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Global Ecology and Conservation

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Original Research Article

Summer activity patterns of four resident south Texas bat species

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ARTICLE INFO

Article history:

Received 21 September 2018

Received in revised form 1 December 2018

Accepted 1 December 2018

Keywords:

Activity

Bat

Foraging

Nocturnal

Resource partitioning

ABSTRACT

Although the activity patterns of bats are recognized to vary widely, both, temporally and spatially, the underlying drivers for those patterns remain poorly understood. Presently, studies focusing on foraging bat ecology have only generalized activity and influence of the environment (across sampling periods, sampling nights, or seasons). The influence of environmental features on foraging bat activity on a finer temporal scale (e.g., throughout a single sampling night) is markedly less studied. The recent emergence of *Pseudogymnoascus destructans*, a cold-adapted fungus and the causative agent of white-nose syndrome (WNS), has led to the precipitous declines in North American bat populations since its arrival in 2006. *P. destructans* has been recently documented in 10 Texas counties and, although WNS primarily affects hibernation cycles, it is recognized to have significant detrimental impacts on summer bat activity. It is imperative we understand and provide a baseline of summer bat activity patterns prior to the arrival of WNS to better manage and protect these, relatively understudied, populations of bat species in south Texas. We used a mixed model approach and acoustic monitoring to quantify how shrub density, canopy height, distance to water, roads, and bare ground coverage influenced nightly foraging activities of four summer resident bat species in south Texas: Eastern Red Bat (*Lasirius borealis*), Cave Myotis (*Myotis velifer*), Evening Bat (*Nycticeius humeralis*), and Brazilian Free-tailed Bat (*Tadarida brasiliensis*). Total bat activity peaked at 2:00-a for all species included in our study. A secondary, smaller peak was notable between 5:00-a and 6:00-a and activity decreased sharply immediately following 6:00-a. However, the trend for total bat activity differed substantially from trends exhibited by the individual species. Eastern red-bats and Evening bats exhibited bimodal nightly activity patterns and showed variable associations with water proximity whereas Cave bats and Brazilian free-tailed bats exhibited unimodal activity patterns and strong associations with canopy height and roads. Our results support the concept that insectivorous bats partition resources, temporally and spatially, in the presence of other sympatric species.

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1. Introduction

Effective, science-based management requires a sound understanding of activity patterns and the factors that drive those patterns (Bender and Hartman, 2015). Foraging activities of North American insectivorous bats are documented to differ seasonally, among species, age classes, and reproductive status (Barclay, 1991; Clare et al., 2011; Hamilton and Barclay, 1998). Although the activity patterns of bats are recognized to vary widely, both, temporally and spatially, the underlying drivers for those patterns remain poorly understood (Bender and Hartman, 2015). For example, certain environmental features, such as illuminated buildings, roads, and stream channelization, are known to depress bat activity possibly due to the decrease or dispersion of prey available to insectivorous bats (Berthinussen and Altringham, 2012; Boldogh et al., 2007; Conlin, 1976). Presently, studies focusing on foraging bat ecology have provided insight on large-scale patterns of activity and influence of the environment (across sampling periods, sampling nights, or seasons). The influence of environmental features on foraging bat activity on a finer temporal scale (e.g., throughout a single sampling night) is markedly less studied. Furthermore, studies are conflicted in defining the unimodal or bimodal nature of bat activity patterns because they vary substantially across geographic regions even among the same species, environmental conditions, and season (Brown, 1968; Davis and Dixon, 1976; Erkert, 1974; Kunz, 1974; Fenton et al., 1977; Gehrt and Chelsvig, 2004). These studies have suggested temporal resource partitioning among insectivorous bats as an underlying mechanism to describe such variable foraging activity patterns among species, particularly in temperate and tropical latitudes where bat biodiversity is high (Adams and Thiabault, 2006; Emrich et al., 2014).

Because of its size and geographic location, Texas has the greatest number of bat species than any other US state (Schmidly, 1994). However, of the 9522 scholarly contributions made to the growing body of scientific literature regarding North American bats since 1950, only 324 of those have discussed Texas bats, specifically. The recent emergence of *Pseudogymnoascus destructans*, a cold-adapted fungus and the causative agent of white-nose syndrome (WNS), has led to the precipitous declines in North American bat populations since its arrival in 2006 (Foley et al., 2011; Lorch et al., 2011; U.S. Fish and Wildlife Service, 2012). *P. destructans* has been recently documented in 10 counties across the state of Texas (unpublished data) and, although WNS primarily affects hibernation cycles, it is recognized to have significant detrimental impacts on summer bat activity (Brooks, 2011; Dzal et al., 2011; Ford et al., 2011). Changes in activity levels and patterns of bats have been used to identify impacts of disease (primarily WNS) and other anthropogenic factors (e.g., installation of wind turbines; Cryan et al., 2014; Grider et al., 2016). It is imperative we understand and provide a baseline of summer bat activity patterns prior to the arrival of WNS to better manage and protect these, relatively understudied, populations of bat species in south Texas.

Our objective was to quantify how shrub density, canopy height, distance to water, roads, and bare ground coverage influenced nightly foraging activities of four summer resident bat species in south Texas: Eastern Red Bat (*Lasirius borealis*), Cave Myotis (*Myotis velifer*), Evening Bat (*Nycticeius humeralis*), and Brazilian Free-tailed Bat (*Tadarida brasiliensis*). We sought to understand what impact, if any, these environmental features have on the presence of these bat species, particularly during crucial foraging hours.

2. Material and methods

2.1. Study site

We conducted our study on the East Foundation's 61,000-ha San Antonio Viejo Ranch (SAV), located approximately 25 km south of Hebbronville, Texas in Jim Hogg and Starr counties (Fig. 1). SAV is located within the South Texas Plains ecoregion and is managed predominantly as a cow-calf operation. Vegetation composition and structure within our study area is characteristic of this ecoregion and consists of a mosaic of grassland and thornscrub. Mean annual temperature within our study site is 22.6 °C and mean annual precipitation is 502.5 mm (PRISM Climate Group, 2018). Mean monthly temperature during our study period (June–September 2017) was 29.6 °C with a maximum daily high of 42.2 °C (PRISM Climate Group, 2018). Mean monthly precipitation during our study period was 29.2 mm with a maximum daily high of 27.7 mm (PRISM Climate Group, 2018).

2.2. Field collection and sampling methods

We randomly generated 43 sampling sites, stratified by vegetation type, across SAV (Fig. 1). We spaced all sampling locations a minimum of 400 m from ranch or pasture boundaries and a minimum of 1 km from other sampling locations and assumed this resulted in samples independent from each other. We were primarily interested in the foraging habits of summer resident bats; thus, we sampled June through September in 2017.

We quantified bat activity by summing passes per hour using acoustic detectors and classifying those calls by species. We defined "pass" according to the standard terms proposed by Kunz and Gustafson (1983), in which one pass by one individual through air space constitutes a bat pass. In this study, we infer bat activity from the number of passes. We recorded ultrasonic bat calls using Pettersson D500X Mk II real-time full spectrum detectors (Pettersson Elektronik, Uppsala, Sweden). We used external microphones connected by 7.62 m (25 ft) long microphone cables and extended to approximately 0.5 m above the canopy of the surrounding vegetation using a telescoping extension pole. We directed the microphones approximately 30° above horizontal and in a northwesterly direction because prevailing winds from the southeast can trigger the detector to

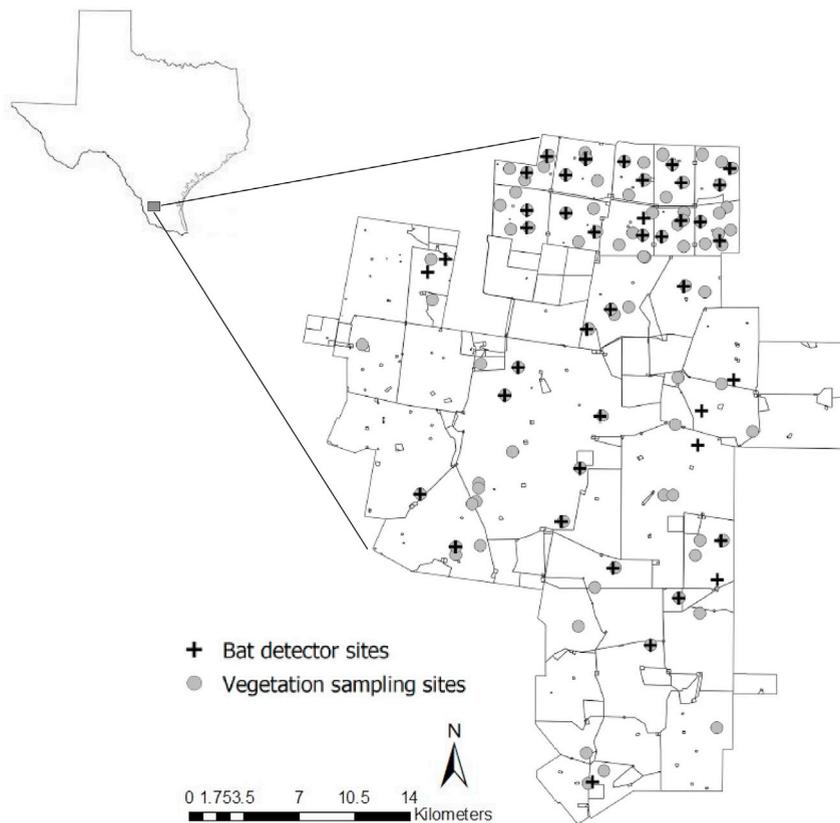


Fig. 1. Locality and representation of study site, East Foundation's San Antonio Viejo Ranch, in south Texas. Acoustic bat detector locations for 2017 sampling are also represented.

record and interfere with the recording of actual bat calls. We surveyed each site for a minimum of 5 consecutive nights before moving detectors (Law et al., 2015; Skalak et al., 2012). If a detector did not successfully record, we assessed the number of successful recording nights and continued sampling until five nights were recorded. We defined a successful night as a night without rain and when equipment did not fail due to dead batteries, corrupt data cards, or unknown reasons. Once all sites were visited, we conducted a second visit to each site for 5 additional successful nights within 3 weeks of the initial sampling period.

Detector settings: On each sampling night, we ran detectors from 15 min before sunset to 15 min after sunrise using the relative timer function on the detector. The relative timer function estimates approximate times of sunrise and sunset based on geographic location. We adjusted detector input volume (gain) on a case by case basis because wind and other environmental factors could trigger unwanted recordings and deplete detector battery life. We set the volume at which a sound would be recorded (trigger level) to 80 dB because a typical bat calls at ~110 dB (Surlykke and Kalko, 2008) and we wanted to detect bats that may call more quietly or indirectly to our microphones. We also programmed detectors to pause for 5 s between recordings (interval) to discourage recording multiple sounds files during a single bat pass. We used a sampling frequency of 500 Hz and turned off the low-frequency attenuation setting (high-pass) to sample the spectrum of frequency ranges utilized by potential bat species on the ranches. Lastly, we adjusted the requirements for the duration of a bat call to trigger a recording (trigger sensitivity) on a case by case basis due to wind and other environmental factors that may trigger the detector. We predominantly used a “low” trigger sensitivity setting, because lower settings generally discriminate against non-bat recordings.

Call classification: We attributed sounds files with meta-data that included site, detector, date, and time-stamp to organize bat recordings prior to processing. We then filtered attributed sound files using the SonoBat 4.2 high-grade batch scrubber. This ensured the clearest bat calls were isolated for species identification and reduced the number of ‘noise’ files that generally included insect, wind, or feedback sound. We processed the filtered sound files using the SonoBat 4.2 regional classifier. The SonoBat classifiers did not assign a species to recordings that contained more than one bat call. For sound files containing more than one bat call, we manually vetted to assign a species classification based on candidate species suggested by the software. Additionally, we manually vetted all automatic classifications made by the software to ensure identification accuracy. We then summarized classified recordings by site, sampling night, and species.

Vegetative data collection: We used vegetative height and density, distance to water, bareground coverage or clearings, and roads as environmental correlates as these features are documented to be utilized by foraging insectivorous bats (Best and Geluso, 2003; Menzel et al., 2005; Rosenstock et al., 1999). To address vegetative influence, we randomly generated 87 sampling locations, stratified by vegetation type, and each within 3 km of a bat detector deployment location, across the SAV ranch in 2017. As part of a long-term grazing study, the 10 northern pastures of the SAV ranch (hereafter referred to as the Coloraditas Grazing Research and Demonstration Area, or CGRDA) were treated with varying cattle grazing regimes resulting in substantially different vegetative communities among pastures during and before our study period. In order to capture the effects of this vegetative variability at the appropriate scale, each pasture was considered a separate vegetation type in the random stratification of sampling locations (Fig. 1). We sampled vegetation using 0.25-m² quadrat frames (for herbaceous coverage) and two 5-m wide belt transects (for woody coverage) along two 25-m transects laid due north from a given point, with the second laid 50 m east of the primary transect. Along each transect, we used 0.25-m² quadrat frames at each 5-m interval to visually estimate percent coverage by litter, woody debris, rock, bare ground, and herbaceous species. We then used the belt transects to sample larger, woody vegetation by identifying all woody species rooted inside the belt extending either side of the transect line. For each woody plant detected, we identified to species, measured canopy height, and collected two, perpendicular canopy diameter measurements.

2.3. Data preparation and analysis

Environmental predictors: We calculated canopy height using data collected in the field as woody vegetation height along belt transects. We imported these values into ArcMap in the ArcGIS® 10.5 suite and used Kriging interpolation to minimize spatial sampling bias and create a continuous surface layer of environmental predictor values. Kriging, or Gaussian process regression, is a geostatistical method through which interpolated values are modeled by a Gaussian process governed by covariances (Van Beers and Kleijnen, 2004). This method of spatial interpolation estimates a continuous surface of values directly based on values at surrounding points weighted according to spatial covariance (Van Beers and Kleijnen, 2004). The Kriging interpolation algorithm is optimal for most eco-spatial modeling because it produces an unbiased prediction and calculates the spatial distribution of uncertainty allowing for an accurate estimate of error at any particular point (Mahmoudabadi and Briggs, 2016). We exported the resulting GeoTIFF and read into R as a raster (R Core Team, 2013). Similarly, we calculated shrub density using the frequency and the two perpendicular canopy diameter measurements and height measurement for woody species <1.8-m in height. We used these values to calculate canopy volume (CV) using the derived canopy volume formula:

$$CV = \frac{2}{3} \pi H(A/2 \times B/2) \quad (\text{Eq. 1})$$

where H is the plant height, and A and B are the two perpendicular canopy measurements. We used this derived, and more sophisticated calculation of canopy volume because it provides a more accurate and reliable representation of plant canopy closure and coverage than the basic ellipsoid equation in which the plant is represented as a cone in 3-dimensional space (Thorne et al., 2002). We multiplied the frequency of each shrub species within each belt transect by each canopy volume value and imported into ArcMap 10.5. We used a Kriging interpolation, similar to canopy height, to minimize spatial sampling bias and to create a continuous surface layer of predictor values and the resulting GeoTIFF was exported and read into R as a raster.

We included bareground coverage by averaging the visual percent cover from the quadrat frames at each transect and each vegetative sampling site. We imported these values into ArcMap used Kriging interpolation to minimize spatial sampling bias and create a continuous surface layer of environmental predictor values. We exported the resulting GeoTIFF and read into R as a raster. We placed a 20-m buffer on both sides of each road located within SAV ranch in ArcMap to represent a biologically significant 'road reach' (i.e., a reasonable distance in which insects that concentrate on roads could likely be found) (Snelgrove et al., 2013). We exported the resulting GeoTIFF and read into R as a raster. To calculate distance to water, we gridded the spatial extent of the SAV ranch into a fishnet (30-m² resolution). We performed a proximity analysis on each pixel centroid using the Near tool in ArcMap to determine distance of each centroid to location of nearest water source, usually a livestock well and holding tank as no natural surface water exists within our study site, and very little exists on the Coastal Sand Plain region of Texas as a whole (Snelgrove et al., 2013). We made considerations for seasonality as not all groundwater pumps are operational year-round on large south Texas cattle ranches and we ensured only those wells known to be active during the summer of 2017 were used in the analysis. We then used Kriging interpolation to create a continuous surface layer of predictor values and the resulting GeoTIFF was exported and read into R as a raster.

Bat recordings and models: We subset our analyses by nightly hour (2000–0600; 8:00-p to 6:00-a) and species. Within each recording hour subset, we performed boosted regression tree analysis (BRT) in R for each species to determine relative influence of environmental factors on occurrence. The Boosted Regression Tree (BRT) is an ensemble, regression-based method that combines the strengths of two commonly used algorithms: regression trees (models that define the response to predictors using binary splits) and boosting (a method for combining multiple simple models to improve performance). We chose to use this approach due to the unique advantage of the BRT to handle collinearity among predictors as well as to simplify and generate candidate models following initial model creation. An initial regression tree is fitted and iteratively improved upon in a forward stagewise manner (boosting) by minimizing the variation in the response not explained by the

model at each iteration. BRT interpretations can be easily summarized to provide powerful ecological insight (Franklin, 2009). Here, we use BRT to examine the relative influence of each predictor variable on bat presence per hour pooled for each successful sampling night in 2017.

In addition to the relative influence of each predictor, we also sought to understand the direction of that influence on the nightly movements of each bat species. For example, if water proximity is a significant correlate, we also define whether it was positively associated or negatively associated with flight activity of bats. To address this, we simplified each BRT model in R by dropping the maximum number of predictors stepwise until candidate models remained containing only explanatory factors. We then used these factors to build simple linear models for each hour per species (number of passes as response variable) to obtain significance (p) and coefficient values. In some instances, night hours did not contain enough records of a species to build any models and so we omitted those hours.

In addition to the subset analyses, we grouped recordings by species and totaled passes per hour across the entire sampling period per successful sampling night in 2017. From these analyses, we were able to quantify the impact, if any, of each environmental feature on the presence (inferred from detection) of each species during crucial foraging hours. While we cannot infer mechanisms for these effects, we can identify important correlates for bat activity throughout the night hours.

3. Results

We surveyed a total of 43 sites across the SAV ranch for a total of 419 successful sampling nights in 2017. 11 sampling nights were unsuccessful due to mechanical failure or weather and were not included in the analyses. We documented a total of 1145 bat passes (Eastern red bat [206], Evening bat [248], Cave bat [460], and Brazilian free-tailed bat [231]). Total bat activity, inferred by recorded bat passes, peaked at 0600 (6:00-a) for all species included in our study (Fig. 2). A secondary peak was notable between 0200 (2:00-a) and 0300 (3:00-a) and activity decreased sharply immediately following 0400 (4:00-a). Activity steadily increased prior to the first peak from 69 passes per hour at 1800 (6:00-p) to 153 passes per hour at 0200 (2:00-a). However, the trend for totaled bat passes per hour differed substantially from trends exhibited by the individual species (Fig. 2).

3.1. Eastern red bat

We observed sporadic peaks in activity that reached a maximum at 0600 (6:00-a; Table 1). Although sporadic, Eastern red bats were most active before 2100 (9:00-p) or after 0200 (2:00-a). Nightly activity of Eastern red bats was significantly, positively associated with canopy height in the early evening (2000; 8:00-p) and just before sunrise (0500; 5:00-a). However, canopy height had a significant negative influence on Eastern red bat activity during the late-night peak (0200; 2:00-a) and the beginning of the sunrise hour (0600; 6:00-a). Water proximity had a significant negative influence on Eastern red bats activity throughout the night as did roads (Table 1). Eastern red bat activity was also significantly associated with areas of high shrub density in the sunrise hour (0600; 6:00-a).

3.2. Evening bat

Evening bats exhibited a bimodal distribution of nightly flight activity throughout the nightly hours with the most pronounced peak at dusk (2000; 8:00-p) and a secondary, more prolonged peak after 0200 (2:00-a) (Table 2). Early evening flight activity by Evening bats was positively influenced by canopy height and water proximity. During the second increase in passes per hour, shrub density and roads had a significant negative influence on Evening bat activity. Although canopy height was a

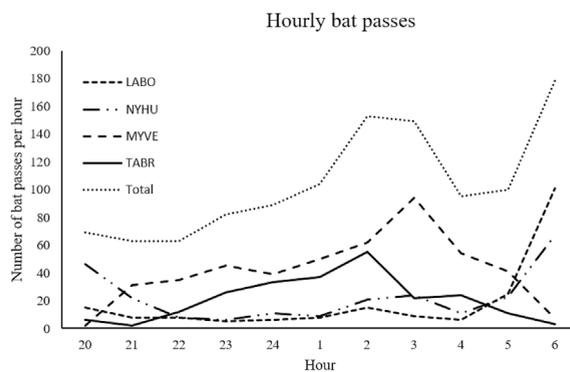


Fig. 2. Number of recorded bat passes per hour pooled for each successful sampling night in 2017 on the East Foundation's San Antonio Viejo Ranch for LABO (Eastern red bat, *Lasirius borealis*), MYVE (Cave bat, *Myotis velifer*), NYHU (Evening bat, *Nycticeius humeralis*), TABR (Brazilian free-tailed bat, *Tadarida brasiliensis*), and Total (Total number of passes for all species). Hours are displayed from 8:00-p (Hour 20) through 6:00-a (Hour 6).

Table 1

Relative influence, as calculated by boosted regression tree analysis (BRT), of several environmental features on nightly movements of Eastern red bat *Lasirius borealis* on the East Foundation's San Antonio Viejo Ranch by hour in 2017. Hours are displayed from 2000 (8:00-p) through 0600 (6:00-a). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; '-' insufficient number of records (n) to build models. (+) denotes positive direction of influence (+coefficient in linear model); (-) denotes negative direction of influence (- coefficient in linear model).

	2000	2100	2200	2300	2400	0100	0200	0300	0400	0500	0600
Shrub density	6.8	–	–	–	–	–	17.9	–	–	5.1	(+) 17.5***
Canopy height	(+) 26.7*	–	–	–	–	–	(-) 44.9*	–	–	(+) 42.9***	(-) 22.9***
Water proximity	(-) 42.4*	–	–	–	–	–	25.2	–	–	(-) 32.5**	38.7
Bareground coverage	1.3	–	–	–	–	–	3.8	–	–	6.86	5.5
Roads	22.8	–	–	–	–	–	8.2	–	–	(-) 12.6*	15.3
n	15	8	8	5	6	8	15	9	6	25	101

Table 2

Relative influence, as calculated by boosted regression tree analysis (BRT), of several environmental features on nightly movements of Evening bat *Nycticeius humeralis* on the East Foundation's San Antonio Viejo Ranch by hour in 2017. Hours are displayed from 2000 (8:00-p) through 0600 (6:00-a). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; '-' insufficient number of records (n) to build models. (+) denotes positive direction of influence (+coefficient in linear model); (-) denotes negative direction of influence (- coefficient in linear model).

	2000	2100	2200	2300	2400	0100	0200	0300	0400	0500	0600
Shrub density	10.2	22.3	–	–	21.4	–	(-) 54.1***	(-) 32.2*	1.9	5.9	(+) 21.3***
Canopy height	(+) 18.5*	(+) 35.4**	–	–	3.7	–	5.5	(+) 23.5*	44.8	54.0	(-) 28.9***
Water proximity	(+) 31.9***	23.5	–	–	(-) 47.8**	–	5.0	22.6	51.3	(+) 16.6**	33.1
Bareground coverage	19.9	7.4	–	–	22.9	–	7.8	9.5	0.98	7.9	8.2
Roads	19.4	11.3	–	–	4.2	–	(-) 27.5*	12.2	0.89	15.5	8.5
n	46	22	8	6	11	9	21	24	11	23	67

significant positive feature for foraging Evening bats through most of the nightly hours, it became a significant negative correlate in the sunrise hour (0600; 6:00-a) (Table 2). In hours leading up to sunrise, water proximity and shrub density became significant positive correlates for Evening bat activity.

3.3. Cave bat

Unlike Eastern red bat and Evening bat, Cave bat activity was relatively unimodal in distribution and steadily increased, reaching a maximum of 94 passes per hour at 0300 (3:00-a), before decreasing rapidly to 7 bat passes per hour by sunrise (Table 3). Shrub density had a consistent, significantly negative influence on Cave bat activity throughout the night. Water proximity was a significant negative correlate for Cave bat activity during the 0200 (2:00-a) hour but a significant positive correlate in the 0400 (4:00-a) hour. This species' nightly foraging activity was also negatively influenced by bareground coverage just before sunrise in the 0500 (5:00-a) hour. However, we observed a significant association in Cave bat activity and roads at 2400 (12:00-a). Canopy height remained a significant positive environmental feature for foraging Cave bats throughout the night (Table 3).

3.4. Brazilian free-tailed bat

Similar to the Cave bat, the Brazilian free-tailed bat exhibited a unimodal distribution of nightly foraging activity, steadily increasing activity throughout the night with a maximum in the 0200 (2:00-a) hour (Table 4). Canopy height and roads remained significant positive features for Free-tailed bat foraging activity through most of the nightly hours, whereas shrub density had a significant negative influence (Table 4).

Table 3

Relative influence, as calculated by boosted regression tree analysis (BRT), of several environmental features on nightly movements of Cave bat *Myotis velifer* on the East Foundation's San Antonio Viejo Ranch by hour in 2017. Hours are displayed from 2000 (8:00-p) through 0600 (6:00-a). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; '-' insufficient number of records (n) to build models. (+) denotes positive direction of influence (+coefficient in linear model); (-) denotes negative direction of influence (- coefficient in linear model).

	2000	2100	2200	2300	2400	0100	0200	0300	0400	0500	0600
Shrub density	–	(-) 57.1***	(-) 33.2***	(-) 30.7***	(-) 62.9***	(-) 65.9***	(-) 41.9***	(-) 34.9***	(-) 25.3***	7.7	–
Canopy height	–	21.5	17.9	(+) 25.4***	(+) 19.7***	(+) 10.7***	(+) 44.5***	(+) 26.5***	(+) 52.6***	(+) 52.6***	–
Water proximity	–	4.0	8.5	23.5	10.5	10.4	(-) 7.5*	10.9	(+) 8.7**	5.4	–
Bareground coverage	–	11.5	19.5	11.6	3.0	7.9	2.7	17.7	11.2	(-) 30.0**	–
Roads	–	5.8	20.8	8.8	(+) 3.9**	5.0	3.4	9.8	2.2	4.3	–
n	2	31	35	45	39	50	62	94	54	41	7

Table 4

Relative influence, as calculated by boosted regression tree analysis (BRT), of several environmental features on nightly movements of Brazilian free-tailed bat *Tadarida brasiliensis* on the East Foundation's San Antonio Viejo Ranch by hour in 2017. Hours are displayed from 2000 (8:00-p) through 0600 (6:00-a). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; '-' insufficient number of records (n) to build models. (+) denotes positive direction of influence (+coefficient in linear model); (-) denotes negative direction of influence (- coefficient in linear model).

	2000	2100	2200	2300	2400	0100	0200	0300	0400	0500	0600
Shrub density	-	-	(-) 51.5**	22.9	(-) 41.0*	(-) 32.3***	(-) 29.7*	3.7	(-) 55.9**	32.6	-
Canopy height	-	-	22.7	(+) 42.7**	16.4	28.6	(+) 29.8**	(+) 64.6**	15.9	6.8	-
Water proximity	-	-	7.0	8.9	4.8	10.8	15.2	7.8	5.3	46.4	-
Bareground coverage	-	-	14.6	10.9	(-) 19.7*	9.6	6.7	1.5	10.1	6.9	-
Roads	-	-	4.2	14.5	(+) 18.0*	18.6	(+) 18.5**	(+) 22.5*	12.8	7.2	-
n	6	2	12	26	33	37	55	22	24	11	3

4. Discussion

Our results demonstrate the importance of separating species when investigating nightly activity patterns of bats. Bats in our study exhibited species-specific responses to vegetative characteristics throughout the night that we would not have observed if we lumped species together. We suspect that these individual species responses are a result of resource partitioning. As suggested by several studies (Arlettaz, 1999; Brown, 1968; Hooper and Brown, 1968; Kunz, 1973; Laval, 1970). Our results add support to this concept as all four species (Eastern red bat, Cave bat, Evening bat, and Brazilian free-tailed bat) exhibited temporally variable activity patterns among species (Fig. 2). Crepuscular and nocturnal insects also exhibit varying nightly activity patterns which could influence the timing of bat emergence and foraging intensity (Corbet, 1961; Rydell et al., 1996). For example, moths (Lepidoptera) tend to reach maximum flight activity near midnight, whereas aquatic insects exhibit two peaks in activity – one between sunset and midnight and another in the few hours before sunrise (Rydell et al., 1996; Williams, 1935). However, temperate, and tropical insectivorous bats are documented to be opportunistic feeders and select from a wide variety of prey including Diptera, Hymenoptera, Homoptera, Coleoptera, and Lepidoptera (Ross, 1961; Whitaker, 1972; Whitaker et al., 1977). We acknowledge that the probability of detection for each species varies according to the species biology, time, and surrounding environment. For example, species that produce loud, mid-to low-range pulses are more likely to be detected a certain distance from a recorder than an individual of similar distance but different species that produces quieter, high-range, or fewer pulses (Adams et al., 2012; Lawrence and Simmons, 1982). Additionally, the surrounding vegetation matrix (e.g., dense canopy) or presence of standing water (concentrating bats) can substantially influence the probability of call detection (Kuenzi and Morrison, 1998; O'Keefe et al., 2014). While we did not adjust for this error, an adjacent study implemented in the CGRDA using the same sampling sites and detectors determined similar detection probabilities for these four species during our study period (ranging from 0.39 to 0.51; unpublished data).

In our study, bats exhibited temporal activity patterns in two distinct groupings: bimodal (Eastern red bat and Evening bat) and unimodal (Cave bat and Brazilian free-tailed bat). Carter et al. (2004) suggested that Eastern red bats and Evening bats alter their prey selection during summer, with red bats consuming more Lepidoptera (taken in greater proportion than their relative availability) and Evening bats consuming more Hemiptera. However, this study consolidated vegetation types and differences in stomach content may have been due to temporal differences in nocturnal foraging activity (Carter et al., 2004). Eastern red bats are recognized to be generalists in terms of prey selection so the nightly activity patterns they exhibit in our study are associated with peaks in total nocturnal flight activity of insects of various orders, both temporally and spatially (Carter et al., 2004; Clare et al., 2009). However, water proximity was a highly influential and significant negative correlate for Eastern red bat activity during crepuscular hours, in which aquatic insect activity is known to peak (Rydell et al., 1996). This suggests an alternative resource targeted by red bats. Evening bats, although exhibiting the same temporal activity pattern as red bats, had differing environmental correlates with nightly activity. For example, water proximity was a highly influential and significant positive correlate for Evening bat activity during crepuscular hours, which may suggest a spatial resource partitioning among these sympatric species. The influence of canopy height varied throughout the night for both; however, canopy height became a significant detractor during the 0600 (6:00-a) hour for both species despite flight activity remaining high. Both, Evening bats and Eastern red bats are tree-roosting species and bats have been known to modify their behavior while commuting to and from roosts when predators (e.g. Great horned owls [*Bubo virginianus*]) are present (Baxter et al., 2006; Menzel et al., 1999, 2001; Speakman, 1991). This sudden aversion to areas of high canopy height (i.e., mature trees) was not seen in the other two species and could suggest considerable predation pressure on these bats during the hours leading to sunrise.

Cave bats and Brazilian free-tailed bats both exhibited strong unimodal activity patterns and had peak flight activity between 0200 and 0400 (2:00-a and 4:00-a). Unlike the Eastern red bats and Evening bats that had similar temporal patterns but differed in spatial associations, Cave bats and Brazilian free-tailed bats shared some of same environmental correlates during periods of high activity (e.g., both were positively associated with areas of high canopy height and negatively associated with areas of high shrub density). Previous studies have suggested a strong association with water and *Myotis* spp. foraging (Cockrum and Cross, 1965; Fenton and Bogdanowicz, 2002). However, water proximity was only a significant positive correlate during the 0400 (4:00-a) hour. This coincides with only the later time period in which aquatic insect activity is known to peak (Rydell et al., 1996). Similarly, Brazilian free-tailed bats, also documented to forage over water in other studies,

were not positively associated with proximity to water at any point during the night (Best and Geluso, 2003; Krutzsch, 1955). Our study only accounted for waterbodies (e.g., cattle tanks) known to exist on the ranch during the sampling period and did not account for other sources of water that could have been available to foraging bats (e.g., shallow puddles, flooded potholes in roads). Bats may have utilized these more fleeting sources of water as a means of resource partitioning among sympatric species active at the same time. Roads were also a significant positive correlate for Cave bat (during the 2400 [12:00-a] hour) and Brazilian free-tailed bat (during the 2400 [12:00-a] and 0200–0300 [2:00-a – 3:00-a] hours). Previous studies are conflicted as to the importance or detriment of lit roads and their effect on foraging efficacy of insectivorous bats (Blake et al., 1994; Rydell, 1991, 1992). However, our roads were not illuminated and, as most were narrow and unpaved, offered only a small clearing in the vegetation. The positive association of free-tailed and Cave bat activity near roads, and negative association with bareground, suggest some advantage to this clearing configuration in the way of protection for bats commuting between foraging or roost sites or a concentration of insects seeking heat held by gravel, caliche, and other road construction materials. Future research should be directed towards understanding the relationship between rural roads and sympatric, insectivorous bats.

5. Conclusions

Nightly activity patterns of sympatric insectivorous bats have rarely been studied in Texas, especially on this fine of a temporal scale. Given the diversity of bat species that occur within this state, describing summer bat activity is essential to inform future management and understanding of these species. Cave bat and Brazilian free-tailed bat nightly utilization of roads should be investigated so that we may understand what resources are provided by these features (e.g., safe passage, concentration of nocturnal insects, heat). With the recent arrival of *P. destructans* in 10 counties across Texas, it is crucial we understand bat activity patterns prior to its arrival to better protect these relatively understudied populations of bat species in south Texas. For example, the strong, positive associations of tree-roosting bat (Eastern red bat and Evening bat) activity with canopy height, temporally variable associations with water proximity, and the evidence of predation pressure in the sunrise hour will help shape effective management should these populations become vulnerable as WNS spreads westward (Zimmerman, 2009). In this way, bat conservation efforts may benefit from active cattle operations, especially in south Texas where natural surface water sources are exceedingly rare.

Acknowledgements

We offer our gratitude to the East Foundation for their generous funding and access to the San Antonio Viejo Ranch, as well as the many field technicians that aided in the ground surveys. This is manuscript number 029 of the East Foundation.

References

- Adams, A.M., Jantzen, M.K., Hamilton, R.M., Fenton, M.B., 2012. Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. *Methods in Ecology and Evolution* 3 (6), 992–998.
- Adams, R.A., Thibault, K.M., 2006. Temporal resource partitioning by bats at water holes. *J. Zool.* 270 (3), 466–472.
- Arletaz, R., 1999. Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. *J. Anim. Ecol.* 68 (3), 460–471.
- Barclay, R.M., 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. *J. Anim. Ecol.* 165–178.
- Baxter, D.J., Psyllakis, J.M., Gillingham, M.P., O'Brien, E.L., 2006. Behavioural response of bats to perceived predation risk while foraging. *Ethology* 112 (10), 977–983.
- Bender, M.J., Hartman, G.D., 2015. Bat activity increases with barometric pressure and temperature during autumn in central Georgia. *SE. Nat.* 14 (2), 231–242.
- Berthiusen, A., Altringham, J., 2012. The effect of a major road on bat activity and diversity. *J. Appl. Ecol.* 49 (1), 82–89.
- Best, T.L., Geluso, K.N., 2003. Summer foraging range of Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) from Carlsbad Cavern, New Mexico. *SW. Nat.* 48 (4), 590–596.
- Blake, D., Hutson, A.M., Racey, P.A., Rydell, J., Speakman, J.R., 1994. Use of lamplit roads by foraging bats in southern England. *J. Zool.* 234 (3), 453–462.
- Boldogh, S., Dobrosi, D., Samu, P., 2007. The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterol.* 9 (2), 527–534.
- Brooks, R.T., 2011. Declines in summer bat activity in central New England 4 years following the initial detection of white-nose syndrome. *Biodivers. Conserv.* 20 (11), 2537–2541.
- Brown, J.H., 1968. Activity patterns of some neotropical bats. *J. Mammal.* 49 (4), 754–757.
- Carter, T.C., Menzel, M.A., Chapman, B.R., Miller, K.V., 2004. Partitioning of food resources by syntopic eastern red (*Lasiurus borealis*), Seminole (*L. seminolus*) and evening (*Nycticeius humeralis*) bats. *Am. Midl. Nat.* 151 (1), 186–191.
- Clare, E.L., Fraser, E.E., Braid, H.E., Fenton, M.B., Hebert, P.D., 2009. Species on the menu of a generalist predator, the eastern red bat (*Lasiurus borealis*): using a molecular approach to detect arthropod prey. *Mol. Ecol.* 18 (11), 2532–2542.
- Clare, E.L., Barber, B.R., Sweeney, B.W., Hebert, P.N., Fenton, M.B., 2011. Eating local: influences of habitat on the diet of little brown bats (*Myotis lucifugus*). *Mol. Ecol.* 20 (8), 1772–1780.
- Cockrum, E.L., Cross, S.P., 1965. Time of bat activity over water holes. *J. Mammal.* 45 (4), 635–636.
- Conlin, M., 1976. Stream Channelization in Illinois – 1976 Update. Illinois Department of Conservation, Springfield, USA.
- Corbet, P.S., 1961. Entomological studies from a high tower in Mpanga forest, X. Observations on Sphingidae (Lepidoptera). *Trans. Ethnol. Soc. Lond.* 113, 351–352.
- Cryan, P.M., Gorresen, P.M., Hein, C.D., Schirmacher, M.R., Diehl, R.H., Huso, M.M., et al., 2014. Behavior of bats at wind turbines. *Proc. Natl. Acad. Sci. Unit. States Am.* 111, 15126–15131. PMID: 25267628.
- Davis, W.B., Dixon, J.R., 1976. Activity of bats in a small village clearing near Iquitos, Peru. *J. Mammal.* 57 (4), 747–749.
- Dzal, Y., McGuire, L.P., Veselka, N., Fenton, M.B., 2011. Going, going, gone: the impact of white-nose syndrome on the summer activity of the little brown bat (*Myotis lucifugus*). *Biol. Lett.* 7 (3), 392–394.

- Emrich, M.A., Clare, E.L., Symondson, W.O., Koenig, S.E., Fenton, M.B., 2014. Resource partitioning by insectivorous bats in Jamaica. *Mol. Ecol.* 23 (15), 3648–3656.
- Erkert, H.G., 1974. Der Einfluß des Mondlichtes auf die Aktivitätsperiodik nachtaktiver Säugetiere [The effect of moonlight on the activity of nocturnal mammals]. *Oecologia* 14 (3), 269–287.
- Fenton, M.B., Boyle, N.H., Harrison, T.M., Oxley, D.J., 1977. Activity patterns, habitat use, and prey selection by some African insectivorous bats. *Biotropica* 73–85.
- Fenton, M.B., Bogdanowicz, W., 2002. Relationships between external morphology and foraging behaviour: bats in the genus *Myotis*. *Can. J. Zool.* 80 (6), 1004–1013.
- Foley, J., Clifford, D., Castle, K., Cryan, P.M., Ostfeld, R.S., 2011. Investigating and managing the rapid emergence of white-nose syndrome, a novel, fatal, infectious disease of hibernating bats. *Conserv. Biol.* 25 (2), 223–231.
- Ford, W.M., Britzke, E.R., Dobony, C.A., Rodrigue, J.L., Johnson, J.B., 2011. Patterns of acoustical activity of bats prior to and following white-nose syndrome occurrence. *J. Fish Wildlife Manage.* 2 (2), 125–134.
- Franklin, J., 2009. *Mapping Species Distributions*. Cambridge University Press, New York, USA.
- Gehrt, S.D., Chelstvig, J.E., 2004. Species-specific patterns of bat activity in an urban landscape. *Ecol. Appl.* 14 (2), 625–635.
- Grider, J.F., Larsen, A.L., Homyack, J.A., Kalcounis-Rueppell, M.C., 2016. Winter activity of coastal plain populations of bat species affected by white-nose syndrome and wind energy facilities. *PLoS One* 11 (11) e0166512.
- Hamilton, I.M., Barclay, R.M., 1998. Diets of juvenile, yearling, and adult big brown bats (*Eptesicus fuscus*) in southeastern Alberta. *J. Mammal.* 79 (3), 764–771.
- Hooper, E.T., Brown, J.H., 1968. Foraging and breeding in two sympatric species of neotropical bats, genus *Noctilio*. *J. Mammal.* 49, 310–312.
- Krutzsch, P.H., 1955. Observations on the Mexican free-tailed bat, *Tadarida mexicana*. *J. Mammal.* 36 (2), 236–242.
- Kuenzi, A.J., Morrison, M.L., 1998. Detection of bats by mist-nets and ultrasonic sensors. *Wildl. Soc. Bull.* 307–311.
- Kunz, T.H., 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. *J. Mammal.* 54 (1), 14–32.
- Kunz, T.H., 1974. Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). *Ecology* 55 (4), 693–711.
- Kunz, T.H., Gustafson, A.W., 1983. Terms commonly used and misused in the literature pertaining to bats. *Bat Res. News* 24, 19–22.
- Laval, R.K., 1970. Banding returns and activity periods of some Costa Rican bats. *SW. Nat.* 15, 1–10.
- Law, B., Gonsalves, L., Tap, P., Penman, T., Chidel, M., 2015. Optimizing ultrasonic sampling effort for monitoring forest bats. *Austral Ecol.* 40 (8), 886–897.
- Lawrence, B.D., Simmons, J.A., 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *J. Acoust. Soc. Am.* 71 (3), 585–590.
- Lorch, J.M., Meteyer, C.U., Behr, M.J., Boyles, J.G., Cryan, P.M., Hicks, A.C., Ballmann, A.E., Coleman, J.T., Redell, D.N., Reeder, D.M., Blehert, D.S., 2011. Experimental infection of bats with *Geomyces destructans* causes white-nose syndrome. *Nature* 480 (7377), 376.
- Mahmoudabadi, H., Briggs, G., 2016. Directional kriging implementation for gridded data interpolation and comparative study with common methods. In: AGU Fall Meeting Abstracts.
- Menzel, M.A., Krishon, D.M., Carter, T.C., Laerm, J., 1999. Notes on tree roost characteristics of the northern yellow bat (*Lasiurus intermedius*), the Seminole bat (*L. seminolus*), the evening bat (*Nycticeius humeralis*), and the eastern pipistrelle (*Pipistrellus subflavus*). *Fla. Sci.* 185–193.
- Menzel, M.A., Carter, T.C., Ford, W.M., Chapman, B.R., 2001. Tree-roost characteristics of subadult and female adult evening bats (*Nycticeius humeralis*) in the Upper Coastal Plain of South Carolina. *Am. Midl. Nat.* 145 (1), 112–119.
- Menzel, J.M., Ford, W.M., Menzel, M.A., Carter, T., Gardner, J.E., Garner, J.D., Hofmann, J.E., 2005. Summer habitat use and home-range analysis of the endangered Indiana bat. *J. Wildl. Manag.* 69 (1), 430–436.
- O'Keefe, J.M., Loeb, S.C., Hill Jr., H.S., Lanham, J.D., 2014. Quantifying clutter: a comparison of four methods and their relationship to bat detection. *For. Ecol. Manag.* 322, 1–9.
- R Core Team, 2013. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rosenstock, S.S., Ballard, W.B., Devos Jr., J.C., 1999. Benefits and impacts of wildlife water developments. *J. Range Manag.* 302–311.
- Ross, A., 1961. Notes on food habits of bats. *J. Mammal.* 42 (1), 66–71.
- Rydell, J., 1991. Seasonal use of illuminated areas by foraging northern bats *Eptesicus nilssonii*. *Ecography* 14 (3), 203–207.
- Rydell, J., 1992. Exploitation of insects around streetlamps by bats in Sweden. *Funct. Ecol.* 744–750.
- Rydell, J., Entwistle, A., Racey, P.A., 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. *Oikos* 243–252.
- Schmidly, D.J., 1994. *The Mammals of Texas*, revised edition. University of Texas Press, Austin, Texas, USA.
- Skalak, S.L., Sherwin, R.E., Bringham, R.M., 2012. Sampling period, size and duration influence measures of bat species richness from acoustic surveys. *Methods in Ecology and Evolution* 3 (3), 490–502.
- Snelgrove, A., Dube, A., Skow, K., Engeling, A., 2013. *East Wildlife Foundation Atlas*. Texas A&M Institute of Renewable Natural Resources, College Station, Texas, USA.
- Speakman, J.R., 1991. Why do insectivorous bats in Britain not fly in daylight more frequently? *Funct. Ecol.* 518–524.
- Surlykke, A., Kalko, E.K.V., 2008. Echolocating bats cry out loud to detect their prey. *PLoS One* 3 (4) e2036. <https://doi.org/10.1371/journal.pone.0002036>.
- Thorne, M.S., Skinner, Q.D., Smith, M.A., Rodgers, J.D., Laycock, W.A., Cerecki, S.A., 2002. Evaluation of a technique for measuring canopy volume of shrubs. *J. Range Manag.* 235–241.
- U.S. Fish, Wildlife Service [USFWS], 2012. North American Bat Death Toll Exceeds 5.5 Million from White-nose Syndrome. USFWS, 26 April 2012. www.fws.gov/whitenosesyndrome/pdf/wns_mortality_2012_nr_final.pdf.
- Van Beers, W.C., Kleijnen, J.P., 2004. Kriging interpolation in simulation: a survey. In: *Simulation Conference, 2004. Proceedings of the 2004 Winter*, vol. 1. IEEE.
- Whitaker Jr., J.O., 1972. Food habits of bats from Indiana. *Can. J. Zool.* 50 (6), 877–883.
- Whitaker Jr., J.O., Maser, C., Keller, L.E., 1977. Food habits of bats of western Oregon. *Northwest Sci.* 51 (1), 46–55.
- Williams, C.B., 1935. The times of activity of certain nocturnal insects, chiefly Lepidoptera, as indicated by a light trap. *Trans. Ethnol. Soc. Lond.* 83, 523–555.
- Zimmerman, R., 2009. Biologists struggle to solve bat deaths. *Science* 324, 1134.