ACOUSTIC AND NETTING SURVEYS OF WESTERN OZARK HIGHLANDS BATS WITH HABITAT SUITABILITY MODELS FOR THREE THREATENED AND ENDANGERED SPECIES

By

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Abstract: Bats in the United States and Canada are experiencing major population declines because of white-nose syndrome (WNS), a fungal disease that kills bats hibernating in caves. First discovered in New York in 2006, WNS has rapidly spread south and west across the United States. Camp Gruber Training Center (CGTC) is a United States National Guard training facility in Muskogee County, Oklahoma. Muskogee County is adjacent to three counties that are suspect for WNS infection as of 2017. I performed acoustic and mist net surveys at CGTC to determine composition of the chiropteran community of the area and if bats in Muskogee County have been exposed to WNS by looking for characteristic damage on wing membranes. Acoustic and mist net surveys determined that the bat community of CGTC is likely dominated by non-endangered species that have not suffered high mortality from white-nose syndrome (*Nycticeius humeralis* and *Lasiurus borealis*). There are at least 2 species that occur rarely within CGTC that are federally endangered (*Myotis grisescens* and *Myotis sodalis*) that, along with the non-endangered *Perimyotis subflavus*, have been known to contract WNS. I found no evidence of WNS symptoms on the bats of CGTC as of summer 2017. I used maximum entropy species distribution modeling (Maxent) to create habitat suitability models for three species that occur in the Ozark Highlands around CGTC, *Myotis grisescens* (endangered), *M. septentrionalis* (threatened), and *M. sodalis* (endangered). These models help explain the community composition of CGTC by revealing habitat preferences of these species and may suggest future range expansions or possible locations of unknown colonies for all three species. I also found that *M. septentrionalis* and *M. sodalis* are highly similar in their habitat preferences, supporting the United States Fish and Wildlife Service decision to combine summer survey guidelines for these species.

PREFACE

The first chapter of this thesis covers two bat surveys (acoustic and netting) performed in eastern Oklahoma and the results thereof, and is formatted for submission to the *Journal of Mammalogy*. The second chapter is formatted for submission to *Diversity and Distributions* and describes habitat suitability models for three species of threatened and endangered Ozark Highlands bats.

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CHAPTER I

ACOUSTIC AND PHYSICAL SURVEYS FOR BATS AT CAMP GRUBER TRAINING CENTER

ABSTRACT

North American bats are facing major population declines due to White-nose syndrome (WNS), and steps must be taken to ensure that these keystone species are not eliminated from much of their ranges in North America. In order to contribute to efforts to understand the spread of WNS, I surveyed a likely habitat for bat species affected by WNS, analyzed relative activity levels and patterns of habitat use of those bats. I also observed bats for signs of WNS infection (wing damage and fluorescent scarring associated with fungal cupping erosions). Acoustic and mist net surveys determined that the bat community of CGTC is likely dominated by non-endangered species that have not suffered high mortality from white-nose syndrome (*Nycticeius humerali*s and *Lasiurus borealis*). There are at least 2 species that occur rarely within CGTC that are federally endangered (*Myotis grisescens* and *Myotis sodalis*) that, along with the non-endangered *Perimyotis subflavus*, have been known to contract WNS. There was no evidence of WNS symptoms on the bats of CGTC as of summer 2017.

INTRODUCTION

Bats are so vital to their ecosystems that they are often referred to as keystone species (Sidhu 2011). Frugivorous bats serve as pollinators to such agriculturally important plants as agave, bananas, and avocados (Marks 2005). Guano of cave-dwelling bats supports both micro- and macrofauna on cave floors (Fenolio et al. 2006) and has had commercial applications ranging from production of fertilizer to gunpowder (Jasinski 2012). Insectivorous bats consume insect species that are harmful to crops and that transmit diseases to humans and other animals, and are particularly important to North American economics. Bats are estimated to be worth at least $3.7 billion/year in agricultural savings, mostly due to reduced crop damage from insects (Boyles et al. 2011). Reduced crop damage leads to reduced insecticide use, meaning fewer insecticides enter the ecosystem overall.

Despite these many ecological and economic benefits, more than a quarter of all bat species are threatened worldwide (Mickleburgh et al. 2002). Most bat populations enter decline due to activities such as poaching, habitat destruction, and wind turbine construction (Mickleburgh et al. 2002; Kunz et al. 2007). Unlike other small mammals, bats live relatively long lives and have low reproductive rates, giving birth to 1 or 2 pups per year (Barclay et al. 2004). This means that bat populations recover slowly from population drops.

White-Nose Syndrome.—A relatively new and major cause of bat population declines in the United States is White-nose syndrome (WNS). WNS is an emerging epidemic among North American bats that is wiping out populations in the northeastern United States and southeastern Canada (United States Fish & Wildlife Service [USFWS]

2017c). WNS is thought to have been introduced to North America via human travel from Europe (Leopardi et al. 2015). In the United States and Canada, more than 5.5 million bats have died from WNS since the first known case in 2006 (Froschauer and Coleman 2012). WNS is caused by the fungus *Pseudogymnoascus destructans* and affects hibernating bat populations (Lorch et al. 2011). *P. destructans* infection often manifests as a white fungal growth around the nasal area and on wings, and results in erratic behavior during hibernation that causes bats to deplete limited fat stores, ultimately leading to starvation (Blehert et al. 2008). Nine bat species from North America are confirmed to be affected by WNS, with an additional 6 species having tested positive for *P. destructans* (USFWS 2017a). Death rates in some hibernacula are as high as 90-100% (USFWS 2017c). A population model by Thogmartin et al. (2013) predicted that, in North America, the overall population of the federally endangered Indiana Bat (*Myotis sodalis*) will be reduced by 86.3% due to WNS.

The first record of WNS in North America is from 2006 in Howes Cave, near Albany, New York (Blehert et al. 2008). Since then, the disease has spread in all directions from the first discovery. Primary movement has been west and south across the eastern United States at a rate of 200-900 km per year, reaching as far as eastern Oklahoma, Nebraska, and Minnesota (Lorch et al. 2016). Counties are classified by USFWS as “suspect” (*P. destructans* DNA is detected on bats) or “confirmed” (histological confirmation of skin invasion) for WNS (WhiteNoseSyndrome.org 2011). In Oklahoma, Ottawa, Sequoyah, Adair, and Cherokee counties are all listed as suspect for WNS and Delaware County has at least one confirmed occurrence of WNS as of August 2017 (WhiteNoseSyndrome.org 2017). In 2016, a little brown bat (*Myotis lucifugus*) tested positive for *P. destructans* near Seattle, Washington (Lorch et al. 2016). This occurrence was much farther west than expected given the previously documented rate of spread for the fungus. Phylogenetic analysis done by Lorch et al. (2016) showed that the Washington occurrence grouped with other isolates from the eastern United States, suggesting that there has not been a reintroduction from Europe to the West Coast. This means that *P. destructans* was likely spread anthropogenically to Washington, and has the potential to be carried to any other location where suitable conditions exist, putting hibernacula all over North America at risk of infection. In January and February of 2017, *P. destructans* was detected on hibernating bats in 6 counties in northeastern Texas (Texas Parks and Wildlife Department 2017). This "jump" to Texas suggests yet another anthropogenic transmittance of *P. destructans* that has the potential to cause thousands to millions of bat deaths. These startling numbers suggest the need for studies in regions likely to be affected by WNS, so that measures can be taken to protect bat populations by preventing infection. It also emphasizes the importance of studies to document chiropteran community composition in areas that are likely to be in the path of WNS before the fungus invades these places.

Although bats can be secretive, there are several reliable survey methods to determine which bat species are present in an area of interest (Kunz and Parsons 2009). I employed 2 of these methods, mist netting and acoustic detection. Mist netting, or bat netting, is a method of capturing bats in the field and is widely used as a method of surveying chiropteran species composition (Kunz and Parsons 2009). For the purpose of capturing bats, mist nets are strung between 2 poles across potential flyways. Common features of flyways include proximity to water or food sources, near exits from caves, or where bats would be funneled into or out of a dense forested area. The nets are not invisible to bats, so they must be arranged in a manner that decreases the bats' ability to maneuver around them. After bats are captured in the pocket of the net, surveyors remove and process them as the study requires.

Acoustic monitoring is the use of ultrasonic detectors to record echolocation calls made by bats in a study area. Acoustic detection coupled with ultrasonic analysis is an emerging field that has revolutionized the way that bat ecology is studied (Britzke et al. 2013). Monitoring can be performed using transects (i.e., the detector is attached to a moving vehicle) or in a stationary manner (the detector is attached to a tree or other object). Anabat Express®, which was used for this study, is a stationary acoustic detector designed for passive monitoring of ultrasonic sounds. Anabat Express® uses a zero-crossings analysis (ZCA) output. ZCA plots frequency over time by quantifying the delay between zero-crossings (instances when the mathematical sign changes) above a threshold, producing a sonogram that represents the strongest frequency components of the sound (Agranat 2012). Species identification relies on differences in acoustic qualities between species (Britzke et al. 2013). Identification can be performed by software programs that compare the ZCA files extracted from the Anabat Express® detectors to a call library of known species calls and make species identifications based on the recorded calls. USFWS has approved several programs for analysis of bat calls: Bat Call ID, Echoclass®, and Kaleidoscope® (USFWS 2016a).

Acoustic monitoring has been used for almost twenty years to study various aspects of bat behavior and ecology. On the individual level, Kazial and colleagues (2008) determined that little brown bat calls communicate significant information (e.g., age, state of lactation, individual identity) from one bat to another in the right circumstances. Hoary bats captured and recorded at 4 different locations throughout the Hawaiian islands had distinct regional variation in echolocation calls (Barclay et al. 1999). Kalcounis et al. (1999) used acoustic monitoring to determine that stand type has a significant effect on bat feeding activity and demonstrated that bats are active above, within, and below the canopy in the boreal forest. Dodd et al. (2012) studied a forested disturbance gradient and showed that bats change their insect foraging patterns across a disturbance gradient to account for different prey and vegetation types. Occurrences collected from acoustic surveys can be used to construct species distribution models (SDM). Depending on the species, SDMs constructed from acoustic data can perform significantly better than those constructed from physical capture data (Barnhart and Gillam 2014). Finally, acoustic monitoring can be used to monitor reduction in activity levels, for example, as a result of WNS mortality (Brooks 2011).

The United States Fish & Wildlife Service has developed guidelines for surveying bats affected by WNS, particularly the Indiana bat (*M. sodalis*) and the Northern-long eared bat (*Myotis septentrionalis*) (USFWS 2017b). These guidelines ensure that independent surveyors use consistent methods to increase confidence in reports and subsequent analyses. I used these guidelines when developing and implementing my acoustic and mist net surveys so that the results could ultimately contribute to large-scale conservation efforts by USFWS.

Study Site.—Camp Gruber Training Center (CGTC) is located in Braggs, OK. This National Guard training facility encompasses 33,027 acres and is used for training exercises by the National Guard and other branches of the U.S. Military, along with training for municipal fire and law enforcement departments. Forty-eight percent of the base consists of closed canopy forest, 27% is open prairies, old pastures, and open woodland, and 17% is water (open water, wetlands, and streams). Only 6% of the land on CGTC is developed (Oklahoma Military Department 2015). This large area that includes closed canopy, edge, and riparian locations represents potentially excellent habitat for bats. CGTC is within the ranges of 7 out of 9 North American bat species affected by WNS (International Union for Conservation of Nature [IUCN] 2015). This includes *M. septentrionalis,* a species affected by WNS that was federally listed as threatened in April 2015. Two endangered species are affected by WNS (*Myotis grisescens and M. sodalis*) and CGTC is within the known range of both. CGTC is located less than 60 miles from Delaware County, which has confirmed WNS infections, and is partially within Cherokee County, which is suspect for WNS (Fig. 1.1). Given the rapid spread of WNS (Lorch et al. 2011, 2016), it is more than reasonable to assume that *P. destructans* may reach bats in CGTC sometime in the near future.

The ultimate goal of this study was to determine the community composition of the bats of CGTC and how they are currently affected by WNS. I had 3 objectives. Objective 1 was to perform an acoustic survey of the bats of CGTC using the three software programs approved by USFWS. Objective 2 was to conduct a physical, or mist net, survey of the bats of CGTC. Objective 3 was to determine how the bats of CGTC are currently affected by WNS, and if they are not, to establish a baseline of community composition and biological data should WNS ever spread to CGTC and Muskogee County.

MATERIALS AND METHODS

Site Selection.—Six "creek" and 4 "edge" sites were selected within CGTC based on suitability of habitat and accessibility by vehicle. Creek sites were selected based on descriptions of suitable foraging habitat from Kunz and Parsons (2009), including a source of water and a closed or partially closed flyway (like closed canopy forest), and based on habitat descriptions for *Lasiurus borealis* (Shump and Shump 1982), *Eptesicus fuscus* (Kurta and Baker 1990), *M. septentrionalis* (Caceres and Barclay 2000), *M. grisescens* (Decher and Choate 1995) and other species known from Muskogee County. Edge sites were selected at locations where forest meets open areas. Jantzen and Fenton (2013) showed that peak activity was found within 20 m of the forest edge in either direction. Edge habitat was shown to have the most bat activity of any habitat type for *E. fuscus, Lasionycteris noctivagans, L. borealis, M. lucifugus,* and *M. septentrionalis* in Ontario, Canada (Jantzen and Fenton 2013).

Objective 1: 2016 acoustic survey.—The acoustic survey took place during summer 2016. Prior to the acoustic survey, 2 Anabat Express® detectors were tested for calibration using ultrasonic pest repellants as described by Larson and Hayes (2000). The detectors consistently gave similar readings, so no action was necessary to calibrate them. Detectors were deployed at all 6 creek sites and 4 edge sites, totaling 10 acoustic monitoring points throughout CGTC (Fig. 1.2). At creek sites, detector microphones were aimed at the creek in order to record bats flying along the creek, either foraging for insects or drinking water. At edge sites, detector microphones were aimed toward the open area. In accordance with the Indiana Bat Summer Survey guidelines (USFWS 2017b), detectors were placed at least 3 m above ground vegetation, at least 10 m from large obstructions, and no detectors were placed within 15 m of a potential roost tree for *M. septentrionalis* (USFWS 2017b).

The creek sites were surveyed with Anabat Express® detectors 2 at a time for 7 nights each, and then this process was repeated at pairs of sites for a total of 84 detector nights from 15 June to 9 August 2016. The edge sites were surveyed 2 at a time for 7 nights each. The detector at Site 2 malfunctioned for 3 nights, causing those data to be lost. Anabat Express® detectors detect and record bat calls 30-100 m away from the microphone (Broken-Brow and Corben 2015). Detectors recorded from 30 min before sunset to 30 min after sunrise. Appendix 1 shows dates, settings, and hours recorded for each acoustic monitoring site.

There are three acoustic identification software programs approved for use in USFWS summer surveys: Echoclass®, Bat Call Identification® (BCID), and Kaleidoscope® (USFWS 2016a). These programs all compare recorded calls to a call library of known species. They provide a maximum likelihood estimate (MLE), which gives the probability that the species was misidentified based on known error rates. The MLE used by all programs was developed on the basis that species identifications are generally more accurate when tested in groups (i.e., aggregate calls from one night) than as individual calls (Britzke et al. 2002). The software programs differ in the number of echolocation pulses that are used for identification and the collection location of the calls used in the call library. Table 1.1 provides a comparison of the three programs used for call identification. I used Echoclass® to conduct my primary acoustic analysis. I also worked with Brian Fuller at the USFWS Oklahoma Ecological Services Field Office in Tulsa to analyze my call files using BCID® and Kaleidoscope®. This allowed for direct comparison between the programs using identical data. After the files were processed in each program, the species and proportions of species detected were determined. For the purpose of calculating captures per unit effort (CPU), a call identified to species was considered a capture, and hours recorded (HR) was used for the unit of effort. Aggregate hourly activity, defined as the number of calls identified to species in 1-hour increments, was determined for all species combined and for each common species. Finally, a two-tailed T-test was used to determine if creek and edge sites showed significantly different bat activity using the average number of identified bat calls per night for 81 creek nights and 28 edge nights.

Objective 2: mist net survey.—The 6 creek sites shown in Figure 1.2 were used for the mist-netting portion of the survey conducted in summer 2017. Edge sites were omitted from the mist net survey because it is more difficult to cover entire openings in that type of habitat, so the ability to funnel bats into nets is diminished. Creek sites were generally similar but had variation in breadth and depth of creek, amount of canopy cover, and proximity to roads. The canopy was dominated by deciduous broadleaf trees like sycamore (*Platanus occidentalis*), black walnut (*Juglans nigra*), redbud (*Cercis canadensis*), pecan (*Carya illinoinensis*), and white oak (*Quercus alba*). Mist nets were erected over likely flyways and in places adjacent to creeks where entire openings could be covered with nets (Kunz and Parsons 2009). In order to comply with USFWS Indiana Bat Summer Survey Guidelines (USFWS 2017b), I used 5 nets per night for 2 nights at each site for a total of 10 net nights per site. To avoid net shyness, where bats apparently learn the location of nets and avoid them on subsequent nights of netting, I adjusted net setups slightly on some nights (as suggested in Tiago Marques et al. 2013). At each site, nets were opened 0-30 minutes before sunset and closed 5-6 hours later. When nets were open, I checked for bats every 10-20 minutes, depending on activity levels, as suggested by the Guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes and Gannon 2016).

Captured bats were transferred to holding cages made with modified minnow traps. After being identified to species, age, sex, reproductive condition, weight, and right forearm length were recorded. Dorsal, ventral, face, and calcar photographs were taken of each bat. Bats were banded with aluminum wing bands (labeled OKCG 001-100) and released as quickly as possible.

Net-area-hours (NAH) was used as a unit of effort to determine capture per unit effort (CPU; similar to Perry et al. 2010). Although 5 nets per night were used at each site, nets of different lengths and heights were used depending on the width of the creek and layout of the site, resulting in slightly different netting effort from site-to-site. NAH for each site was calculated by multiplying the height and width of each net used to determine area of open net in square meters. This was multiplied by the number of hours each net was open to determine NAH for each site and total NAH. A Pearson Product-Moment correlation coefficient was calculated to show the relationship between NAH and number of captures for each night. Hourly capture histograms were constructed using the time of capture for each bat. Ninety-five percent confidence intervals were constructed to determine which acoustic identification program most closely aligned with mist net results.

The Simpson Diversity Index (D_1) was used to estimate and compare species diversity as determined by acoustic (as identified by Echoclass®) and mist-net surveys.

This index accounts for richness (number of species), evenness of species distribution, and proportional abundance of species to estimate community diversity (Morris et al. 2014). Simpson Diversity Index values range from 0 to 1. Diversity increases with increasing values, and the value itself represents the probability that 2 randomly selected individuals are different species (Morris et al. 2014).

Objective 3:evidence of WNS.—For each bat captured during the mist net survey, wing damage from white-nose syndrome was scored using the Wing-Damage Index developed by Reichard and Kunz (2009). Dorsal and ventral surfaces of wing membranes were observed under longwave ultraviolet light (368-385 nm) to check for fluorescence characteristic of fungal cupping erosions caused by WNS infection (Turner et al. 2014).

The methods used in this study were approved by the Oklahoma State University Institutional Animal Care and Use Committee under Animal Care and Use Protocol AS-16-6. Endangered species were trapped and handled under USFWS Native Endangered and Threatened Species Recovery Permit number TE00540C-0. All other animals were trapped and handled under Oklahoma Department of Wildlife Conservation Scientific Collector Permit number 6877. Because of the risk of WNS transmission, survey personnel used a new pair of nitrile gloves over leather gloves to handle each bat captured. Additionally, equipment that came into contact with bats was decontaminated in accordance with the United States Fish and Wildlife Service WNS National Decontamination Protocol (USFWS 2016b) and guidance from the USFWS Oklahoma Ecological Services Field Office located in Tulsa, Oklahoma. Briefly, porous equipment (i.e., nets) were immersed in hot (>55˚C) water and nonporous equipment was cleaned with Clorox® Disinfecting Wipes.

RESULTS

Objective 1.—Activity was recorded for 10.5-11.3 hours per night over the course of the survey. There were 109 detector nights and 1172.96 hours recorded. See Appendix 1 for detailed descriptions of the acoustic survey schedule.

Fourteen species were captured via acoustic analysis. Table 1.2 shows which species were identified by the three programs, along with the proportions and classifications of each species. Species were categorized as common (>5.00% of all captures), uncommon (1.00-4.99% of captures), and rare (<0.99% of all captures). Three species were common across all programs: *L. borealis*, *Nycticeius humeralis*, and *P. subflavus*. *E. fuscus* was categorized as either common or uncommon by all programs. Other species that were common or uncommon in two out of three programs were *L. noctivagans*, *Lasiurus cinereus*, and *M. lucifugus*. A capture was defined as a call file identified to species. Overall captures per unit of effort (CPU) was 7.67. Table 1.3 shows CPU for each site and Table 1.4 for each species as identified by Echoclass®. The Simpson Diversity Index for the acoustic survey (as identified by Echoclass®) was $D_1 =$ 0.451.

Acoustic activity for all bat species combined tended to peak twice per night, once about an hour after sunset (9:00 pm) and again about 8 hours later (5:00 am; Fig. 1.3). Individual species generally followed this trend, but had minor differences in peak activity times (Fig. 1.4). *E. fuscus* showed peak activity levels around 9:00 pm (34.0% of all activity), and tapered-off throughout the night with no pre-sunrise peak. *L. borealis* was fairly active all night long, but had moderate activity peaks (36.0% of all activity) around 9:00 pm and 5:00 am. The majority of *N. humeralis* activity (51.4%) was during post-sunset and pre-sunrise peaks. *P. subflavus* had very evenly distributed activity throughout the night, with small post-sunset and pre-sunrise peaks (23.5% of all activity).

Average number of bat calls identified to species was highly variable for both creek and edge sites. According to Echoclass® analysis, creek sites had an average of 87.7 (SD ± 72.4) identified bat calls per night with a range of 0-267 calls per night over 80 nights. Edge sites had an average of 70.9 (± 95.5) and a range of 1-343 calls per night over 28 nights. A two-tailed T-test showed that there was no significant difference between average calls per night in creek and edge environments; $t(38) = 0.85$, $p = 0.40$.

Objective 2.—The netting effort was 5 nets open per night for 12 nights, totaling 60 net nights. Nets were open for approximately 5 hours per night, totaling 62 hours and 11,795 net-area-hours (NAH). Thirty-eight individual bats were captured. Five of those individuals were observed in nets but escaped before they could be removed and processed, resulting in 33 bats identified to 5 species. The captures per unit effort (CPU) for combined sites was 0.003. There was a significant correlation between NAH and number of captures ($n = 12$, $r = 0.5583$, $p = 0.03$). See Table 1.5 for netting effort and CPU by site.

The species captured via mist net were *L. borealis*, *M. grisescens*, *M. sodalis*, *N. humeralis*, and *P. subflavus*. Only 1 individual was captured for: *M. grisescens*, *M. sodalis*, and *P. subflavus*. Eighteen *N. humeralis* and 12 *L. borealis* were captured. Overall, there were 23 females and 10 males. The age distribution was 20 adults, 12 sub-adults, and 1 juvenile. There were no signs of pregnancy in females and no males were scrotal. One adult female was actively lactating and 3 were post-lactating. See Table 1.6 for measurement and age breakdown by species. *N. humeralis* made up the majority of captures (54.6%, CPU = 1.53 x 10^{-3}). *L. borealis* was second most abundant at 36.4% (CPU = 1.02 x 10^{-3}). *M. grisescens, M. sodalis,* and *P. subflavus* were all single captures representing a proportion of 3.0% each (CPU = 0.085 x 10^{-3}). The Simpson Diversity Index for the mist net survey was D_1 = 0.585. Table 1.7 shows the proportions of species captured in mist nets with 95% confidence intervals on those proportions.

Peak capture time was about 2 hours after sunset (10:00-11:00 pm). From the peak time, capture rate gradually went down until nets were closed. *L. borealis* were captured between 9:00 pm and 2:00 am. All *N. humeralis* were captured in a 3-hour window between 9:00 pm and midnight. The single individual of *M. grisescens* was captured around 11:30 pm, *M. sodalis* around 10:00 pm, and *P. subflavus* around 9:30 pm. Figure 1.5 shows hourly activity levels for *L. borealis,* for *N. humeralis,* and for all species combined.

Objective 3.—All individuals except one scored a zero on the WDI, meaning there was minimal to no damage evident on wings. One adult female *L. borealis* scored a 1 due to several scars and holes on the wings. No individuals showed evidence of ultraviolet fluorescence associated with WNS scarring.

DISCUSSION

Objective 1.—Echoclass®, BCID®, and Kaleidoscope® were in agreement about three common species (*L. borealis, N. humeralis,* and *P. subflavus). E. fuscus* was common or uncommon in all three analyses. *L. noctivagans, L. cinereus,* and *M.*

lucifugus were common or uncommon in two out of three analyses. Aside from these species, there was little agreement between the three programs.

Species of the genus *Myotis* occurring in the eastern United States are famously difficult to differentiate acoustically (Kalcounis et al. 1999; O'Farrell 1999; Britzke et al. 2002; Broders et al. 2004; Clement et al. 2014). The prominence of *M. lucifugus* in the Kaleidoscope® analysis (and BCID®, to a lesser extent; see Table 1.2) is unexpected because the species typically concentrates activity in uncluttered habitat unlike our survey sites (Broders et al. 2004), and because it was not captured in the mist net survey. Given the physical capture of two other species of *Myotis* in the area, the simplest explanation is that one or both of those species were misidentified as *M. lucifugus* by BCID® and Kaleidoscope®.

Maximum Likelihood Estimations.—Table 1.2 shows which species were detected with high confidence ($p \leq 0.05$, indicated by asterisk). Interestingly, Echoclass® was never able to confidently identify *N. humeralis* (Table 1.2), the most commonly physically captured species. This could indicate a weakness of Echoclass® in identifying *N. humeralis* or significant regional variation in *N. humeralis* calls (as demonstrated in Murray et al. 2001) for which Echoclass could not compensate. BCID® and Kaleidoscope® estimated *N. humeralis* proportions much more accurately and with confidence, so it is not likely a recording quality issue.

Another interesting MLE result is how many species were detected with confidence on at least one night during the acoustic survey. Echoclass® confidently identified 8 out of 12 species in its call library; BCID® identified 11 out of 11 species with confidence; Kaleidoscope® identified 12 out of 13 species with confidence. This could be a result of the survey effort. There were 109 detector nights totaling 1172.96 hours recorded during the 2016 acoustic survey. The sheer number of recording hours increases the likelihood of random variations in acoustic activity compounding to produce unexpected or misleading results. Even using a lower number of minimum pulses, Echoclass® appears to be more conservative than BCID® or Kaleidoscope® in calculation of MLE p-values.

Echoclass® apparently has difficulty identifying *N. humeralis* calls and greatly overestimates *L. borealis* presence. Beyond this issue, Echoclass® closely matched the proportions of the other three species captured physically (*P. subflavus*, *M. grisescens*, and *M. sodalis;* see Table 1.7). It is difficult to construct a complete picture of how well BCID® performs with the species present at CGTC because *M. sodalis* was not included in the preliminary analysis. However, BCID® and Kaleidoscope® both performed better than Echoclass® at estimating relative proportions of *N. humeralis* and *L. borealis*. BCID® and Kaleidoscope® also both had more *P. subflavus* captures than physical or Echoclass® captures. Overall, the program that most closely matches the proportions of species captured in mist nets is Kaleidoscope®. Echoclass® performed the worst by greatly overestimating *L. borealis* and underestimating *N. humeralis*. BCID® was likely the second best, but it is not possible to say without *M. sodalis* being included in analysis.

Community composition.—In spite of the 2016 acoustic survey detecting 14 species and the mist net survey detecting only 5, the Simpson Diversity Index showed that the acoustic community was less diverse than the mist net community. This is because of the dominance of *L. borealis* in the Echoclass® analysis. The mist net captures were dominated by *N. humeralis* and *L. borealis* together, resulting in a more diverse sample overall.

In an acoustic survey in South Carolina, *N. humeralis* was rarely detected below the forest canopy, and was detected at 3 times the rate above the forest canopy (Menzel et al. 2005). This was taken to mean that *N. humeralis* was foraging above the canopy much more. In the present study, *N. humeralis* were captured with high success below the canopy. This may be because of differences in geographic location and forest composition, but it is possible that *N. humeralis* calls get lost or distorted in the cluttered area below the canopy, which could lead to lower detection below the canopy. Regardless, this example of *N. humeralis* versus *L. borealis* dominance reinforces the need for bat population surveys to be comprehensive and undertaken with a thorough understanding of individual species ecology and the abilities of the survey methods being employed.

Activity patterns.—Acoustic activity consistently peaked one hour earlier (9:00 pm) than netting activity (10:00 pm). The acoustic detectors can survey activity much higher than nets can reach, possibly as high as 40 m (Broken-Brow and Corben 2015). It is possible that bats forage higher earlier in the night, and then fly below the canopy to drink water. Future research is needed to determine whether bats forage at different heights throughout the night, and what factors might cause this.

There are interesting differences between species activity levels (Figs. 1.4 and 1.5). *N. humeralis* and *L. borealis* showed distinct differences in apparent activity patterns during the mist net survey (Fig. 1.5). *L. borealis* was captured in low numbers throughout the netting period (5-6 hours), whereas *N. humeralis* seemed to have a burst of activity over a 3-hour period, peaking at 10:00 pm. The acoustic activity of both species shows similar patterns. *L. borealis* showed much more even distribution of acoustic activity and *N. humeralis* had 2 peaks in acoustic activity. Since netting only took place for 5 hours per night, there was no opportunity to detect the *N. humeralis* pre-sunrise peak of activity. The tendency for bat species occupying the same area to forage at different times has been demonstrated (Kunz 1973; Erkert 1982). The species within CGTC distributing their foraging activity differently throughout the night may be an example of temporal niche apportioning (Adams et al. 2006).

Survey effort and capture success.—Bats can be unpredictable, and this is demonstrated in how much the CPU varied from site-to-site and night-to-night. The correlation between NAH and number of captures per night was moderately strong (r = 0.558) and significant (p = 0.030). It is intuitive that increased sampling effort should lead to increased captures, and such CPU values as are presented here can be useful guidelines or starting points for surveyors. However, there are many factors that affect how many bats are captured in a night or at a site. This includes the phenomenon of net shyness, or the tendency for bat captures to decrease during subsequent nights of netting in the same location (Kunz and Kurta 1988; Tiago Marques et al. 2013). Other factors shown to have an effect on bat activity are light (sunset, sunrise, moon phase) or ambient temperature (Erkert 1982; White et al. 2014).

As an example of the multitude of factors that can affect capture rate, I captured no bats at my first sampling location, site 3. I expected it to be a high quality foraging and netting location based on the closed canopy and slow-flowing creek. One possible explanation is that Camp Gruber and the surrounding area received around 6 inches of rain the week before I arrived to survey site 3 (Oklahoma Mesonet 2017). This meant that the creek was higher than usual and possibly caused a short term disturbance in the macroinvertebrate community (Robinson et al. 2004) shortly before I began netting. Bats have been shown to move their foraging activity and location in response to a disturbance in insect habitat (Dodd et al. 2012). I observed bats foraging over the canopy at this location, so it is possible that the bats were responding to the disturbance by foraging higher than usual. At the next 5 sites, enough time had passed since the large rain event that the creek was back to normal levels, and I had higher capture success at all other sites.

For both acoustic and physical data, there seem to be sites that were more productive than others regardless of survey effort (Tables 1.3 and 1.5). While it is always important to choose high quality survey locations, it will not always guarantee higher capture success. I found that extent of effort (NAH) for netting surveys is significantly correlated with number of captures. Expending a small amount of additional effort when netting (e.g. putting up one more net) will increase net area and will likely increase capture success. It should also increase likelihood of capturing rare species. Apparent quality of location did not always prove a useful selection criterion on its own for netting (Site 3 example). This is not as true for acoustic surveys. Extent of survey effort (HR) was significantly correlated with acoustic capture success, but not as strongly as physical capture success. Site selection, and possibly other unaccounted for variables like weather conditions, would seem to better determine capture success via acoustic detection.

Perry et al. (2010) performed an 8 year mist net survey in the Ouachita Mountains in Arkansas (approximately 160 – 420 km from CGTC). The authors used a net-meterhours metric to standardize capture rates, which I modified into the net-area-hours unit used in this study. They captured 3 of the same species as were captured at CGTC, which allows me to compare capture rates between surveys which took place in the same month and in geographically close locations. In July, *N. humeralis* capture rate for Perry et al. (2010) was roughly the same as in my survey; *L. borealis* and *P. subflavus* capture rates were both approximately 10-15 times greater than my survey. One possible explanation for these differences is that the habitats are not identical at CGTC and the Ouachita Mountains, so *L. borealis* or *P. subflavus* may be more common in the latter habitat. Another explanation is that Perry et al. (2010) performed their survey over 8 years, which may have allowed them to account for population cycles. Because I only did mist netting over one month, it is impossible to know whether 2017 was a low, high, or average year in terms of population sizes for the species captured.

Total CPU for all acoustic data (2016 and 2017) was 7.55. Total CPU for mist net data was 0.003. Capture success was roughly 2,300 times greater with acoustic survey methods than traditional mist net methods. Acoustic surveys are incredibly efficient and will result in higher capture rate with much less effort expended. Acoustic detectors can be left alone and require little to no maintenance when recording. Every hour that a mist net is open must be monitored by qualified surveyors, greatly increasing the time and personnel required. However, it is important to recognize that mist net surveys involve more than just species identification. Mist net and other physical surveys yield more and different data, for example, size, weight, sex, reproductive condition, disease, and parasite load. Acoustic surveys are also reliant on software programs that can have flaws which can result in inaccurate identifications.

Evidence of WNS.—Only one individual showed enough evidence of wing damage to warrant anything but a score of zero on the WDI. Since the bat showed no signs of white-nose syndrome-associated fluorescence, I judged the damage to be a result of age or mechanical injury. It seemed more likely that the wing damage was a result of injury or age because *L. borealis* has never been recorded with WNS symptoms to date (although it has been recorded with *P. destructans*) and because this female was the largest *L. borealis* captured in both mass and forearm length. Given the lack of membrane damage on captured bats, there is no evidence of WNS survival in the bats of CGTC in Muskogee County. It is important to note that the 2 most commonly captured species, *L. borealis* and *N. humeralis*, have tested positive for *P. destructans*, but have never developed symptoms of WNS. The other 3 species that were captured, *M. grisescens, M. sodalis,* and *P. subflavus* are known to contract WNS and have experienced significant population decline due to WNS (Cryan and Ellison 2017). The single captured *P. subflavus* was a juvenile, meaning it has not yet had its first winter and likely has not ever had the opportunity to be exposed to the fungus in a hibernaculum. Adults of *M. grisescens* and *M. sodalis* were captured, neither of which showed any evidence of WNS damage.

Conclusions.—Acoustic and physical survey results suggest slightly different community composition. Most species that were captured by mist net were also identified with confidence by Echoclass®, BCID®, and Kaleidoscope®. *N. humeralis* was never detected with confidence by Echoclass® and *M. sodalis* was not included in the BCID® analysis. Given the low CPU for netting, it is possible that more of the species detected acoustically occur rarely or incidentally in CGTC. The bat community of Camp Gruber

Training Center is likely dominated by non-endangered species that have never been recorded with white-nose syndrome (*N. humeralis* and *L. borealis*). There are at least 2 species that occur rarely within CGTC that are federally endangered (*M. grisescens* and *M. sodalis*) that, along with the non-endangered *P. subflavus*, have been known to contract WNS. I found no evidence of WNS symptoms on the bats of CGTC as of summer 2017, so my data provide a baseline should WNS ever move into Muskogee County.

CHAPTER II

COMPARATIVE HABITAT SUITABILITY MODELS FOR THREE OZARK HIGHLANDS BAT SPECIES AFFECTED BY WHITE-NOSE SYNDROME

ABSTRACT

I used maximum entropy species distribution modeling (Maxent) to create habitat suitability models for three species that occur in the Ozark Highlands around CGTC, *Myotis grisescens* (endangered), *Myotis septentrionalis* (threatened), and *Myotis sodalis* (endangered). These models help explain the community composition of CGTC by revealing habitat preferences of these species and may suggest future range expansions or possible locations of unknown colonies for all three species. I also found that *M. septentrionalis* and *M. sodalis* are highly similar in their habitat preferences, supporting the United States Fish and Wildlife Service decision to combine summer survey guidelines for these species.

INTRODUCTION

Significance.—Ecological niche modeling (ENM), also called species distribution modeling and habitat suitability modeling, is a field that has considerable potential in understanding species distributions and aiding conservation efforts (Peterson 2001; Phillips et al. 2004). The ability to analyze habitat preferences and model suitable habitat for species (endangered, invasive, or otherwise of interest) can inform land-use decisions, conservation plans, and ecological risk assessment (Peterson et al. 2000; Miller 2010).

As white-nose syndrome (WNS) continues to threaten bat populations throughout the United States and Canada (Froschauer and Coleman 2012), it is becoming increasingly important to understand and protect bat species that are or could potentially be impacted by WNS. The use of ecological niche modeling could be instrumental in developing plans to protect bats threatened by WNS. The disease itself can be studied, as in Flory et al. (2012), where the environmental conditions associated with mortality from WNS were modeled and locations where mortality is most likely were revealed.
ENM can also be used to examine the potential impact of WNS on bat species (Thogmartin et al. 2013; Alves et al. 2014). There is also a growing need to determine ideal habitat for species affected by WNS so those areas can be surveyed, protected, or treated (Barnhart and Gillam 2014).

Many studies of habitat suitability in temperate bats focus on the eastern United States (Loeb and Winters 2013; Pauli et al. 2015; Hammond et al. 2016). This is the epicenter of the white-nose syndrome (WNS) outbreak and certainly the area that has experienced the greatest number of deaths due to WNS (Froschauer and Coleman 2012). However, as the fungus spreads to hibernacula further west each year, it is necessary to study other regions of the US to determine the potential impact on bat species in the central and western United States.

In 2016 and 2017, I conducted both acoustic and physical bat surveys at Camp Gruber Training Center (CGTC) in Braggs, Oklahoma. One purpose of these surveys was to determine the presence or absence of the threatened species, *Myotis septentrionalis.*

This species and two endangered species, *Myotis grisescens* and *Myotis sodalis*, were captured via acoustic detection, but only *M. grisescens* and *M. sodalis* were captured in the mist net survey. These results suggest the need to analyze the suitability of this general area for each species on a larger geographic scale.

The northern long-eared bat, *M. septentrionalis,* and the Indiana bat, *M. sodalis* are similar in ecology. For example, the United States Fish & Wildlife Service (USFWS) guidelines for summer surveys are identical for *M. septentrionalis* and *M. sodalis* (USFWS 2017b). Loeb and Winters (2013) modeled suitability for Indiana bat maternity colonies in the eastern United States for both current and future climate conditions. The study area did not include Oklahoma. Ideal conditions that predicted Indiana bat occurrence were average daily temperature of 23.4-27.4˚C, along with higher May precipitation and elevation of 120-330 m. Pauli et al. (2015) used presence-only modeling to determine environmental variables that predict roost occupancy for *M. septentrionalis* and *M. sodalis* maternity colonies in Indiana. *M. sodalis* preferred roosting sites that had >80% local cover, but <40% cover within 1 km of the roost site, along with distance to streams (within 1 km of perennial streams). They also found a negative relationship between quality of an area for foraging and likelihood of maternity colonies. For northern long-eared bats, roost occupancy was positively related to increased proportion of forests. Distance to major roads (within 2 km) also decreased likelihood of roost occupancy for northern long-eared bats. Hammond et al. (2016) used presence-only modeling to predict suitable roosting habitat for *M. sodalis* at the landscape-scale in the Southern Appalachians. The most important variables were elevation and forest type (mixed pine-hardwood forests at 260-575 m).

Very little modeling work has been done with the gray bat, *M. grisescens*, so there are not many examples of predictive variables in the literature, unlike *M. septentrionalis* and *M. sodalis, M. grisescens* is a cave-obligate species preferring limestone caves, and very rarely storm drains, for both summer and winter use (Decher and Choate 1995). Because of their dietary preferences for insects found near water *M. grisescens* usually roosts in caves that are within 1-2 km of water (Decher and Choate 1995). Foraging distances of adult *M. grisescens* are remarkably large compared to other North American *Myotis* species. In Missouri, *M. grisescens* captured over streams and banded were recaptured at caves a mean distance of 12.5 km away from the original site, and as much as 35.4 km away (LaVal et al. 1977). Bats in Kansas marked with reflective bands at the roost entrance were recorded as far as 14.3 km away (Decher and Choate 1995).

Newly volant bats have exceptionally high metabolic demands, which is exacerbated by cold cave temperatures (Tuttle 1975). To alleviate the stress of cave roosting on juveniles, *M. grisescens* selects particularly warm caves (13.9-26.3˚C; Tuttle 1976b). Roosting in large groups and selecting caves with domed ceilings was also hypothesized to increase cave temperatures, therefore increasing juvenile growth rates (Tuttle 1975). Growing juvenile bats do not forage as far as adults. Tuttle (1976) demonstrated that mean weight of juvenile bats was negatively correlated with distance of the maternity roost from water. This suggests that the extra metabolic costs of summer cave-roosting makes *M. grisescens* more likely to choose maternity roosts close to quality foraging locations (Tuttle 1976a). This distinctly differs from the apparent preference of *M. sodalis* for maternity roosts far from good foraging locations (Pauli et al. 2015). Adult *M. grisescens* (mostly males) were observed leaving a cave roost and flying directly cross-country without demonstrating any foraging behavior (LaVal et al. 1977). It is possible that the area close to the roost is too crowded with young bats, so the fully-grown adults seek foraging locations farther away.

Meyer (2017) modeled *M. grisescens*, *M. septentrionalis*, and *M. sodalis* habitat under future climate scenarios and found that habitat for those species would be significantly reduced and fragmented by 2070. The models also showed possible range shifts for all three species, meaning they will have to disperse from currently suitable areas to find new habitat. This work indicates that even in a best-case scenario, climate change will likely negatively affect these already threatened and endangered species.

This chapter has two goals. The first goal is to use maximum entropy species distribution modeling to create large-scale habitat suitability models for *M. grisescens*, *M. septentrionalis*, and *M. sodalis*. The second goal is to create modified versions of these models that focus on CGTC and surrounding Ozark Plateau counties, that can be used to predict locations of likely occurrence for these federally listed species as WNS moves westward into Oklahoma.

MATERIALS AND METHODS

Study Area.—The study area for this project comprises four states in the central US: Arkansas, Kansas, Missouri, and Oklahoma (where CGTC is located). This study area covers a large portion of the range for all three species and therefore maximizes the number of occurrence points that can be used. This area also includes counties that are currently experiencing rapid spread of white-nose syndrome infection (WhiteNoseSyndrome.org 2017).

*Species Occurrence Data.—*Occurrence data for all three species came from the United States Geological Survey (USGS) BISON database (USGS 2015) and the Oklahoma State University Collection of Vertebrates. Only records with precise location information (latitude and longitude) were used. The 2017 occurrences of *M. grisescens* and *M. sodalis* from Camp Gruber Training Center were also included in their respective models. Occurrence points having identical latitude and longitude data were removed. Spatial rarefication was used to reduce auto-correlation and account for sampling bias, which can reduce model quality (Kramer-Schadt et al. 2013; Boria et al. 2014). Versions of each model were created with non-rarefied, 5 km rarefied, and 10 km rarefied occurrence data and the best performing model was chosen.

*Variable Selection and Prioritization.—*Environmental variables considered in initial analyses were 19 bioclimatic variables elevation, and distance to water. Bioclimatic variables provide information about temperature and precipitation at a very fine scale (Hijmans et al. 2005). Elevation has been shown to contribute to occurrence of several *Myotis* species (Bellamy et al. 2013; Barnhart and Gillam 2014; Hammond et al. 2016). The GTOPO30 dataset from USGS was used to obtain fine-scale elevation information (United States Geological Survey Long Term Archive 1996). Temporally sensitive variables, like land cover type and leaf area index, were not included because occurrence points were from a broad range of years (roughly 1890-2015). The National Hydrography Dataset Plus (NHDPlus) Snapshot combines information from the National Hydrography Dataset, National Elevation Dataset, and the National Watershed Boundary Dataset to yield highly detailed information about most water sources in the United States (McKay et al. 2012). The distance from a water source to each pixel centroid in the study area was calculated to produce a Distance to Water environmental variable. The resolution of all environmental variables was 1 km.

Collinearity, or environmental variable values being linearly related to one another, can cause model results to be difficult or impossible to interpret (Dormann et al. 2012). To avoid this, Pearson correlation coefficients were calculated for each variable to determine degree of collinearity. The correlation threshold was $r \geq 0.7$ because this value has been shown to be as effective at reducing collinearity problems as more restrictive thresholds (Dormann et al. 2012). When two variables are at or above the correlation threshold, one variable is chosen to keep and one is eliminated based on which is deemed higher priority or more important to the model considering the ecology of the species at hand.

Maxent Models.—The Maximum Entropy Species Distribution Modeling algorithm (Maxent) is a presence-only modeling program that is widely used in ecological studies (Phillips et al. 2004; Elith et al. 2011). Maxent was used to model the suitable habitat for *M. grisescens, M. septentrionalis, and M. sodalis* based on selected environmental variables. The default settings were used as Maxent is regularly updated to include the best default settings and these generally perform best (Elith et al. 2011). For example, a recent Maxent software update changed the default output format from logistic to complementary log-log, or cloglog (Phillips et al. 2017). The cloglog format was used in this study. Ten crossvalidation replicates were performed for each model and the average output was taken. For each model, Maxent created images of the study area and created response curves for variables. Individual response curves show the relationship between probability of species occurrence and variation in environmental variables. Maxent also calculates percent contribution, which assigns each variable used in the model a value that represents how much that variable is responsible for occurrence probability. For each species, several versions of the model were constructed using different rarefication levels and non-correlated variables until a single best performing model emerged. In the end, a single model for each species was created where every 1 km pixel in the study area received a value representing the probability that the species would occur there.

Model performance was assessed using the area under the receiver operating curve (Test AUC) and fractional predicted area (FPA). The receiver operating curve (ROC) plots true positives (the model predicted a test occurrence as present) versus false positives (the model predicted a background point as present) (Fielding and Bell 1997). Test AUC values of 0.5-0.7 or less are considered poor because the model is not predicting true positives better than random chance; values of 0.7-0.9 are reasonably predictive and appropriate for interpretation; values of 0.9 or greater are of high predictive value and quality (Pearce and Ferrier 2000). FPA is a value related to omission rates that represents the proportion of the study area that is estimated to be suitable habitat. Eleven thresholds are estimated by Maxent when a model is created; balance threshold FPA was used for evaluation in this study.

After final models were constructed, niche overlap (Schoener's D) was calculated using ENMTools (Warren et al. 2010). Schoener's D is a ecological statistic in which values range from 0 to 1 and represent the amount of overlap between two niches (Warren et al. 2008). This is a tool used to estimate how similar two species are to one another in their environmental preferences.

Camp Gruber Training Center Occurrence Probability.—The final versions of each habitat suitability model were extracted to the three counties surrounding Camp Gruber Training Center (CGTC): Muskogee, Cherokee, and Sequoyah. The highest probability of occurrence within CGTC was recorded for each species. The balance cloglog threshold was used to create binary output maps for this smaller study area, in which each pixel is classified as either suitable or not suitable.

RESULTS

Species Occurrence Data.—Within the study area, there were 75 non-rarefied occurrences of *M. grisescens*, 56 of *M. septentrionalis*, and 51 of *M. sodalis.* Models created using non-rarefied occurrence data were of poor quality due to overfitting based on FPA from the balance threshold. Although the use of spatial rarefication reduced model performance in terms of AUC, overfitting was greatly reduced. Spatial rarefication at 10 km was used in all final models. After rarefication, there were 42 *M. grisescens*, 38 *M. septentrionalis*, and 32 *M. sodalis* occurrences.

Environmental Variable Contributions.—Collinearity tests resulted in the removal of most of the bioclimatic variables. Variables that provided information about temperature ranges (both daily and seasonally), precipitation extremes (e.g. precipitation of wettest/driest quarter), and interaction between temperature and precipitation (e.g. mean temperature of wettest quarter) were prioritized. Elevation was not utilized in any of the final models because of correlation with a large number of precipitation-related variables. When elevation was included in preliminary models, it was unresponsive and contributed very little for all three species. Distance to water was only responsive enough to be included in the final model for one species, *M. septentrionalis*. Table 2.1 lists the final variables used across all three models and provides a brief explanation of their meaning (O'Donnell and Ignizio 2012).

M. grisescens.—The mean Test AUC value from ten crossvalidation replicates for the *M. grisescens* model was 0.886 (SD = 0.065). The mean FPA was 0.431. In order of contribution, the environmental variables used in the final *M. grisescens* model were mean temperature of wettest quarter, precipitation of the warmest quarter, temperature seasonality, mean temperature of the warmest quarter, and precipitation of the wettest month (Table 2.2). Probability of occurrence showed an inverse relationship with mean temperature of warmest quarter (Fig. 2.1-D). The other response curves showed peak probability of occurrence under the following conditions: mean temperature of wettest quarter around 20.0˚C (Fig. 2.1-A), precipitation of about 300 mm during the warmest quarter (Fig. 2.1-B), low-to-moderate temperature seasonality (Fig. 2.1-C), and precipitation of about 140 mm during the wettest month (Fig. 2.1-E).

The highest probability of occurrence for *M. grisescens* is in southwest Missouri, northwest Arkansas, and east Oklahoma (Fig. 2.2). Most of Kansas and Oklahoma do not have high probability of occurrence. The highest probability of occurrence within CGTC was 0.623 (Fig. 2.4). Binary transformation showed that all of CGTC and all of Muskogee and Cherokee Counties are suitable for *M. grisescens* (Fig. 2.5).

M. septentrionalis.—The mean Test AUC value from ten crossvalidation replicates for the *M. septentrionalis* model was 0.825 (SD = 0.101). The mean FPA was 0.516. In order of contribution, the environmental variables used in the final *M. septentrionalis* model were mean temperature of the warmest quarter, isothermality, precipitation of the warmest quarter, distance to water, and mean temperature of the wettest quarter (Table 2.2). Mean temperature of the warmest quarter (Fig. 2.6-A) and distance to water (Fig. 2.6-D) both had inverse relationships with probability of occurrence. Isothermality had a positive relationship with occurrence (Fig. 2.6-B). Precipitation of around 320 mm during the warmest quarter (Fig. 2.6-C) and mean temperature of about 22.0˚C during the wettest quarter (Fig. 2.6-E) both showed peak probability.

M. septentrionalis has high probability of occurrence in southern Missouri, northern Arkansas, and most of Kansas. There is low-to-moderate probability in Oklahoma (Fig. 2.7). The highest probability of occurrence within CGTC was 0.264 (Fig. 2.9). Binary transformation showed limited suitable habitat for *M. septentrionalis* in CGTC and Muskogee County (Fig. 2.10).

<u>*M. sodalis*</u>.—The mean Test AUC value from ten crossvalidation replicates for the *M. sodalis* model was 0.811 (SD = 0.144). The mean FPA was 0.725. In order of contribution, the environmental variables used in the final M. sodalis model were mean temperature of the wettest quarter, mean temperature of the warmest quarter, precipitation of the warmest quarter, temperature seasonality, and isothermality (Table 2.2). Mean temperature of the warmest quarter had an inverse relationship with probability of occurrence (Fig. 2.11-B). Isothermality had a positive relationship with occurrence (Fig. 2.11-E). The other response curves showed peak probability of occurrence under the following conditions: mean temperature of around 18.0˚C during the wettest quarter (Fig. 2.11-A), precipitation around 280 mm during the warmest quarter (Fig. 2.11-C), and low-to-moderate temperature seasonality (Fig. 2.11-E).

High probability of occurrence for *M. sodalis* is shown throughout Missouri, in northern Arkansas, eastern Oklahoma, and extreme northern Kansas (Fig. 2.12). The highest probability of occurrence within CGTC was 0.363 (Fig. 14). Binary transformation showed all of CGTC and all of Muskogee, Cherokee, and Sequoyah counties suitable for *M. sodalis* (Fig. 15).

Niche Overlap.—The niches for *M. grisescens* and *M. septentrionalis* overlap by 55.4% according to Schoener's *D*. *M. sodalis* and *M. grisescens* overlap by 65.2%. *M. septentrionalis* and *M. sodalis* overlap by 77.2%.

DISCUSSION

M, grisescens.—The model for *M. grisescens* was the highest performing with an AUC of 0.825. This model also had the least fractional area predicted present at 0.431. Considering the FPA value and the concentration of high probability in the Ozark Highlands (Fig. 4), the *M. grisescens* model was likely the most overfit. The model still predicts suitability in locations outside the known range. In 1939, it was thought that the distribution limit for *M. grisescens* was in the Ozarks of Oklahoma (Blair 1939). Given the result of the current model, it is possible that *M. grisescens* could or already has experienced a range shift into central Oklahoma.

Based on the final habitat suitability model, *M. grisescens* is most likely to occur in the Ozark Highlands and surrounding area (Fig. 4). *M. grisescens* is most sensitive to temperature during wet periods and precipitation during warm periods (Table 2.2). It is likely that both of these contribute to ideal cave temperature and humidity, since *M. grisescens* roosts in caves year-round (Decher and Choate 1995). Another significant contributor (23.6%) to *M. grisescens* occurrence was temperature seasonality, or low standard deviation of yearly temperature. There are more *M. grisescens* mortalities during the twice-yearly migration season, likely due to stressful and dangerous conditions associated with migration (Tuttle and Stevenson 1977). Recovery from migration stress may be aided by ideal environmental conditions during the summer (Decher and Choate 1995). In this context, the apparent preference of *M. grisescens* for low temperature seasonality makes sense, as predictable temperature would help ensure ideal summer habitat for recovering from migration stress.

M. septentrionalis.—The model for *M. septentrionalis* performed well with an AUC of 0.825 and fractional predicted area of 0.516. *M. septentrionalis* had high likelihood of occurrence in large parts of the study area, including in large parts of western Kansas (Figs. 6 and 7). *M. septentrionalis* was most sensitive to temperatures and precipitation during warm periods, isothermality, and distance to water (Table 2.2). Temperatures and precipitation during warm periods could be related to roost tree and foraging location selection during summer. The positive relationship of occurrence with isothermality, or how much daily temperature oscillates relative to annual temperature, reveals that *M. septentrionalis* prefers habitat where the daily temperature range is closer to the annual temperature range (higher values of isothermality). Pauli et al (2015) found that *M. sodalis* responds more to distance to water than *M. septentrionalis*. The models from this study reveal the opposite: *M. septentrionalis* relies more on closeness to water than *M. sodalis*.

M. sodalis.—This model performed worst of the three, but still performed well with an AUC of 0.811. *M. sodalis* had the most area predicted suitable (FPA = 0.725). Although highest probability of occurrence was concentrated in the Ozark Highlands and

Ouachita Mountains, almost all of the study area was predicted suitable (Figs. 8 and 9). This contradicts Thomson (1982), who stated that the western edge of the species' range was the Ozark Plateau in Oklahoma. *M. sodalis* was sensitive to temperatures during warm and wet periods and precipitation during warm periods. The highest probability of occurrence happened at mean temperature of about 23.5˚C and 260 mm of precipitation during the warmest quarter. Both of these align with the findings of Loeb and Winters (2013).

General Trends.—Models with more occurrence points performed better than those with fewer. Model AUC was inversely related to FPA. All species had high probability of occurrence in the area surrounding the Ozark Highlands. This is expected as much sampling takes place in the numerous caves and forests in that area and many occurrence points were concentrated in that area. All species also had suitable habitat predicted outside of known areas of occurrence, suggesting that range shifts or unknown colonies could be possible. The two species that were least similar were *M. grisescens* and *M. septentrionalis*. As expected, *M. sodalis* and *M. septentrionalis* were more similar to each other than to *M. grisescens*. The great amount of niche overlap between *M. sodalis* and *M. septentrionalis* in this part of their range provides support for the USFWS decision to combine summer survey guidelines for these species. *M. grisescens* and *M. sodalis*, which were captured in the same general location (CGTC), overlap a moderate amount.

Implications for Camp Gruber Training Center.—Both species that were captured in Camp Gruber Training Center (*M. grisescens* and *M. sodalis*) had suitable habitat throughout CGTC and the surrounding counties. It is important to note that occurrences at CGTC were included in both species models, so it would be surprising if CGTC was not predicted suitable. *M. septentrionalis* had sparse areas of suitable habitat in CGTC surrounded by non-suitable habitat. It is unlikely that *M. septentrionalis* currently occurs in CGTC, but an incidental occurrence from a nearby county would not be impossible. If range shifts are happening, CGTC management should prepare for more occurrences of *M. grisescens* and *M. sodalis*

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TABLES AND FIGURES

Table 1.1. Comparison of the three call identification programs used. Minimum number of pulses required for ID refers to the number of individual echolocation pulses in a single call sequence (usually less than one second long). The program will not make an identification if the minimum number of pulses are not present and of good quality.

Program	Min. num. pulses required for ID	Call library location
Echoclass®	3 – not changeable	VA, NC, TN , KY, IN, OH, IL, AR, MO, IA
Bat Call ID	5 – changeable in settings	Northeast and Midwest US
Kaleidoscope®	5 – changeable in settings	North America

Table 1.2. Aggregate 2016 acoustic data. Proportions and classifications of species detected by each program in descending order of detection rate. * = species with MLE values $p \leq 0.05$.

Species	Echoclass® Proportion	Classification
*Lasiurus borealis**	72.84%	Common
Nycticeius humerialis	8.58%	Common
*Perimyotis subflavus**	7.58%	Common
*Eptesicus fuscus**	6.99%	Common
*Myotis grisescens**	1.68%	Uncommon
*Lasiurus cinereus**	1.03%	Uncommon
*Lasionycteris noctivagans**	0.69%	Rare
Myotis septentrionalis	0.14%	Rare
Myotis austroriparius	0.13%	Rare
Myotis leibii	0.13%	Rare
*Myotis sodalis**	0.13%	Rare
*Myotis lucifugus**	0.08%	Rare
Corynorhinus townsendii	-	Not analyzed
Tadarida brasiliensis	-	Not analyzed
Species	**BCID® Proportion**	**Classification**
*Nycticeius humeralis**	49.53%	Common
*Perimyotis subflavus**	19.29%	Common
*Lasiurus borealis**	17.17%	Common
*Lasionycteris noctivagans**	7.68%	Common
*Myotis lucifugus**	3.18%	Uncommon
*Eptesicus fuscus**	2.09%	Uncommon
*Myotis grisescens**	0.42%	Rare
*Lasiurus cinereus**	0.34%	Rare
*Corynorhinus townsendii**	0.18%	Rare
*Myotis septentrionalis**	0.08%	Rare
*Myotis leibii**	0.03%	Rare
Myotis austroriparius	-	Not analyzed
Myotis sodalis	-	Not analyzed
Tadarida brasiliensis	-	Not analyzed
Species	**Kaleidoscope® Proportion**	**Classification**
*Lasiurus borealis**	42.23%	Common
*Nycticeius humeralis**	24.87%	Common
*Perimyotis subflavus**	15.28%	Common
*Myotis lucifugus**	5.42%	Common
*Eptesicus fuscus**	5.23%	Common
*Lasionycteris noctivagans**	3.93%	Uncommon
*Lasiurus cinereus**	1.29%	Uncommon
*Myotis grisescens**	0.87%	Rare
Tadarida brasiliensis	0.48%	Rare

*Corynorhinus townsendii**	0.16%	Rare
*Myotis septentrionalis**	0.11%	Rare
*Myotis sodalis**	0.09%	Rare
*Myotis leibii**	0.05%	Rare
Myotis austroriparius	-	Not analyzed

Table 1.3. 2016 acoustic CPU data by site. Hours Recorded (HR), number of captures, and captures per unit effort (CPU) are given. x.1 or x.2 values represent the first and second times each site was surveyed. Total CPU was 7.67.

Site	HR	Captures	CPU
1.1	73.79	149	2.02
1.2	74.14	727	9.8
2.1	42.17	712	16.9
2.2	74.14	930	12.5
3.1	73.15	21	0.287
3.2	75.08	890	11.9
4.1	73.15	201	2.75
4.2	75.08	1074	14.3
5.1	73.5	105	1.43
5.2	76.24	920	12.1
6.1	73.5	45	0.612
6.2	76.24	1241	16.3
7	77.47	147	1.9
8	77.47	1538	19.9
9	78.92	55	0.697
10	78.92	246	3.12

Table 1.4. CPU for each species captured via acoustic detection according to Echoclass in 2016.

Species	Captures	Proportion	CPU
Lasiurus borealis	6556	72.84%	5.59
Nycticeius humeralis	772	8.58%	0.658
Perimyotis subflavus	682	7.58%	0.581
Eptesicus fuscus	629	6.99%	0.536
Myotis grisescens	151	1.68%	0.129
Lasiurus cinereus	93	1.03%	0.079
Lasionycteris noctivigans	62	0.69%	0.53
Myotis septentrionalis	13	0.14%	0.011
Myotis austroriparius	12	0.13%	0.010
Myotis leibii	12	0.13%	0.010
Myotis sodalis	12	0.13%	0.010
Myotis lucifugus	7	0.08%	0.006

Table 1.5. Mist net CPU data. Hours of netting, net-area-hours (NAH), number of captures, and captures per unit effort (CPU) organized by site. All dates were in 2017. Total CPU was 3.22 x 10^{-3}.

Date	Site	Hours	Net Area	NAH	Captures	CPU
5 July	3	5.2	122.2	635.44	0	0
6 July	3	5	122.2	611	0	0
7 July	6	5.3	241.8	1281.54	8	6.24 x 10^{-3}
8 July	6	5.1	241.8	1233.18	1	0.81 x 10^{-3}
9 July	5	5	200.2	1001	1	0.99 x 10^{-3}
10 July	5	5	200.2	1001	1	0.99 x 10^{-3}
17 July	1	5.1	218.4	1113.84	1	0.90 x 10^{-3}
18 July	1	5	218.4	1092	2	1.83 x 10^{-3}
19 July	4	4.9	189.8	930.02	8	8.60 x 10^{-3}
20 July	4	6.25	226.2	1413.75	11	7.79 x 10^{-3}
21 July	2	5	148.2	741	5	6.75 x 10^{-3}
22 July	2	5	148.2	741	0	0

Table 1.6. Number of individuals of each species captured during the 2017 mist net survey. Mass (g), and right forearm (RFA, mm) measurements are reported by species and age class. In groups where n > 1, mean measurements are reported with standard deviation in parentheses.

Species	**Adult**		**Subadult**		**Juvenile**	
	Mass	*RFA*	*Mass*	*RFA*	*Mass*	*RFA*
Lasiurus borealis (n = 12)	11.5 (2.89)	41.4 (1.44)	9.38 (0.98)	39.9 (1.78)	7	39.3
Myotis grisescens (n = 1)	12.25	41.7	-	-	-	-
Myotis sodalis (n = 1)	9	35.4	-	-	-	-
Nycticeius humeralis (n = 18)	10.2 (1.00)	37.0 (2.50)	9.14 (0.96)	37.9 (2.61)	-	-
Perimyotis subflavus (n = 1)	-	-	5.5	34.5	-	-

Table 1.7. Proportions of confirmed species (those captured in mist nets) across each capture method along with 95% confidence intervals for proportions of physical captures. * = species with MLE values p≤0.05 in the respective program.

Species	**Physical**	**95% CI**	**Echoclass®**	**BCID®**	**Kaleidoscope®**
Nycticeius humeralis	54.5%	36.7-71.5%	8.58%	49.53%*	24.87%*
Lasiurus borealis	36.4%	20.0-52.8%	72.84%*	17.17%*	42.23%*
Perimyotis subflavus	3.0%	0.00-8.88%	7.58%*	19.29%*	15.28%*
Myotis grisescens	3.0%	0.00-8.88%	1.68%*	0.42%*	0.87%*
Myotis sodalis	3.0%	0.00-8.88%	0.13%*	N/A	0.09%*

Table 2.1. Environmental variables used in final models with units and interpretations (based on O'Donnell and Ignizio 2012).

Variable	Unit	Interpretation
Isothermality (Bio3)	Percent	Measures how much daily temperature oscillates relative to annual temperature.
Temperature Seasonality (Bio4)	Degrees Celsius	Standard deviation of mean monthly temperature. Measures annual temperature variability.
Mean Temperature of Wettest Quarter (Bio8)	Degrees Celsius	Mean temperature during the three consecutive months of the year with the most

		precipitation.
Mean Temperature of Warmest Quarter (Bio10)	Degrees Celsius	Mean temperature during the warmest three consecutive months of the year.
Precipitation of Wettest Month (Bio13)	Millimeters	Amount of precipitation during the month of the year with the most precipitation.
Precipitation of Warmest Quarter (Bio18)	Millimeters	Amount of precipitation during the warmest three consecutive months of the year.
Distance to Water	Kilometers	Distance from pixel centroid to nearest body of water.

Table 2.2. Variables used in final models and percent contribution of each.

Myotis grisescens	
Variable	**Contribution**
Mean Temperature of Wettest Quarter (Bio8)	40.8%
Precipitation of Warmest Quarter (Bio18)	26.2%

Temperature Seasonality (Bio4)	23.6%
Mean Temperature of Warmest Quarter (Bio10)	7.9%
Precipitation of Wettest Month (Bio13)	1.7%

Myotis septentrionalis

Variable	**Contribution**
Mean Temperature of Warmest Quarter (Bio10)	55.5%
Isothermality (Bio3)	17.0%
Precipitation of Warmest Quarter (Bio18)	15.0%
Distance to Water	10.1%
Mean Temperature of Wettest Quarter (Bio8)	2.3%

Myotis sodalis

Variable	**Contribution**
Mean Temperature of Wettest Quarter (Bio8)	40.5%
Mean Temperature of Warmest Quarter (Bio10)	34.4%
Precipitation of Warmest Quarter (Bio18)	15.9%
Temperature Seasonality (Bio4)	5.9%
Isothermality (Bio3)	3.3%

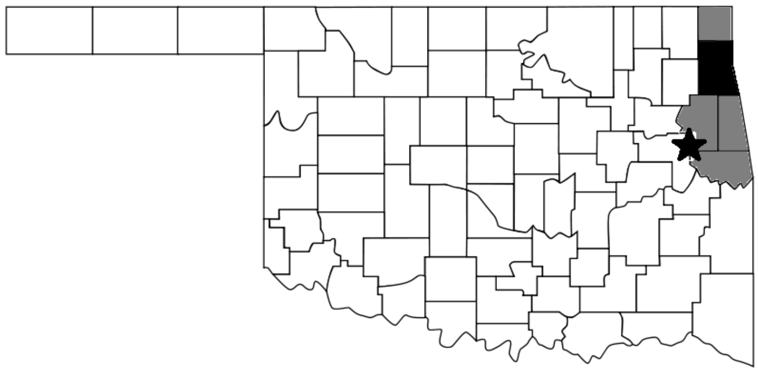


Figure 1.1. Ottawa, Sequoyah, Adair, and Cherokee Counties (gray) are suspect for WNS and Delaware County (black) is confirmed. CGTC is located in Muskogee County (approximate location shown with black star).

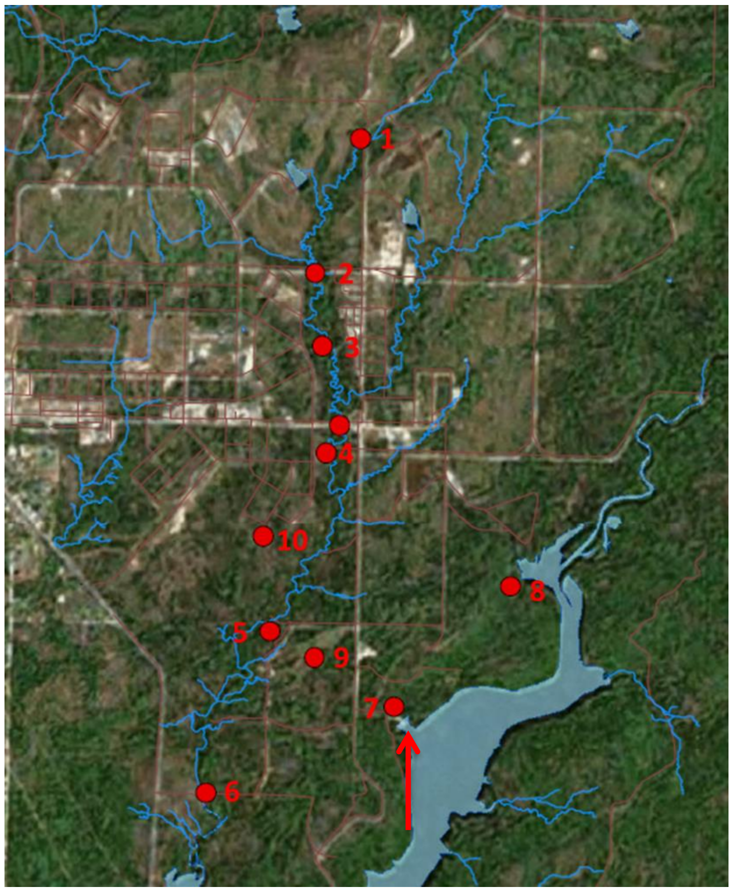


Figure 1.2. Acoustic monitoring sites within Camp Gruber Training Center. Sites 1-6 are on Little Greenleaf Creek. Sites 7-10 are edge habitat between forest and open area. One unnumbered point was initially considered but not utilized. The red arrow indicates north on the map.

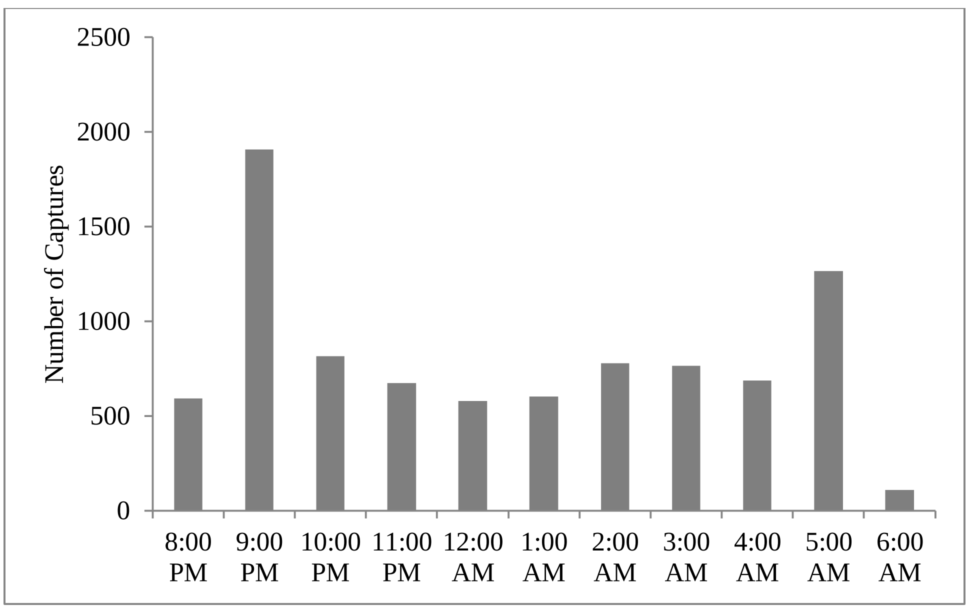


Figure 1.3. 2016 aggregate acoustic activity (number of captures per hour) for all species as identified by Echoclass®.

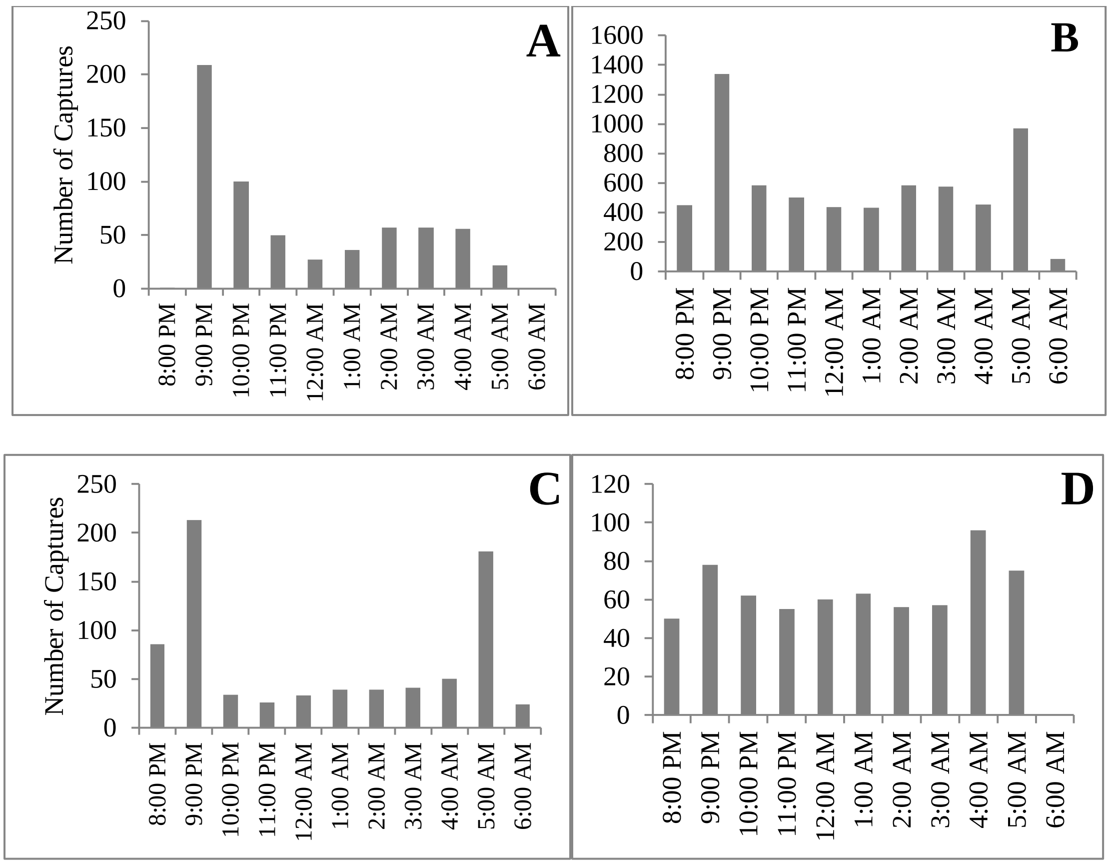


Figure 1.4. Hourly acoustic activity patterns of the four most common acoustically detected species in 2016. Note different y-axis values. A) *Eptesicus fuscus*, B) *Lasiurus borealis*. C) *Nycticeius humeralis*. D) *Perimyotis subflavus*.

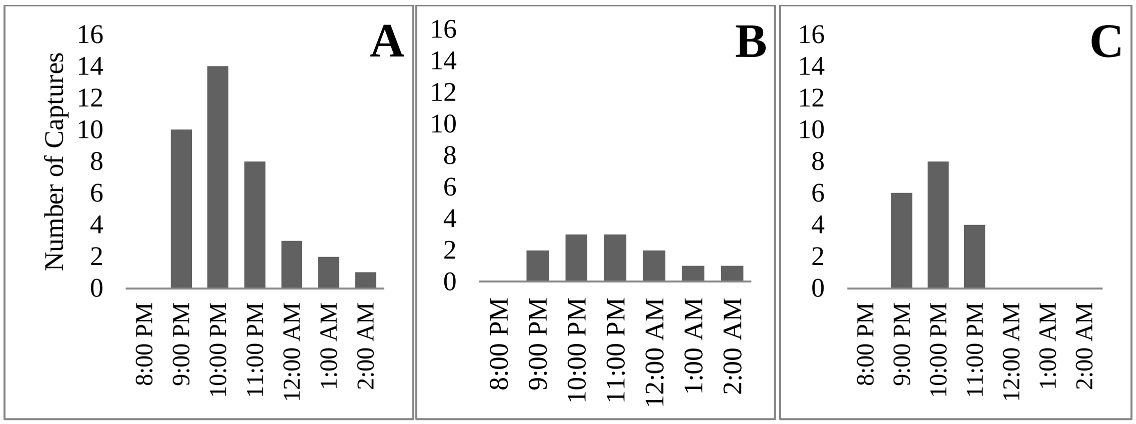


Figure 1.5. Mist net captures by hour. (A) all captures, including escapes. (B) *Lasiurus borealis* captures. (C) *Nycticeius humeralis* captures.

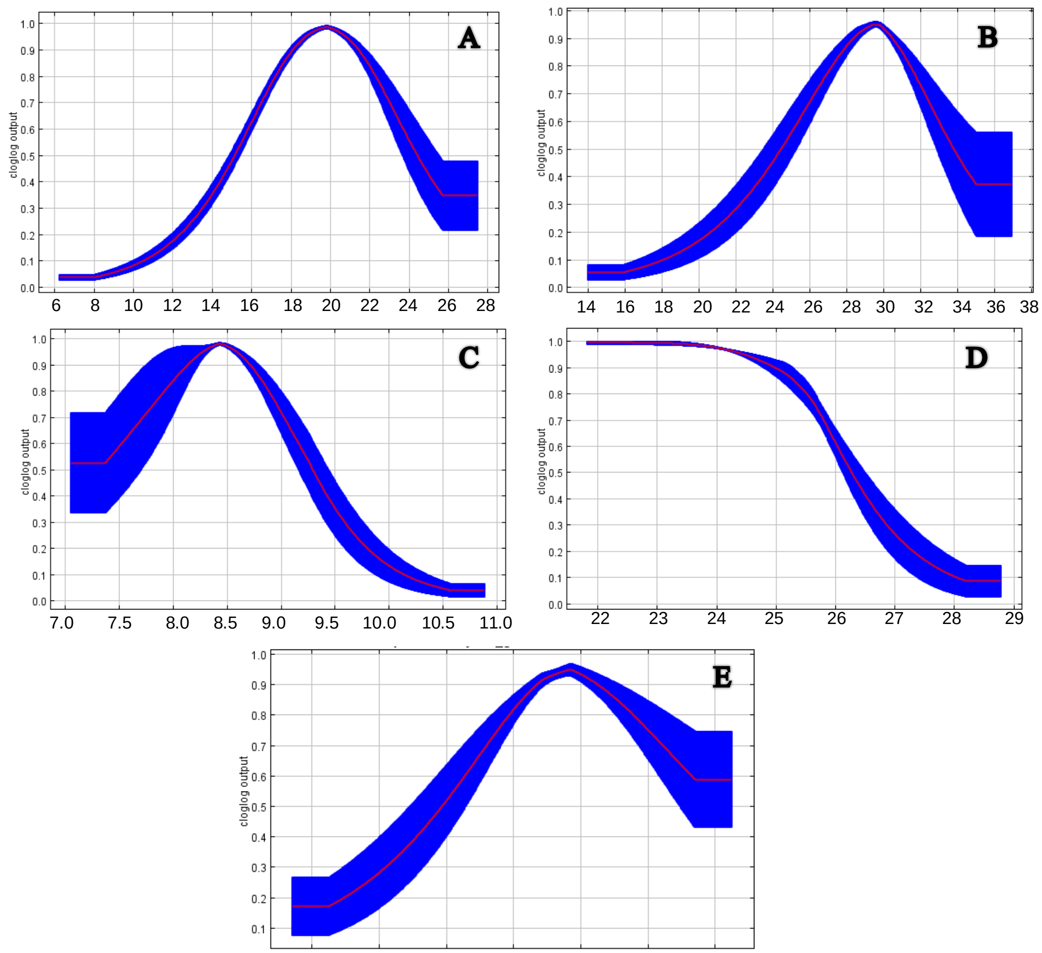


Figure 2.1. Probability of *Myotis grisescens* occurrence (cloglog output) as it responds to environmental variables. A) Mean Temperature of Wettest Quarter (Bio8; unit is degrees Celsius). B) Precipitation of Warmest Quarter (Bio18; millimeters). C) Temperature Seasonality

(Bio4; degrees Celsius). D) Mean Temperature of Warmest Quarter (Bio10; degrees Celsius). E) Precipitation of Wettest Month (Bio13; millimeters).

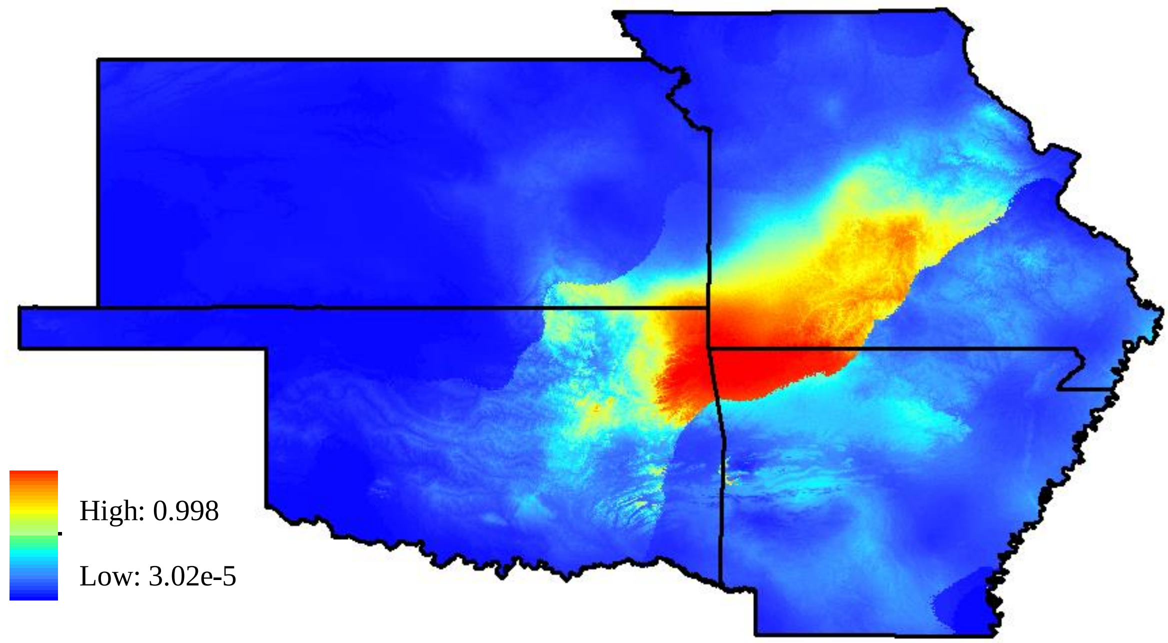


Figure 2.2. Heatmap showing probability of *Myotis grisescens* occurrence in Missouri, Arkansas, Oklahoma, and Kansas.

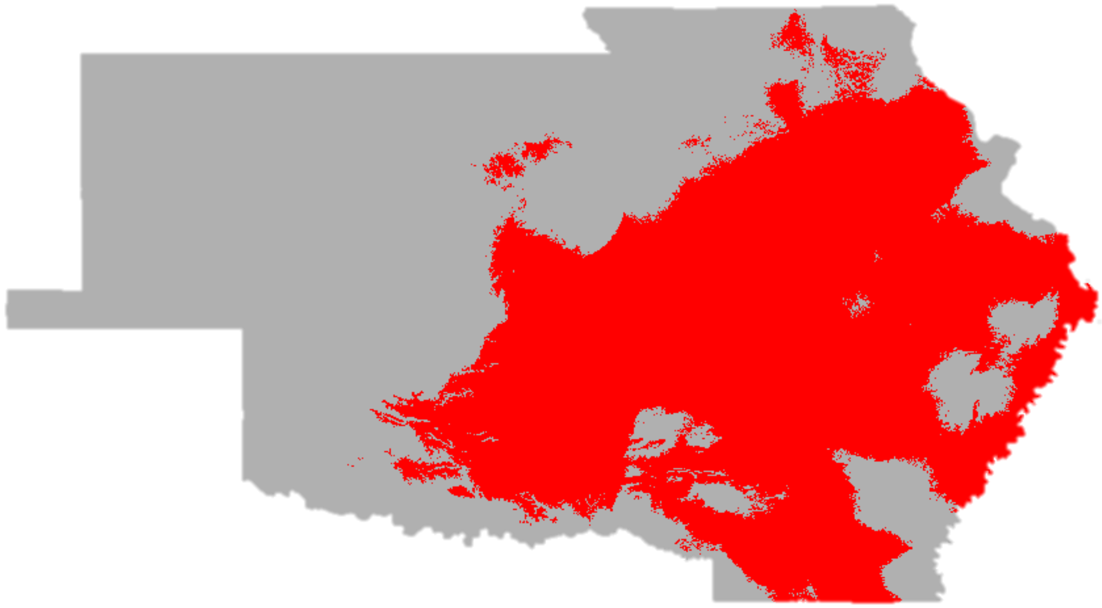


Figure 2.3. Transformed binary map (not shown in text) showing suitable (red)/not suitable (gray) habitat for *Myotis grisescens.*

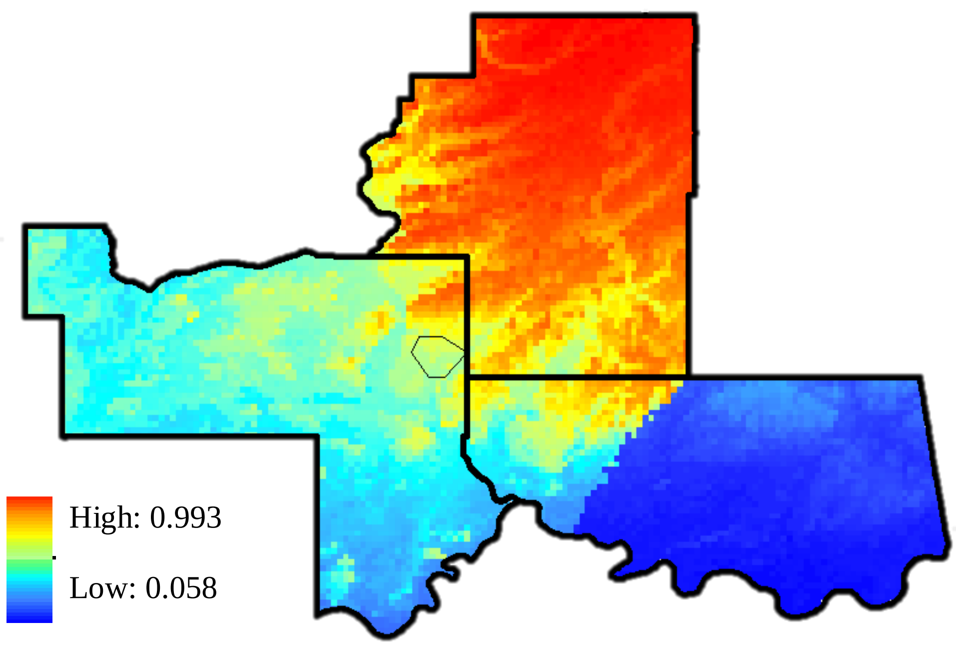


Figure 2.4. Heatmap showing probability of *Myotis grisescens* occurrence in Muskogee (left), Cherokee (top), and Sequoyah (right) counties. Light outline represents CGTC.

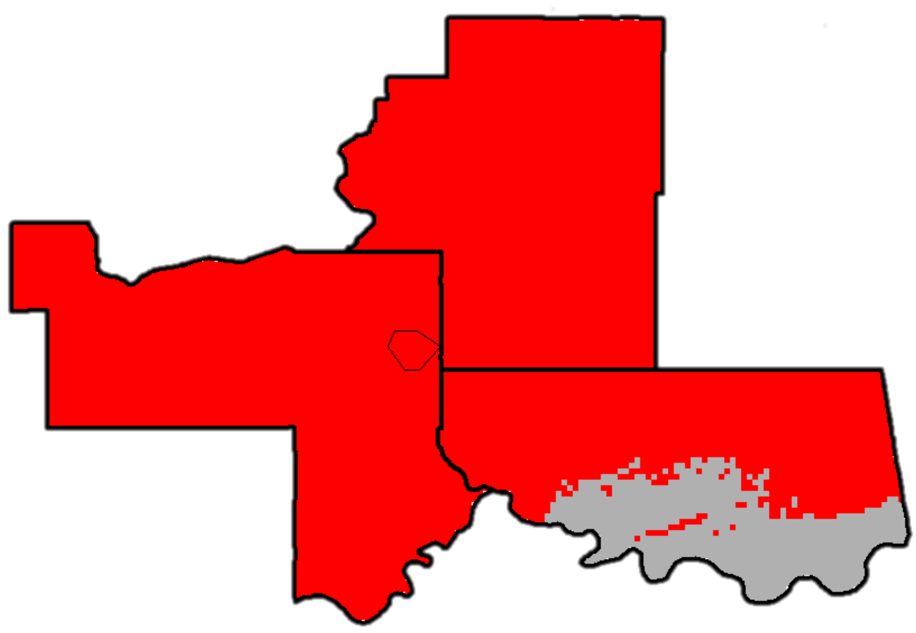
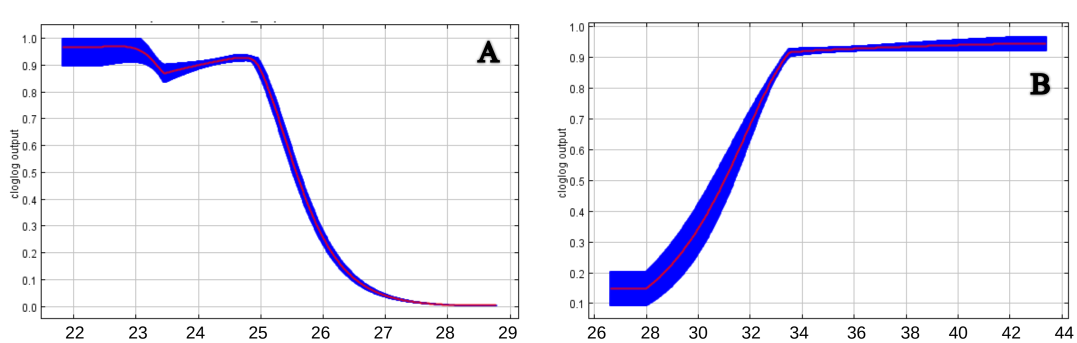


Figure 2.5. Transformed binary map showing suitable (red)/not suitable (gray) habitat for *Myotis grisescens.*



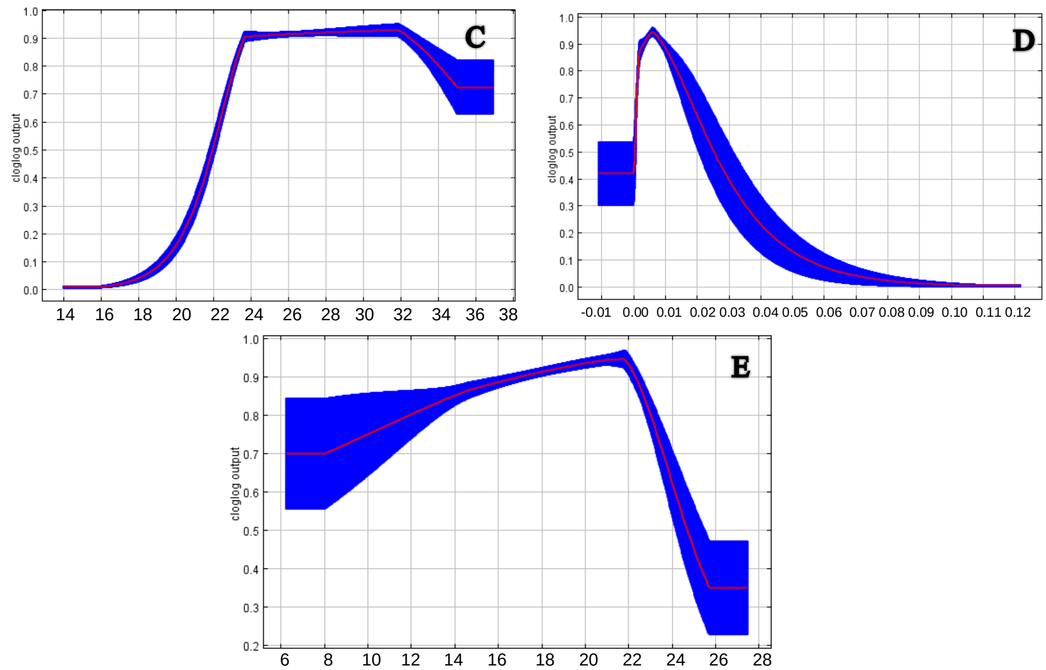


Figure 2.6. Probability of *Myotis septentrionalis* occurrence (cloglog output; y-axis) as it responds to environmental variables (x-axis). A) Mean Temperature of Warmest Quarter (Bio10; unit is degrees Celsius). B) Isothermality (Bio3; percent). C) Precipitation of Warmest Quarter (Bio18; millimeters). D) Distance to Water (kilometers). E) Mean Temperature of Wettest Quarter (Bio8; degrees Celsius).

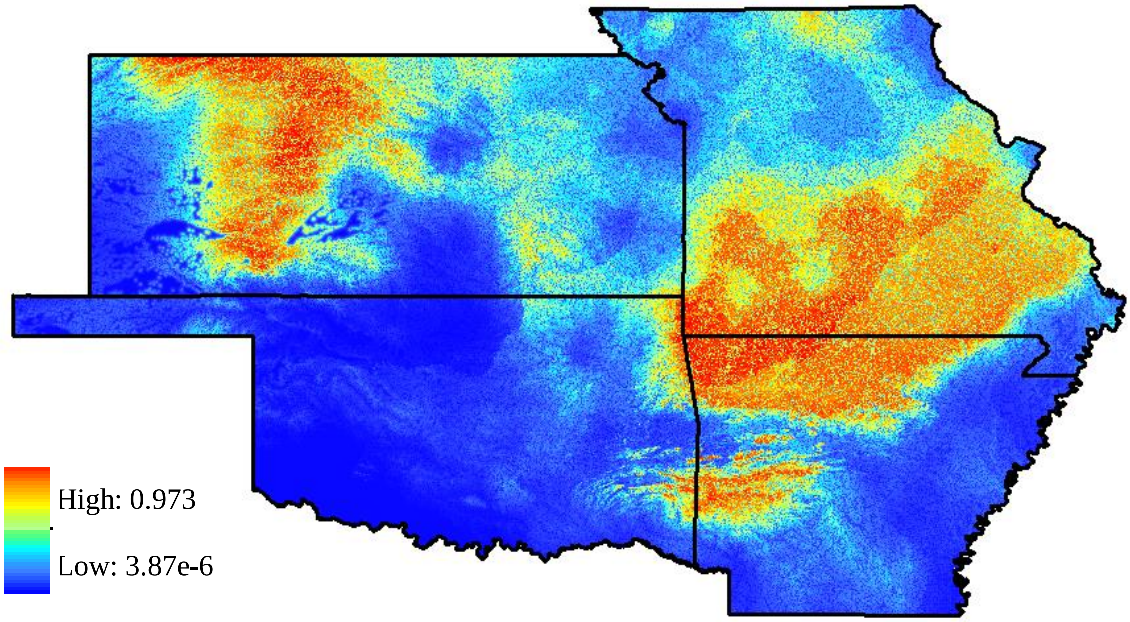


Figure 2.7. Heatmap showing probability of *Myotis septentrionalis* occurrence in Missouri, Arkansas, Oklahoma, and Kansas.

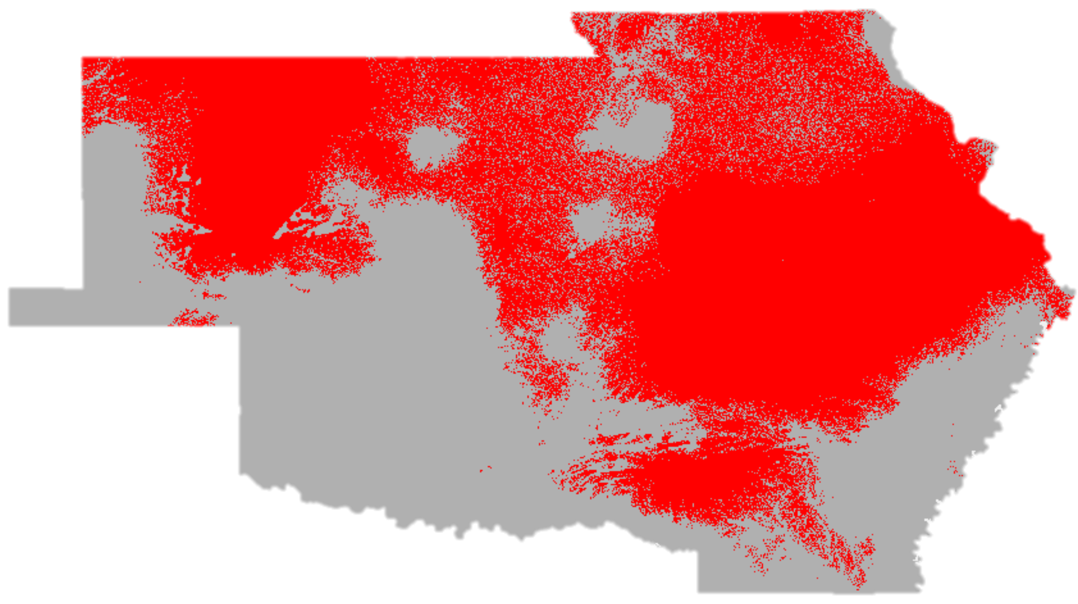


Figure 2.8. Transformed binary map (not shown in text) showing suitable (red)/not suitable (gray) habitat for *Myotis septentrionalis.*

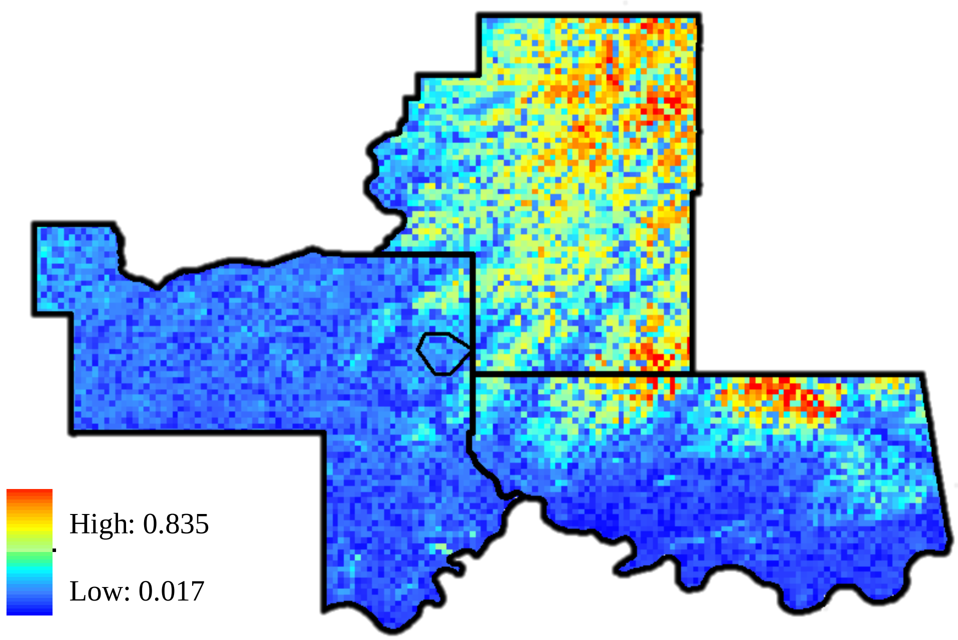


Figure 2.9. Heatmap showing probability of *Myotis septentrionalis* occurrence in Muskogee (left), Cherokee (top), and Sequoyah (right) counties. Light outline represents CGTC.

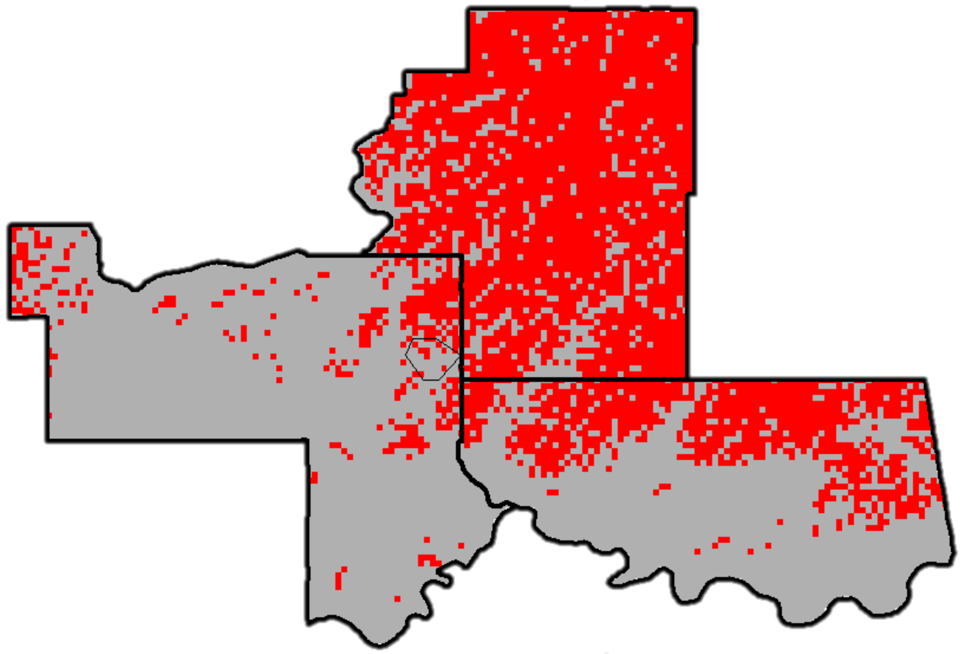
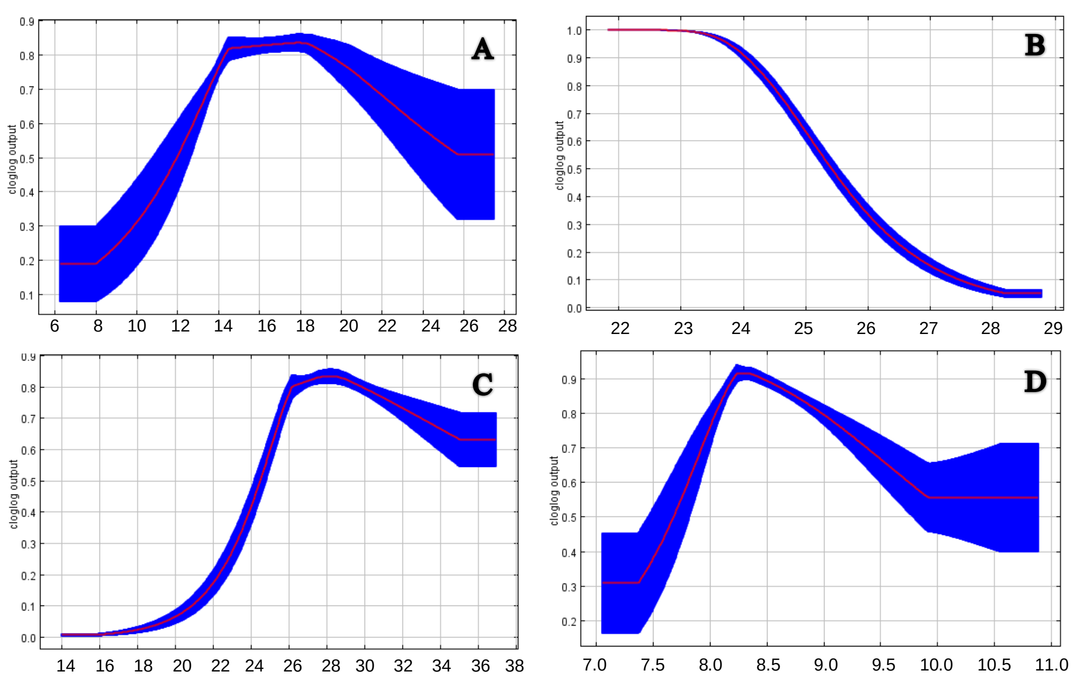


Figure 2.10. Transformed binary map showing suitable (red)/not suitable (gray) habitat for *Myotis septentrionalis.* Light outline represents CGTC.



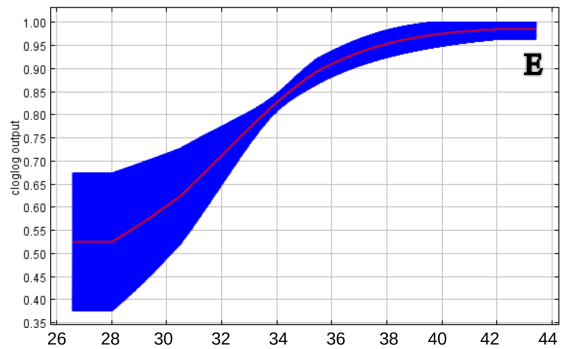


Figure 2.11. Probability of *Myotis sodalis* occurrence (cloglog output) as it responds to environmental variables. A) Mean Temperature of Wettest Quarter (Bio8; unit is degrees Celsius). B) Mean Temperature of Warmest Quarter (Bio10; degrees Celsius). C) Precipitation of Warmest Quarter (Bio18; millimeters). D) Temperature Seasonality (Bio4; degrees Celsius). E) Isothermality (Bio3; percent)

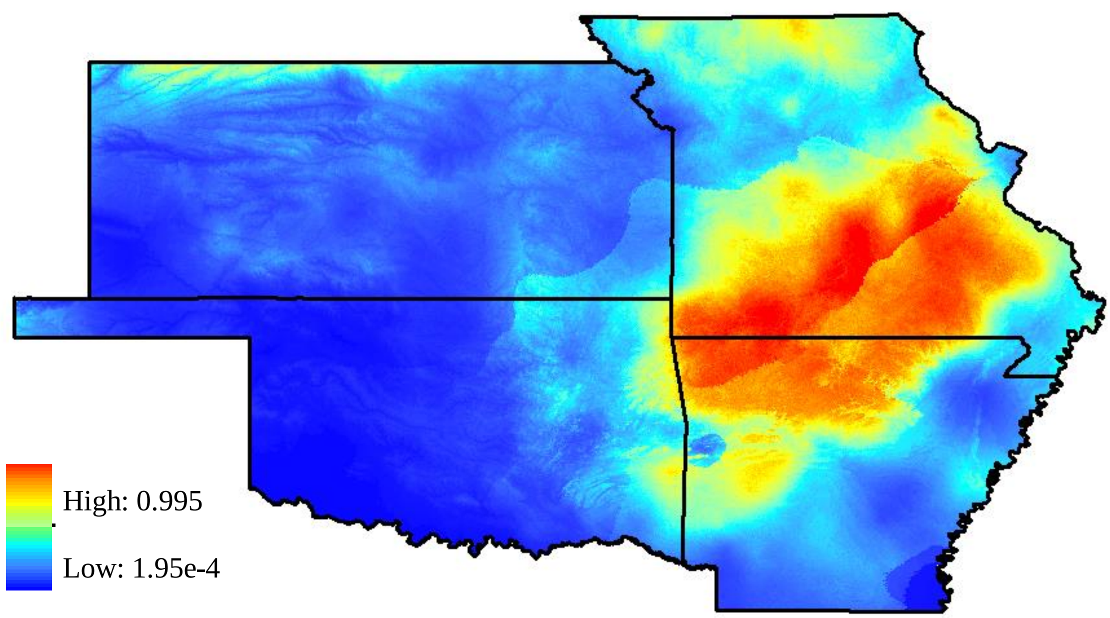


Figure 2.12. Heatmap showing probability of *Myotis sodalis* occurrence in Missouri, Arkansas, Oklahoma, and Kansas.

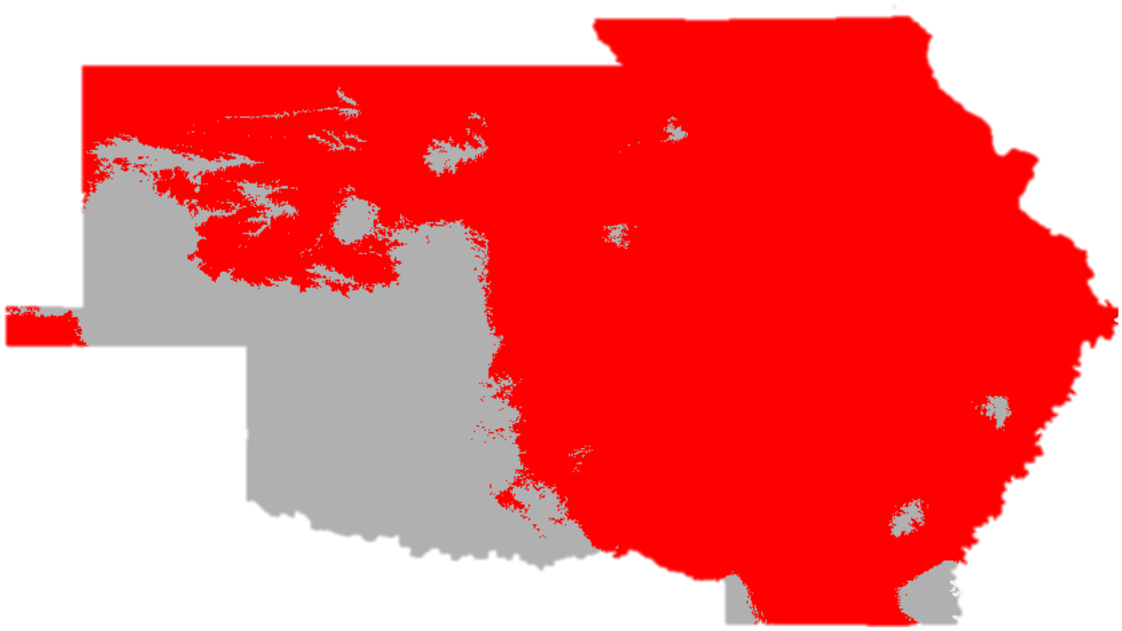


Figure 2.13. Transformed binary map (not shown in text) showing suitable (red)/not suitable (gray) habitat for *Myotis sodalis.*

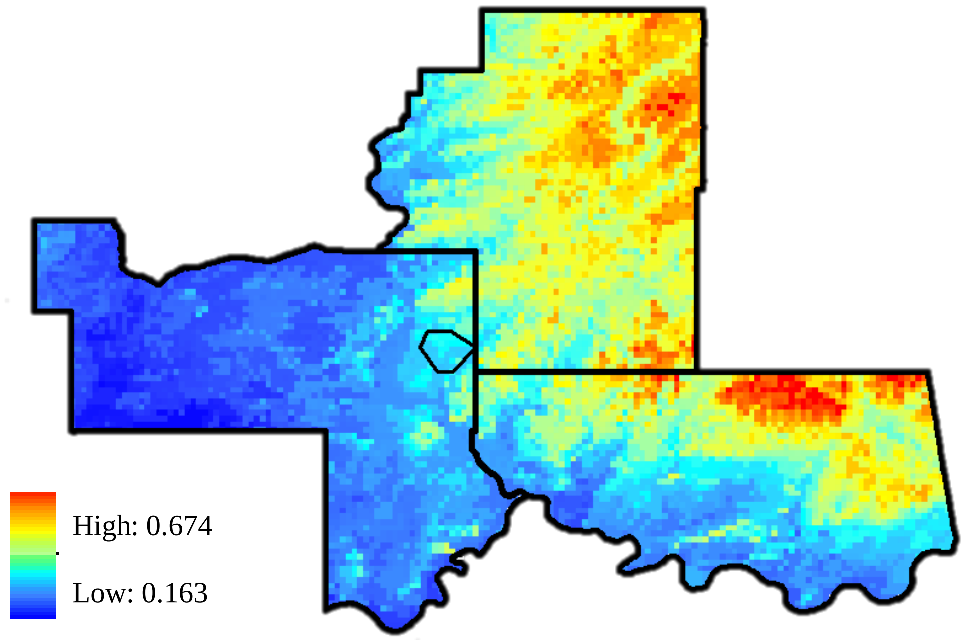


Figure 2.14. Heatmap showing probability of *Myotis sodalis* occurrence in Muskogee (left), Cherokee (top), and Sequoyah (right) counties. Light outline represents CGTC.

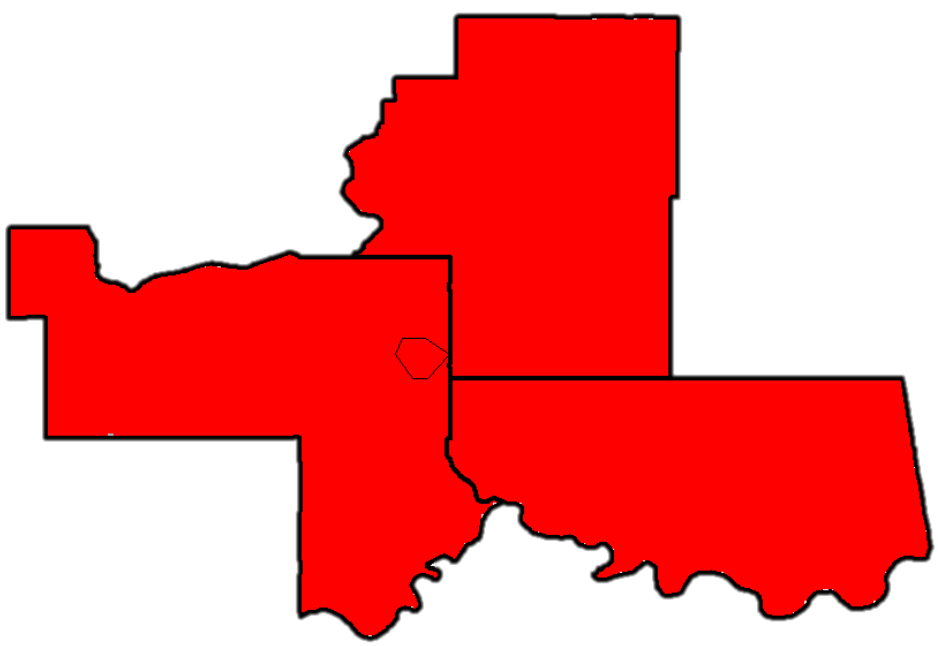


Figure 2.15. Transformed binary map showing suitable (red)/not suitable (gray) habitat for *Myotis sodalis.* Light outline represents CGTC.

APPENDIX 1: Dates, recording settings, number of nights, and mean hours recorded per night used at each site during the 2016 acoustic survey. Schedule refers to user-input recording schedule. At the two sites where the Schedule setting was used, the detectors were set to record from 30 minutes before sunset to 30 minutes after sunrise. The Night Only setting records for the same duration, so it was used exclusively after the first week.

Site Number	Dates Surveyed	Recording Schedule	No. of Detector Nights	Mean HR Per Night
Site 1	15 June 2016 - 21 June 2016	Schedule	7	73.79
Site 2	15 June 2016 - 21 June 2016	Schedule	4	42.17
Site 3	22 June 2016 - 28 June 2016	Night Only	7	73.15
Site 4	22 June 2016 - 28 June 2016	Night Only	7	73.15
Site 5	29 June 2016 - 5 July 2016	Night Only	7	73.5
Site 6	29 June 2016 - 5 July 2016	Night Only	7	73.5
Site 1	6 July 2016 - 12 July 2016	Night Only	7	74.14
Site 2	6 July 2016 - 12 July 2016	Night Only	7	74.14
Site 3	13 July 2016 - 19 July 2016	Night Only	7	75.08
Site 4	13 July 2016 - 19 July 2016	Night Only	7	75.08
Site 5	20 July 2016 - 26 July 2016	Night Only	7	76.24
Site 6	20 July 2016 - 26 July 2016	Night Only	7	76.24
Site 7	27 July 2016 - 2 August 2016	Night Only	7	77.47
Site 8	27 July 2016 - 2 August 2016	Night Only	7	77.47
Site 9	3 August 2016 - 9 August 2016	Night Only	7	78.92
Site 10	3 August 2016 - 9 August 2016	Night Only	7	78.92
			Total: 109	**Total: 1172.96**

VITA

A. Rachel Ritchie

Candidate for the Degree of

Master of Science

Thesis: ACOUSTIC AND NETTING SURVEYS OF WESTERN OZARK HIGHLANDS BATS WITH HABITAT SUITABILITY MODELS FOR THREE THREATENED AND ENDANGERED SPECIES

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