EXAMINING BAT ECOLOGY IN AN UNDERSTUDIED REGION: THE TEXAS

GULF COAST

by

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DEDICATION

Dedicated to the memory of Michael James Farrand (1960–2019).

ACKNOWLEDGEMENTS

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LIST OF ABBREVIATIONS

Abbreviation	Description
AIC	Akaike Information Criterion
CBH	Columbia Bottomland Hardwood forest
DBH	Diameter at Breast Height
LABO	Eastern red bat (*Lasiurus borealis*)
LACI	Hoary bat (*Lasiurus cinereus*)
LAIN	Northern yellow bat (*Lasiurus intermedius*)
MYVE	Cave myotis (*Myotis velifer*)
NWR	National Wildlife Refuge
NYHU	Evening bat (*Nycticeius humeralis*)
PESU	Tricolored bat (*Perimyotis subflavus*)
RAWS	Remote Automatic Weather Station
TABR	Brazilian free-tailed bat (*Tadarida brasiliensis*)
SBNWR	San Bernard National Wildlife Refuge
WNS	White-nose Syndrome

ABSTRACT

I assessed activity and habitat associations of bats in and surrounding San Bernard National Wildlife Refuge on the Gulf Coast of Texas from May to August 2018 and 2019. My objective was to examine two major components of bat ecology in a region with no prior data: 1) nighttime activity and habitat use of all species and 2) day-roost use of evening bats (*Nycticeius humeralis*). I used autonomous acoustic detectors to assess nighttime activity of bats in various habitats across the refuge and recorded vegetation surrounding the deployment sites. I then conducted generalized linear mixed-effect models to assess drivers of bat activity. I also conducted Kruskal-Wallis non-parametric analysis of variance tests to determine differences in activity among habitats. For both analyses, I used the number of bat calls of each species in each year as response variables and habitat types and vegetation estimates as independent variables. Seven species of bats were detected and used all available habitats. Activity increased throughout the summer, likely because bat pups reached volancy. Alongside acoustics, I utilized radio telemetry to assess day-roost use of evening bats, an abundant species in the region. I radiotracked 11 evening bats to 9 unique roost locations. All bats roosted within a <1.0 km^2 area of an urban neighborhood, 3–5 km from a protected area. No bats switched roosts, contrary to most literature, which documents regular roost switching in evening bats. Roost trees were over twice as tall and generally greater in DBH, with less surrounding canopy cover and nearly 20-fold less understory vegetation than trees in the protected area. This study has determined baseline ecological data surrounding bats in an area with no previous

data. Acoustic detectors can continue to be deployed by biologists and allow long-term, year-round monitoring of bats. Repeated sampling of the refuge may allow researchers to examine changes in activity after the arrival of the disease white-nose syndrome. Preservation of large trees in the urban area has created bat roosts and allowed a population of tree-roosting bats to be present in a city. However, bats regularly use the protected tract of land potentially as foraging habitat. The combination of large trees with no understory clutter in the city and the preserved old-growth forest on the refuge may together provide the needed food and habitat resources for these bats. The telemetry study is the southernmost research on roosting ecology of evening bats, and as such, this population may be one of the first impacted by critical maximum temperatures.

I. DRIVERS OF BAT ACTIVITY ON THE COAST OF TEXAS

Introduction

Bats patrolling the night skies help control insect populations, decrease dependence on pesticides, and improve crop yields on farmlands, saving farmers billions of dollars annually. Insectivorous bats, one of the only predators of night-flying insects, deliver vital pest reduction and suppression in agricultural areas (Boyles et al. 2011). For example, the value of pest suppression ranged from $12 to $173 per acre in a cotton-dominated agricultural landscape in south-central Texas (Cleveland et al. 2006). These results extrapolate to bats being valued at tens of billions of dollars annually to the United States agricultural industry (Boyles et al. 2011).

In addition to pest-control services, abundant and diverse bat assemblages are excellent bioindicators of overall land management and habitat quality (Jones et al. 2009) because bats fill a wide range of ecological niches and are sensitive to environmental stressors (Jones et al. 2009, Stahlschmidt and Brühl 2012). This information becomes paramount as habitat fragmentation, disease, and anthropogenic stressors continue to affect bat populations negatively (Krusic et al. 1996). Using bats as indicators of system-level threats can inform land management with broad ecosystem goals. Specifically, determination of habitat use by bat species, or groups of species, provides baseline data vital to management and conservation of many species.

Texas has the greatest bat diversity of any U.S. state and is home to the largest known bat colony in the world (Iskali and Zhang 2015); however, the state faces numerous conservation challenges. Bats throughout the world, including Texas, face a suite of threats including wind energy, climate change, and disease (Frick et al. 2017,

Adams and Hayes 2018, Razgour et al. 2018). Texas produces more wind energy than any other state and is creating new large-capacity wind-energy facilities at a rapid rate (Sağlam 2018, American Association of Wind Energy 2019), which may negatively influence bat populations. The annual mean temperature in East Texas increased 0.7 °C, and annual precipitation increased 16.3% between 1970 and 2009 (Heo et al. 2015), which may be shifting selection pressures for wildlife species. Additionally, sea level is rising in Galveston Bay in southeastern Texas at a rate of 3.0–4.0 mm/year (Epps and Khan 2016). Rising sea levels may restrict access to roost sites and, when combined with tropical storms, impact bat populations (Sherwin et al. 2013). In January 2017, *Psuedogymnoascus destructans*, the fungus that causes White-nose Syndrome (WNS) was detected in Texas for the first time (Texas Parks and Wildlife 2017). As of March 2020, the first case of WNS has been confirmed in Texas (Texas Parks and Wildlife 2020).

Additionally, compared to some non-volant mammals, bats have been more difficult to research because of an unusual combination of life-history traits. Flight, nocturnality, diverse and dynamic home ranges, and relative taxonomic uncertainty for some groups are unique challenges to researching bats (Lim and Engstrom 2001). However, developments in acoustic technology now allow us to study these animals with a different approach.

Acoustic detectors record the high-frequency sounds emitted by echolocating bats and eliminate the need to capture, handle, stress, or alter the behaviors of the animals being monitored (Schwab and Mabee 2014). Acoustic studies also provide researchers with the ability to study multiple sites simultaneously and are generally less labor

intensive than capturing the animals. These methods provide a powerful approach to studying the distribution, ecology, and behavior of bats (Towsey et al. 2014). Technological advancements have allowed acoustic detectors to become a standard in the study and survey of bats globally (Rydell et al. 2017). However, acoustic analysis and species-identification software have limitations; thus, researchers should implement a method of cross-validation (Brigham et al. 2004, Russo and Voigt 2016).

To determine management actions that aim to benefit a specific taxa, it is important to consider habitat use at the landscape level, among stands within a landscape, and within stands (Krusic et al. 1996). Due to the drastic reductions in bat populations worldwide, it is crucial we develop a far greater understanding of the ecological requirements of bats. This information will allow the development of appropriate management plans and conservation policies. In understudied regions such as the Gulf Coast of Texas, baseline data becomes more critical to landowners when facing wildlife-management decisions.

The goal of this study was to assess the species-specific drivers of bat activity by analyzing habitat, environmental, and temporal variables on the Gulf Coast of Texas. Specifically, I 1) compared activity among habitats (bottomland hardwood, saline prairie, and upland prairie); 2) examined the effects of habitat (canopy cover and vegetation height) on bat activity; and 3) assessed the influence of weather on bat activity. I hypothesized that bottomland hardwood habitats would have greater activity than saline prairie and upland prairie habitats, because bottomland hardwood habitats are dominated by large trees and provide more roosting sites for bats. I predicted Julian day would have a positive relationship with activity of all bat species, as pup activity increases over

summer months (Davis et al. 1962). I also predicted canopy cover would affect bat

activity of some species positively and some negatively, due to variation of size, wing

loading, and aspect ratio among bat species (O'Keefe et al. 2014). Further, there is a

knowledge gap surrounding overall ecology of bats along the Gulf Coast of Texas. Land

managers often aim to create or conserve wildlife habitat by using various management

techniques and my goal is to use my results to inform these decisions.

Methods

I sampled bats at San Bernard National Wildlife Refuge (SBNWR) from May to

August 2018 and from May to July 2019. SBNWR is an 18,506-ha refuge located on the

Gulf Coast of Texas that is managed by the U.S. Fish & Wildlife Service (Figures 1–3).

The refuge features a diverse landscape of various habitat types and ages. U.S. Fish &

Wildlife Service staff conduct active management on some of the refuge and rest the

remaining stands. The three major habitat types include upland prairies, saline prairies,

and inland old-growth Columbia bottomland hardwood forests (CBH) (Rosen et al.

2008). These habitats are dispersed among the main refuge and 26 tracts of land across

Brazoria and Matagorda counties.

I surveyed bat activity acoustically at fixed points using autonomous acoustic

recording devices (Pettersson D500X Ultrasound Detector/Recorder, Pettersson

Elektronic, Sweden), commonly referred to as "detectors". I used 5–8 acoustic detectors

simultaneously on a rotating schedule around SBNWR, for 3-day intervals in 2018 and 4-

day intervals in 2019. I systematically surveyed 60 sites in 2018 (Figure 2) and 24 sites in

2019 (Figure 3) across the refuge. Sampling at each site was temporally replicated to

include 2 or 3 primary sampling occasions per year.

I placed microphones at a height of 3.5 m, angled upward at 45 degrees, in a direction with minimal clutter and obstructions that could negatively impact call quality. All detectors were set to identical sensitivity settings (trigger window = 2 s; file length = 15 s; division ratio = 8). All devices began recording at sunset and stopped recording at sunrise for each sampling period. In the event of equipment failure during deployment, all data were deleted and devices were redeployed at a later date.

I defined a bat pass as a sequence of 2 or more pulses separated by at least 2 seconds between passes (MacAodha et al. 2018). I used Sonobat 4.3.0 (Sonobat Bat Call Analysis Software, USA) to remove files that contained only noise, then used Sonobat auto-identification software (region pack TX[c20180819] southeast Texas) to classify and identify all acoustic files to seven common species based on region. However, the software combines *Lasiurus borealis*, and *L. seminolus*, because their calls are too similar to differentiate. Thus, both species are grouped as *L. borealis*.

I compared Sonobat 4.3 auto-identification outputs to combined identifications of two observers with less than one year of experience with manual identification. I matched greater than 25% of manually identified bat calls from Sonobat's most confident species identification in 2019 (n = 2,916). Observers matched Sonobat auto-identification output 81.1%. When assessing identification at a broader scale (high-frequency or low-frequency sonic groups), the software and manual observers match 94.9% of identifications. Due to the percentage of matches, I used the auto-identification software to classify this large, multi-season dataset. If the call is of high quality (greater echolocation signal than noise) the software provides an identification, if low quality (greater noise than echolocation signal), the call is omitted and identified as noise

(MacAodha et al. 2018). I selected the most likely species output by Sonobat as identification.

I collected weather measurements from the Remote Automatic Weather Station (RAWS) located on SBNWR property (28.86472 N, 95.56794 W) and operated by the Western Regional Climate Center. The RAWS is located 41.5 km from the furthest sampling location and less than 6.5 km from more than half of all sampling locations. The data collected by RAWS is public and can be accessed via the RAWS website (www.raws.dri.edu). I recorded: mean wind velocity (m/s), total precipitation (mm), minimum, mean, and maximum air temperature (°C), and relative humidity (%). To create independent variables, I averaged the weather variables, except precipitation, over each 3- or 4-day deployment period.

I also surveyed the structure and composition of vegetation surrounding each acoustic monitoring device. I conducted vegetation surveys along three, 25-m-long transects. Transects began at the detector and radiated outward in 3 directions: 0°, 120°, and 240°. Each transect had six sampling points at 5-m increments, beginning 1 m from the detector. Using a 2-m-tall Robel pole (Robel et al. 1970), I counted the frequency with which vegetation touched the pole at points spaced at 1-dm intervals along the pole (Fritts et al. 2016). I then averaged height of the 30 total points to create an index of vegetation height. I assessed canopy cover using a concave densiometer at the identical 30 points and used the mean of the readings to create an index of canopy cover. All vegetation and canopy cover measurements were recorded within the last 14 days of the 2018 and 2019 seasons to minimize temporal variation.

I scaled all numerical predictors (Skaug et al. 2011) using the equation: $x = \frac{x - \bar{x}}{x_{sd}}$

and then conducted correlation analysis (Pearson 1931). After omitting variables greater

than |0.7| until no remaining predictors correlated, I conducted 16 separate generalized

linear mixed-effect models (Skaug et al. 2011) to assess drivers of bat activity split by

individual species and year: seven individual species models for each of the 2 years as

well as a full activity model, not split by species, for both years. Independent fixed effects

included Julian day, total precipitation, and canopy cover. I constructed a global model of

uncorrelated predictors, outlined below:

$$Bat\ calls \sim Julian\ day +\ total\ precipitation\ +\ canopy\ cover$$

$$+\ (1\ |\ detector\ site)$$

I then determined the distribution of each species' calls to use as the response

variables. I fit each of the 16 individual models to distributions using Akaike's

Information Criterion corrected for small sample sizes (AICc) (Akaike 1974).

Distribution tests included: Poisson, zero-inflated Poisson, negative binomial, and zero-

inflated negative binomial. Of the 16 models, 12 fit the negative binomial distribution,

with *L. intermedius* 2018, *L. cinereus* 2019, and *L. intermedius* 2019 fitting zero-inflated

negative binomial, zero-inflated Poisson, and zero-inflated negative binomial

distributions, respectively. The 2018 and 2019 complete call models both fit a zero-

inflated negative binomial distribution.

To assess differences in activity among habitat types, I conducted 16 separate

Kruskal-Wallis non-parametric analysis of variance tests followed by Dunn's test for

multiple comparisons (Kruskal and Wallis 1952, Dunn 1961) and applied a Bonferroni

correction to p-values (Bonferroni 1935). The Kruskal-Wallis method was selected over

one-way ANOVA, because the response variables were not normally distributed (Akaike

1974). The non-Gaussian distribution is accounted for in the Kruskal-Wallis analysis by implementing a ranking system of response variables (Kruskal and Wallis 1952). Tests were structured as follows:

Mean calls per sampling night ~ Habitat type

A 95% confidence interval that does not overlap zero was used to determine statistical significance of bat activity. All analyses were completed, and figures created in R using packages "dunnTest," "FSA," "extrafont," "glmmADMB," "ggplot2," "ggpubr," "MASS," "MuMIn," and "stats" (R Core Development Team, 2020).

Results

In 2018, Sonobat automatically identified to species 32,596 bat call files obtained over 3,442 monitoring hours on 85 sampling nights. The software analyzed 70,834 total files and filtered 54% as noise. Species composition consisted of 27% Brazilian free-tailed bats (*Tadarida brasiliensis*) (TABR), 22% Northern yellow bats (*Lasiurus intermedius*) (LAIN), 17% Eastern red bats (*Lasiurus borealis*) (LABO), 14% hoary bats (*Lasiurus cinereus*) (LACI), 12% tricolored bats (*Perimyotis subflavus*) (PESU), 6% evening bats (*Nycticeius humeralis*) (NYHU), and 2% cave myotis (*Myotis velifer*) (MYVE). In 2019, Sonobat automatically identified to species 11,763 bat call files obtained over 1,092 monitoring hours on 65 sampling nights. The software analyzed 53,321 total files and filtered 78% as noise. Species composition consisted of 37% LACI, 16% TABR, 15% PESU, 11% LABO, 9% LAIN and NYHU, and 3% MYVE. I recorded all 7 species in each of the 3 habitats (CBH, saline prairie, and upland prairie).

I detected bats in bottomland hardwood forest habitats at (mean ± SD) 49 ± 20 and 35 ± 19 calls per detector night in 2018 and 2019, respectively. Detections in saline

prairie sites resulted in 47 ± 26 and 17 ± 9 calls per detector night in 2018 and 2019, respectively. I detected bats in upland prairie habitats at 27 ± 11 and 14 ± 3 calls per detector night in 2018 and 2019, respectively (Table 1). Bottomland hardwood forest habitat detections increased 8% whereas saline habitat detections dropped 12% of total calls from 2018 to 2019. Meanwhile, upland prairie habitat remained consistent, comprising 21% of calls per detector night during both seasons. There were no significant differences among habitat use of all bats in 2018 ($\chi^2 = 2.22$, $p = 0.33$) or 2019 ($\chi^2 = 2.78$, $p = 0.25$).

The effects of Julian day varied among species. In 2018 total bat activity increased throughout the summer. Bat activity increased 0.02% per day and 2.4% from 18 May to 10 August 2018 (Table 2; Figure 4). Activity was greatest from 25 July to 3 Aug, encompassing nearly one quarter of all calls recorded in 2018. LABO activity increased throughout the summer season in 2018 (Table 2; Figure 4) at a rate of 1.4% per day. This extrapolates to an activity increase of 42.9% every 30 days, and 120.3% over the 84-day season. LAIN activity increased throughout the summer of 2018 (Table 2; Figure 4). Activity increased at a rate of 0.9% per day. This extrapolates to 25.6% every 30 days and 45.1% over the 84-day 2018 season. NYHU activity increased during both 2018 and 2019 summers (Tables 2–3; Figures 4–5). In 2018, activity increased at a rate of 0.04% per day, which extrapolates to 1.1% every 30 days and 3.2% over the 84-day season. In 2019 the association still trended positively, NYHU activity increased 0.03% per day, 0.9% every 30 days, and 2.6% among the entire season. PESU exhibited a positive relationship with Julian day in 2019 (Table 3; Figure 5). PESU activity increased 1.6% per day beginning 18 May 2019. TABR is the only species to have a positive

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relationship between Julian day and activity one season, and a negative relationship the next. In 2018, TABR activity increased 1.9% per day, 56.1% every 30 days and 154.6% over the 84-day season. In 2019, TABR activity decreased 1.9% per day, 61.8% every 30 days, and 109.2% over the 53-day season (Tables 2–3 Figures 4–5). Julian day did not influence activity of LACI, MYVE, nor PESU in 2018 as well as LABO, LAIN, MYVE, or all species in 2019 (Tables 2–3; Figures 4–5).

Precipitation only significantly influenced activity of 2019 LACI. The effect on LACI activity was minimal but noteworthy, with activity decreasing nearly 1% for every 5 cm of rain (Table 3; Figure 5). Precipitation did not influence activity of any other bat species, or combined species, in 2018 or 2019 (Tables 2–3; Figures 4–5).

Canopy cover negatively affected two species of bats and positively influenced one. LAIN activity decreased by 3.8% with every 10% increase in canopy cover during 2018. In 2019, the association was still followed a negative trend at 1.6% decrease in activity with every 10% increase in canopy cover (Tables 2–3; Figures 4–5). TABR is the second species in this study to exhibit a negative trend of activity and canopy cover in both 2018 and 2019 (Tables 2–3; Figures 4–5); activity decreased 1.8% in 2018 and 0.2% in 2019 for each 10% increase in canopy cover. MYVE in 2018 is the only species to exhibit a positive association with canopy cover ($\beta = 0.46$, $SE = 0.13$, $Z = 3.62$, $p < 0.01$) (Tables 2–3; Figures 4–5). Every 10% increase in canopy cover increased MYVE activity by 1.8% in 2018. Contrarily, 55% of MYVE activity was detected in saline prairie habitat, which has a mean canopy cover index of 3.9%. Canopy cover did not have a significant influence on any other species or combined species in 2018 or 2019 (Tables 2–3; Figures 4–5).

Only 2018 PESU and TABR differed in activity among habitats. In 2018, PESU was more active in bottomland hardwood habitat than saline prairie ($Z = 3.46$, $p < 0.01$) and upland prairie habitats ($Z = 3.03$, $p < 0.01$) (Figure 6). Furthermore in 2018, TABR was more active in saline prairie habitats than bottomland hardwood habitats ($Z = 3.03$, $p < 0.01$) (Figure 7). No differences among habitat use were detected for any other species.

Discussion

Results identify that bottomland hardwood forests are critical habitats for bat activity. Bottomland hardwood forest habitats may be more accessible to tree-roosting bats, such as LACI and LABO, than saline and upland prairie habitats. Bats that roost in forests may require less distance to foraging areas than those that use saline and upland prairie habitats. Changes in species composition among years likely are due to sampling locations and occasions, as opposed to a shift in overall bat species composition. LACI and LABO are both foliage-roosting bats and utilize forest habitats (Jung et al. 1999). These species may benefit from the preservation of trees and refuge management (Carter et al. 2007).

TABR is generally abundant throughout Texas and produces loud echolocation pulses relative to other bats, which may be why I detected them more often (Simmons et al. 1978). Results that indicated TABR as more active in saline prairie habitat than bottomland hardwood forest habitat may have been due to increased detection in saline prairie, which has less clutter (O'Keefe et al. 2014). Additionally, the Sonobat auto-identification software may inflate the abundance of low-frequency bats (LACI, LAIN, and TABR in this study) by misidentifying low-frequency insect noise as a potential low-frequency bat.

The lack of effect on activity by weather variables likely was due to minimal weather variation and because I averaged variables over primary sampling periods which consisted of several days. Coastal Texas is generally consistent with high temperatures and humidity throughout the summer months. Many other studies detect great variation in bat activity from weather influences; however, these studies occur in different ecoregions that experience more diverse weather patterns (Erickson and West 2002, Wolcott and Vulinec 2012, Smith and McWilliams 2016). Moreover, nightly and hourly weather patterns may affect bat activity more than grouped patterns over a multi-day sampling period.

Activity of most species increased during summer months, which may have been because bat pups reached volancy. In Texas, most species give birth between May and July, and young begin flying about 3 weeks after birth. Consequently, it was expected that bat activity would increase, among all species, as Julian day increased (Davis et al. 1962). I assume the instances of negative association between activity and Julian day was not due to migration or a seasonality related event. Likely, this observation was due to the limited number of sites I was able to sample simultaneously and the presumed greater quality of habitat in certain sites than others. I would ideally compensate for this by sampling all sites simultaneously throughout the entirety of the season; however this was not possible due to limited resources. Some sites appeared consistently more active than others, and if emphasis was placed on less active sites at the end of the season, it could lead to an apparent decrease in activity.

The influence of canopy cover had various effects on species, but whether clutter affected activity and/or detection is unknown. Generally, clutter specialist bats would be

more active in areas with greater canopy cover, however, an increase in clutter reduces detection probability (O'Keefe et al. 2014). Large bats with greater wing aspect ratios, such as LACI and LAIN, may prefer habitats with low canopy cover, as they are generally less acrobatic flyers (Aldridge and Rautenbach 1987).

Precipitation totals may affect the availability of insect prey, but also impede bats ability to fly. However, this study did not examine precipitation during activity periods only, and included precipitation that occurred throughout the day. The strong positive association between TABR activity and total precipitation in 2019 may be due to roosting habits or a possible increase in insect availability following a rain event. Structure roosting bats like TABR (Davis et al. 1962) may have greater protection from environmental conditions, as well as a wider selection of potential roosting habitat, and exercise the ability to start and stop foraging as weather varies throughout a single night. Further, as long-distance foragers (Lee and McCracken 2002) TABR may be able to escape certain weather events and continue to forage with less competition, while other bats remain in roosts.

Sonobat 4.2 auto-identification software may be a useful tool, especially for those with less than one year of manual acoustic identification experience (Jennings et al. 2008), but results should be cross-validated with another available recognizer (e.g. Kaleidoscope Pro, Wildlife Acoustics, USA) and netting surveys. To conduct acoustic monitoring concurrently with netting, one may instill more confidence in the software analysis. However, auto-identification software utilizes numeric parameters to make identifications and lacks the bias of a human (Russo and Voigt 2016, Rydell et al. 2017, Caldwell et al. 2019).

This study has determined baseline ecological data surrounding bats in an area with no prior information. Acoustic detectors can be deployed by biologists with minimal training, and SBNWR can conduct small-scale long-term monitoring of bats. Repeated sampling of SBNWR may allow the refuge to examine changes in activity after the arrival of WNS. For example, tricolored bats, which comprised 12% of total activity in 2018 and 15% in 2019, are experiencing significant and dramatic declines in other regions due to WNS (Frank et al. 2019, O'Keefe et al. 2019). This species is a year-round resident of Texas and has been documented with the fungus that causes WNS in Texas (Texas Parks and Wildlife 2017).

Future researchers should conduct year-round monitoring, as opposed to only during summer months. Bat activity and diversity may fluctuate based on seasonality and migration. Year-round monitoring may also improve our understanding of the influences of weather and habitat availability on activity in this area. Comparison of winter activity and summer activity may yield robust results. A long-term acoustic study at SBNWR and adjacent areas will help to fill the knowledge gap surrounding bats of the Texas Gulf Coast. Further, an emphasis to determine activity patterns of a single species— such as PESU which is a candidate for protection in the U.S.— may allow the researcher to focus on specific habitat types and locations, and thus increase detections.

II. URBAN TREE ROOST USE BY EVENING BATS IN TEXAS

Introduction

Bats spend more time roosting than in any other activity and do so in numerous natural and anthropogenic structures. Roosts promote energy conservation, provide protection from predators and environmental conditions, and space for social interaction (Barclay and Kurta 2007). Further, roost sites often are listed as a major limiting resource for bats (Scheel et al. 1996, Fenton 1997); thus, if managers prioritize maintaining appropriate roost sites, they may increase abundance and diversity of bats.

Roosting habits are influenced by the availability of suitable sites, abundance of food, and the physical environment (Scheel et al. 1996, Barclay and Kurta 2007). Roost selection in trees and anthropogenic structures alike, especially among reproductive females, often accounts for cavity size, proximity to foraging areas and water, and surrounding stand composition (Henry et al. 2002, Willis et al. 2006, Perry and Thill 2007). For example, tall, large-diameter trees, are critical roost sites for many species of bats with various roosting strategies (Carter et al. 2007). A meta-analysis of 12 North American bat species by Fabianek et al. (2015) determined that most roost trees are taller and have a larger diameter at breast height (DBH) (n = 66 data sets) than non-occupied trees. Another meta-analysis by Kalcounis-Rüppell et al. (2005) suggested similar results (n = 22 data sets). However, many knowledge gaps among species and locations remain. Thus, a thorough understanding of roosting ecology, in every region, is potentially vital information for bat conservation.

Bats often roost in urban areas as urbanization encroaches on native habitat. "Urban habitats" are areas of intense human development interspersed with green spaces,

characterized by residential, industrial, and commercial buildings. This provides wildlife

with some suitable habitat surrounded by unusable space (McCleery et al. 2014).

Urbanization may lead to an increase in human-wildlife interactions; these interactions

raise concerns of human health and property damage, but also present opportunities for

education and outreach (Breuste et al. 2008, McCleery et al. 2014).

In urban areas there is often an increase in the availability of insect prey— due to

artificial lighting, roosts— in the form of bridges, buildings, or preserved large trees, and

water— as lakes, rivers, or residential swimming pools. However, urban areas can lead to

greater predation, possible loss of roost sites through construction and tree removal, and

greater human disturbance and activity (Breuste et al. 2008). Further, different factors of

urbanization can affect distribution and behavior of wildlife— structure, road density,

and human population size all impact bats differently (Mager and Nelson 2001, Breuste

et al. 2008, McCleery et al. 2014, Muthersbaugh et al. 2019).

Urban wildlife conservation is becoming an increasingly vital field of research as

urbanization increases (Duchamp et al. 2004, Adams and Lindsey 2009). When

approaching conservation at an ecosystem scale, the importance of understanding

abundant species becomes clearer. Abundant bats provide greater ecosystem services

than rare and uncommon bats in most cases (Agosta 2002). Gathering data on common,

as opposed to rare and endangered species, is important for bat conservation as a whole.

This becomes especially true as bat diversity continues to decline due to anthropogenic

stressors, climate change, and disease. If bat diversity decreases, we must retain healthy

populations of abundant species in order to maintain the wide variety of niches bats fill.

Evening bats (*Nycticeius humeralis*) are small (5–10 g) and inhabit various rural

and urban habitats. *Nycticeius humeralis* is distributed throughout most of the eastern United States, westward to Nebraska, and southward into northeastern Mexico. Further, the geographic range of evening bats may be expanding in Texas, Nebraska, Kansas, New Mexico, Michigan, and Wisconsin (Watkins 1972, Münzer 2008, Auteri et al. 2016, Andersen et al. 2017, Kaarakka 2018). These bats are usually abundant, except along the northern edge of their range. *Nycticeius humeralis* occupies a great diversity of roosts in cavities of live and dead trees, exfoliating bark, tree foliage, moss, leaf litter, underground burrows (one documented occurrence in winter), and buildings sometimes shared with *T. brasiliensis* (Menzel et al. 2001, Boyles et al. 2005, Münzer 2008, Hein et al. 2009). During spring and summer, male and female *N. humeralis* typically segregate. Pregnant females form maternity colonies in roosts where they will birth their pups, while males and non-reproductive females roost solitarily or in smaller groups (Barclay and Kurta 2007). Because female bats aggregate into separate colonies, maternity roost sites are critical to populations of evening bats.

My objectives were to: 1) assess roost selection in *N. humeralis* at the roost- and stand-scale of an urban landscape with a nearby preserved tract of old-growth forest habitat; and 2) compare roost site potential between the urban and nearby preserved areas. I hypothesized bats would roost in the nearby, small, continuous tracts of protected forest due to less anthropogenic disturbance. I also hypothesized bats would use large trees as maternity roosts because the urban and forest areas of the study site have an abundance of trees. I predicted tall trees with greater DBH would be most often used as roosts (Kalcounis-Rüppell et al. 2005, Fabianek et al. 2015).

Methods

The study occurred during June and July of 2018 and 2019. I surveyed bats at Dow Woods (29.08083 N, 95.46030 W), a 130-ha tract of Columbia bottomland hardwood (CBH) old-growth forest (Figure 1). Columbia bottomland hardwood forest is characterized by live oak (*Quercus virginiana*), pecan (*Carya illinoinensis*), and palmettos (*Sabal mexicana*). The vegetation structure causes CBH to resemble less of a swamp than traditional bottomland hardwood habitat, which is generally dominated by gum (*Nyssa* spp.), cypress (*Taxodium spp.*), and tupelo (*Nyssa* spp.) trees (Clark and Benforado 1981). This property is a satellite unit owned and managed by San Bernard National Wildlife Refuge (SBNWR) of the U.S. Fish & Wildlife Service acquired in 2006. The management strategy from acquisition to present day has been to rest the plot with minimal active management, other than maintenance of grass and public pathways. Dow Woods is located approximately 3 km away from the city of Lake Jackson, TX, USA (pop. approximately 26,000).

I used mist-nets to capture *N. humeralis* within the Dow Woods tract. Mist-netting began at sunset and ceased 4 h after sunset. To increase capture success, I deployed 10-m tall mist-nets near water sources and across flyways (i.e. corridors in the woods and forested edges of open areas). I checked nets every 5–15 min, depending on activity. After capture, I recorded forearm length (mm), body mass (g), age (sub-adult or adult, by degree of ossification of finger joints) (Kunz and Anthony 1982, Jones et al. 2009), sex, and reproductive condition (scrotal or non-reproductive in males and pregnant, lactating, post-lactating, or non-reproductive in females— determined by abdominal palpation and inspection of mammary glands). I temporarily held bats in an individual drawstring

cotton bag as they awaited processing. After use, the bags were washed/decontaminated. Bats were not held longer than 1 hour. Typical handling time was 15 minutes. Over two seasons, I experienced zero causalities. All methods were approved by Texas State University (IACUC #20181302465) and followed national sampling guidelines regarding WNS.

I used radio telemetry to identify day roosts of *N. humeralis*. I attached radio transmitters (Holohil BD-2X, 0.35g: Holohil Systems Ltd., Canada) to reproductive female and sub-adult bats. Only adult females and sub-adults were selected for telemetry because locating the day roost of an adult female or sub-adult is likely to be a maternity roost. Transmitters did not exceed 5% of body mass (mean = 3.68% ± 0.85%) (O'Mara et al. 2014). I glued transmitters to the skin in the middle of the back, between the shoulder blades, with Perma-Type surgical cement (Perma-Type Company Inc., USA). I carefully removed fur from this area with scissors before attachment. After attachment, I held bats for up to 10 min while the glue dried, then released bats near the capture site. I tracked bats at least one hour, once per day, between sunrise and sunset using 3- or 5-element Yagi antennae and a telemetry receiver (ATS R-4000, Advanced Telemetry Systems, USA) for the life of the transmitter ($\leq$ 21 days).

After a roost was located, I collected a variety of data about the roost. For tree roosts, I determined species and condition (dead/alive), height (m) with a clinometer (SUUNTO PM-5, Finland), understory vegetation density using a Robel pole in 4 cardinal directions within a 0.1-ha plot around the roost tree (Robel et al. 1970), and DBH (cm) with DBH tape. For the single anthropogenic roost I recorded building age (years), footprint area (m^2), height of exit (m), size of exit (cm^2) and roof and structure

material. For all roosts, I also collected relevant landscape data including roost site distance to capture site (km) and nearest road (m) measured manually with meter tape or in ArcMap software (Esri Geographic Information Systems, USA).

After identifying the roost, I conducted emergence counts to estimate colony size and identify exit points. Experienced observers counted individual bats exiting the roost from 30 min prior to sunset to 60 min after. By silhouetting bats against the dusk sky, observers estimated the number of bats using the specific roost at the time of the survey.

I used ArcGIS to select at random a presumed non-roost focal tree for each located tree roost (Miller et al. 2003, O'Keefe and Loeb 2017). The random focal tree was within the Dow Woods tract to assess differences in trees between the protected and residential habitat. The Dow Woods site was gridded into 1-ha blocks, from which I randomly selected a single plot. I then selected the nearest tree to the center of the block which was as similar to roost trees as possible (i.e. species, condition, size) and designated it as a "focal tree" (O'Keefe and Loeb 2017). I then recorded identical roost and landscape characteristics for focal trees as previously for roost trees. Due to low sample size of anthropogenic roosts (n = 1), I omitted the focal roost analysis of these data.

I compared roost trees with assumed non-roost trees using four univariate t-tests for height, DBH, canopy cover, and understory vegetation. T-tests were deemed an appropriate analysis due to low sample size and highly correlated variables. After conducting the t-tests, I applied a Bonferroni correction to account for multiple comparisons. A 95% confidence interval that does not overlap zero was used to determine statistical significance. All analyses were completed, and figures created in R

using packages "extrafont," "ggplot2," "gridExtra," "stats," and "wesanderson" (R Core Development Team, 2020).

Results

I captured 127 bats of 3 species during the summers of 2018 and 2019. Captures included 120 evening bats (*N. humeralis*), 5 Eastern red bats (*L. borealis*), and 2 Brazilian free-tailed bats (*T. brasiliensis*). I tracked 11 evening bats from Dow Woods to 9 unique roost locations. Overall, 7 bats were tracked to cavities of 5 different tree roosts all of which were alive, tall, large, live oak trees (*Quercus virginiana*) (height: 27–31 m; DBH: 108–201 cm), with moderate canopy cover (33–70%) and low understory vegetation (0.5–1.94 dm) (Figure 8; Table 4) on private property. A single bat was tracked to the attic of a 2-story residential home 3.8 km from the capture site. The home was 40 years old, constructed of brick and shingles, and 306.4 m^2 in footprint area. The exit point used by bats in the home was 2.7 m high, 22.5 cm^2 in area, 37.2 m from the nearest road, and 24 bats were recorded leaving the roost. I also tracked 3 bats to 3 different parcels of private land, but I was denied access and could not confirm whether the bats roosted in a tree or anthropogenic structure. Nevertheless, I was confidently able to triangulate a location (represented by circles in Figure 9). I tracked multiple bats to the same tree in both 2018 and 2019, with similar colony sizes both years. The study site is dominated by large *Q. virginiana*, which all tree-roosting individuals used as roost sites (Table 4).

All roosts were located 3.6–4.5 km from the same capture site, within a 0.92 km^2 area of an urban neighborhood (Figure 10). Colony size of bats occupying the roosts ranged from 16 to 500+ bats. When roost trees were compared to focal trees, bats used

trees which were over twice as tall ($t = -9.46$, $p < 0.01$, *95% CI* [-17.45, -10.38]) and

generally greater in DBH ($t = -3.38$, $p = 0.10$, *95% CI* [-106.32, -11.68]), with less

surrounding canopy cover ($t = 4.05$, $p = 0.02$, *95% CI* [12.19, 49.12]) and nearly 20-fold

less understory vegetation ($t = 66.05$, $p < 0.01$, *95% CI* [18.10, 19.62]) (Figures 8 & 11).

All bats, including those on properties I was denied access to, stayed in roosts for the full

life of the transmitter (5–21 days) and no roost switching occurred.

Discussion

The preservation of large trees in the city of Lake Jackson has created bat roosts

and allowed a population of evening bats to be present on an urban landscape. However,

bats regularly use the Dow Woods tract, potentially as foraging habitat. The combination

of large trees with no understory clutter in Lake Jackson, and the preserved CBH habitat

at Dow Woods may be excellent resources for these bats on the Gulf Coast of Texas.

Low diversity of bat captures was unexpected based on region, as eight different

species' range overlap the study site (Ammerman et al. 2012). However, many

environmental and habitat variables affect capture success of bats. Utilizing acoustic data

to identify the presence of other species has allowed us to estimate other species

occupying SBNWR (Rogers, Ch. 1). The coupling of acoustics and captures will provide

more robust information regarding management of specific species, including potential

threatened and endangered species (Brigham et al. 2004).

This is the southernmost study on roosting ecology of *N. humeralis*, and as such,

this population may be one of the first impacted by climate change, which may alter

species behavior (Adams and Hayes 2018). This information may be relevant to

populations in northern latitudes that are more susceptible to contracting WNS. No

evening bats have tested positive for WNS and, if they are resistant to the disease, may need to fill the open niches from declining populations of bat species. Biologists must understand ecological requirements of the particular species to develop proper management strategies, and basic ecological research is the critical first step in conservation efforts (Munns 2006).

No bats I radiotracked switched roosts. Bats with alternative roosts are more likely to survive predation, microclimate changes, and destruction of roosts, compared to species that rely on a single tree or building (Willis et al. 2006). Most literature documents regular roost switching in evening bats every 1–4 days (Menzel et al. 2001, Boyles and Robbins 2006, Münzer 2008). Additionally, many trees in the study area have been damaged in hurricanes, including Hurricane Harvey in 2017, which broke branches and created cavity openings for these bats. Results suggest evening bats in this area do not have great roost availability, which promotes roost switching (Willis et al. 2006). Perhaps the lack of roost switching I observed is a behavioral effect of urbanization. In the urban area, potential roosts may be less accessible due to surrounding powerlines and structure, at greater risk of mortality from predators such as cats, and more likely to be destroyed by a private landowner.

From a management perspective, this study could aid strategic acquisition of land by private, state, and federal entities. Preserving large trees as roosts and acquiring small tracts of land near urban areas may benefit bats in various regions (Russo and Ancillotto 2015). Roosts in Lake Jackson could continue to be located and documented by the public with minimal training and lead to long-term monitoring of bat roosts, year-round, through citizen science. Managers should aim to create more roosts by allowing the

growth of large trees, while keeping understory clutter at a minimum. Convincing the public to preserve large trees near their homes in an area that experiences regular hurricanes may be a difficult task. However, if properly trained to conduct an emergence survey and identify characteristics of roosts, a landowner should be able to determine if their tree is occupied or has potential to act as a bat roost. Thus, ecologically intelligent removal of trees may be possible. These experiences may also increase education and outreach opportunities where landowners may learn the benefits of bat conservation (Medellin 2003, Hoffmaster et al. 2016).

Future researchers should conduct long term monitoring of roosts, including during the winter months, as roosting habits in bats tend to change seasonally (Boyles and Robbins 2006). Studies should also attempt to locate more roosts in Lake Jackson to develop a better understanding of roost density in this area. Further, the examination of bachelor colony roosting behavior could provide more insight into *N. humeralis* life history. Perhaps bachelor colonies utilize different strategies than maternity colonies bats in this habitat.

Table 1. Environmental characteristics and bat activity of three habitat types in summer 2018 and 2019 at San Bernard National Wildlife Refuge in Brazoria and Matagorda counties, Texas, USA. BLH = bottomland hardwood forest, SP = saline prairie, UP = upland prairie, CC = canopy cover, UV = understory vegetation.

Year	Habitat	Mean calls/night	Mean CC %	Mean UV
2018	BLH	49.2 ± 20.2	78.3 ± 22.3	11.1 ± 2.9
2018	SP	47.4 ± 25.6	17.2 ± 10.2	10.2 ± 3.5
2018	UP	14.1 ± 11.1	0.0 ± 0.0	12.5 ± 3.7
2019	BLH	34.9 ± 18.5	82.3 ±19.7	15.1 ± 2.6
2019	SP	17.3 ± 8.5	22.0 ± 11.4	11.1 ± 3.1
2019	UP	27.3 ± 11.1	0.0 ± 0.0	10.9 ± 0.3

Table 2. Drivers of bat activity at San Bernard National Wildlife Refuge in Brazoria and Matagorda counties, Texas, USA, May–August 2018. Values were calculated using linear mixed-effects models, with number of bat calls as the response variable, and canopy cover, Julian day, and precipitation as predictors. Each species was analyzed individually, totaling eight separate models.

	Lasiurus borealis				*L. cinereus*			
	Beta Value	SE	Z	p	Beta Value	SE	Z	p
Intercept	3.89	0.13	29.34	< 0.01	3.72	0.15	24.84	< 0.01
Julian day	0.29	0.10	0.43	< 0.01	-0.11	0.09	-1.20	0.23
Precipitation	0.08	0.10	0.10	0.45	-0.06	0.11	-0.58	0.56
Canopy cover	0.16	0.09	0.09	0.07	-0.03	0.10	-0.32	0.75
	L. intermedius				*Myotis velifer*			
	Beta Value	SE	Z	p	Beta Value	SE	Z	p
Intercept	3.11	0.17	18.04	< 0.01	1.37	0.18	7.44	< 0.01
Julian day	0.68	0.15	4.55	< 0.01	0.19	0.11	1.73	0.08
Precipitation	0.18	0.13	1.39	0.17	0.08	0.12	0.66	0.51
Canopy cover	-0.51	0.17	-2.91	0.01	0.46	0.13	3.62	< 0.01

Table 2 continued.

	Nycticeius humeralis				Perimyotis subflavus			
	Beta Value	SE	Z	p	Beta Value	SE	Z	p
Intercept	2.89	0.12	23.37	< 0.01	3.12	0.28	11.33	< 0.01
Julian day	0.27	0.10	2.63	0.01	0.07	0.12	0.58	0.56
Precipitation	0.15	0.09	1.71	0.86	-0.16	0.16	-1.03	0.31
Canopy cover	0.13	0.09	1.43	0.15	0.31	0.14	2.18	0.29
	Tadarida brasiliensis				All Species			
	Beta Value	SE	Z	p	Beta Value	SE	Z	p
Intercept	1.68	0.17	9.60	< 0.01	3.59	0.08	22.66	< 0.01
Julian day	0.37	0.05	7.23	< 0.01	0.17	0.05	-0.03	0.98
Precipitation	0.27	0.06	4.21	< 0.01	0.05	0.05	1.79	0.07
Canopy cover	-1.01	0.17	-5.88	< 0.01	0.02	0.06	-0.24	0.81

Table 3. Drivers of bat activity at San Bernard National Wildlife Refuge in Brazoria and Matagorda counties, Texas, USA, May–July 2019. Values were calculated using linear mixed-effects models, with number of bat calls as the response variable, and canopy cover, Julian day, and precipitation as predictors. Each species was analyzed individually, totaling eight separate models.

	Lasiurus borealis				*L. cinereus*			
	Beta Value	SE	Z	p	Beta Value	SE	Z	p
Intercept	2.67	0.19	13.47	< 0.01	1.91	0.45	2.67	< 0.01
Julian day	0.05	0.12	0.43	0.67	-0.43	0.07	-5.81	< 0.01
Precipitation	0.01	0.12	0.08	0.94	-0.22	0.07	-3.03	0.01
Canopy cover	0.21	0.16	1.34	0.18	0.55	0.52	1.06	0.29
	L. intermedius				*Myotis velifer*			
	Beta Value	SE	Z	p	Beta Value	SE	Z	p
Intercept	2.09	0.19	11.24	< 0.01	1.25	0.23	5.48	< 0.01
Julian day	0.01	0.14	0.09	0.93	0.22	0.14	1.56	0.12
Precipitation	-0.05	0.15	-0.34	0.74	-0.11	0.16	-0.68	0.50
Canopy cover	-0.64	0.16	-3.91	< 0.01	0.29	0.17	1.71	0.09

Table 3 continued.

	Nycticeius humeralis				*Perimyotis subflavus*			
	Beta Value	SE	Z	p	Beta Value	SE	Z	p
Intercept	2.35	0.24	9.84	< 0.01	2.60	0.30	8.79	< 0.01
Julian day	0.26	0.13	2.05	0.04	0.31	0.13	2.30	0.02
Precipitation	0.07	0.13	0.50	0.62	0.19	0.14	1.40	0.18
Canopy cover	0.12	0.19	0.63	0.53	0.37	0.23	1.59	0.11
	Tadarida brasiliensis				All Species			
	Beta Value	SE	Z	p	Beta Value	SE	Z	p
Intercept	3.05	0.32	9.43	< 0.01	2.88	0.13	21.02	< 0.01
Julian day	-0.44	0.17	-2.51	0.01	0.01	0.54	0.12	0.90
Precipitation	0.02	0.18	0.08	0.94	0.08	0.58	1.39	0.16
Canopy cover	-0.48	0.19	-2.46	0.01	-0.32	0.11	-0.28	0.78

Table 4. Characteristics of roost trees (tree) occupied by evening bats (*Nycticeius humeralis*) and randomly selected focal trees (focal), as well as the single anthropogenic roost (bottom portion) during summer in 2018 and 2019 in Lake Jackson, TX, USA. Ht = height, DBH = diameter at breast height, CC = canopy cover, UV = understory vegetation. Bold denotes same roost was used by bats in 2018 and 2019, colony sizes were similar both years.

| Roost type	Bats	Ht (m)	DBH (cm)	CC (%)	UV (dm)	Tree species	Condition	Capture site (km)	Road (m)
Tree	**500**	**31**	**201**	**67.3**	**1.94**	***Q. virginiana***	**Alive**	**4.6**	**38.6**
Tree	16	27	120	33.3	0.53	*Q. virginiana*	Alive	4.0	16.4
Tree	295	28	168	50.2	0.88	*Q. virginiana*	Alive	4.2	7.5
Tree	180	29	169	48.6	0.41	*Q. virginiana*	Alive	3.6	10.1
Tree	170	27	108	69.7	0.61	*Q. virginiana*	Alive	4.5	14.1
Focal	0	15	98	83.0	19.63	*Q. virginiana*	Alive	NA	NA
Focal	0	14	85	81.1	19.53	*Q. virginiana*	Alive	NA	NA
Focal	0	10	91	77.7	19.89	*Q. virginiana*	Alive	NA	NA
Focal	0	18	103	98.2	19.84	*Q. virginiana*	Alive	NA	NA
Focal	0	15	94	82.4	19.79	*Q. virginiana*	Alive	NA	NA
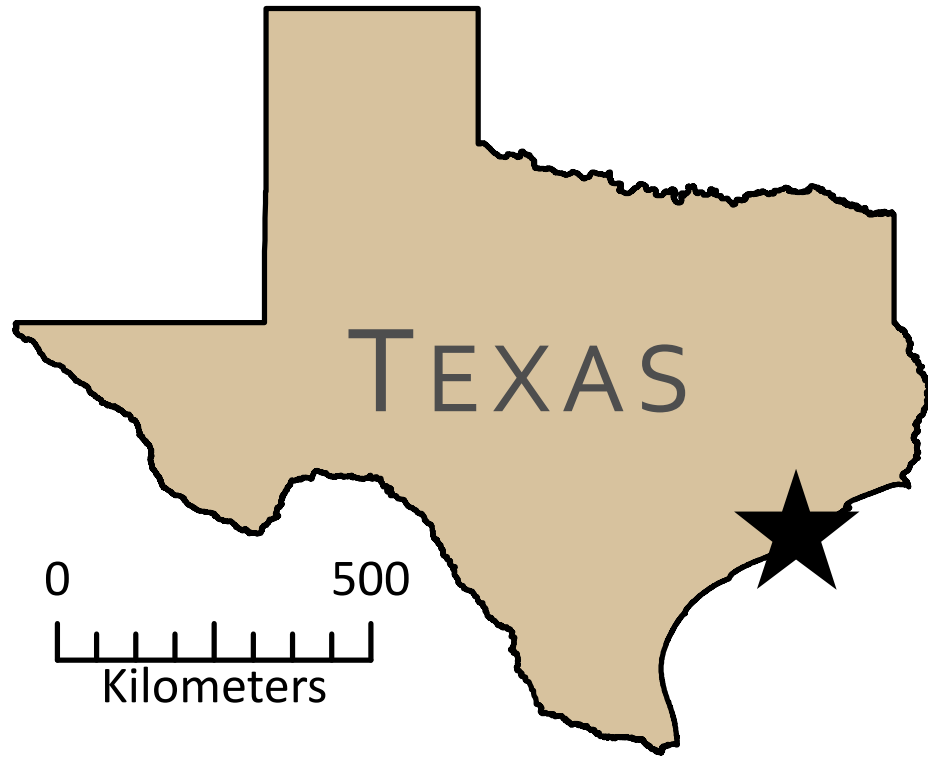
Figure 1. Study area where we investigated bat ecology during summer months of 2018 and 2019. San Bernard National Wildlife Refuge in Brazoria and Matagorda counties, Texas, USA.
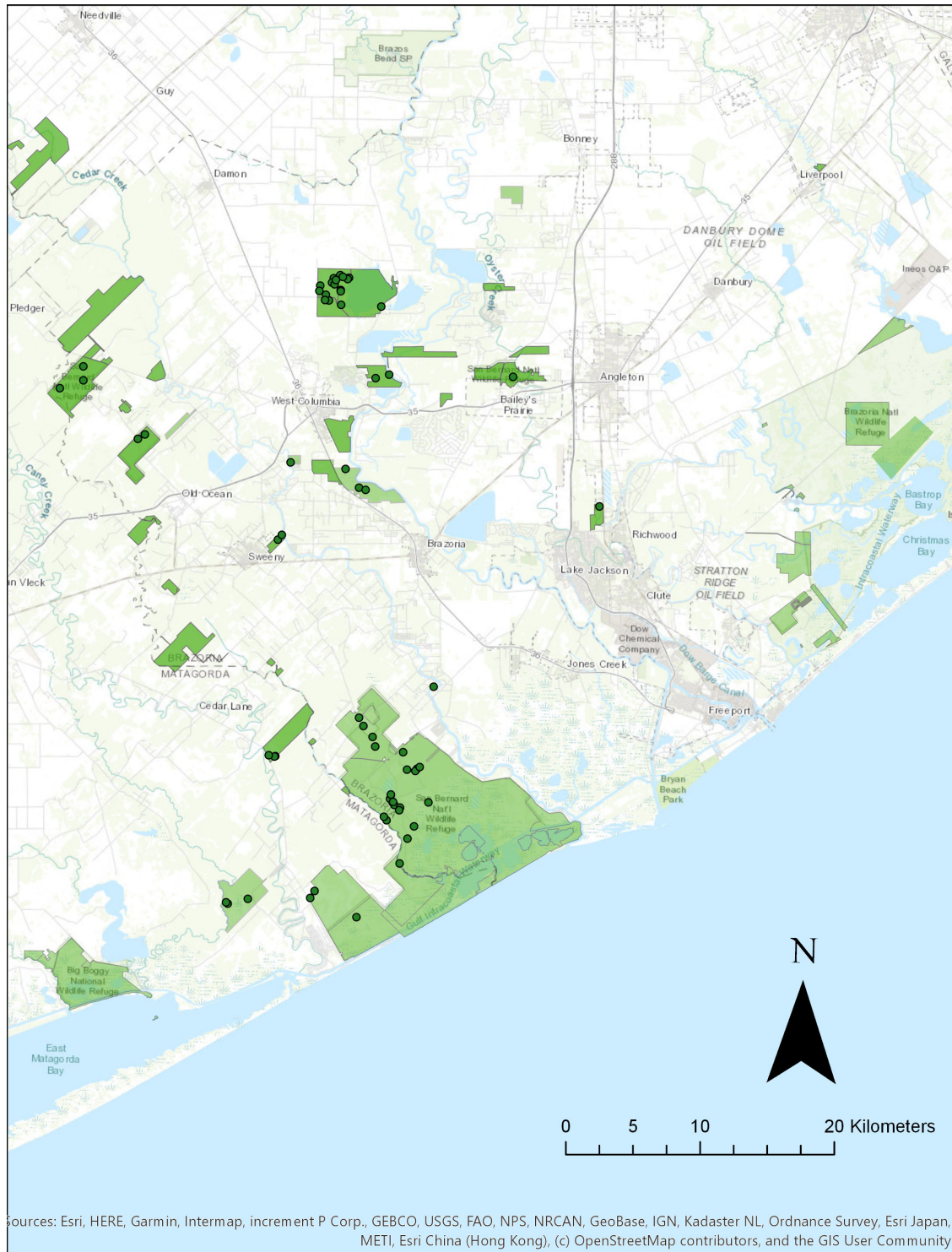
Figure 2. Locations of bat activity surveys using acoustic detectors among 60 sites distributed across San Bernard National Wildlife Refuge during summer 2018 in Brazoria and Matagorda counties, Texas, USA. Each site was temporally replicated at least two times.
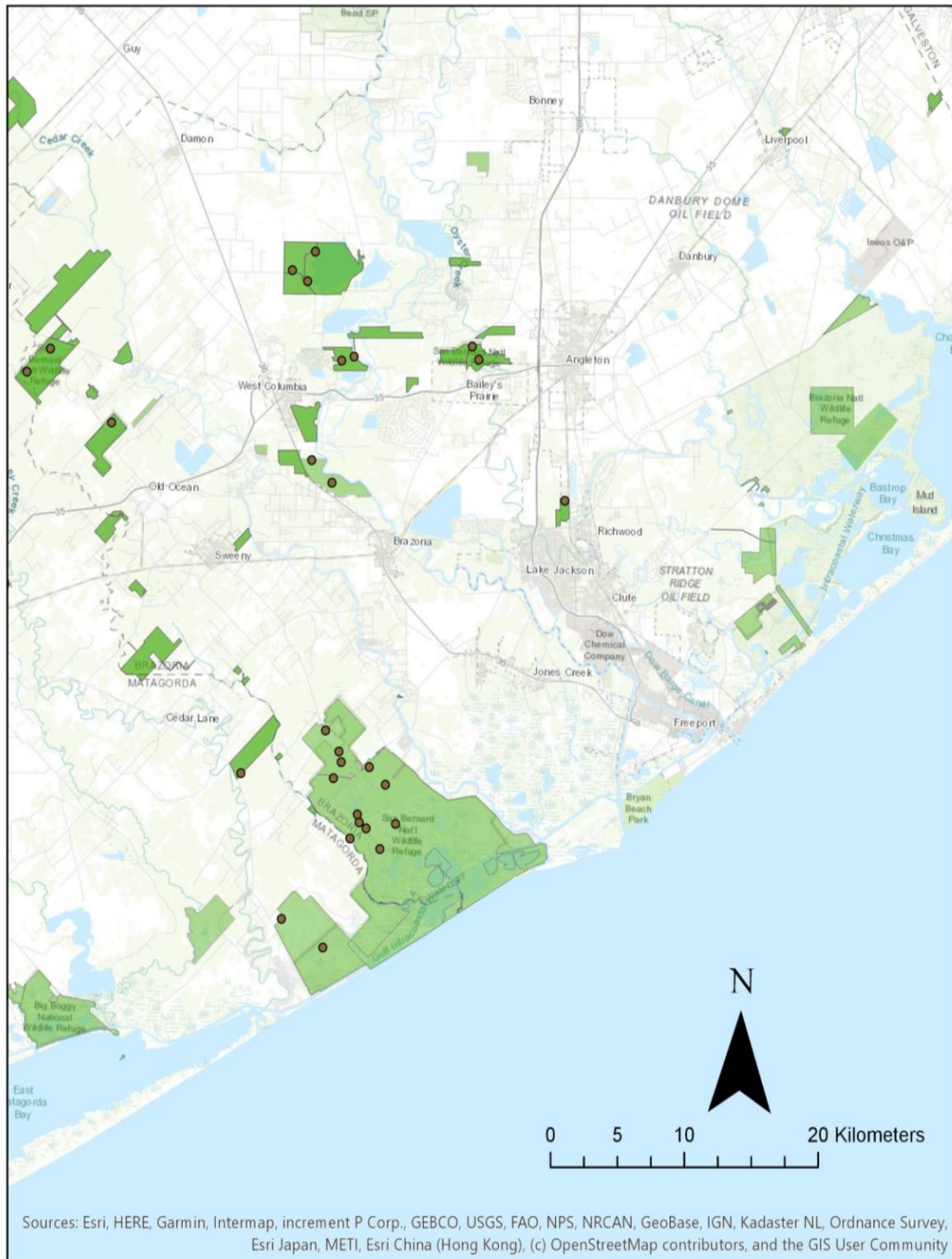
Figure 3. Locations of bat activity surveys using acoustic detectors among 27 sites distributed across San Bernard National Wildlife Refuge during summer 2019 in Brazoria and Matagorda counties, Texas, USA. Each site was temporally replicated three times.
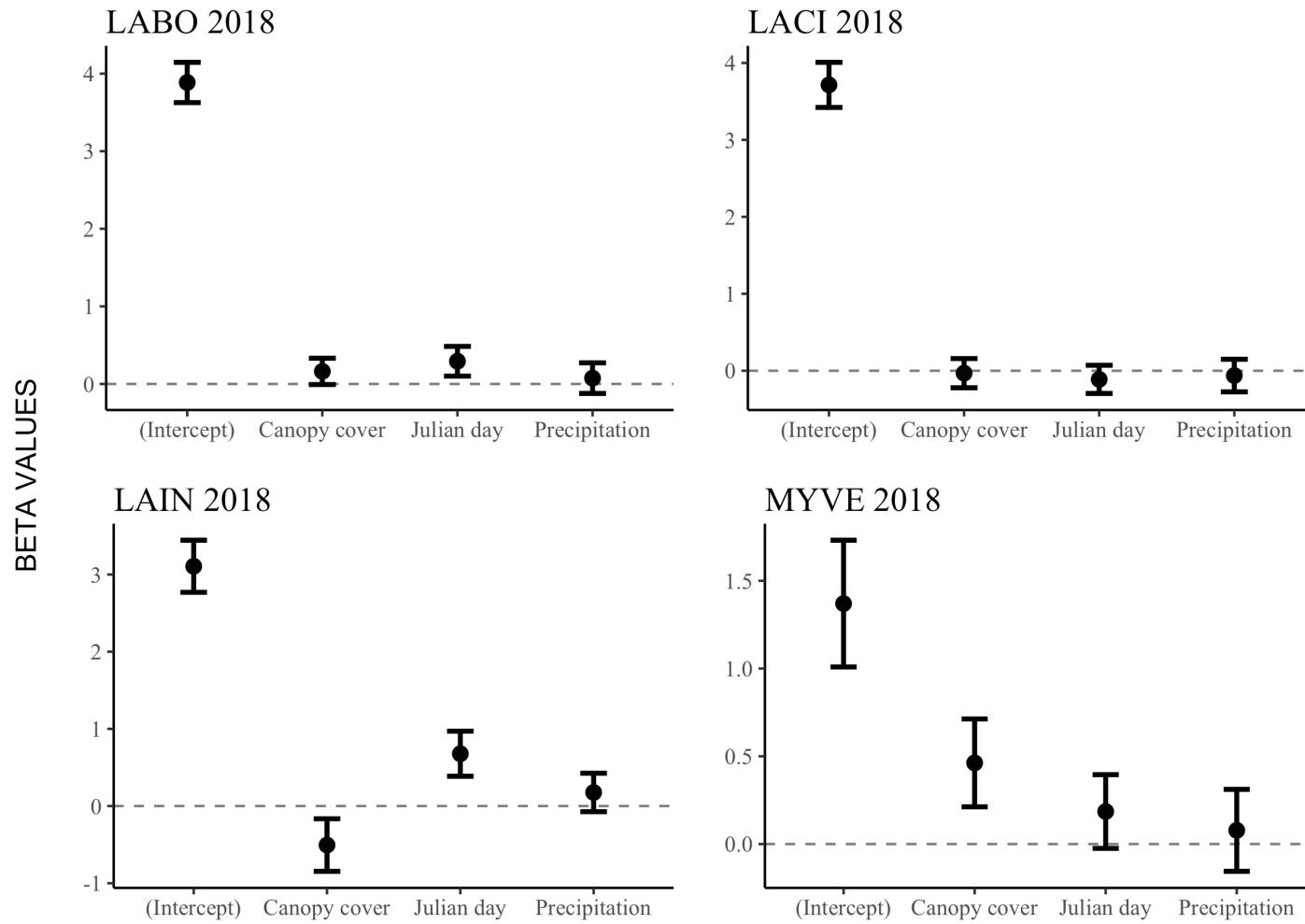
Figure 4. Beta values and 95% confidence intervals of drivers of bat activity at San Bernard National Wildlife Refuge in Brazoria and Matagorda counties, Texas, USA, May–August 2018. Values were calculated using linear mixed-effects models, with number of bat calls of each species as the response variable, and canopy cover, Julian day, and precipitation as predictors.
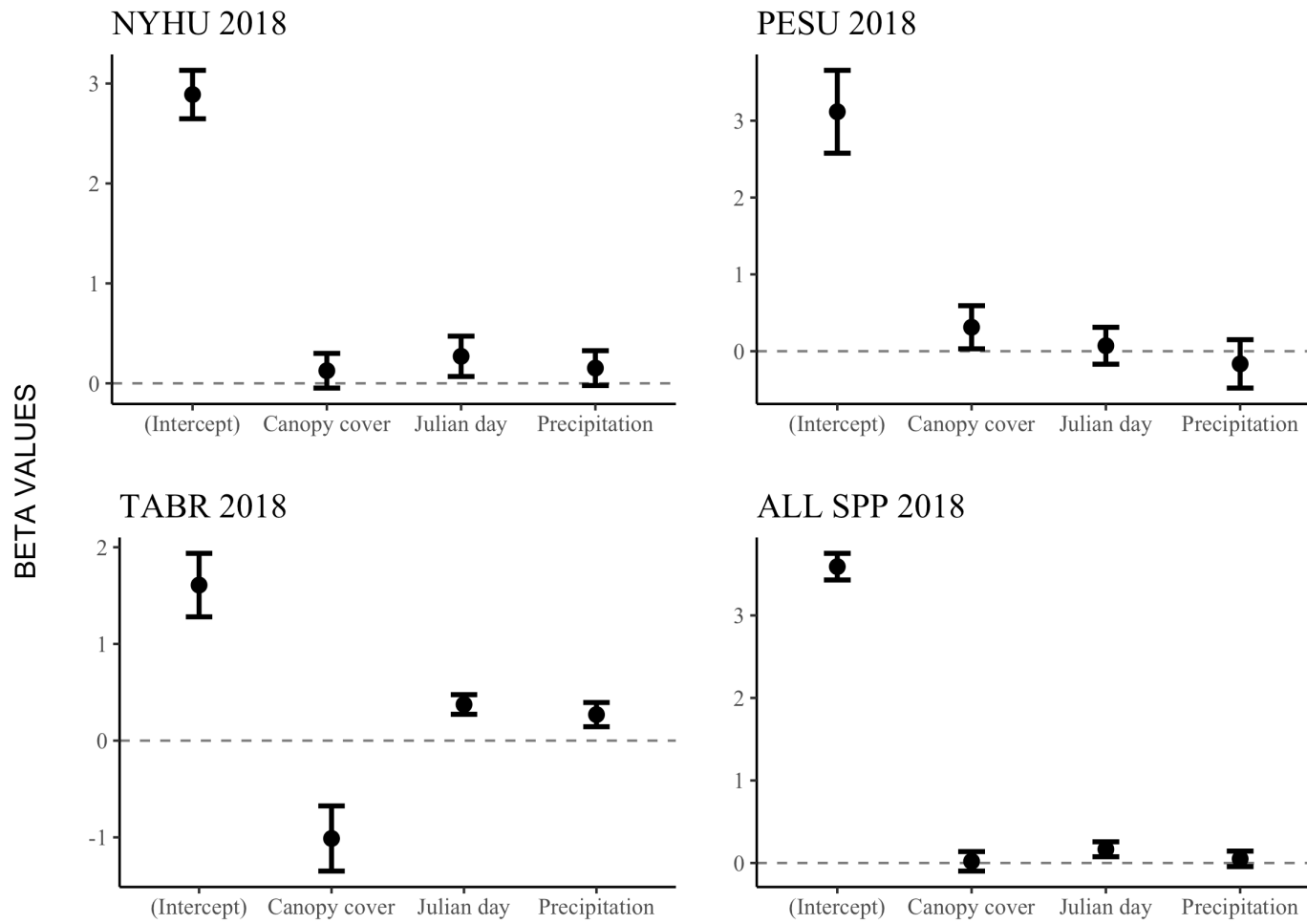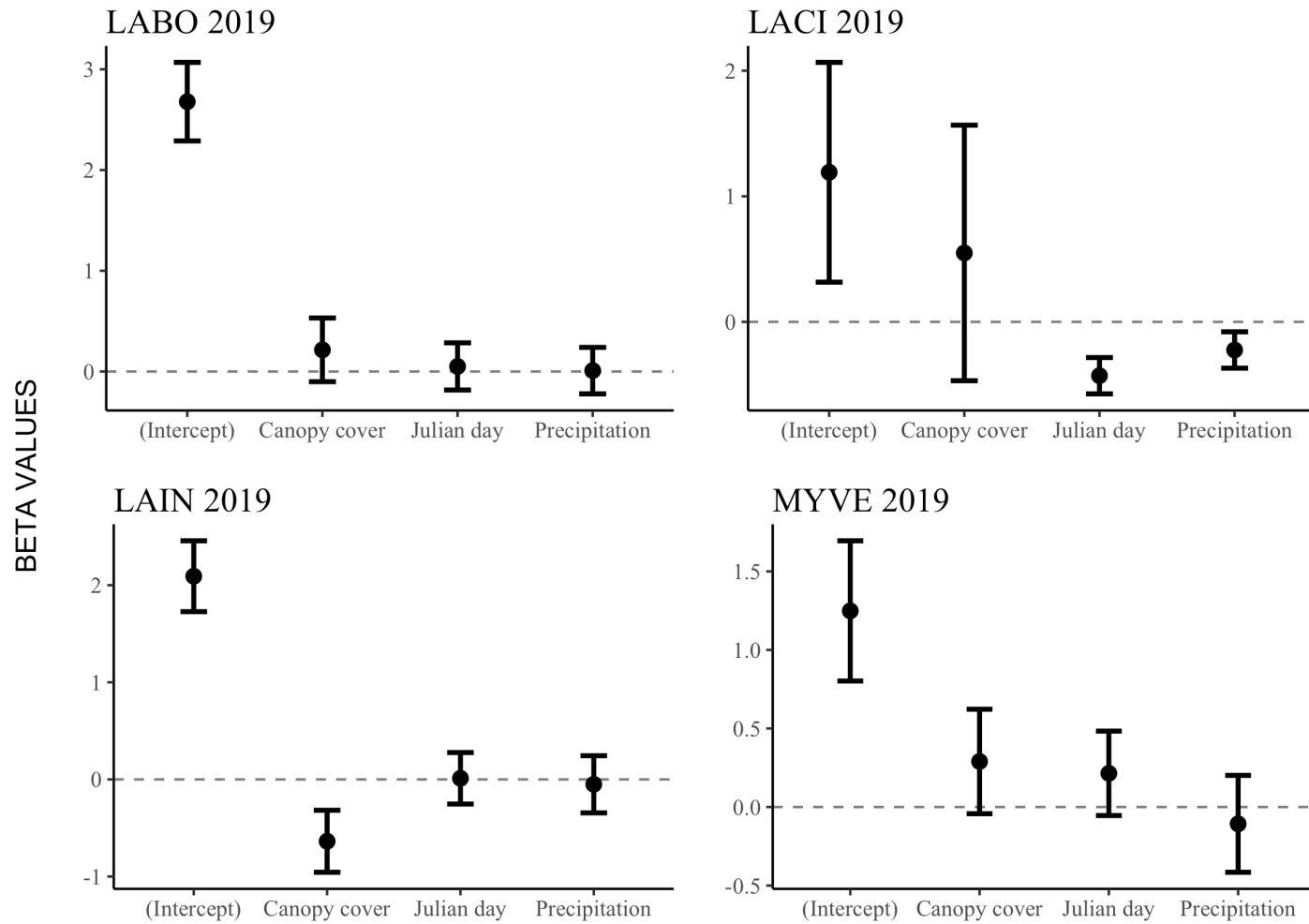
Figure 4. Continued.

Figure 5. Beta values and 95% confidence intervals of drivers of bat activity at San Bernard National Wildlife Refuge in Brazoria and Matagorda counties, Texas, USA, May–July 2019. Values were calculated using linear mixed-effects models, with number of bat calls of each species as the response variable, and canopy cover, Julian day, and precipitation as predictors.

NYHU 2019

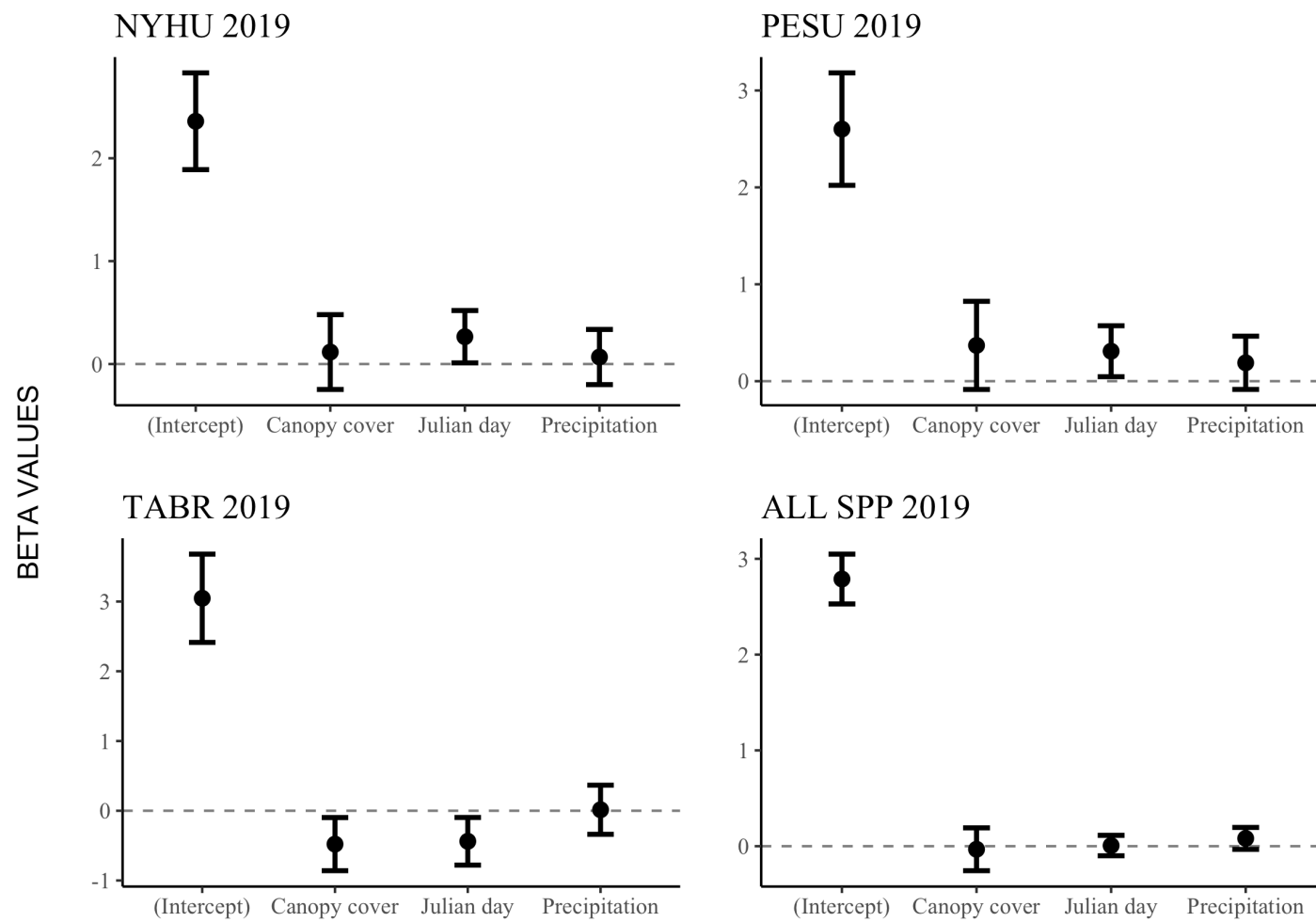PESU 2019

TABR 2019

ALL SPP 2019
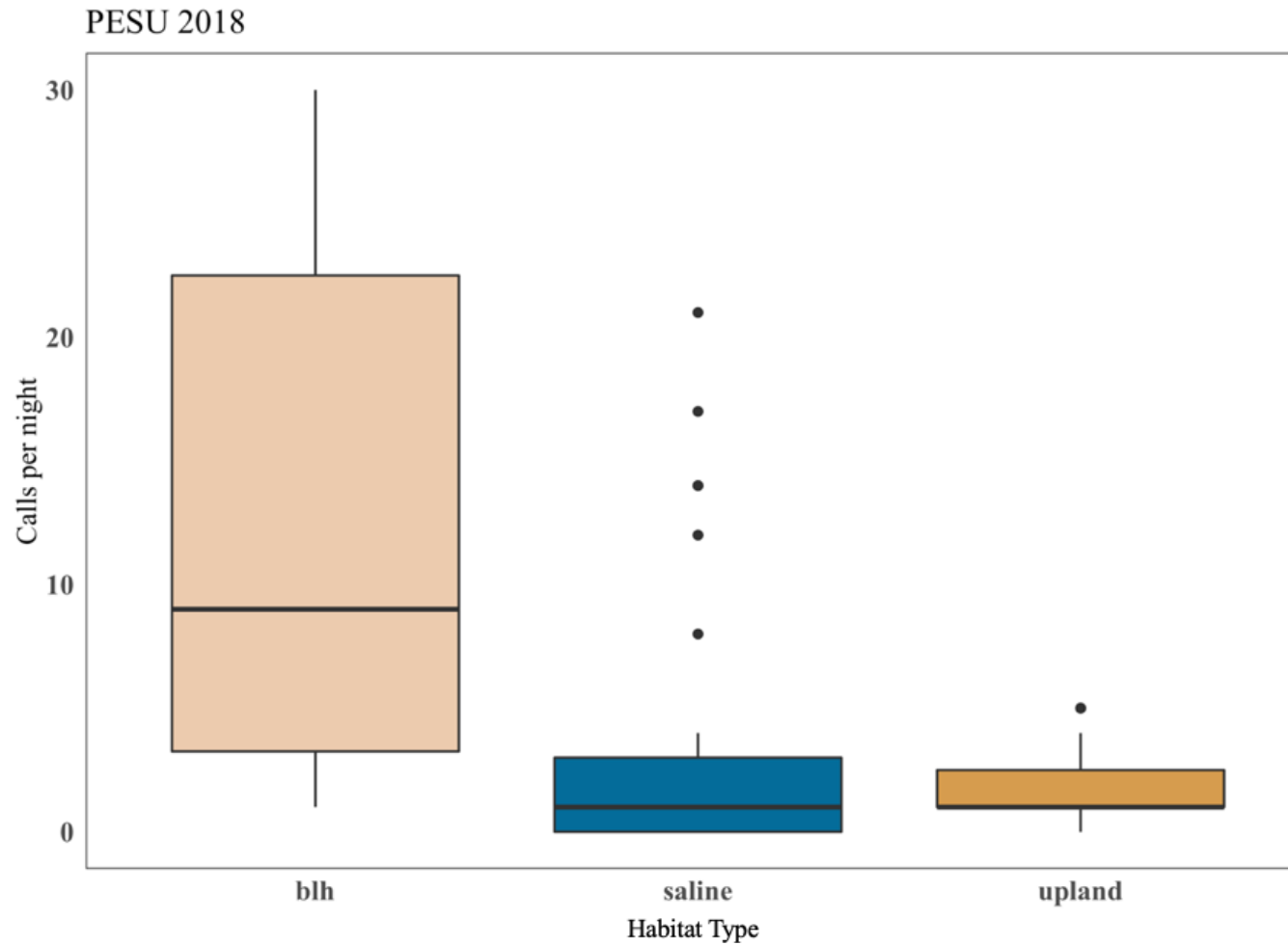
BETA VALUES

Figure 5. Continued.

Figure 6. Mean (dark line) and distribution (boxes) of calls per night for tricolored bats (*Perimyotis subflavus*) in three different habitat types at San Bernard National Wildlife Refuge in Brazoria and Matagorda counties, Texas, USA May–August 2018. Values were calculated using Kruskal-Wallis and Dunn's tests. BLH = bottomland hardwood forest, saline = saline prairies, and upland = upland prairies.
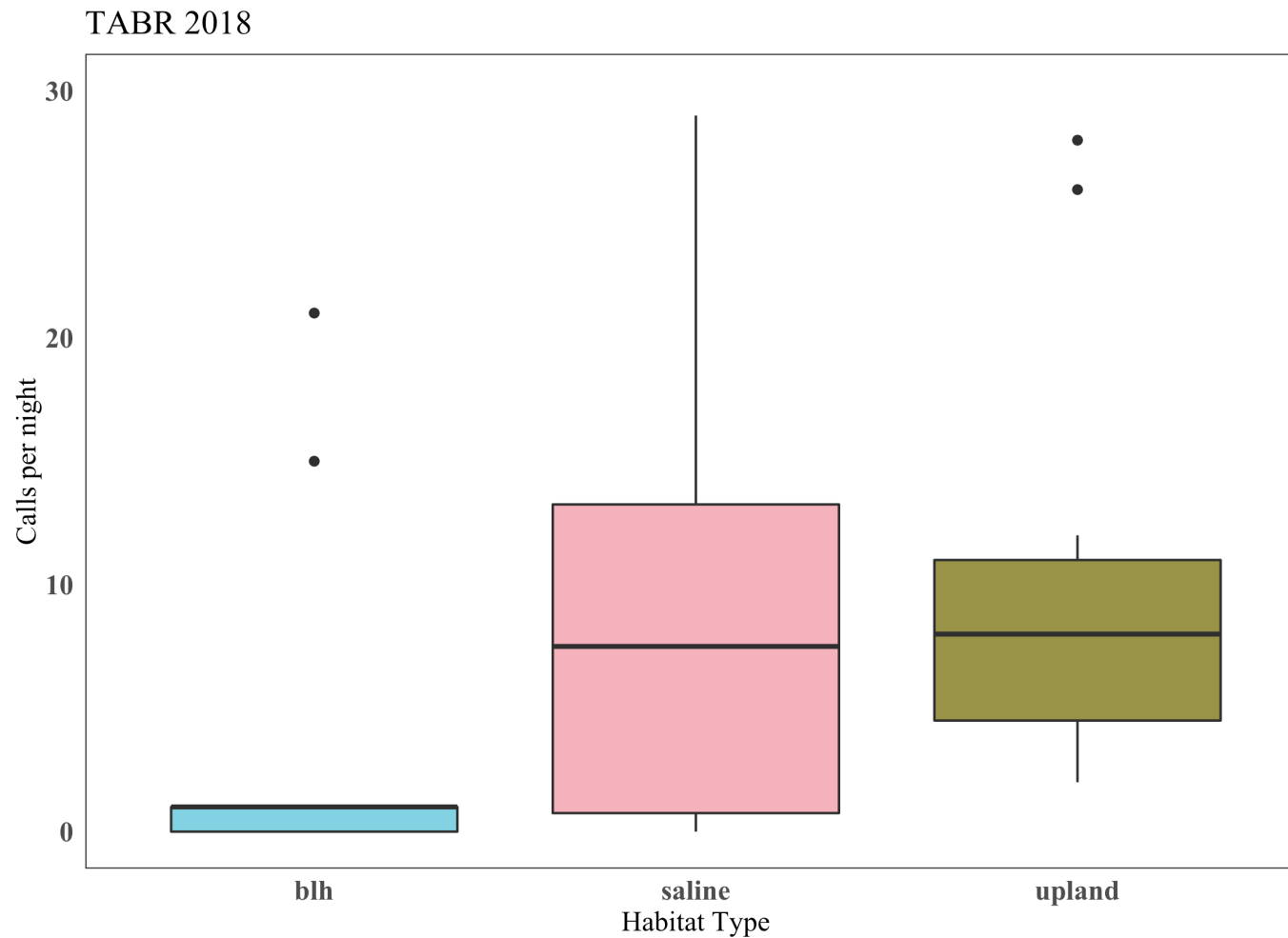
TABR 2018

Figure 7. Mean (dark line) and distribution (boxes) of calls per night for Brazilian free-tailed bats (*Tadarida brasiliensis*) in three different habitat types at San Bernard National Wildlife Refuge in Brazoria and Matagorda counties, Texas, USA, May–August 2018. Values were calculated using Kruskal-Wallis and Dunn's tests. BLH = bottomland hardwood forest, saline = saline prairies, and upland = upland prairies.

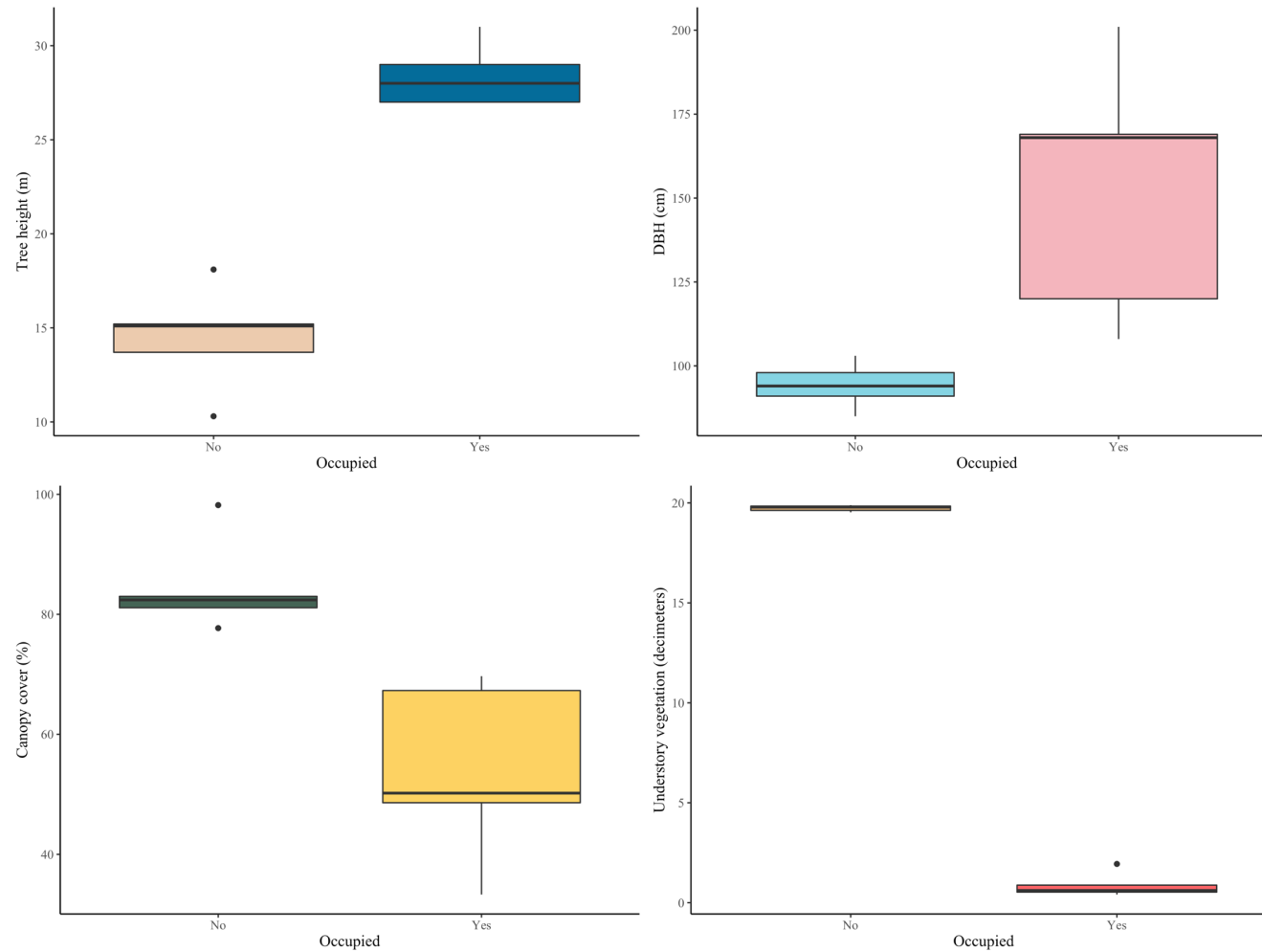Figure 8. Mean (dark line) and distribution (boxes) of characteristics of unoccupied random trees (left box) and roost trees (right box) used by evening bats (*Nycticeius humeralis*) during summer 2018 and 2019 in Lake Jackson, Texas, USA. Measurements include tree height (top left), diameter at breast height (DBH) (top right), canopy cover percentage (bottom left), and understory vegetation (bottom right).

Figure 9. Locations of capture site and nine unique roosts used by evening bats (*Nycticeius humeralis*) during summer in 2018 and 2019 in Lake Jackson, Texas, USA. Shapes represent the type of roost and colors denote which year the roost was discovered.

Figure 10. Locations of capture site and density of nine unique roosts used by evening bats (*Nycticeius humeralis*) during summer in 2018 and 2019 in Lake Jackson, Texas, USA. Shapes represent the type of roost and colors denote the year the roost was discovered. Blue polygon represents the total area that encompassed all located roosts.

Figure 11. An example of an urban tree roost used by evening bats (*Nycticeius humeralis*) during summer 2019 in Lake Jackson, Texas, USA.

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