range 160–184), and 245 tph (SE = 32, range 213–277) for heavy, moderate, and light thinning treatments, respectively. Untreated (unthinned and unburned) control stands with densities of 1201 tph (SE = 311) were used for comparison. Treatments and controls were arranged in 3 blocks (FVEF blocks; Fig. 1).

Nightly Activity

We conducted passive acoustic surveys from July to August 2006 and May to August 2007 to compare activity levels (call rates) of bats among restoration-treated areas in FVEF. We used 4 Anabat II Bat Detectors and a zero-crossings analysis interface module (ZCAIM) with an incorporated timer (Titley Scientific, Brendale, Queensland, Australia) and remote transducers (15 × 30-cm Plexiglas reflector plate with rubber microphone housing to protect the microphone from precipitation) to record calls. We placed microphones on a 45° angle from horizontal against a tree bole at a height of 2 m. In each stand, we designated 5 survey points (center, northeast, northwest, southeast, and southwest) ≥60 m from stand edges or other survey points. Because differences in vegetative clutter may affect echolocation calls (Patriquin and Barclay 2003), we placed the detectors in open patches (>10 to 20 m diameter) near each survey point to standardize the location of microphones among treatments and the detectability of bat calls. We tested the distance from which microphones detected bats with the Bat Chirp Board (Nevada Bat Technology, Las Vegas, Nevada, USA) and positioned detectors so they faced similar opening sizes. We sampled each block 14 times (6 in 2006 and 8 in 2007) with one detector in each treatment type per night. We randomized the sequence of blocks, order of sampling points, and assignment of detector for each point. Detectors recorded calls from sunset to sunrise in each sample night. We calibrated detectors with the Bat Chirp Board at the start and midpoint of each field season to ensure equal detection capability among detectors.

We reviewed all Anabat files with AnalookW (version 3.5e, Titley Scientific) software and eliminated files that did not contain sequences

Fig. 1. Capture sites, roost locations for bats, and Fort Valley Experimental Forest (FVEF) restoration stands (outlined) used for acoustically monitoring nightly activity in a 6000-ha study area in northern Arizona. Blocks are indicated by 1, 2, or 3; C = control (unthinned); treatments include the following: L = lightly thinned, M = moderately thinned, and H = heavily thinned. We compared nightly activity in the FVEF stands during summers of 2006 and 2007 and located bat roosts throughout the study area.

of ≥ 5 calls by bats or calls identifiable as bats. Because of the difficulty in distinguishing species by calls for many *Myotis* bats in the southwestern United States, we grouped bats into 2 categories to evaluate activity levels. Using a species list based on captures in the study area during summer 2007, we categorized bat calls as either *Myotis* or non-*Myotis* (Table 1; Crampton and Barclay 1998, Humes et al. 1999, Erickson and West 2003) using characteristic frequency (F_c) and slope (S_c) of calls (O'Farrell and Gannon 1999, Hayes et al. 2009; J.M. Szwczak, Humboldt State University Bat Lab, personal communication). We identified call sequences with $F_c > 35$ kHz or

with $S_c > 150$ octaves per second (OPS) and calls of fringed myotis (*Myotis thysanodes*; which has an $F_c < 30$ kHz but an $S_c > 150$ OPS and is one of the few readily identifiable *Myotis* calls) as *Myotis*, and all other calls with $F_c < 30$ kHz and $S_c < 100$ OPS as non-*Myotis* (C. Corben, AnaBat Detector and AnaLook Software developer, personal communication). On a case-by-case basis we compared questionable sequences and those between 30 and 35 kHz to an existing call library of bats in northern Arizona (O'Farrell and Gannon 1999). We calculated average call rate per hour by night for each stand for all calls, *Myotis* calls only, and non-*Myotis* calls only.

We pooled data across summer months each year to represent the reproductive period for bats in the area (i.e., when pregnant females, nursing mothers, and volant young are present) and calculated an average call rate per stand for each summer. Surveys in 2006 may underrepresent activity of pregnant females because we started in July.

To test the null hypothesis that call rates did not differ between treatment types, we used a one-way ANOVA, with block and treatment as model effects and each block-year ($n = 6$) as a separate unit (Ott and Longnecker 2001). We treated years separately to account for potential differences between years; block-by-treatment interactions were accounted for by the blocking factor and placed in the error term of the model. Because the blocking design accounted for variation in nightly (e.g., temperature, humidity, rainfall) and within-season (e.g., moon phase, insect blooms, pup volancy) factors across survey dates, we did not include these factors in analyses. We compared differences between means of each pair post hoc with Student's t test using JMP 5.0.1.2 (SAS 2002). We set $\alpha = 0.05$ for all analyses.

Roost Locations

To identify roosts, we captured bats over water throughout the 6000-ha study area using mist nets on 22 nights between 12 June and 16 July 2007. We netted at 4 earthen water catchments, 4 water-filled plastic pools (1.5 m diameter), and 1 artificial resin roost (Chambers et al. 2002) (Fig. 1). We opened nets 30 min after sunset and kept them open until we had captured at least 2 reproductive females of our focal species (long-eared myotis and Arizona myotis) or until ≥ 3 h had elapsed after sunset and capture rates had slowed to < 1 bat per hour. We recorded species, sex, age (adult or juvenile based on the absence of cartilaginous epiphyseal plates in the phalanges of juveniles; Brunet-Rossinni and Wilkinson 2009), reproductive status, and weight (to the nearest 0.2 g) for all bats captured. We determined reproductive status for females by palpation of the abdomen to determine pregnancy and examination of the mammary glands to determine lactation or postlactation. Capturing and handling of bats conformed to guidelines established by the American Society of Mammalogists (Kirkland et al. 1998) under a protocol approved by the

Northern Arizona University Institutional Animal Care and Use Committee.

We attached radio transmitters (LB-2N, Holohil Systems Ltd., Ontario, Canada) using nontoxic latex adhesive (Torbot Bonding Cement, Torbot Group Inc., Cranston, RI) to reproductive (pregnant or lactating) females of our focal species that weighed ≥ 7 g. Radio transmitters weighed $\leq 5\%$ of the individual's body mass (Aldridge and Brigham 1988). We limited the number of radio transmitters we deployed to 2 per species per night at each site to avoid oversampling bats that shared the same roosts. We released bats that were fitted with a radio transmitter at the capture site within 30 min and located roosts of radio-tagged bats on a daily basis until the radio transmitter failed or dropped from the bat. We calculated distance between roosts and capture sites for each radio-tagged bat that we tracked. We tested for differences between focal species in travel distances between consecutive roosts using a Wilcoxon's signed-ranks test (JMP 5.0.1.2; SAS 2002). We conducted exit counts at roosts from 10 min prior to sunset until bats ceased emerging or for ≥ 30 min to confirm the use and location of roosts.

We measured characteristics of each roost and a randomly selected comparison snag. We selected comparison snags that were the same species as roost snags (ponderosa pine), that met a minimum size requirement for use by bats (≥ 31.2 cm dbh, ≥ 3 m in height—dimensions based on snags used in our study and previous studies; Rabe et al. 1998, Morrell et al. 1999, Hinman and Snow 2003), and that were > 150 m from the roost, based on the minimum distance bats traveled between roosts (Vonhof and Barclay 1996). We chose the snag matching these criteria that was closest to a random point generated by a geographic information system (GIS; Rabe et al. 1998), then visually searched for signs of bats (presence of guano) to avoid selecting a snag that was used by bats. We measured the same variables at roosts and comparison snags: dbh, height of snag, top condition (intact or broken), and presence of exfoliating bark. We measured characteristics of the microplot surrounding each roost or comparison snag following methods of Rabe et al. (1998); we centered a 0.04-ha (11.3-m radius) plot on the roost and measured the number of live trees by diameter, percent canopy cover (calculated using a

spherical densiometer), and number of snags ≥ 1.4 m tall and ≥ 20 cm dbh. We treated each roost as an experimental unit and considered multiple roosts used by a single individual to be independent, because roost switching is common and roosts are usually used by multiple bats, indicating a simultaneous decision by multiple individuals (Lewis 1995, Vonhof and Gwilliam 2007). In addition, a 2-person survey team conducted a snag census by counting the number of snags (≥ 31.2 cm dbh, ≥ 3 m in height) in a 1-ha plot centered on each roost. Surveyors counted snags by simultaneously walking 30 m apart.

To describe landscape characteristics surrounding roosts that bats selected, we calculated mean canopy cover within a 7.1-ha plot of the roost (150-m radius, based on the minimum distance bats traveled between roosts) and categorized percent canopy cover as 0% to 10% (meadows and forest clearings), 11% to 50% (open forest), and 51% to 100% (dense forest). We used a GIS (ArcGIS v9.2, Environmental Systems Research Institute, Redlands, CA) 30-m-resolution canopy cover raster layer developed from a Landsat image and digital elevation model. We categorized percent canopy cover within a 1613-m radius (corresponding to the average distance from capture sites to roosts) around all sites where we captured bats ($n = 6$) for comparison. We derived elevation, aspect, and slope for each roost.

To compare snag densities among FVEF restoration treatments with those found near roosts, we censused snags on 15 ha in one heavily thinned stand (expected to have the greatest reduction in snag density because of mechanical treatments and prescribed burning) and one unthinned stand (expected to have the least reduction in snag density). We walked simultaneous transects in pairs spaced 60 m apart in one heavily thinned stand and 30 m apart in one unthinned stand to account for lower visibility. We calculated the number of large snags (≥ 31.2 cm dbh, ≥ 3 m in height) per hectare by treatment type (heavily thinned or unthinned) and noted snag recruitment or loss based on snags marked during a previous survey in 1999 (V. Alm and C. Chambers, unpublished data).

We determined which attributes predicted roost use by using contingency analysis for categorical measurements and single-variable logistic regression likelihood-ratio chi-square

tests with receiver operating characteristic (ROC) curves for significant variables (Hosmer and Lemeshow 2000). The ROC value reports the probability that the variable accurately identifies a bat roost. A ROC value of 0.50 to 0.70, 0.70 to 0.90, and >0.90 indicates low, moderate, and very high accuracy, respectively (Swets 1996). We used separate analyses for each focal species. We set $\alpha = 0.05$ for all statistical analyses.

RESULTS

Nightly Activity

During 188 detector-nights, we collected 3313 audio files, some containing multiple bat calls. After discarding unusable files, we retained 1874 (57%) files for analyses. From these files we identified 1969 bat calls, of which 45% were *Myotis*, 40% were non-*Myotis*, and 15% could not be assigned to either group. We did not detect a difference in mean number of echolocation calls for all bats among treatments ($F_{3,5} = 1.86$, $P = 0.2$; Fig. 2) nor for *Myotis* spp. among treatments ($F_{3,5} = 2.24$, $P = 0.1$). However, call rates of non-*Myotis* differed ($F_{3,5} = 5.42$, $P = 0.01$), with fewer calls in unthinned compared to heavily thinned stands (Fig. 2). There were also higher call rates in unthinned stands for *Myotis* compared with non-*Myotis* ($F_{1,10} = 49.6$, $P \leq 0.0001$; Fig. 2).

Roost Locations

We captured 55 long-eared myotis (32 female) and 29 Arizona myotis (17 female) and placed radio transmitters on 10 long-eared myotis and 8 Arizona myotis at 6 sites. We captured focal species at 3 locations within FVEF stands and 3 locations ≤ 2 km north, west, or south of FVEF. Most captures (85%) and all roosts for long-eared myotis occurred in the eastern portion of the study area; 90% of captures and all roost locations for Arizona myotis were in the western portion of the study area (Fig. 1).

We tracked bats for an average of 5 days ($SE = 1$, range 1–11), locating 24 roosts: 16 roosts for long-eared myotis and 8 roosts for Arizona myotis (Fig. 1). Most roosts (71%) were in unthinned areas; only 7 roosts occurred in thinned areas (5 and 2 roosts for long-eared myotis and Arizona myotis, respectively). Roosts for long-eared myotis were in ponderosa pine snags ($n = 11$), buildings ($n = 2$),

Fig. 2. Call rates of the entire bat assemblage (all calls), *Myotis* bats, and non-*Myotis* bats by stand type (unthinned control, lightly thinned, moderately thinned, and heavily thinned) in Fort Valley Experimental Forest, northern Arizona, from nightly activity surveys conducted in the summers of 2006 and 2007. For all calls, $P = 0.22$ and SE is represented by the error bars. For *Myotis* and non-*Myotis* call rates, lowercase letters indicate differences between these groups in unthinned controls, and capital letters indicate differences within non-*Myotis* call rates between unthinned controls and heavily thinned stands. $P \leq 0.05$ indicates significance; standard error is represented by the error bars.

rock crevices ($n = 2$), and a live ponderosa pine tree (damaged and with exfoliating bark; $n = 1$). Arizona myotis roosts were in ponderosa pine snags ($n = 6$), a Douglas-fir (*Pseudotsuga menziesii*) snag ($n = 1$), and an artificial bark roost on a snag ($n = 1$). We conducted exit counts at 17 of the 24 roosts and found 5 bats (SE = 3, range 1–16) at 12 long-eared myotis roosts and 17 bats (SE = 4, range 1–39) bats at 5 Arizona myotis roosts. Exit counts confirmed that roosts in snags and trees were beneath exfoliating bark.

Snag roosts used by both species had larger dbh (long-eared myotis: ROC = 0.73; Arizona myotis: ROC = 0.96; Table 2), higher frequency of broken tops (long-eared myotis: roosts = 81%, comparison snags = 29%, $P = 0.02$; Arizona myotis: roosts = 71%, comparison snags = 37%, $P = 0.04$), and more frequent presence of loose bark (for both species, 73% of snags with loose bark, 22% of comparison snags with loose bark; $P = 0.001$) than comparison snags. Roosts for Arizona myotis had higher numbers of excavated (ROC = 1.0) and natural cavities (ROC = 0.85) and were surrounded

by higher snag densities (ROC = 0.82) than comparison snags (Table 2).

Both species used an average of 1.8 roosts per individual (SE = 0.2, range 1–3) and moved 860 m (SE = 256, range 155–2860) when switching roosts. Arizona myotis moved greater distances ($n = 5$; 1737 m, SE = 319) between consecutive roosts than long-eared myotis ($n = 7$; 234 m, SE = 28 m; $Z = 8.1$, $P = 0.004$), and mean distance from capture site to roost was 1613 m (SE = 280, range 338–4227 m). Although only 3 roosts were found within FVEF stands (2 long-eared myotis roosts in unthinned control stands and 1 Arizona myotis roost in a moderately thinned stand), 5 roosts occurred in areas thinned within the last 5 years. The remaining roosts were in areas that had not been recently treated and exhibited a wide range of tree densities (Fig. 3). On average, the landscape surrounding roosts of long-eared myotis was characteristically denser forest (51%–100% canopy cover, ROC = 0.81) than random comparison, and neither species used areas with low canopy cover for roost sites (0%–10% canopy cover)

TABLE 2. Roost (tree or snag), microplot (0.04 ha surrounding the snag), and surrounding landscape characteristics in ponderosa pine (*Pinus ponderosa*) forest were evaluated to determine which variables were predictive of long-eared myotis (*Myotis evotis*) and Arizona myotis (*Myotis occultus*) roosts in comparison to snags randomly selected in 2007 in northern Arizona. Mean, SE, and P value are reported from single-variable logistic regression.

Scale	Variable	Long-eared myotis					Arizona myotis				
		Roost site		Random-comparison		P	Roost site		Random-comparison		P
		$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE	
Roost	dbh	68	4.1	55	3.8	0.02	73	5.0	42	2.8	0.0001
	height	21	3.4	22	2.8	0.9	22	4.3	16	2.1	0.06
	number of limbs	12	3.3	10	2.5	0.6	17	4.1	11	5.9	0.3
Microplot	excavated cavities	3	0.8	3	1.0	0.9	5	1.1	0	0.0	0.0001
	natural cavities	2	1.3	1	0.5	0.3	3	1.7	0	0.0	0.001
	degree of lean	7	1.1	5	0.8	0.3	7	1.4	9	3.8	0.4
	tph	798	140.5	968	296.6	0.6	556	156.8	279	110.5	0.2
	canopy cover	57	3.7	62	6.1	0.5	45	7.3	54	9.4	0.4
	basal area	117	11.3	133	17.9	0.4	94	23.0	122	24.3	0.3
	stems <12.5	452	112.0	568	223.5	0.6	350	130.2	114	101.9	0.2
	stems 12.5–30.2	232	42.6	304	81.1	0.4	106	16.2	57	20.9	0.09
	stems 30.3–45.5	82	16.2	59	19.7	0.4	75	26.7	57	31.2	0.7
	stems 45.6–61.0	21	9.0	20	6.5	0.9	19	7.8	43	18.7	0.2
Surrounding landscape	stems >61	11	5.1	18	5.5	0.3	6	4.1	7	4.6	1.0
	logs/ha	91	20.5	64	15.9	0.3	125	31.6	100	29.4	0.5
	snags/ha	38	10.7	25	3.7	0.3	69	9.1	32	13.0	0.05
	0%–10% CC (%)	3	0.0	19	0.1	0.001	5	0.0	19	0.1	0.01
	11%–50% CC (%)	34	0.3	34	0.0	0.9	41	0.0	34	0.0	0.1
	51%–100% CC (%)	63	0.0	48	0.0	0.05	54	0.1	48	0.0	0.2
	150-m-radius %CC	55	2.0	50	3.8	0.2	51	3.1	49	4.0	0.7

Fig. 3. Live tree density (trees per hectare estimated based on 11.3-m-radius plot) for roosts of long-eared myotis and Arizona myotis compared to published tree density for Fort Valley Experimental Forest (FVEF) forest restoration treatments.

(long-eared myotis: ROC = 0.94; Arizona myotis: ROC = 0.90; Table 2).

The snag census in the FVEF treatments found more snags ≥ 31.2 cm dbh, a size that bats were likely to use for roosting, in the thinned FVEF stands (thinned = 8.0 snags/ha, unthinned = 5.6 snags/ha). New snags ≥ 31.2 cm dbh were recruited in both thinned and unthinned stands (37% and 144% recruitment, respectively).

DISCUSSION

Bat Habitat Use

Using 2 approaches to categorize forest habitat for bats, we found no distinct “best” treatment to recommend, likely because some bat species are better adapted to open-canopy and some to closed-canopy forest. Bats used both thinned and unthinned forest for roosting, commuting, and foraging habitat.

Differences in nightly bat activity levels among treatment types may be attributed to species differences in morphology, maneuverability, and detectability (Aldridge and Rautenbach 1987, O’Farrell and Gannon 1999, Kingston et al. 2000). Bats can use large areas for foraging (e.g., maximum areas of 30 to 3000 ha, a range based on 13 studies; Lacki et al. 2007) and can travel long distances (e.g., 1.5 km, an average based on 15 studies; Lacki et al. 2007) to forage or obtain water, thus potentially traveling through multiple stands in an evening (Clark 1993, de Jong 1995). Bats adapted to open forest environments will travel through low-clutter areas, and those adapted to dense forest will travel through high-clutter areas as they attempt to feed throughout the night (Verboom and Spoelstra 1999, Schnitzler and Kalko 2001). We hypothesized higher activity in thinned stands compared to unthinned controls. The only difference we detected was for the non-*Myotis* group, species with lower maneuverability

and thus better adaptation to low-clutter environments such as thinned forests. The *Myotis* group used thinned and unthinned stands because bats adapted to both open and dense forest comprised this group.

Foraging and roosting are intrinsically linked. Accessibility between roosting sites and foraging areas is an important factor in roost site selection (Brigham 1991, Waldien et al. 2000). Captures took place at open water sources in early to midevening. Bats likely visited water sources soon after emergence to drink at sites relatively close to roost sites (Kunz and Kurta 1988). Thus, we assume that capture locations were a reflection of, rather than a bias in, where roosts were located. Availability and locations of roosts are often the focus of bat habitat studies and can differ between species (e.g., Kunz 1982, Lewis 1995, Vonhof and Barclay 1996, Rabe et al. 1998, Henry et al. 2002). Although we captured bats throughout the 6000-ha study area, each species used spatially distinct regions for roosting, with the Arizona myotis roosts in an area of more open forest on generally steeper slopes and the long-eared myotis roosts in a more closed-canopy forest area.

The Arizona myotis demonstrated more specialization in its roost selection than the long-eared myotis. Snag roosts occurred in areas with high snag density relative to surrounding areas and were similar to roosts identified for this species by Saunders (2015). Specialization was also demonstrated by the farther distance to capture site from roost and higher roost fidelity by the species as a whole; almost half of the radio-collared bats were found in the same roost as previously identified by another Arizona myotis tracked during the study. Arizona myotis were found only in snags and the artificial resin roost (which simulated exfoliating bark and was located on a snag; Chambers et al. 2002), also suggesting less flexibility in selection of

roosting structures. In contrast, the long-eared myotis roosted in a variety of structures (snags, trees, buildings, and rock crevices), with no bats roosting in the same location used by another bat tracked during the study.

Seven of the 10 species that we captured are known to roost in ponderosa pine snags in northern Arizona (Rabe et al. 1998, Bernardos et al. 2004, Solvesky and Chambers 2009). The characteristics of roosts in snags were similar between species in this study and reconfirm the findings of previous studies, with bats selecting ponderosa pine snags with large dbh and decay (e.g., loose bark; Brigham et al. 1997, Rabe et al. 1998, Solvesky and Chambers 2009, Saunders 2015). Larger snags may provide more space under exfoliating bark needed to create a suitable microclimate for maternity colonies. The artificial roost in this study is one example of a smaller snag (dbh = 46 cm versus 69 cm to 89 cm for other roost snags used by Arizona myotis) used as a roost, possibly because the artificial roost created a large exfoliating bark structure similar to those on larger snags (Chambers et al. 2002). Other snag characteristics were likely correlated with the overall decay class of the snag and presence of exfoliating bark (Thomas et al. 1979).

Habitat Management

It is important to provide a forest structure that will allow for development of suitable roosting snags while providing a mosaic of forest structures suitable for species with different flight adaptations. When thinning dense, untreated areas, resource managers should retain or create large-diameter ponderosa pine snags for roosting structures. Although we counted more large snags in thinned stands (Johnson 2008), higher recruitment in unthinned stands is likely due to increased mortality in densely forested areas as a result of drought, disease outbreak, and suppression (Smith 1986). Prescribed fire and windthrow in the thinned stands may remove existing snags without recruiting equal numbers of replacements (Randall-Parker and Miller 2002, Chambers and Mast 2005, Ganey and Vojta 2005). Protecting (e.g., raking away debris and litter) and monitoring snags during prescribed fire to reduce snag mortality, retaining mature ponderosa pine during thinning operations, or using live, mature trees to

create snags (Walter and Maguire 2005) is critical. Educating personnel trained in prescribed fire implementation and management about the habitat provided by snags can also protect this important habitat element. When snags appropriate for roosting are not available, resource managers can temporarily supplement natural roosts with artificial roosts (Chambers et al. 2002, Mering and Chambers 2012, 2014).

Heterogeneity in forest structure and tree density within forest treatment areas will promote roosting and foraging habitat for a diversity of bats. Live tree densities around roosts in our study were between the densities of unthinned and heavily thinned restoration stands (Fig. 3). We suspect that neither extreme provided ideal habitat, but that FVEF stands may represent a dominant forest density that existed in ponderosa pine prior to Euro-American settlement (Cooper 1960, Covington and Moore 1994), to which bats in this forest are adapted. Past management recommendations for wildlife (e.g., Reynolds et al. 1992) have suggested retaining approximately 5 to 7 snags per hectare, one group of 3 to 5 mature ponderosa pine trees per hectare in openings >0.4 ha, small forest openings between 0.2 and 1.6 ha, and a diversity in forest structures from young saplings to old growth arranged in clusters. Based on our study, these recommendations are still a generally appropriate forest structure for bat habitat, especially if large-scale treatments with thinning and prescribed fire, such as those demonstrated in FVEF, are conducted throughout southwestern ponderosa pine forests where a diverse bat assemblage resides.

All habitat managers should understand the adaptations of the bat assemblage in their region and how differences in these adaptations may affect habitat selection. While patterns of bat habitat use identified in this study may be generally useful to guide management actions elsewhere, specific management implications from this study should be applied primarily to ponderosa pine forests in the Southwest. Use of multiple techniques (e.g., mist netting, radio-telemetry, and acoustic detection) can aid in developing forest management recommendations which address both use and availability of roosting sites and foraging areas for the species assemblage under consideration.

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