



Impact of land use and climate on the distribution of the endangered Florida bonneted bat

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Understanding the distributions and environmental associations of rare species is a critical 1st step in their conservation and management. Federally endangered Florida bonneted bats (*Eumops floridanus*) are endemic to southern Florida and are believed to have one of the most limited geographic distributions of any bat in the United States. We conducted a large-scale acoustic survey of 330 points spread across approximately 38,000 km² over a 2-year period and used a hierarchical Bayesian approach accounting for imperfect detection to model the distribution and environmental associations of the Florida bonneted bat. Bat occupancy was negatively correlated with the amount of developed land within 5 km of the sampling point and positively correlated with the amount of crop-based agriculture within 5 km of the sampling point. Bat occupancy probabilities increased with the 30-year mean for minimum spring temperature and levels of annual precipitation, and decreased with the 30-year mean for levels of spring precipitation. Bat detection was positively influenced by Julian date and minimum temperature of the survey night. This study offers new insight into the habitat use of this endangered species. Results confirm that predicted changes in land cover and climate will be threats to the Florida bonneted bat.

Key words: acoustics, Chiroptera, conservation, endangered species, Florida, occupancy

Federally endangered Florida bonneted bats (*Eumops floridanus*; Family Molossidae) are endemic to southern Florida and are believed to have one of the most limited geographic ranges (approximately 12,000 km²) of any North American bat (Belwood 1992; Florida Fish and Wildlife Conservation Commission [FWC] 2011). The Florida bonneted bat (hereafter bonneted bat) is 1 of just 9 species of bat listed as endangered under the U.S. Endangered Species Act (ESA). Previous arbitrary acoustic survey efforts documented bonneted bats in 7 counties in southern Florida (U.S. Fish and Wildlife Service [USFWS] 2013). However, these surveys were limited by their equipment, temporal sampling windows, and systematically biased in favor of presumably “good” habitat (e.g., pine-dominated natural areas). Accordingly, the distribution of this endangered bat remains largely unknown (Marks and Marks 2012; FWC 2013).

Environmental factors that influence the occurrence of bonneted bats also are virtually unknown. Bonneted bats have been

detected in a variety of habitats including urban, agriculture, uplands, and wetlands (Marks and Marks 2008, 2012; USFWS 2013), but there is not rigorous information on selection or preference. What information does exist is largely speculation based on incidental observations. Other species of molossid bats appear to benefit from urbanization and selectively forage in developed areas (Scanlon and Petit 2008; Threlfall et al. 2011). The bonneted bat was first reported from urban areas in southeastern Florida, where it has been documented roosting under barrel tiles on roofs, in chimneys of houses, and in palm trees since the 1930s (Barbour 1936; Belwood 1992; Timm and Genoways 2004; Gore et al. 2015). It has also been suggested that bonneted bats select pineland, based on records of roosts in longleaf pine and slash pine (*Pinus palustris* and *P. elliottii*—Belwood 1992; Angell and Thompson 2015; Braun de Torrez et al. 2016), and forage in pine flatwoods (USFWS 2013).

The lack of reliable information on the distribution and environmental associations of the bonneted bat hinders the

development of effective conservation and management plans for this species. Changes in climate and land cover are listed as 2 major threats (USFWS 2013). Southern Florida is expected to undergo extreme land cover changes over the coming decades as a result of increasing development. In addition, most climate models suggest that the temperature of tropical southern Florida will increase as a result of climate change (Misra et al. 2011). The bonneted bat's restricted range provides a unique opportunity to investigate the factors that influence a bat's distribution throughout its entire geographic range.

The goal of this study was to investigate the distribution and environmental associations of the bonneted bat. The specific objectives of our study were to 1) investigate the distribution of the bonneted bat throughout its geographic range, 2) identify environmental associations that influence the distribution of the bonneted bat, and 3) determine factors influencing detection of the bonneted bat, which can be used to make recommendations for monitoring efforts. Other bats within the genus *Eumops* have a Neotropical distribution (Best et al. 1997; Barquez et al. 2012); thus, we predicted bonneted bats would be found more often in areas with higher minimum temperatures. We also predicted that bonneted bats would be found more often in pine forest and in developed areas, based on previous observations of the species.

MATERIALS AND METHODS

Study area.—Our research was conducted in all counties in southern Florida with a known or suspected occurrence of the bonneted bat (Fig. 1A). South Florida has a subtropical to tropical climate, with a wet summer and a dry season that extends

from mid-autumn through late spring (Duever et al. 1994). The major source of rainfall is thunderstorms (Duever et al. 1994). Highest mean annual precipitation totals are found along the east coast (Hialeah = 178.77 cm) compared to the west coast (Venice = 128.22 cm—Southeast Regional Climate Center [SERCC] 2015).

Temperatures rarely drop below freezing in most of the study area, but the northern portion (Polk and Osceola counties) averages 1–2 freeze days annually (SERCC 2015). The warmest month is August, with average temperatures around 27°C in the northern part of the study area and 28.5°C–29°C south of Lake Okeechobee. The coolest month is February, when temperatures average 15.5°C in the interior and northern part of the study area.

Site selection.—Using ArcMap 10.1 (ESRI, Redlands, California), we established a grid system comprised of 5 × 5 km cells across southern Florida, similar to the Bat Grid and North American Bat Monitoring Program (NABat) survey protocols (Hayes et al. 2009; Loeb et al. 2015). To assure access, we excluded grid cells that were located > 2 km from any roads. We classified land use of grid cells in the study area by simplifying the Florida Natural Areas Inventory (FNAI) classifications into 4 major categories: agriculture, developed, upland, and wetland (Supplementary Data SD1—FNAI 2012). We used the ‘Tabulate Area’ feature in the Spatial Analyst toolbox in ArcMap to determine the most abundant land cover type in each grid cell. We classified each cell according to this land cover type, and then randomly selected 17 grid cells of each of the 4 land cover types for bat sampling during 2 field seasons. We used the ‘Create Random Points’ feature in the Data Management toolbox in ArcMap 10.1 to place 5 random

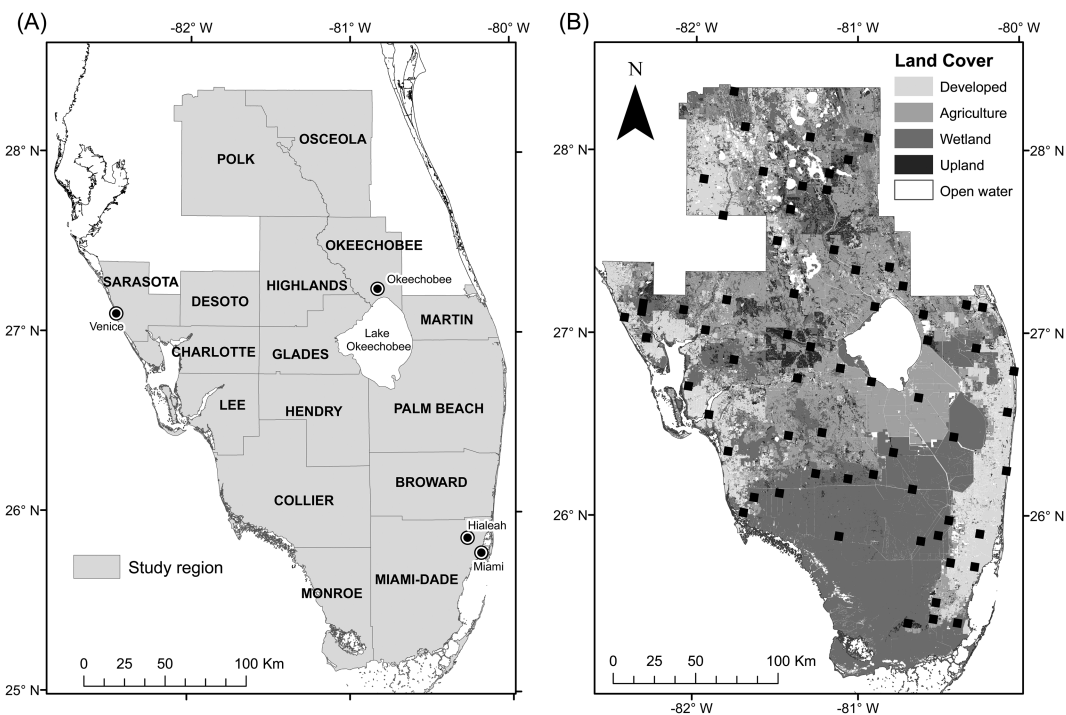


Fig. 1.—Our study area in southern Florida. Maps show (A) all counties included in our study area and (B) land cover of our study area. Black squares represent grid cells that were acoustically sampled for bonneted bats (*Eumops floridanus*) from January–June 2014 and January–May 2015.

sampling points in each cell to reduce biases from spatial variation (Hayes 2000). We placed each point > 400 m from other points.

Acoustic surveys.—We used acoustic recording equipment to survey for bonneted bats. Acoustic methods are effective for bat species with distinctive echolocation calls (Hayes 2000; Hayes et al. 2009). Bonneted bats have a low-frequency call that is easily distinguishable from that of other species of bats in southern Florida (Belwood 1992). We used SM2BAT+ detectors with SMX-US microphones (Wildlife Acoustics, Maynard, Massachusetts) for acoustic surveys. All detectors were set to record continuously from 15 min before sunset to 15 min after sunrise. We elevated each microphone to 3.4 m and positioned them horizontally with a slight downward tilt (Agranat 2014). We tested microphones once per week with an ultrasonic calibrator (Wildlife Acoustics), and replaced them when the calibrator read -36 dB.

We surveyed 20 January–13 June 2014 and 13 January–12 May 2015, visiting each cell 3 times each year, separating each visit by > 3 weeks. During each visit, detectors recorded bat activity 2–3 nights. We placed each detector in a location < 100 m from each randomly generated point to maximize the probability of detecting bats (e.g., in open areas—Ormsbee 2010). The majority of points in developed and agricultural cells were located on private land. If access permission was denied, we moved to the next closest property until permission was granted.

During 2014, we set out a detector at each of the 5 points per cell during the 1st visit. Due to equipment and logistical issues, we sampled only 4 points in each cell during the 2nd and 3rd visits. We randomly rotated the 1 point that was not sampled, ensuring each point was surveyed for ≥ 4 nights per year. In 2015, we sampled all 5 points during all visits.

Detection covariate sampling.—Many bats are more active as temperatures increase (Rodhouse et al. 2015). To quantify the influence of temperature on detection, we programmed the SM2+ detectors to record the minimum temperature from each survey night (*surveytemp*). To account for potential changes in detectability resulting from seasonal movements, phenology, and increases in detection of volant juveniles, we converted the date of each survey to Julian date (*Jdate*) and used it as a covariate.

Occupancy covariate sampling.—We used ArcGIS 10.1 to derive a number of metrics to reflect patterns of land cover. We estimated the average canopy cover (*cc*) in each grid cell using the National Land Cover Dataset (NLCD—Homer et al. 2015) and the % pine in each grid cell dominated by pine (*Pinus* spp.), as identified by FNAI.

We divided the 4 original land cover categories used to stratify cells into 8 subcategories. We divided agricultural land cover into rangeland (improved pasture or unimproved-woodland pasture) and crop-dominated agriculture, and separated uplands into non-forested uplands (i.e., dry prairies, palmetto prairies, scrub, shrub and brushland, and barren and outcrop communities identified by FNAI) and forested uplands (Supplementary Data SD1). We also separated wetlands into

3 categories: open water, non-forested wetlands, and forested wetlands (Supplementary Data SD1). We calculated the percent of each cell covered by forested wetlands (*forest.wetland*), non-forested wetlands (*non.wetland*), forested uplands (*forest.upland*), non-forested uplands (*non.upland*), crop-dominated agricultural areas (*ag*), rangeland (*range*), developed areas (*developed*), and open water (*water*).

We used the National Oceanic and Atmospheric Administration's 1981–2010 climate normals available from the Southeast Regional Climate Center (SERCC) to represent historical climate data. We determined the average annual minimum temperature (*mintemp*), average annual precipitation amounts (*precip*), average spring (January–May) minimum temperatures (*spring.mintemp*), and average spring precipitation amounts (*spring.precip*) from the climate center nearest each survey point.

Data analysis.—We analyzed acoustic files in Kaleidoscope Pro 3.1.0 using the “Bats of Florida 3.1.0” classifier (Wildlife Acoustics). Kaleidoscope Pro compares recorded calls to a known call library containing 1,631–130,435 calls for each species (Agranat 2012). We programmed Kaleidoscope Pro to identify to species each call sequence (a series of ≥ 2 calls with < 5-s gap between them—Britzke et al. 2002). We then manually looked at all calls identified by Kaleidoscope as either bonneted bat or NoID to ensure that no bonneted bat calls were missed or that no Brazilian free-tailed bat (*Tadarida brasiliensis*) calls were erroneously identified as bonneted bats. We classified calls with minimum frequency 10–18 kHz and maximum frequency 16–22 kHz as bonneted bat calls (B. Miller, Bat Sound Services, pers. comm.; C. Marks, Florida Bat Conservancy, pers. comm.).

We used Bayesian hierarchical occupancy models to investigate the distribution of the bonneted bat and elucidate the influence of environmental factors on its occurrence. We used a Bayesian approach to integrate hierarchical effects that address potential spatial autocorrelation among points in each grid cell. We also accounted for imperfect detection when estimating the state of occupancy (Royle and Dorazio 2008). We modeled the observation process as conditional on the latent occupancy state, $y_j(i) | z(i,k) \sim \text{Bern}(z[i] * p_{ij})$, where p_{ij} is the probability of detection during survey j given presence at point i , under a Bernoulli distribution. $Y_j(i)$ represents the detection history, with each taking a value of 1 or 0 representing “detection” or “non-detection” for survey j at site i . To speed Markov chain Monte Carlo (MCMC) convergence and improve interpretability, we standardized all covariates (Gelman and Hill 2007). We did not include correlated covariates ($r^2 > 0.60$ —Rodhouse et al. 2015) in interactive models.

We created models by 1st holding occupancy constant at the latent occupancy state and modeled the effects of *surveytemp* and *Jdate* on detection. We used JAGS v 3.4.0 (Plummer 2003) launched from Rstudio v.0.98 with the R2jags library (Su and Yajima 2015) to implement Bayesian estimation of model parameters via MCMC samples of posterior distributions. We input each covariate into the model as a random effect using vague, normally distributed [$N(0, 0.01)$] priors on all logit-scale

parameters (Kery and Royle 2015). Posterior summaries were based on 10,000 MCMC samples of the posterior distributions from 3 chains run simultaneously, thinned by a factor of 10, following an initial burn-in of 2,000. We assessed convergence of MCMC chains with trace plots and the Gelman–Rubin diagnostic (\hat{R}); convergence was reached for all parameters according to the criteria $|\hat{R} - 1| < 0.1$ (Ntzoufras 2009).

We evaluated models using a stepwise comparison predictive performance of each, removing covariates where the 95% credible intervals crossed zero and re-running the model after each covariate was removed (Kery and Schaub 2012). This approach was used rather than the deviance information criterion (DIC) because it is more robust when evaluating predictive performance of hierarchical models (Gelman et al. 2013). After a final model was selected for detection, we evaluated occupancy with *pine*, *mintemp*, *spring.mintemp*, *precip*, *spring.precip*, *developed*, *forest.upland*, *non.upland*, *forest.wetland*, *non.wetland*, *range*, *ag*, and *water* as covariates. Again, we used a stepwise approach, holding detection constant as a function of the best-fitting model found above. We reported all beta estimates and credible intervals from the final selected model and graphed the effects of all covariates included in the final model.

To better visualize the distribution of the bonneted bat, we rasterized the climate and land cover layers using the “raster” package in RStudio. We then converted the logit estimates to probabilities using the link function from the final model. Using these probabilities, we mapped the probabilities of bonneted bat occupancy throughout the study area.

RESULTS

Due to poor recording quality, we excluded 1 cell classified as agriculture and 1 classified as uplands from analysis. This left 330 points (66 cells) that were sampled during 2014 and 2015 (Fig. 1B). We recorded > 500 bonneted bat call sequences at 60 points. The best model for detection included *surveytemp* and *Jdate* as covariates. Julian date (*Jdate*) had the strongest effect on detection, with bonneted bats more likely to be detected later in the year ($\beta = 0.70$ [95% credible interval: 0.42–0.80]; Supplementary Data SD2). Minimum temperature of each survey night (*surveytemp*) was positively associated with detection probabilities ($\beta = 0.26$ [95% credible intervals: 0.03–0.50]; Supplementary Data SD2). Overall nightly detection probability was 0.29 (0.23–0.35). Based on the estimated detection probabilities, it would take 9 survey nights (1 detector per night) to determine with 95% certainty whether bonneted bats are present at a sampling point (Supplementary Data SD3).

The final model for occupancy included *developed*, *precip*, *spring.mintemp*, *spring.precip*, and *ag* as covariates that influenced bonneted bat occupancy probabilities. Developed areas (*developed*) had the largest effect ($\beta = -1.20$ [–1.92 to –0.63]), with occupancy probability decreasing with increasing amount of developed land (Fig. 2A). Precipitation (*precip*) had the 2nd largest effect ($\beta = 0.87$ [0.42–1.32]), the probability of occurrence increased with increasing precipitation levels recorded between 1981 and 2010 (Fig. 3A). Average spring

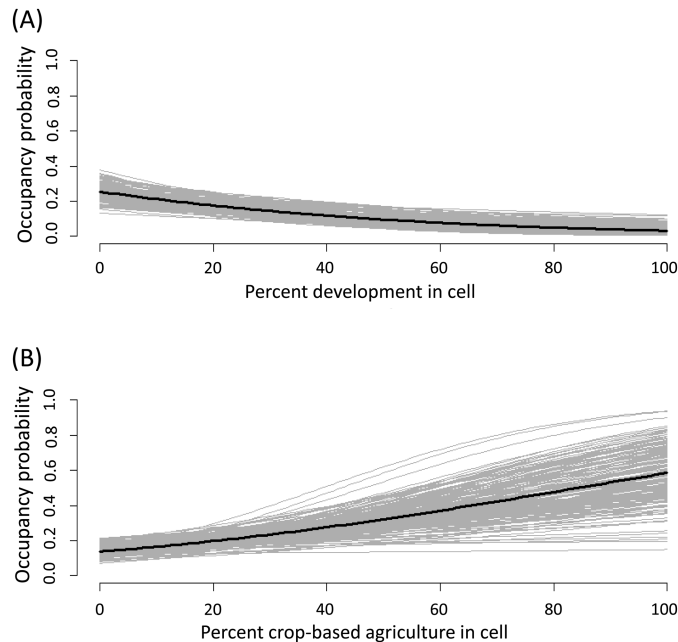


Fig. 2.—Association between the percent of grid cell classified as (A) developed land or (B) crop-dominated agriculture and the occupancy probability of bonneted bats (*Eumops floridanus*) acoustically surveyed in southern Florida in January–June 2014 and January–May 2015. Black lines show the posterior mean, and gray lines show the relationships based on a random posterior sample of size 200 to visualize estimation uncertainty.

precipitation levels (*spring.precip*) were negatively associated with occupancy ($\beta = -0.69$ [–1.10 to –0.32]; Fig. 3B). Average spring minimum temperature (*spring.mintemp*) had a relatively large effect ($\beta = 0.74$ [0.26–1.25]), with occupancy probability increasing with average spring minimum temperature recorded between 1981 and 2010 (Fig. 3C). Agriculture (*ag*) had a positive effect on occupancy ($\beta = 0.52$ [0.21–0.85]), with occupancy increasing with the amount of crop-based agriculture in the grid cell (Fig. 2B).

The final model estimated bonneted bats were present at about 77 (66–91) points, compared to our observed 60 points (Supplemental Data SD4). Mapping occurrences identified areas with relatively high predicted occurrence probabilities for bonneted bats throughout the southern portion of the peninsula, along the west coast, and just south of Lake Okeechobee (Fig. 4).

DISCUSSION

We determined that the range of the Florida bonneted bat is larger than previously known. The detection of bonneted bats in the northern portion of the study area suggests that the range of the bonneted bat may be even larger than documented in this study. Future surveys in additional counties along the northern portion of our study area would help elucidate the northern limit of bonneted bat presence in Florida. Although distribution cannot be directly linked to abundance, it is considered a reliable method for assessing population status at broad spatial scales (MacKenzie and Royle 2005; Jones 2011). Overall, bonneted

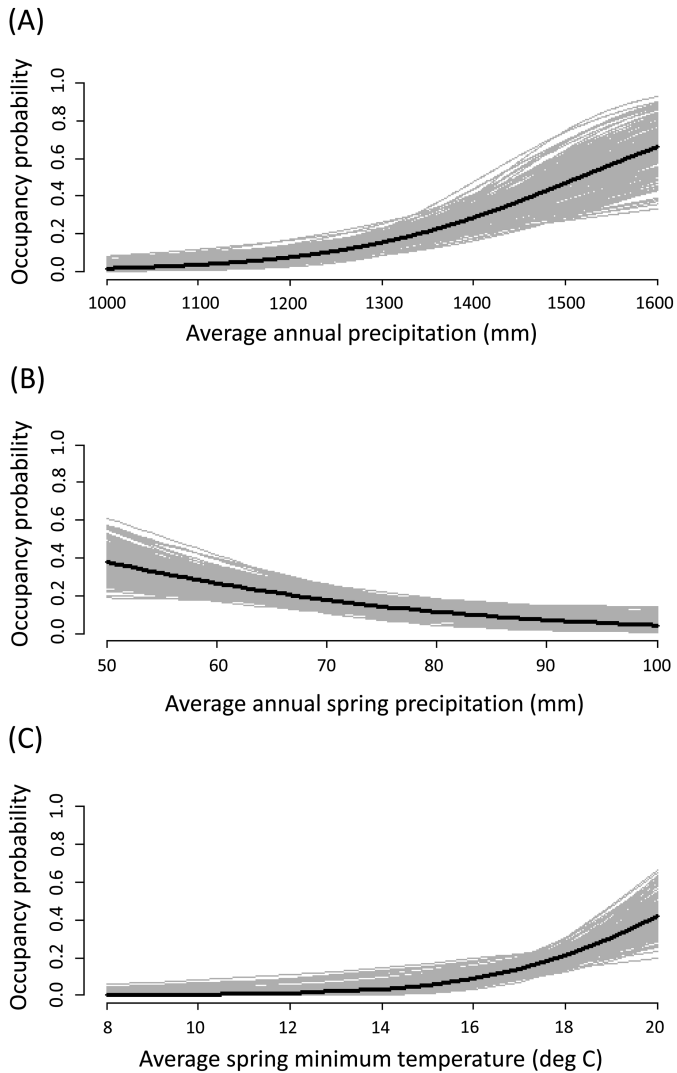


Fig. 3.—Association between (A) average annual precipitation, (B) average annual spring precipitation, (C) spring minimum temperature and the occupancy probability of bonneted bats (*Eumops floridanus*) acoustically surveyed in southern Florida in January–June 2014 and January–May 2015. Black lines show the posterior mean, and gray lines show the relationships based on a random posterior sample of size 200 to visualize estimation uncertainty.

bats were estimated to be present in > 20% of our study area, indicating that these bats may be more common than originally thought (Marks and Marks 2012; USFWS 2013).

Bonneted bats were detected in all land cover types investigated in this study; however, the environmental associations we found did not support our predictions. While previous studies have documented bonneted bats roosting and foraging in pine-lands (Belwood 1981; USFWS 2013), our results suggest that bonneted bats do not use these areas more than other land cover types. The belief that bonneted bats preferentially use pine forests was likely a result of the limited scope of previous investigations into environmental associations, or an indication that bats roost there and forage in other land use types.

Also contrary to our predictions, increased developed land was negatively associated with bonneted bat occurrence.

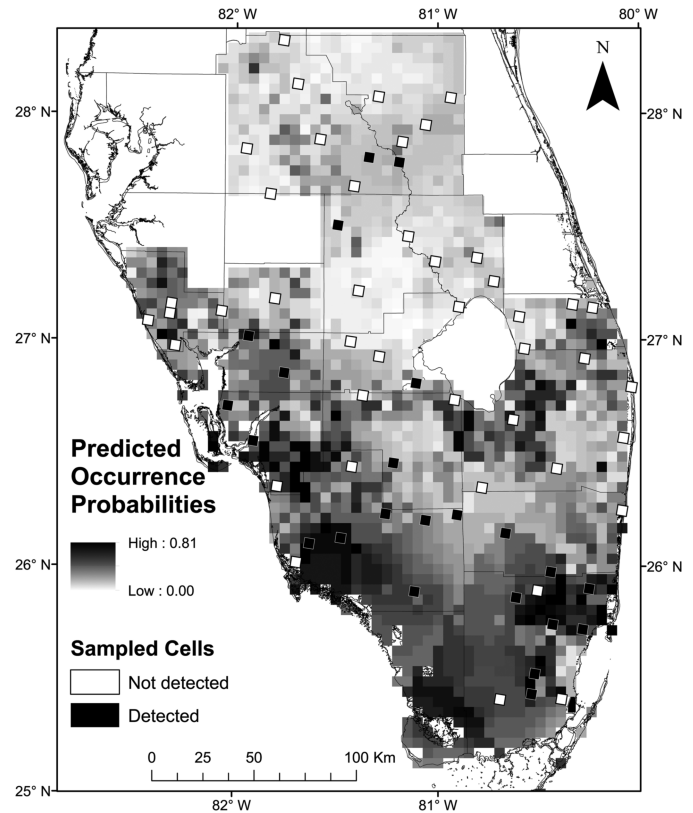


Fig. 4.—Predictive map showing the probability of occurrence of bonneted bats (*Eumops floridanus*) throughout the study area. Probabilities are derived from a Bayesian occupancy model including effects of amount of surrounding developed land and crop-based agriculture, and historical minimum temperatures, annual precipitation and spring precipitation levels. Sampled cells are included on the map; white outlined cells show where bonneted bats were not detected, and black outlined cells show where bonneted bats were detected.

Other studies have suggested molossid's wing structure pre-adapts them for foraging in urban areas where they can successfully exploit concentrations of insects around streetlamps (Scanlon and Petit 2008; Threlfall et al. 2011). Bonneted bats were first described from urban roosts in the 1930s (Barbour 1936), and have since been intermittently documented using urban environments (Timm and Genoways 2004; Gore et al. 2015). Despite this, Avila-Flores and Fenton (2005) noticed a similar trend to our study with the western mastiff bat (*E. perotis*), which was not recorded in Mexico City, Mexico, but was detected in forests surrounding the city. They hypothesized that the larger molossid (i.e., *Eumops* spp.) were not maneuverable enough to exploit insect prey amid the structural clutter that comes with development. This could explain why bonneted bats were negatively associated with urbanization, despite being observed roosting in urban areas (Timm and Genoways 2004; Gore et al. 2015). Our study also did not attempt to measure structural clutter in urban areas. Further data on the height of structures in relation to the foraging height of bonneted bats and into the abundance of prey in these areas could help to explain the negative association with urban areas observed in this study,

and why bonneted bats may be found in some urban areas but not others.

In contrast to developed land, crop-based agriculture is largely devoid of structural clutter (Williams-Guillen et al. 2016). In addition, well-irrigated crop fields often foster an abundance and diversity of insects, particularly in areas that experience prolonged dry seasons like southern Florida (Noer et al. 2012). Increased occurrence of bonneted bats in agricultural areas likely is a result of the combination of insect abundance in these areas and the ability of bats to successfully forage in these open spaces. Other species of molossidids, including Brazilian free-tailed bats (Cleveland et al. 2006), little free-tailed bats (*Chaerephon pumilus*), and Angolan free-tailed bats (*Mops condylurus*—Noer et al. 2012) have been documented selecting agricultural areas for foraging habitat.

Tropical temperatures of southern Florida create conditions that support a large number of Caribbean and Neotropical species (Webb 1999). The low probabilities of occurrence of bonneted bats in areas where historical mean minimum temperatures were below 15°C suggests bonneted bats are limited to southern Florida due to temperature, as predicted. This would be expected in the Americas, as the Molossidae family primarily is distributed throughout the Neotropics (Barquez et al. 2012). Additional evidence of cold sensitivity comes from a cold spell in 2010 resulting in the permanent disappearance and presumed mortality of one-half of the bonneted bats using a bat house in Lee County (USFWS 2013).

Bonneted bats were more common in areas with higher historical mean annual rainfall, but seemed to prefer areas with lower rainfall during the spring. System-wide productivity is consistently positively correlated with precipitation (Williams 1951; Silva et al. 2011); thus, it is expected that bonneted bats were found more commonly in areas with higher levels of precipitation. The negative association between bonneted bat occurrence and levels of spring precipitation may have to do with the diel timing of precipitation events. The majority of rainfall in southern Florida occurs during the summer wet season (Webb 1999), when maximum precipitation occurs during early to mid-afternoon (Schwartz and Bosart 1979). In contrast, maximum precipitation during the dry season (winter and spring) occurs during early to late evening (Schwartz and Bosart 1979), which roughly corresponds with peak insect activity (Kunz 1973). Nighttime precipitation has been shown to decrease activity levels of other species of bats (Kunz 1973; Fenton et al. 1977), likely as a result of increased thermoregulatory costs and decreased prey activity (Burles et al. 2009). If this was indeed occurring, we would expect to see a similar trend with other species of bats in southern Florida. When we ran a similar analysis on other species of bats recorded in southern Florida, we did not see the same trends in any other species. In addition, the variance in levels of spring precipitation between locations is small ($\sigma = 0.15$), indicating that the association is unlikely to be biologically significant. It is also possible that bonneted bats are responding to some other variable that we did not explicitly measure, which is correlated with levels of spring precipitation.

Southern Florida is an area that is expected to undergo dramatic changes in the coming decades. The human population of Florida is expected to grow by nearly 20,000,000 people by 2060, and the landscape of southern Florida is expected to become mostly urbanized (Zwick and Carr 2006). Southwestern and south-central Florida are expected to undergo the most extreme land cover changes in the state, with nearly all agricultural and private natural lands predicted to be converted to developed land (Zwick and Carr 2006). If these predicted land use changes occur, bonneted bats could see a dramatic contraction of suitable foraging areas.

These land cover changes likely will lead to changes in climate as well, with higher levels of development being associated with lower levels of annual precipitation and higher temperatures in southern Florida (Pielke et al. 1999). Additionally, scenarios for the state of Florida predict that temperatures will increase and rainfall patterns will shift as a result of climate change (van der Valk et al. 2015). The results from this study can be used to help predict how the bonneted bat will respond to these predicted changes.

These future scenarios highlight the need for continued monitoring of the bonneted bat to document potential shifts in the geographic range and status of this endangered species. Future monitoring efforts should survey each sampling point for ≥ 9 nights to have a 95% chance of detecting bonneted bats if they are present. Our results suggest that future monitoring efforts should be focused on warm nights later in the spring to maximize detection probabilities. The higher detection probabilities observed in the later months of both field seasons likely are a result of increased insect abundance due to increased temperatures, humidity, and precipitation (Williams 1951) influencing the bats' activity. Unfortunately, we cannot reliably extrapolate our results beyond May. While it is possible that detection probabilities of bonneted bats are higher during the summer months, surveying during this season would be difficult due to wet weather limiting access to many natural areas (Webb 1999).

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SUPPLEMENTARY DATA

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

Supplementary Data SD1.—Florida Natural Areas Inventory (FNAI) state-level land cover types grouped into broad land

covers used during site selection for acoustic surveys conducted for bonneted bats (*Eumops floridanus*) throughout southern Florida.

Supplementary Data SD2.—Association between (a) Julian date and (b) minimum temperature during each survey night and detection probability of bonneted bats (*Eumops floridanus*) acoustically surveyed in southern Florida from January–June 2014 and January–May 2015. Black lines show the posterior mean, and gray lines show the relationships based on a random posterior sample of size 200 to visualize estimation uncertainty.

Supplementary Data SD3.—The relationship between P^* , the probability of detecting bonneted bats (*Eumops floridanus*) at a point acoustically at least once during n surveys, and number of detector nights. The dashed line indicates 95% certainty to detect the species when present.

Supplementary Data SD4.—Posterior distribution of the number of points occupied by the bonneted bat (*Eumops floridanus*) based on acoustic surveys conducted in southern Florida in January–June 2014 and January–May 2015. Vertical line indicates the observed number of 60 occupied points.

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