Patterns of Florida Bonneted Bat Occupancy at the Northern Extent of Its Range

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Abstract

The Florida bonneted bat *Eumops floridanus* is a rare, endemic bat of South Florida that roosts in woodpecker cavities and anthropogenic structures such as roofing tiles, chimneys, and bat houses. The northernmost occurrences of the bonneted bat are from mature pine forests at the Avon Park Air Force Range, Florida. We used ultrasonic acoustic recorders to understand bonneted bat activity and habitat occupancy. We modeled occupancy using a hierarchical Bayesian analysis and included site- and time-specific covariates of detection probability and site-specific covariates of occupancy. Probability of detection was low throughout Avon Park Air Force Range but increased with Julian date. In most habitats, occupancy was poorly estimated, except for flatwood mature pinelands where occupancy was low (0.23 ± 0.06). As distance from red-cockaded woodpecker colonies increased, occupancy decreased ($\beta = -1.19 \pm 0.26$ SD). At the northernmost extent of the range, and throughout much of the historic range, increasing the expanse of mature, fire-maintained forest systems will increase habitat for the bonneted bat and lead to faster population recovery.

Keywords: *Eumops floridanus*; Florida bonneted bat; forest cover; longleaf pine; red-cockaded woodpecker

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Introduction

The Florida bonneted bat *Eumops floridanus* (herein called "bonneted bat") is a federally endangered species endemic to South Florida, with a limited range in seven counties (U.S. Endangered Species Act [ESA 1973, as amended]; USFWS 2013). It is a large (40–65 g; Figure 1) bat that is active year-round and roosts in anthropogenic structures such as tile roofing, chimney structures, or bat houses and in palms and woodpecker cavities of live mature pines and dead pine snags (Angell and Thompson 2015; Gore et al. 2015; Braun de Torrez et al. 2016; Webb et al. 2021). The bonneted bat roosts in small colonies, which makes studying its population ecology and habitat needs challenging (Gore et al. 2015; Bailey et al. 2017a). Bonneted bats will roost in red-cockaded woodpecker *Picoides borealis* (RCW) cavities, and likely used these more frequently when distribution of mature southern pines, such as longleaf pine *Pinus palustris* and slash pine *Pinus elliottii*, was greater (Walker 2000). These fire-adapted ecosystems provided ideal open forests for bonneted bats to forage and roost (Angell and Thompson 2015; Braun de Torrez 2018a; Braun de Torrez et al. 2018b).

Figure 1. Photographs of the Florida bonneted bat *Eumops floridanus* and bonneted bat habitat from southern Florida, including (A) a Florida bonneted bat from Fred C. Babcock–Cecil M. Webb Wildlife Management Area, Florida, 2018; (B) typical longleaf pine *Pinus palustris* forest at Avon Park Air Force Range (APAFR), Florida; (C) biologists looking into a bonneted bat roost, APAFR, 2019. Photographs taken by R.A.S., K.A.P.

The northernmost roosts of the bonneted bat occur at Avon Park Air Force Range (APAFR), where there are stands of mature longleaf forest (Angell and Thompson 2015). Five active and inactive bonneted bat roosts at APAFR are in RCW cavities. As with RCWs, bonneted bats may have been more prevalent at APAFR when mature longleaf and slash pine forests were ubiquitous in south-central Florida (Belwood 1992). The bonneted bat roosts at APAFR are considerable distances from the nearest bonneted bat population along the Peace River approximately 40 km southeast. The isolation of populations provides representation, and conservation of these populations is critical for recovering bonneted bat populations and delisting the species (Smith et al. 2018; Austin et al. 2022). The discovery of bonneted bats at APAFR (Angell and Thompson 2015) gives promise that other roosts exist in similar forested systems in south-central Florida, and it heightens the importance of conserving each isolated small population.

Current land management at APAFR is a balance between maintaining historic habitat types, managing pine plantations, conserving native species, reducing natural fuel hazards, and conducting daily military activities. The APAFR actively conserves habitat for rare species, like the RCW, Florida scrub jay *Aphelocoma coerulescens*, and Florida grasshopper sparrow *Ammodramus savannarum*, and bonneted bats. To accommodate the varied land-use demands, APAFR needs to understand where these rare species are, how they use the available habitats, and how to minimize land management activities that threaten the species and their habitats. For bonneted bats, biologists identify habitat use by collecting ultrasonic acoustic records throughout the range. In this study, we use those recordings to estimate bonneted bat habitat use and use environmental and location-specific covariates to inform habitat occupancy and detection probability.

Study Site

We conducted this study at APAFR, which is a 42,900-ha air-to-ground training complex with 40,000 ha undeveloped lands in Polk and Highland counties, Florida (elevation = 37 m; Figure 2). Wildfires regularly occur at APAFR, ignited by lightning strikes and unintentionally by ongoing military training. In addition, prescribed fire is used to reduce fuel loads and maintain pyrogenic-adapted land cover types, such as longleaf pine forest, oak *Quercus* scrub, and dry prairie. The application of prescribed fire at APAFR contrasts the surrounding lands where fire was suppressed in past decades. The wet season of APAFR typically lasts from mid-May to November, with warm temperatures (18–32°C) and ample precipitation (89 ± 27cm/y), and the dry season (November to mid-May) has comparatively cooler temperatures and less precipitation (12–25°C, 42 ± 15cm/y; Duever et al. 1994; Slocum et al. 2010).

Roosting areas for the bonneted bat at APAFR are a mosaic of hydric flatwoods of South Florida slash pine *P. e. densa* and pine flatwood-savannahs of longleaf pine (Figure 1). The understory vegetation of hydric flatwoods is dominated by cutthroat grass *Panicum abscissum*, whereas longleaf pine flatwoods and savannahs are dominated by wiregrass *Aristida beyrichiana* and patchy woody shrubs, such as saw palmetto *Serenoa repens*. Other abundant land cover of APAFR includes managed mixed pine plantations of North Florida slash pine, South Florida slash, and longleaf pine, swamps of pond cypress *Taxodium ascendens* and bald cypress *Taxodium distichum*, hardwood hammocks, oak and pine scrublands, marshes, and grassland prairies (Figure 2). Less than 5% of APAFR is developed lands that include a cantonment area, roads, and a runway.

Methods

Acoustic call collection and analysis

We conducted acoustic surveys from November 21, 2018 to March 10, 2020, deploying autonomous recording units (ARU) with ultrasonic microphones (SM4BAT acoustic recorders and SMM_U2 microphones; Wildlife Acoustics, Inc., Maynard, MA) at 508 sites (Data S1, *Supplemental*

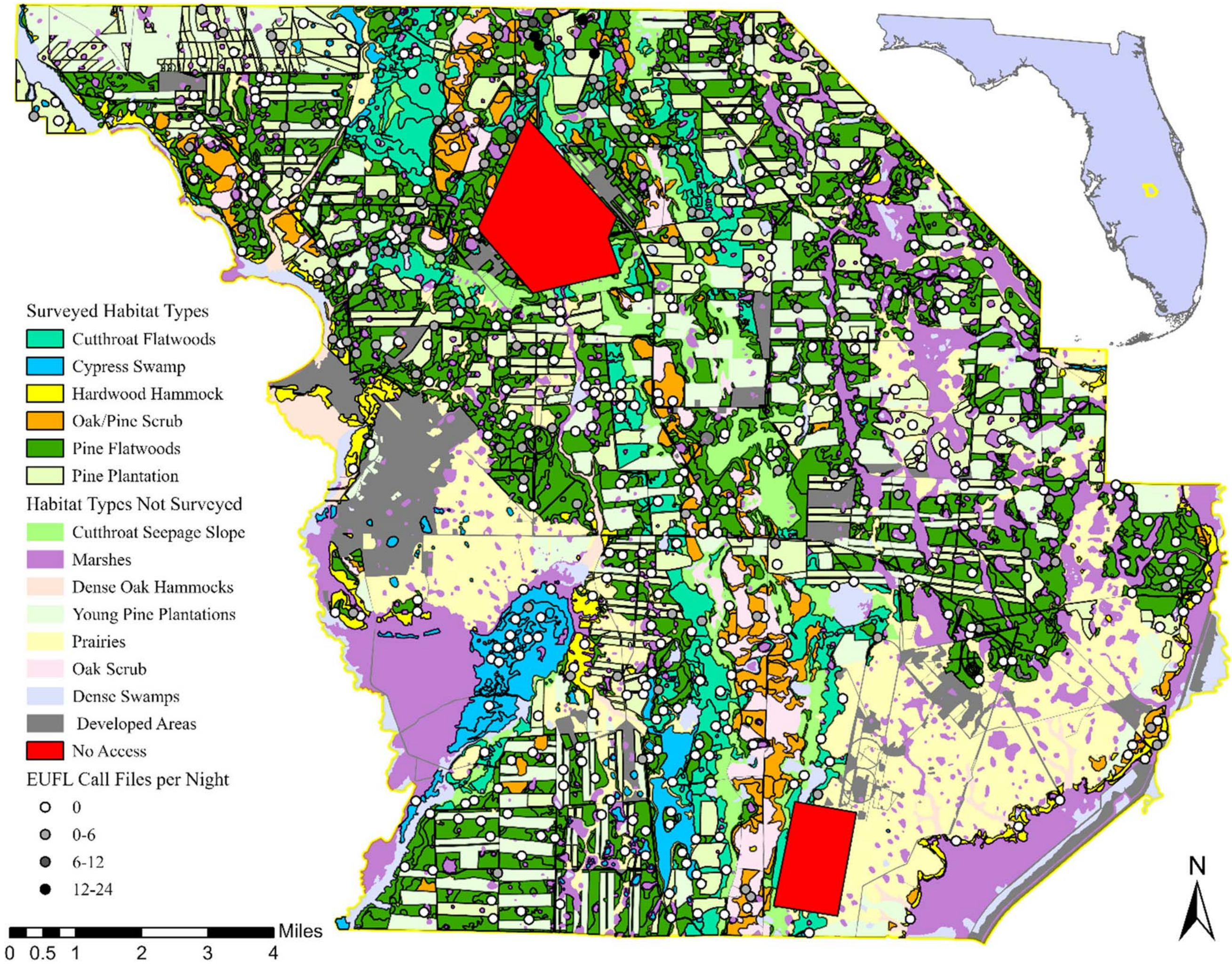

Figure 2. Map of Avon Park Air Force Range (APAFR) location in Florida and the land cover types and autonomous recording unit locations on APAFR, 2018–2020.

Material). We focused our surveys in areas that had high potential for bonneted bat roosting habitat and areas with higher potential for tree cavities or snags. We surveyed hydric flatwoods, pine flatwoods and savannahs, pine plantations over 15 y old, cypress swamps, hardwood hammocks, and oak and pine scrub, with some random points occurring in nearby grasslands, which encompassed 21,000 ha. We randomly selected ARU deployment locations that were separated by $>$100 m. We mounted ARUs on a pole and tripod, with microphones at the top of the pole (4.9 m) and started recording 30 min before sunset and ended 30 min after sunrise. We set ARUs to record with a minimum trigger frequency of 8 kHz because bonneted bats emit low-frequency calls between 10 to 18 kHz (Belwood 1992). Also, we set ARUs at a sample rate of 256 kHz, volume trigger level at 12 dB, minimum trigger window to 2 s, and minimum call duration of 2 ms (Braun de Torrez et al. 2018a). We deployed each ARU for more than three consecutive nights.

To analyze recorded call files we used Kaleidoscope Pro 5.4.1 (Wildlife Acoustics, Inc.) and the Bats of North America 5.4.0 classifier for Florida (Agranat 2013). We processed call files using the balanced or neutral setting to filter out noise, low-quality calls, or non-bat call files (Reichert et al. 2018), then used the auto-identification function software to identify bonneted bats. We defined a call file as a recording that had at least three distinct pulses (bat-emitted ultrasound) lasting between 2 and 15 s. We manually vetted all call files identified as bonneted bats, removing any false positives and removing bat social calls, insect noise, and bird vocalizations. We classified a call as coming from bonneted bat when the call had a characteristic frequency of 10–18 kHz, a maximum frequency of 16–22 kHz, average call duration of 10.2 ms, and an average call/s of 5.5.

Temporal and habitat-specific analysis covariates

We collected regional precipitation and temperature covariates from a weather station on APAFR and collected site-specific temperature using the summary files generated by the ARU at each survey location (Data S2, *Supplemental Material*). We calculated habitat covariates for each survey

Table 1. Covariates and their predicted impact on occupancy and detectability of Florida bonneted bat *Eumops floridanus* at Avon Park Air Force Range, Avon Park, Florida, 2018–2019.

Covariate	How applied	Predicted impact	
		Occupancy	Detectability
Autonomous recording unit (ARU) nightly temperature (mean, maximum, minimum)	Daily	—	Increase
Scotophase	Daily	—	Decrease
Nightly temperature (mean, maximum, minimum)	Daily	—	Increase
Nightly precipitation	Daily	—	Decrease
Nightly wind (mean, maximum, minimum)	Daily	—	Decrease
Tadarida brasiliensis activity	Daily	—	Decrease
Acoustic noise	Daily	—	Decrease
Distance from nearest *Picoides borealis* cluster	Site	Decrease	—
Distance from nearest *Citrus sinensis* grove	Site	Decrease	—
Area of nearest *Citrus sinensis* grove	Site	Increase	—
Distance from nearest wetland	Site	Increase	Increase
Area of nearest wetland	Site	Increase	Increase
Habitat type	Site	Decrease/increase	Decrease/increase
Distance from nearest tree within 100 m	Site	Increase	—
Height of nearest tree within 100 m	Site	Increase	—
Canopy radius (m) of nearest tree within 100 m	Site	Decrease	—
Canopy cover within 100 m	Site	Decrease	—
Percent canopy cover within 100 m	Site	Decrease	—
Crown area (m^2) within 100 m (mean, maximum, minimum)	Site	Decrease	—
Height of trees within 100 km (mean, maximum, minimum)	Site	Decrease	—
Canopy radius (m) of trees within 100 km (mean, maximum, minimum)	Site	Decrease	—
Days since last forest fire	Site	Decrease	—

location in ArcGIS Pro 2.6.5 (ESRI, Redlands, California) using land cover feature layers, and used remote-sensed light detection and ranging (LIDAR) data (October 2018) in R (v 3.5.0) to determine tree stand covariates within 100 m of each ARU (Beucher and Meyer 1993; Popescu and Wynne 2004; Plowright 2018; R Core Team 2018). We identified individual trees and their canopy in the "Forest Tools" package by setting the minimum tree height to 2 m and defining the dynamic window size (lin $\leftarrow$ function(x){x0.05 $+$ 2}; Popescu and Wynne 2004). Using burn history data, we determined the date since last burn at each ARU location.

For modeling detection probability (p), we used weather covariates of maximum, minimum, and mean overnight temperature range on ARU environmental data and from a nearby weather station (Avon Park, FL; 27.61°N, 81.51°W). We used weather station data of total nightly precipitation, and maximum, minimum, and mean wind speed. We used ARU-specific covariates of total number of call files autoidentified as Brazilian free-tailed bat *Tadarida brasiliensis* (TABR) calls and noise. Also, we used habitat covariates that aggregated the major habitat types at APAFR, including mature flatwood pinelands (flatwoods, which included hydric flatwoods and pine flatwoods), pine plantations (plantations), scrubby flatwoods and sandhills (scrub), oak hammock (oak), and cypress swamplands (swamp). An additional habitat type (prairies) was not included in the original sampling design; however, some ARUs were placed in pine plantations that had been clearcut and resembled grassland prairies. We used Julian date because bonneted bats have increased detection probability later in the year, and we created a covariate for winter and summer months when dominant male bonneted bats show higher activity (January–March, July–August; Braun de Torrez et al. 2020).

For modeling occupancy, we used covariates of the six major habitat types used to model p, and distances to and sizes of particular land features (Table 1). We used distance to nearest RCW cluster, distance to nearest orange *Citrus sinensus* grove, area of nearest orange grove, distance to nearest wetland, and area of nearest wetland. Also, we used ARU-specific landscape measurements within a 100-km radius pertaining to forest canopy cover, forest crown area, tree heights, and canopy radius (Table 1). In addition, we used days since last fire as a covariate. To test if bonneted bat detections are lower during periods of high TABR activity, we calculated the number of call files autoidentified as TABR at each ARU and used those as ARU-specific covariates of detection. To detect if high levels of insect noise interfered with our ability to detect bonneted bats, we calculated the number of noise call files recorded at each ARU location.

Models and analysis

We used Bayesian hierarchical occupancy models to estimate occupancy probability assuming imperfect detection (Royle and Dorazio 2008; Bailey et al. 2017). We mean-centered and standardized occupancy and detection covariates to speed Markov chain Monte Carlo (MCMC) convergence and modeled detection probability first, while holding occupancy time dependent (Morin et al. 2020). We used JAGS v 4.3.0 launched from RStudio v 1.3.1073 with the R2jags library (Su and Yajima 2021) for Bayesian estimation of model parameters via MCMC samples of posterior distributions. We input each covariate as a random effect using a vague, normally distributed (N[0,0.01]) prior on logit-

Table 2. Covariates with ≥50% inclusion in variable selection runs and estimated effect size (β) and 95% credible interval (CI) for occupancy and detectability of Florida bonneted bats *Eumops floridanus* at Avon Park Air Force Range, Florida, 2018–2019.

Detectability (habitat)	Percent inclusion	β (95% CI)	Parameter (95% CI)
Flatwoods	100	−2.52 (−2.74, −2.32)	0.08 (0.06, 0.09)
Grass/prairie	50	−2.67 (−3.11, −2.28)	0.07 (0.04, 0.09)
Oak	100	−4.19 (−5.54, −2.84)	0.02 (0.00, 0.06)
Pine plantation	100	−2.65 (−3.04, −2.28)	0.07 (0.05, 0.09)
Scrub	100	−2.39 (−2.89, −1.93)	0.09 (0.05, 0.13)
Swamp/marsh	100	−2.33 (−3.24, −1.58)	0.10 (0.04, 0.17)
Julian date	100	0.41 (0.27, 0.55)	0.60 (0.57, 0.63)
Occupancy (habitat)			
Flatwoods	100	−1.25 (−1.72, −0.72)	0.23 (0.15, 0.33)
Grass/prairie	57	−0.55 (−8.80, 8.82)	0.38 (0.00, 1.00)
Pine plantation	53	−0.47 (−8.87, 8.92)	0.39 (0.00, 1.00)
Area of nearest wetland	50	−0.26 (−8.80, 9.00)	0.44 (0.00, 1.00)
Distance to nearest *Citrus sinensus* grove	72	−0.43 (−8.17, 8.15)	0.40 (0.00, 1.00)
Distance to nearest *Picoides borealis* colony	100	−1.19 (−1.70, −0.72)	0.24 (0.15, 0.33)

scale parameters (Kery and Royle 2015). Posterior samples were ranged on 50,000 MCMC samples of posterior distributions of three chains, following a burn-in of 10,000. We assessed convergence of MCMC chains using trace plots and Gelman–Rubin diagnostics ($\hat{R}$). Convergence was reached for all parameters according to the criteria $|\hat{R} - 1| < 0.1$ (Ntzoufras 2009). We standardized all covariates to speed MCMC convergence.

We evaluated models using an indicator variable selection process (Hooten and Hobbs 2015). We built parameter weights for covariates, which depict the percentage of time a particular covariate was included in the model iteration (Kuo and Mallick 1998). We ran models with the full suite of covariates and removed any covariates that were included in less than 50% of the iterations. We reran the analysis with covariates that were included in ≥50% of iterations.

Results

We conducted acoustic recording at 498 sites at APAFR and deployed ARUs from 3 to 25 nights (mean: 5 nights). Acoustic analysis was not conducted at nine ARUs because of recording errors. Some ARUs recorded for multiple weeks because weather and military activity prevented retrieval. We recorded bonneted bats at 128 locations and estimated that bonneted bats could be at 166 locations (95% credible interval [CI]: 149 – 188). The best model for detection probability included covariates of Julian date and habitat type. Detection probability was comparably low in all habitat types ($p = 0.07$–0.10 ± 0.01–0.04 SD), but detection probability was substantially lower in oak habitats ($p = 0.02 \pm 0.01$ SD, Table 2). Including the covariate Julian date increased p ($\beta = 0.41 \pm 0.07$ SD).

The best model for occupancy included three habitat types, including pine plantations, prairies, and flatwoods. Occupancy was greatest in plantations ($\psi = 0.39 \pm 0.33$ SD), then prairies ($\psi = 0.38 \pm 0.32$ SD), and then flatwoods ($\psi = 0.23 \pm 0.06$ SD), but was poorly estimated in all but flatwood habitats (coefficient of variation [CV] > 50%). Occupancy decreased as distance to a RCW colony increased ($\beta = -1.19 \pm 0.26$ SD, Figure 3). Also, occupancy decreased as the area of nearest wetland increased ($\beta = -0.26 \pm 4.01$ SD) and as distance to nearest orange grove increased ($\beta = -0.42 \pm 3.05$ SD), but these impacts are poorly estimated.

Discussion

Bonneted bats were detected in all the APAFR habitat types included in this analysis, including scrub, swamp, flatwoods, prairies, and pine plantations, but only occurred in pine plantations, flatwoods, and prairies often enough to produce estimates of occupancy. Additionally, only occupancy estimates in flatwoods habitats produced reasonable estimates of variability. Flatwoods habitats include all native, old-growth longleaf and slash pine where bonneted bat roosts occur at APAFR. It is these mature pine stands where RCWs and the cavities they build are more available as bonneted bat roosts. Thus, it is not surprising that two of the best predictors of bonneted bat occupancy are the presence of flatwoods habitat types and the distance to RCW clusters. At APAFR there are 45 active clusters and 8

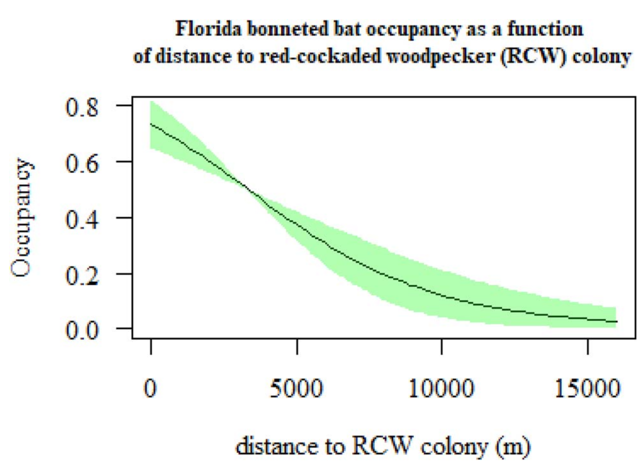

Figure 3. Florida bonneted bat *Eumops floridanus* occupancy and distance to red-cockaded woodpecker *Picoides borealis* colony at Avon Park Air Force Range, Florida, 2018–2019.

inactive clusters, with 229 artificial cavities and 119 natural cavities in 348 cavity trees. The land cover throughout the bonneted bat's range includes developed and undeveloped lands, and the rangewide analysis of Bailey et al. (2017b) did not find bonneted bats preferentially using pinelands. We believe our analysis at APAFR showed bonneted bat occupancy closely associated with flatwood pinelands because bonneted bats roost in tree cavities of mature pines, and our analysis did not include developed areas that were a minor land cover at APAFR. Although we did not include developed areas as a habitat type for this study, there were multiple ARUs near developed areas that likely would have detected bonneted bats if they occurred in developed areas. We would like to include a covariate of distance to developed lands that includes areas off APAFR as a follow-up analysis.

The inclusion of prairie habitats for bonneted bat occupancy may allude to bonneted bats' need for open foraging habitat (Voigt and Holderied 2012). Bonneted bats frequently use agricultural lands, likely as feeding habitats, and the most-similar, open habitat types on APAFR are prairie grasslands (Bailey et al. 2017b). The nearest agricultural lands at APAFR are orange groves, and distance to nearest orange grove was an informative, albeit poorly estimated, covariate for estimating bonneted bat occupancy. We believe that prairie habitats and nearby orange groves provide necessary, proximate insect-rich feeding sites (Simanton 1960; Swengel 2001). The loss of southern longleaf and slash pine forests and suppression of low-intensity, short-return fire intervals that limited understory development in most remaining forests have greatly reduced the availability of open prairies in mature forests (Croker 1987). Broad swaths of recently burned forest, with limited vegetative clutter, may have been the primary hunting grounds of bonneted bats. Agricultural lands may now act as surrogate hunting resources for molossid bats (Cleveland et al. 2006; Noer et al. 2012), which may explain their inclusion in bonneted bat occupancy analyses. However, agricultural lands may not provide lepidopteran prey that molossid bats prefer (Krauel et al. 2018). These habitats may not include as much moth diversity and biomass as natural, fire-maintained southern pine grasslands (Armitage and Ober 2012).

Pine-dominated landscapes cover a large proportion (50%) of APAFR, but only a small fraction ($\sim$13%) of these pinelands has the mature longleaf and slash pines that would provide roosting habitat for bonneted bats. Currently, there is one active bonneted bat roost, one inactive roost, and three roosts that are no longer viable. All roosts are in woodpecker cavities in mature longleaf pines, except a temporary roost that was under loose bark. The inviable roosts are in trees damaged by hurricanes, in cavities degraded by woodpecker activity, or in use by other species, such as big brown bats *Eptesicus fuscus* or Brazilian free-tailed bats. Efforts to increase bonneted bat habitat at APAFR will require expanding the availability of mature pinelands for the woodpeckers that create bonneted bat roosts. Actively managing forests with historic burning regimes will increase forest types and structure that support habitat for bonneted bats and other rare species (Van Lear et al. 2005; Braun de Torrez et al. 2018a; 2018b). Restoration of longleaf pine forests at APAFR using natural fire regimes and appropriate silviculture practices (Brockway et al. 2005) will increase habitat suitability for bonneted bats by increasing expanses of mature pines for roost availability and open space for hunting prey and the insect communities they feed on (Braun de Torrez 2018b).

Of interest, all active and inactive bonneted bat roosts are only along the northern edge of APAFR where mature pinelands are most abundant. Bonneted bat distribution models suggest that additional habitat exists in the southern sections of APAFR and Polk County (Bailey et al. 2017b). Expanding mature longleaf forests southward would increase the availability and viability of habitat for bonneted bats and RCW that create cavity roosts. Contiguous forests would increase the success of recovery efforts by connecting bonneted bat habitat and populations and increasing security from stochastic weather events such as the increasing frequency and severity of hurricanes (Zampieri et al. 2020). Besides creating forests more attractive to the woodpeckers that create natural cavities, artificial bat boxes have proved to be viable bonneted bat roosting alternates (Bailey et al. 2017a). However, even in areas where bat boxes have been successful, there is an abundance of flatwood forests similar to the mature pine stands of APAFR (FWC 2003). Installation of bat boxes in mature pine stands may provide roosting alternatives for bonneted bats when RCWs are unavailable to build natural roosts.

This study is the first to assess bonneted bat habitat use at APAFR; however, because we did not deploy ARUs in all available habitats we cannot assess habitat use in unsampled land cover types (developed areas). Although bonneted bats tend to avoid developed areas (Bailey et al. 2017b), future sampling in these habitats will aide in understanding use patterns at APAFR. As further acoustic sampling refines bonneted bat habitat use at APAFR, sampling tools that optimize detection of rare or clustered species can increase efficiency of future sampling design (Brown et al. 2013).

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Florida bonneted bat *Eumops floridanus* (EUFL) ultrasonic acoustic data from 2018 through 2020 from Avon Park Air Force Range, Polk and Highland counties, Florida. The first column represents the location label, and each subsequent column is the detection (1) or failure to detect (0) nightly EUFL acoustic file detection history.

Available: https://doi.org/10.3996/JFWM-22-055.S1 (32 KB XLSX)

Data S2. Site-specific landscape and vegetation covariates from 2018 through 2020 used for modeling Florida bonneted bat *Eumops floridanus* occupancy at Avon Air Force Base, Polk and Highland counties, Florida. The first column represents the location of acoustic recording and each column represents the landscape- or vegetation-specific attributes of that site. There is a separate tab in the worksheet to define the covariates and their abbreviations.

Available: https://doi.org/10.3996/JFWM-22-055.S2 (184 KB XLSX)

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