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GRAY BAT MIGRATION IN MISSOURI

A Master's Thesis

Presented to

The Graduate College of
Missouri State University

In Partial Fulfillment

Of the Requirements for the Degree

Master of Science, Biology

By

Cheyenne Gerdes

July 2016

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GRAY BAT MIGRATION IN MISSOURI

Biology

Missouri State University, July 2016

Master of Science

Cheyenne Gerdes

ABSTRACT

Migration is an important and understudied aspect of the life histories of many species, particularly bats. Migration impacts conservation efforts, including efforts to manage the impacts of wildlife disease. The federally endangered gray bat (*Myotis grisescens*) is a migratory species with documented infections by *Pseudogymnoascus destructans*, the fungus that causes White-nose Syndrome (WNS). To better understand migration as it might relate to WNS, I quantified the timing and location of gray bat movements in Missouri using acoustic detectors and bat banding. I recorded calls at 4 maternity sites from January to May 2015, and used the R package PVAClone to generate estimates of r and K as measures of arrival rate and an index of population size at the maternity sites respectively. These values were plotted against each cave's distance from a major hibernaculum to examine whether there was an effect on the arrival of gray bats at a site. Values of r varied between 0.3 and 0.9, and values of K varied between 981 and 3020 among the maternity roosts: estimates were consistent whether considering observation error or not. While bats arrived at the closest maternity colony quicker and in greater numbers, the remaining rates and indices were equivocal with distance. Over 1,000 gray bats were banded and 18 were relocated, revealing previously undocumented connections between gray bat caves across the region. The acoustic methodology used in this thesis could be useful for management officials wanting to monitor the timing of bat migration and site activity, both of which could be affected by WNS. The cave network used by gray bats in Missouri could yield insight into how WNS spreads across cave networks.

KEYWORDS: gray bats, *Myotis grisescens*, migration, acoustic monitoring, bat banding

This abstract is approved as to form and content

Dr. Lynn Robbins
Chairperson, Advisory Committee
Missouri State University

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July 2016

Approved:

Dr. Lynn Robbins

Dr. Sean Maher

Dr. Xin Miao

Dr. Julie Masterson: Dean, Graduate College

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TABLE OF CONTENTS

Introduction.....	1
Bat Migration	1
Gray Bats	5
Objectives	10
Using acoustic detectors to document arrival of gray bats (<i>Myotis grisescens</i>) at maternity colonies	11
Abstract	11
Introduction.....	12
Methods.....	13
Results.....	16
Discussion.....	18
Literature Cited	24
Using bat banding to document connections between gray bat caves	35
Introduction.....	35
Methods.....	36
Results.....	37
Discussion.....	38
Literature Cited	39
Conclusion	43
Literature Cited	45

LIST OF TABLES

Table 1. Description of gray bat acoustic monitoring sites	26
Table 2. Coefficients generated by PVAClone models with 10,000 clones.....	27
Table 3. Bat banding site details.....	40

LIST OF FIGURES

Figure 1. Example acoustic detector setup	28
Figure 2. Map of gray bat acoustic monitoring sites	29
Figure 3. Timelines of bat activity showing the number of bat calls per day recorded from January 1 -May 31, 2015	30
Figure 4. Logistic models accounting for detection error, generated from package PVAClone in R, shown in red. Black lines represent 95% confidence interval	31
Figure 5. Logistic models not accounting for detection error, generated from package PVAClone in R, shown in red. Black lines represent 95% confidence interval	32
Figure 6. Gray bat calls per day at hibernacula site CC, with comparison to the migratory timing at maternity caves (colored bars). The migratory period of a maternity site was defined as the time between the PVAClone model starting date and the day that the data had a value equal to the site's carrying capacity.....	33
Figure 7. A) The effects of distance between maternity caves and a major hibernaculum on the rate of gray bat arrival based on logistic growth models with observation error B) The effects of distance between maternity caves and a major hibernacula on the rate of gray bat arrival based on logistic growth models without observation error. C) The effects of distance between maternity caves and a major hibernaculum on the rate of gray bat arrival based on the PVAClone logistic model starting date.. ..	34
Figure 8. Map of gray bat banding efforts by Missouri State University between 2013 and 2015.....	41
Figure 9. Map of gray bat band returns from bats banded 2013 – 2015 by Missouri State University.....	42

INTRODUCTION

Bat Migration

Migration can be defined as a seasonal, two-way movement from one location to another to seek favorable climatic conditions and avoid unfavorable ones (Fleming and Elby 2003). For bats living in temperate climates, migration likely evolved due to pressure from seasonal environmental shifts (Fleming and Elby 2003). Tree bat species with seasonal migration likely move in response to seasonal fluctuations in temperature. However, migration in cave roosting bats likely is related to cave microclimate needs during different parts of the bat's annual cycle (Rodrigues and Palmeirim 2008). At current count, at least 15 genera of bats from 4 families (Molossidae, Vespertilionidae, Phyllostomidae, Pteropodidae) are known to migrate, although this may be an underestimate (Popa-lisseanu and Voigt 2009).

Bats use migration to varying degrees. Fleming and Eby (2003) classify 3 categories of spatial behavior in bats: sedentary species (seasonal movements ≥ 50 km), regional migrants (One-way migrations 100–500km), and long-distance migrants (One-way migrations >1000 km). These categories are associated with habitat preferences; long distance migration is associated with tree roosting species, while cave-roosting species are more likely to be regional migrants or sedentary (Roer 1995). Females of many bat species move farther during migration than males, generally due to their more selective requirements for maternity roosts (Fleming and Elby 2003). In some species, such as the gray bat (*Myotis grisescens*) and the little brown bat (*M. lucifugus*), females leave

hibernacula earlier than males and make similarly rapid migrations back to the hibernacula during the fall (Tuttle 1976).

Like many migratory species, bats utilize stopover habitat during migration, however some evidence suggests that tree roosting bats, unlike birds, use stopover as a temporary refuge rather than an extended place to refuel energy stores (Mcguire et al. 2012). Cave-roosting bats, including gray bats, utilize transient caves as stopover roosting habitats (Guthrie 1933). Short-term visits to transient habitat, as well as more general “wandering” behavior can occur during migration for some species of temperate bats, particularly in males and juveniles (Davis and Hitchcock 1965, Dwyer 1966, Humphrey and Cope 1976).

Migration can have energetic benefits and costs. Giavi et al. (2014) showed that the Liesler’s bat (*Nyctalus liesri*) was found to have a very low mortality during migration compared to other seasons, suggesting that the costs of migration, at least to survival, can be low. However, in gray bats, the cost of migration was considered to be fairly high, especially for juveniles (Tuttle and Stevenson 1977). More broadly, migration’s costs on bats’ life history traits are still poorly understood due to the lack of detailed life tables and demographic data (Fleming and Elby 2003). Migration might also have benefits or costs relating to the effects of disease on a species.

Migration and Disease. In some biological systems, migration might lessen the burden of disease on a population. Hall et al. (2014) showed that animals with a greater migratory propensity can be less likely to transmit pathogens, in part because transmission of pathogens only occurs during a single stage of the migration cycle. Migration might allow individuals to minimize exposure to habitats that are infected

through migratory escape (Loehle 1995; Bartel et al. 2011). If individuals carrying disease are less likely to survive migration, then long and strenuous migrations might play a role in limiting disease spread through migratory culling (Bradley and Altizer 2005).

Alternatively, animals might instead contribute to transmission by carrying pathogens with them as they move. Long distance dispersal events have already been suggested as a method of transport for disease such as rabies (Russell et al. 2005), and movements of hosts can spread a novel pathogen outwards from its point of introduction (White et al. 2000). In some cases, even a few translocated individuals can transport pathogens great distances and introduce them to novel areas (Daszak et al. 2000). If transmission, spread, and introduction of pathogens can be affected by migratory movement, then understanding that movement is important for understanding outbreaks of disease. Given that migratory species of bats are affected by or implicated in the spread of emerging infectious diseases (Blehert et al. 2008; Wood et al. 2012), they are relevant study taxa for this line of inquiry.

Bat banding. Bat banding began in Europe and North America during the first half the 1900s, and it continues to be used as a tool to study bat movements. Bat banding in the United States started with the use of bird bands on the legs of tricolored bats (*Perimyotis subflavus*) in 1916 (Allen 1921). An official Bat Banding Program (BBP) was established in the United States in 1932 (Ellison 2008), and at this time, bird bands had been approved for use on bats. During the early years of the BBP many researchers attempted to determine the best way of marking bats, experimenting with various methods including tattooing (Griffin 1934) staining (Poole 1932), ear tagging (Mohr

1939), leg bands, and stenciling as well as forearm banding (Trapido and Crowe 1946). For many years, leg banding was the norm for bats, until forearm banding was popularized in the 50's and 60's. When bird bands were used on bats, the sharp edges of the bands cut into bat tissue and caused skin to grow over the bands. Because of these injuries, a new, safer band design with lipped edges was developed in the mid-1950s (Herreid et al. 1960). Despite this, bird bands were issued through the BBP for use on bats until the program was disbanded.

A moratorium on bat banding was proposed in the fall of 1972. Bat banding had been documented to disturb bats directly through band injuries and roost disturbances, with 22 species suffering declines linked to banding efforts (Ellison 2008). Clyde Jones, then Chief of the Mammal Section of the Bird and Mammal Laboratories of the United States Fish and Wildlife Service, solicited information from bat researchers attending the 1970 Symposium on Bat Research. These researchers recommended protective legislation for bats and the establishment of a permitting system for bat research. They proposed the moratorium on issuing new bat bands through the BBP, as well as an evaluation of the program and its records, and establishment of a treaty for the protection of bats similar to that provided for migratory birds. Members of the American Society of Mammalogists ratified the moratorium in 1973 (Ellison 2008).

Over 2 million bands were used on 36 species of bats across North and Central America between 1932 and 1972, the years that the BBP was active (Ellison 2008). The data collected from bat banding studies can be used to study many aspects of bat natural history, including migratory movements, longevity, site fidelity, hibernation ecology, and other important biological information (Keen et al. 1980; Roer 1995; Ellison 2008; Perry

2011; Humphrey and Oli 2015). The Bat Banding Program records contain data on somewhere between 300,000 to 1.5 million banded bats, all stored on index cards. In her report on the Bat Banding Program for the US Geological Survey, Ellison (2008) said, “Banding bats is still ongoing to this day, but no official clearinghouse or program exists, nor are banding efforts coordinated in any way despite a definite need.”

Gray Bats

General Ecology. The gray bat is a North American bat in the genus *Myotis* that occurs throughout the karst regions of the eastern and midwestern United States. The species occurs primarily in the Appalachia and Ozark regions, but the species can range as far south to Florida, north to Illinois, and west to Oklahoma and Kansas (Decher and Choate 1995). This range overlaps many congeners, including the Indiana bat (*M. sodalis*), the threatened northern long-eared bat (*M. septentrionalis*), as well as the little brown bat.

Gray bats are cave obligates, requiring them for roosting during all parts of their lifecycle (Decher and Choate 1995). They often roost in caves that contain other species of bats, including the Indiana bat, and they have been known to roost in physical contact with these species (Elliot 2008). Individuals of both sexes utilize hibernacula during winter, though males and females often roost in bachelor and maternity colonies, respectively, during the summer. Caves used for hibernacula are usually cold, while summer maternity caves are typically warm and near a water source (Tuttle 1976), and bats will travel between these caves annually. Gray bats were listed as endangered under

the Endangered Species Act of 1973, primarily because human disturbance to their roosts led to large declines (Greenwalt 1976).

Gray bats have clearly defined annual cycles similar to those of other temperate, cave-roosting species. They mate in the fall and females store the sperm until the following spring (McNab 1974). Pregnancy typically begins in April and May with parturition occurring in May and June (Guthrie 1933a; Rice 1955; Barker 1986), which means that females are pregnant during spring migration. Females cannot breed until their second year because ovarian follicles are not mature until their second spring. Neonates are born hairless and with a full set of deciduous teeth, and lactation is usually complete by the end of July (Guthrie and Jeffers 1938; Saugey 1978). Individuals of all sexes and age classes migrate to hibernacula in the fall.

Migration. Gray bats have average flight speeds of approximately 11 mph, and they are capable of significantly long regional migrations between summer and winter caves (Kennedy and Best 1972; Tuttle 1976). Gray bats typically travel between the few large winter colonies and more numerous scattered summer colonies (Tuttle 1976). Gray bats are known to use multiple caves during both seasons, as well as transient caves during migration (Elder and Gunier 1978; Laval and Laval 1980). Gray bats are also known to be philopatric, returning to the same winter, summer, and transient caves for multiple years (Tuttle 1976). Tuttle (1976) suggested seasonal classifications of gray bat activity periods: Spring Migration (26 March – 24 May), Summer Period (25 May – 22 August) which includes the maternity season (4 June – 6 July), Fall Migration (23 August – 20 November), and Winter Period (21 November – 25 March).

Average one-way migration distance in gray bats has been documented at approximately 200 km, though one movement between Missouri and Illinois was 640 km (Elder and Gunier 1978) and another between Tennessee and Florida was approximately 775 km (Tuttle 1976). While gray bats can move significant distances, they are typically considered regional migrants rather than long distance migrants like *Lasiurus* species, which often move more than 1,000 km between seasonal habitats (Holland 2007). Female gray bats are known to have longer migrations than males (Tuttle 1976). This is likely due to the selection of warm caves to decrease the energetic cost of thermoregulation during maternity season (Tuttle 1975, 1976). Conversely, males are less likely to travel long distances, as they are less particular in their cave requirements. They often roost in cool summer caves where they enter daily torpor to conserve energy. These tendencies might also serve an additional benefit of reducing intraspecific competition for food as the sexes segregate across the landscape (Fleming and Elby 2003). Migration has been suggested to be a cause of increased mortality for gray bats due to a study that found that most public recoveries of banded gray bats (individuals that had died) occurred during spring and fall migration seasons (Tuttle and Stevenson 1977).

Known Gray Bat Movement, with an Emphasis on Missouri. The first documentation of migratory behavior in gray bats occurred in Missouri (Guthrie 1933b) and several studies have documented the movement of gray bats in Missouri and the surrounding states (Elder and Gunier 1978; LaVal and LaVal 1980). These studies were primarily banding studies. Elder and Gunier (1978) focused banding efforts around the gray bat hibernacula at Marvel Cave. Marvel Cave is now a part of the Silver Dollar City Theme Park near Branson, Missouri. Because of modifications to the cave, the gray bat

population there has fallen drastically and migration patterns in the area have likely changed. LaVal and LaVal (1980) prepared a report for the Missouri Department of Conservation that documented the banding of approximately 5,000 gray bats. Over 1,000 of these bats were recaptured, a recapture rate of approximately 29 %. Most movements recorded in the study were those between caves in the Meramec area of eastern Missouri, but some movement was documented from the Meremac area towards major hibernacula and maternity caves in central Missouri. Sasse et al. (2007) described gray bat populations in Missouri, Arkansas, and Oklahoma as 3 roughly independent subpopulations (Southern, Northern, and Eastern), consisting of bats that used regional maternity caves and an associated hibernacula. No major gray bat banding studies have been completed in Missouri during the last two decades.

Recent studies have documented gray bat movement in Kentucky and Tennessee (Holliday et al. 2010). Movements in Kentucky and Tennessee showed trends similar to those in Missouri, with a few scattered hibernacula each populating a large radius of maternity caves. Some movements between northern Arkansas and Missouri have been documented, as well as movements between Missouri and Illinois, Missouri and Oklahoma, Missouri and Kansas, Kansas and Arkansas, and Kansas and Missouri (Tuttle 1976; Elder and Gunier 1978; Robertson 2003). The longest known gray bat migration was between Tennessee and Florida, when a male gray bat moved approximately 775 km (Tuttle 1976).

Gray bat movement and activity has also recently been documented in Missouri through the use of NEXRAD weather radar (Hedgepeth et. al. 2015). A large maternity colony in southwestern Missouri was discovered using weather radar, followed by

investigation on foot. The radar signatures occur during emergence, bat outflights large enough and close enough to the radar tower can be detected as sudden increased reflectivity from a small area on the landscape. Future work using weather radar to document gray bat activity could focus on how the reflectivity values of these outflights changes over different seasonal periods, which could serve as a way to document migratory activity. As aeroecology and radar biology develops as a field, more data on gray bat movement will be within reach.

Gray Bats and WNS. White-nose Syndrome (WNS) is a disease causing mass mortality of North American bats. The fungus *Pseudogymnoascus destructans* is the causal agent of the disease (Lorch et al. 2011). Clinical signs of the condition include white fungal growth on the wings and muzzle of infected bats, lesions on wings, and disruption of hibernation (Blehert et al. 2008). The fungus can be transmitted from bat to bat, and between cave environments and bats that live there. Disease spread is also possible due to humans moving between caves (Lindner et al. 2011; Lorch et al. 2011). This disease has caused the deaths of at least 5.7 million bats as of 2012 (Froschauer and Coleman 2012). The fungus is native to Eurasia, but arrived in the United States around 2006 in New York. It has expanded outward from New York each year and as of January 2016 has been detected as far west as Nebraska, as far south as Alabama, and as far north as Canada (Heffernan 2016).

The fungus is known to infect gray bats, however, gray bat mortality from WNS has not yet been documented (Cryan et al. 2013). Other species that share hibernacula with the gray bat, such as the Indiana bat, northern long-eared bat, and little brown bat, have been heavily impacted by WNS (Dzal et al. 2011; Thogmartin et al. 2012). It is

possible that gray bats, due to their migration, possible resistance to infection, year round use of cave roosts, and direct contact with susceptible species could serve as a major vector for *P. destructans* between and among caves. If this is the case, an increased understanding of gray bat movements and cave networks is needed.

Objectives

The overall objective of this thesis is to better describe gray bat migration in Missouri and the surrounding area. I first describe the timing of spring migratory activity, as gray bats leave their hibernaculum and travel to their summer roosts. I also estimated the rate of growth and other population parameters at several maternity colonies during the migration season, and determine whether any differences in those parameters relate to the distance between the hibernaculum and maternity caves. Finally, I used bat banding to document gray bat movements and show connections between regional caves, which could serve as pathways for disease spread. All activities for this project were performed under IACUC protocol number 14-027.0-A.

**USING ACOUSTIC DETECTORS TO DOCUMENT ARRIVAL OF GRAY BATS
(*MYOTIS GRISESCENS*) AT MATERNITY COLONIES**

Abstract

Migration is a critically important and understudied aspect of the life histories of many species, particularly bats. Migration affects conservation efforts, including efforts to manage the impacts of wildlife disease. The gray bat (*Myotis grisescens*) is a migratory species with documented infections by *Pseudogymnoascus destructans*, the fungus that causes White-nose Syndrome (WNS). Despite infections, there are no documented mortalities of gray bats from the disease at current time. Gray bats are cave-obligate, and migrate between discrete hibernacula and maternity caves annually. I documented the timing of gray bat migration in Missouri using acoustic detectors and analyzed patterns of arrival using growth curves. I recorded calls at 4 maternity sites from January to May 2015, and used the R package PVAClone to generate estimates of r and K as measures of arrival rate and an index of population size at the maternity sites. I also plotted values of r and K of each cave against that cave's distance from a major hibernaculum to examine whether there was an effect on the arrival of gray bats at a site. Values of r varied between 0.3 and 0.9 and values of K varied between 981 and 3020 among the maternity roosts, and estimates were consistent whether considering observation error or not. While bats arrived at the closest maternity colony quicker and in greater numbers, the remaining rates and indices were equivocal with distance. This method could be useful for wildlife management officials who want to monitor the phenology of bat migration and the changes in population size at sites with seasonal aggregations.

Introduction

Migration affects many aspects of a species' life history and ecology as well as its conservation needs (Bradley and Altizer 2005; Wilcove and Wikelski 2008; Hall et al. 2014). One major conservation issue for bats in the United States is White-nose Syndrome (WNS), a disease caused by the fungus *Pseudogymnoascus destructans* (Lorch et al. 2011; Cryan et al. 2013). The disease is characterized by white fungal growth on bat skin and disruption of hibernation and it has caused the deaths of at least 5.7 million bats as of 2012 (Froschauer and Coleman 2012). The fungus is likely transmitted from bat to bat, and between cave environments and the bats that live there (Lindner et al. 2011; Lorch et al. 2011), making migration a potentially important contributor to the disease spread.

The federally endangered gray bat (*Myotis grisescens*) is a migratory species that has been documented with WNS. Despite the infection, the gray bat has had no documented mortality from WNS (Cryan et al. 2013). Gray bats are cave-obligate, and migrate between hibernacula and maternity caves annually (Guthrie 1933; Decher and Choate 1995). Tuttle (1976) suggested seasonal classifications of gray bat activity periods: Spring Migration (26 March – 24 May), Summer Period (25 May – 22 August) which includes the maternity season (4 June – 6 July), Fall Migration (23 August – 20 November), and Winter Period (21 November – 25 March).

Bats use echolocation calls to navigate their environment, and acoustic detectors that record bat calls can be used to study many aspects of bat biology, including migration. For example, several studies used acoustic monitoring to study the seasonal movements of tree bats such as *Lasiurus* spp., as well as the relationship between bat migration and mortality due to wind turbines (Johnson et al. 2011a; b). Long-term

acoustic monitoring projects have documented migratory patterns of various species in coastal and northern regions of the United States (Peterson et al. 2014; Reimer et al. 2014). Acoustic monitoring has also been used to study the effects of WNS in the eastern United States (Ford et al. 2011). Acoustic data can help define migration phenology, such as estimating arrival times at maternity or hibernacula sites (Rydell et al. 2014). Bat activity as recorded by ultrasonic acoustic detectors can be assumed to serve as a rough index of site use (Frick 2013).

In Missouri, Parris (2013) used acoustic monitoring to record the winter activity of gray bats at Missouri caves, discovering that gray bats appear to be more active in winter than previously thought. Using similar methods, I monitored gray bat caves in Missouri to record bat activity during and after the spring migration season. This allowed me to generate an estimated index of growth rate at maternity caves as bats arrived at seasonal sites.

My goal was to determine a timeline of gray bat activity using acoustic detectors, which I predicted would be similar to the timing described from Tuttle's (1976) observations. I also sought to determine whether or not the distance of a maternity cave from a hibernaculum affected the rate of arrival of individuals. I predicted that gray bats would arrive later and more slowly at maternity sites that were farther away from a large hibernaculum.

Methods

Detector Setups. Anabat I and II bat detectors (Titley Electronics, Ballina, New South Wales, Australia) were deployed 3 – 20 January, 2015 and remained in the field

until 30 April – 12 May, 2015. Detectors were enclosed in Pelican Cases (Pelican Products, Inc, Torrance, CA) and attached to 12-volt batteries (Batteries Plus LLC, Hartland, WI) that were connected to solar panels (SunWize Technologies, Inc., San Jose, California) depending on light levels at sites, which allowed for slow-recharging to extend battery life. Microphones were placed inside a 45° angled PVC tube funnel (Fig. 1). The sensitivity of the detectors was adjusted based on the ambient noise at the site, but was between 4 and 7 units, and the division ratio was set to 16. Detectors were mounted on trees or rocks with funnels aimed at areas expected to collect clear gray bat vocalizations during emergence. Detectors mounted on trees were placed on hunter's tree seats, and both tree and rock mounted detectors were chained to prevent theft. Detector data were stored on a Compact Flash (CF) card. Each CF card was set to record from 6pm to 6am each night to capture bat activity. Calls were downloaded every 1—2 weeks.

Study area. Seven detectors were deployed at caves in southern, central, and western Missouri (Table 1). One of these caves was a hibernaculum, one a transient cave, and five were maternity colonies (Figure 2). The hibernaculum monitored in this study is considered the largest gray bat cave in the state, with an estimated population approximating 400,000 — 500,000 bats (Elliott 2007). All transient and maternity sites in this study have been documented to house bats that were found at Coffin Cave (Laval and Laval 1980, Gerdes unpublished data).

Acoustic Data Analysis. All calls were downloaded from CF cards using the CF Read application (Titley Electronics, Ballina, New South Wales, Australia). Calls were classified using Bat Call Identification Software (BCID; Bat Call Identification, Inc. Kansas City, Missouri) using the default Missouri species list and requiring a minimum

of five pulses for identification. Results of these classifications were exported to an excel spreadsheet. The filenames of each call were converted into appropriate timestamps and then the individual excel files were combined by site and converted to a .csv file. The data were imported into Program R (R Development Core Team 2014). Calls classified as gray bats were selected and daily counts of gray bat calls were calculated.

To determine the approximate timing of migration, a timeline of calls for each site was generated. I used the status files of each download period to determine when detectors were functional. Some periods of time were missing data due to battery failure or card errors. Days that had errors or missing data for any part of the set recording time were considered NA values and were excluded from analysis.

PVAClone (Nadeem and Lele 2012) was originally designed to perform population viability analysis by generating a variety of models using count data. The package uses data cloning in a Bayesian framework to generate growth curves for time series count data with missing values (Nadeem and Lele 2012). It works by using Markov Monte Carlo Method (MCMC) to approximate a likelihood variable after the original input data have been cloned. The package can also account for observation error in its models. This allowed us to create a logistic growth model of the increase in gray bat activity as individuals arrived at their maternity colonies during and after migration.

Logistic growth models were generated to describe spring migratory activity using the package PVAClone (version 0.1-5) in R (version 3.2.2), as well as JAGS (version 3.4). Because the PVAClone package can only create models if the starting and ending values are nonzero, models in this study were built using a subset of the time series data collected. I selected the broadest period of dates with nonzero values that the

package could successfully generate a model – the earliest Julian date that allowed PVAClone to generate a model was considered the “model starting date”. Essentially, this means that dates from early in the study period were excluded from the model because most days had no detected gray bat calls.

The data were fit using the package’s theta-logistic method based on the following equation $x_t = x_{t-1} + r \left[1 - \left(\frac{e^{x_{t-1}}}{K} \right)^\theta \right] + \varepsilon_t$. The package generated estimates for r (Growth rate), K (Carrying capacity), Σ (Process error), τ (Observation error). It also provides an estimate of \hat{r} (The Bayesian potential scale reduction factor) which represents how well the model has stabilized to represent the underlying distribution. For this work theta was set to unity so that the model would be a logistic growth model. The data were cloned 10000 times to generate each model. Models were run twice, once assuming no observation error and once assuming normally distributed observation error. Confidence intervals (95%) were calculated using the confint function in R. Because there were missing values in the data, I was unable to run PVAClone’s AIC model selection tool to determine which models explain the most variation in the data. After coefficients for the logistic growth model were generated, I plotted cave distance from a major hibernaculum (Site CC) against the coefficients r and K , as well as against the model starting date to determine if the distance from a major hibernaculum had an impact the arrival of bats at maternity colonies.

Results

Timelines generated for maternity colonies showed an approximately logistic growth pattern as bats arrived at breeding colonies, while the trend at the hibernaculum

showed an increase and subsequent decrease as bats emerged from torpor and left for summer habitats (Figure 3). The earliest documented activity at hibernaculum site CC was recorded on 23 March. However, bats might have been active at this site proceeding that date, during a period with missing data. Bat activity at site CC declined in early April and returned to zero by 8 May. The earliest model start date at maternity caves was at site BQ on 5 March, followed by site ES on 8 March, site RC on March 27, and site ML on March 29.

Two detectors were excluded from the results. The detector at the transient cave (SC), which was located in a public park, experienced repeated problems with attempted theft, excess humidity, and battery failure, leading to the collection of only 16 days of reliable data. One detector at the westernmost maternity cave (PK) recorded for most of the study period, but only picked up a total of 66 gray bats calls during the entire season, likely due to a combination of detector location/angle and high levels of ambient noise from an immediately adjacent highway.

Values of \hat{r} in logistic growth models approached 1.0 at 10,000 clones for all sites with both types of errors. Estimated r and K coefficients for all sites were significantly different from zero ($P < 0.05$), regardless of whether or not observation error was included in the model (Table 2). Process error (σ) was also significant in all models ($P < 0.05$). In models including normally distributed detection error, the detection error values (τ) were significant in 3 of 4 sites ($P < 0.05$), with the exception of site BQ.

For each site, there were no significant differences in r values between models that included detection error and those that did not. Site ML had the highest r value for both the model including observation error (0.7548 ± 0.2621) and the model that did not

include observation error (0.9290 ± 0.2951). This site also had the highest standard error for r in both models. There were no significant differences between the r values of the remaining models for sites BQ, RC, and ES, regardless of whether or not detection error was included in the model (Table 2). Estimates of K were likewise highest at site ML regardless of whether detection error was included in the model (3020.00 ± 277.50) or not (3014.00 ± 249.00), while remaining sites all had similar estimated carrying capacities.

Estimated detection error (τ) was highest at site RC ($\tau=0.4425 \pm 0.0897$) and lowest at BQ ($\tau=0.0230 \pm 0.3943$), where detection error was not significant. Generally, there was little difference between model coefficients that included detection error and those that did not. However, process error values (σ) were reduced for site RC when observation error was included in the model. The inclusion of observation errors did not affect process error values for sites BQ, ML, and ES (Table 2). The 95% confidence intervals for site RC were reduced when detection error was accounted for (Figure 4-5).

Sample size ($n=4$) precludes whether I could test for trends in model coefficients with respect to the distance between maternity caves and a major hibernaculum. When this distance was plotted against model coefficients (r , K , and model starting date), no obvious trends emerged for models with or without detection error. The lack of a clear trend might simply be an effect of the very small sample size (Figure 6).

Discussion

I successfully used acoustic data to create a timeline of bat activity at 1 hibernaculum and 4 maternity caves in Missouri during the spring of 2015. Bat activity

appeared to begin as early as March, when bats at the site CC hibernaculum had aroused from torpor. The number of calls-per-day seemed to increase until April, and by the beginning of May virtually all activity at the hibernaculum had vanished. This pattern matches with what was documented at maternity caves, where the number of calls-per-day rose until they approached their carrying capacities by mid-April. There was no apparent effect of the distance between the maternity caves and the hibernaculum on the rate or timing of gray bat migration, though sample size ($n=4$) was too small for statistical testing.

PVAClone. I chose to use PVAClone's Bayesian method estimation of detection error, something that likelihood methods would be unable to do. I also chose this method because it can account for missing data, an important factor when dealing with acoustic data that had gaps due to occasional equipment failures. The package uses count data, and here I chose to use an index of (calls/day) as a count that would represent activity. The fact that PVAClone uses a time series format also made it appealing, because calls-per-day are temporally auto-correlated and the package takes that into consideration. Despite the fact that PVAClone was originally designed for performing population viability analysis, I believe its ability to create growth models is a useful tool that has a variety of other applications, including studying migration.

Data considerations. Acoustic data have certain limits, for example, Anabat detectors are extremely sensitive to the placement and direction of the microphone (Weller and Zabel 2002). Because each cave in this study has a different shape and size, detector placement could not be standardized. Detectors were placed at varying heights and distances away from cave openings, which could limit the ability to compare K

values between caves. Sensitivity levels on detectors also differed between sites due to ambient noise ranging from the sounds of people, traffic, and running water. For future studies using this method over multiple years for long-term monitoring, it is important that detector placement is standardized at each cave over time.

It is also important to remember that in this context, Anabat count data does not represent a true measure of abundance or density at a site, but rather an index of population size at a specific time. Measures of growth are not direct measures of individuals, but of an increase in the number of calls. The relationship between bat echolocation activity and abundance of bats is not clearly defined and, at this time, echolocation activity recorded this way cannot be used to directly infer population densities (Hayes et al. 2009). Nevertheless, it is reasonable to assume that changes in detected activity over time indicate changes in use of the habitat of interest (Frick 2013).

PVAClone is designed to handle missing data; however, large gaps of missing values during the population growth period might push back the model starting date and therefore affect model results. This might have been the case with site ML, which had a large gap of missing values (18 days) immediately preceding PVAClone's model starting date. The site also had the highest r value and latest model starting date. For the purpose of this analysis, I assumed that model outputs at site ML were not skewed by this missing data, but researchers using detectors to study migration in the future should be especially diligent about preventing data loss during the growth period at maternity sites.

Interpretation. The acoustic activity index timelines for the maternity sites show a roughly logistic growth pattern beginning early in the year. These timelines show the period of time that gray bat activity at maternity sites increases due to migration of bats

that have emerged from torpor and left the hibernaculum. It is worth noting that I detected bat activity at sites BQ and ES slightly earlier by model starting date (8 March and 5 March respectively) than Tuttle's (1976) suggested migration period beginning 26 March. This may be due to stray bats overwintering in summer caves, but is more likely the result of migrants, as there were also many calls slightly preceding Tuttle's estimates at the CC hibernaculum (23 March).

Three of the sites (BQ, RC, and ES) had model outputs that were relatively similar. Site ML had the highest number of calls of all the sites, with a peak calls-per-day value of about 4,000; double that of the other 3 maternity colonies. It also had the highest carrying capacity, with an estimated K value of over 3000 calls per day. While some of this likely had to do with detector placement and cave shape, it's also due to the large maternity population at the site. Site ML also had the highest r value for both types of models (0.9390 without detection error, 0.7548 with detection error). The remaining sites (BQ, RC, ES) had fairly similar model outputs, with growth rates between 0.3 — 0.5 and K values between 900 — 1500.

The r and K values in all models were significant ($p < 0.01$). In this context, a significant P -value simply describes a value that is effectively different from zero. The models document population growth at these sites. Models that accounted for observation error generally had lower standard errors of their r and K values. Site ML had a much higher standard error for r than any of the other sites, regardless of the model used. Site RC had the highest standard error for its K values, and the model without observation error for that site also had the widest 95% confidence interval.

Coefficients did not appear to be distinctly related to distance from site CC affecting on the rate of growth or the model start date. This is possibly due to a small sample size of only 4 sites, but might also be due to contributions of migrating bats from other hibernacula. Because site CC is the largest gray bat hibernaculum in the state, and band returns link this cave to all of the maternity sites in this study (Laval and Laval 1980, Chapter 2), I assumed that at least some proportion of maternity cave populations originated at site CC. Site CC has an estimated population in the hundreds of thousands, it seems likely that this hibernaculum is a major contributor to maternity caves throughout this part of Missouri.

If straight-line distance from a major hibernaculum has no effect on the time or rate of gray bat arrival at maternity sites, there might be other factors at play. For instance, gray bats are known to move along waterways, so it is possible the length of the bat migration route is related to the length of rivers rather than a straight-line distance. Future work should investigate length of major waterways between caves in addition to straight line distance, to determine if distance travelled over water is a better estimator of time of arrival. Alternatively, distance might not play a factor at all – gray bats might simply be arriving at the same rate regardless of distance, covering large distances in the same number of nights as they cover short ones. A larger sample size of caves monitored is needed to determine any differences in the arrival of bats at maternity colonies.

Context and future applications. The continuous logistic growth model relies on the assumption of a closed population, where immigration and emigration are typically assumed to be zero. In that scenario, growth occurs because the birth rate exceeds the death rate; in this case, growth reflects individuals arriving at maternity colonies. Because

bats do not give birth during this time period, it can be safely assumed that growth at maternity caves is driven primarily by migration rather than reproduction. Essentially, this approach uses immigrants as births and emigrants as deaths, although the number of emigrants is unknown.

This method for analyzing acoustic data could be used to study any species that makes recordable vocalizations and seasonally migrates to a discrete location such as a cave (bats), a vernal pool (frogs), or an island (breeding sea birds). Placement of long-term acoustic detectors allows researchers to record dates that animals begin to arrive at seasonal sites, and fitted growth models can be used to monitor populations and compare model coefficients over many years. Estimates of r allow researchers to understand how quickly populations at a seasonal site are growing due to an influx of migrating individuals. Comparing timing of migration as well as the logistic growth parameters among years could be useful for studying the effects climate change or other disturbances on migratory behavior. Long term data sets can compare the population growth rates and the estimated first arrival dates between years, as well as compare how management, weather/climate, and other factors affect model coefficients.

In the context of disease ecology, particularly WNS, this method could be useful for quantifying effects of disease on migration and population size. Understanding the rates of migration to specific sites between years could provide insight into how WNS affects populations and the timing of movements. Using a permanent detector set up at a cave (While keeping detector location standardized) could provide those who manage caves with an index of activity that can then be monitored over the years. Using our method of analysis could allow them to gain estimates of a carrying capacity of calls/day

(K) that can be compared between years. This method is useful not only for gray bats, but any bats that use seasonal caves and are identifiable using automated software. This includes the endangered Indiana Bat (*Myotis sodalis*), the threatened northern long-eared bat (*M. septentrionalis*), and the declining little brown bat (*M. lucifugus*), all of which are impacted by WNS. Monitoring caves this way is that it is a relatively low-cost, low-effort, and minimally invasive way to get continuous time-series data for understanding relative activity levels, the effects of disease, and the timing of seasonal movements.

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Table 1. Description of gray bat acoustic monitoring sites.

Site	Cave Type	Active Detector Days	Total Days	#Calls	Distance To CC
CC	Hibernaculum	4 Jan—18 Feb, 22 Mar—9 May	93	19,242	—
BQ	Maternity	20 Jan—27 Jan, 1 Feb—21 Mar, 29 Mar—11 Apr, 24 Apr—30 Apr	82	38,635	24
ML	Maternity	4 Jan—9 Mar, 29 Mar—2 May	100	101,672	10
RC	Maternity	17 Jan—1 Mar, 28 Mar—12 May	90	44,683	132
ES	Maternity	21 Jan—2 Feb, 6 Feb—18 Feb, 4 Mar—4 May	89	37,591	103
PK	Maternity	21 Jan—18 Feb, 3 Mar—4 May	92	66	169
SC	Transient	15 Jan—23 Jan, 14 Feb—15 Feb, 29 Apr—4 May	16	*	76

Table 2. Coefficients generated by PVAClone models with 10,000 clones. Models that included observation error are in italics. Asterisks represent coefficients that had p-values less than 0.05.

	r	K	Σ	τ	\hat{f}
BQ	$0.4668 \pm 0.1277 *$	$1167.0 \pm 191.3 *$	$0.4728 \pm 0.0525 *$		1.000
	<i>$0.4666 \pm 0.1283 *$</i>	<i>$1167.0 \pm 189.3 *$</i>	<i>$0.4722 \pm 0.0579 *$</i>	<i>0.023 ± 0.412</i>	<i>1.280</i>
ML	$0.9390 \pm 0.2951 *$	$3014.0 \pm 249.0 *$	$0.4475 \pm 0.0554 *$		1.001
	<i>$0.7548 \pm 0.2621 *$</i>	<i>$3020.0 \pm 277.5 *$</i>	<i>$0.3372 \pm 0.0805 *$</i>	<i>$0.256 \pm 0.091 *$</i>	<i>1.002</i>
RC	$0.4321 \pm 0.1900 *$	$1265.0 \pm 335.1 *$	$0.7002 \pm 0.0746 *$		1.000
	<i>$0.3952 \pm 0.1169 *$</i>	<i>$1329.0 \pm 266.9 *$</i>	<i>$0.4129 \pm 0.1006 *$</i>	<i>$0.442 \pm 0.091 *$</i>	<i>1.002</i>
ES	$0.3283 \pm 0.0902 *$	$981.2 \pm 200.2 *$	$0.4260 \pm 0.0400 *$		1.001
	<i>$0.3031 \pm 0.0766 *$</i>	<i>$1021.0 \pm 198.8 *$</i>	<i>$0.3400 \pm 0.0904 *$</i>	<i>$0.203 \pm 0.105 *$</i>	<i>1.006</i>



Figure 1. Example acoustic detector set up. Detectors were placed on trees or rocks with a 45° cone pointed upward toward possible bat flyways. Anabat detectors were powered with 12 volt batteries connected to either 1 or 2 solar panels.

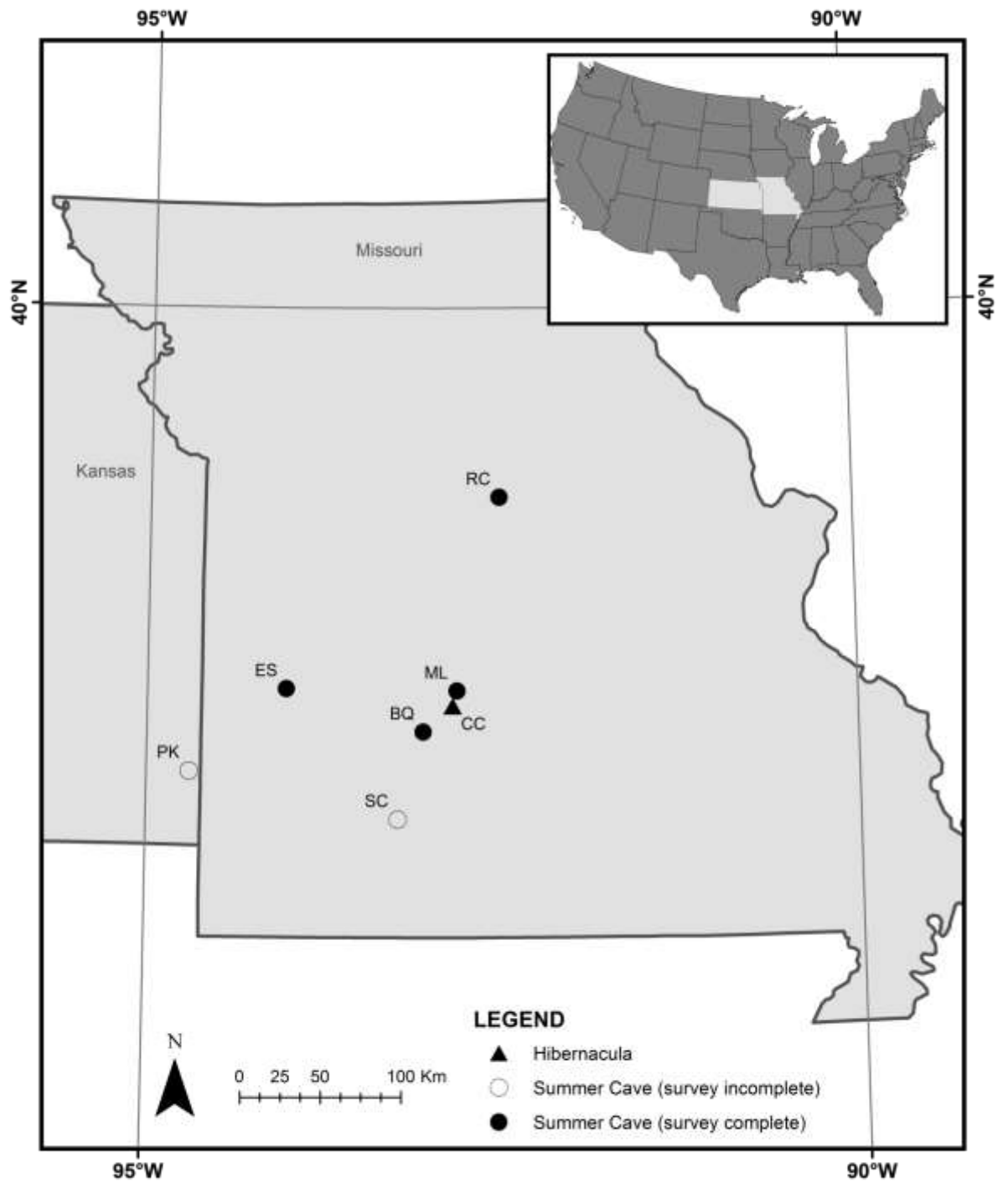


Figure 2. Map of gray bat acoustic monitoring sites.

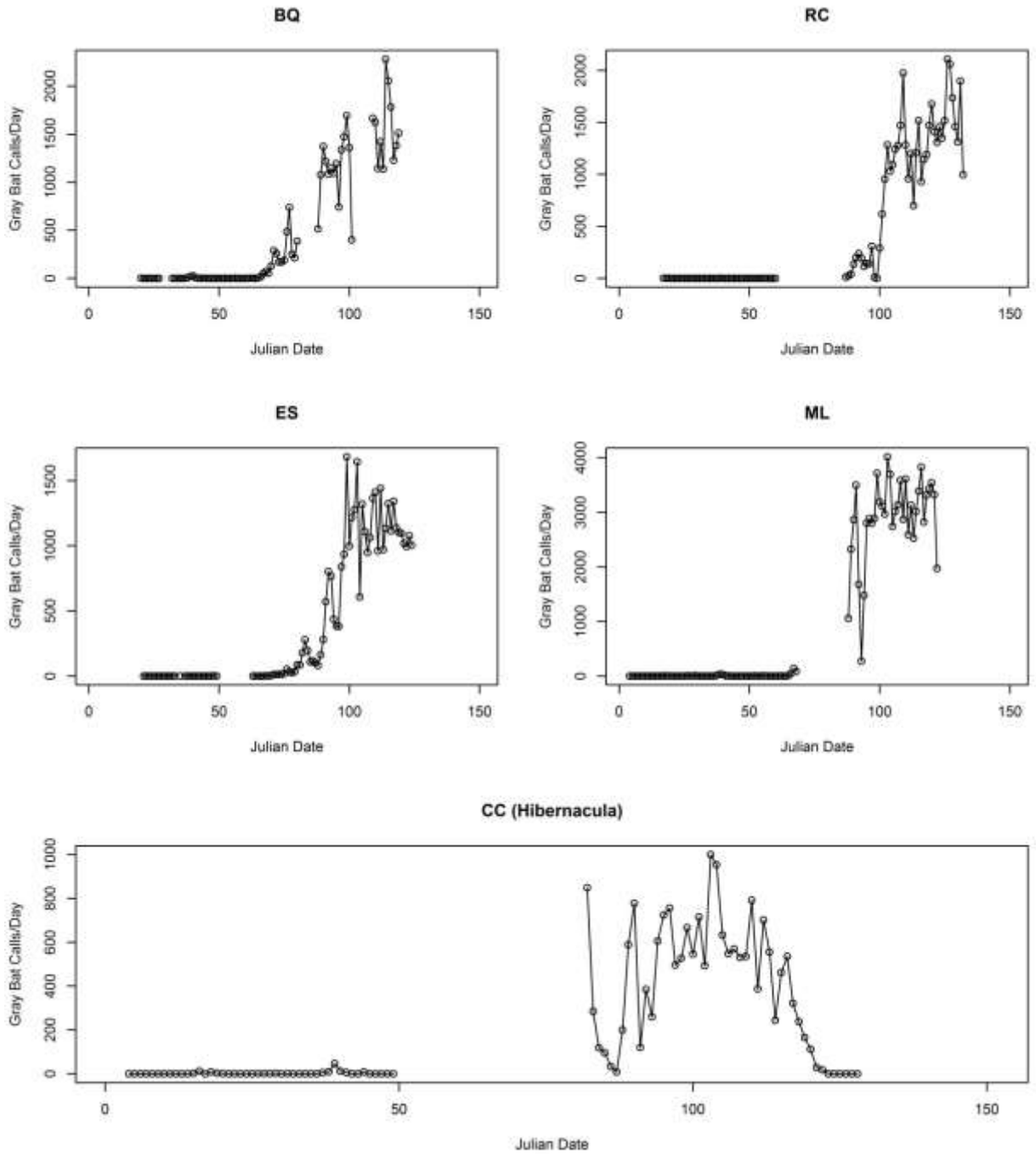


Figure 3. Timelines of bat activity showing the number of bat calls per day recorded from January 1 -May 31, 2015.

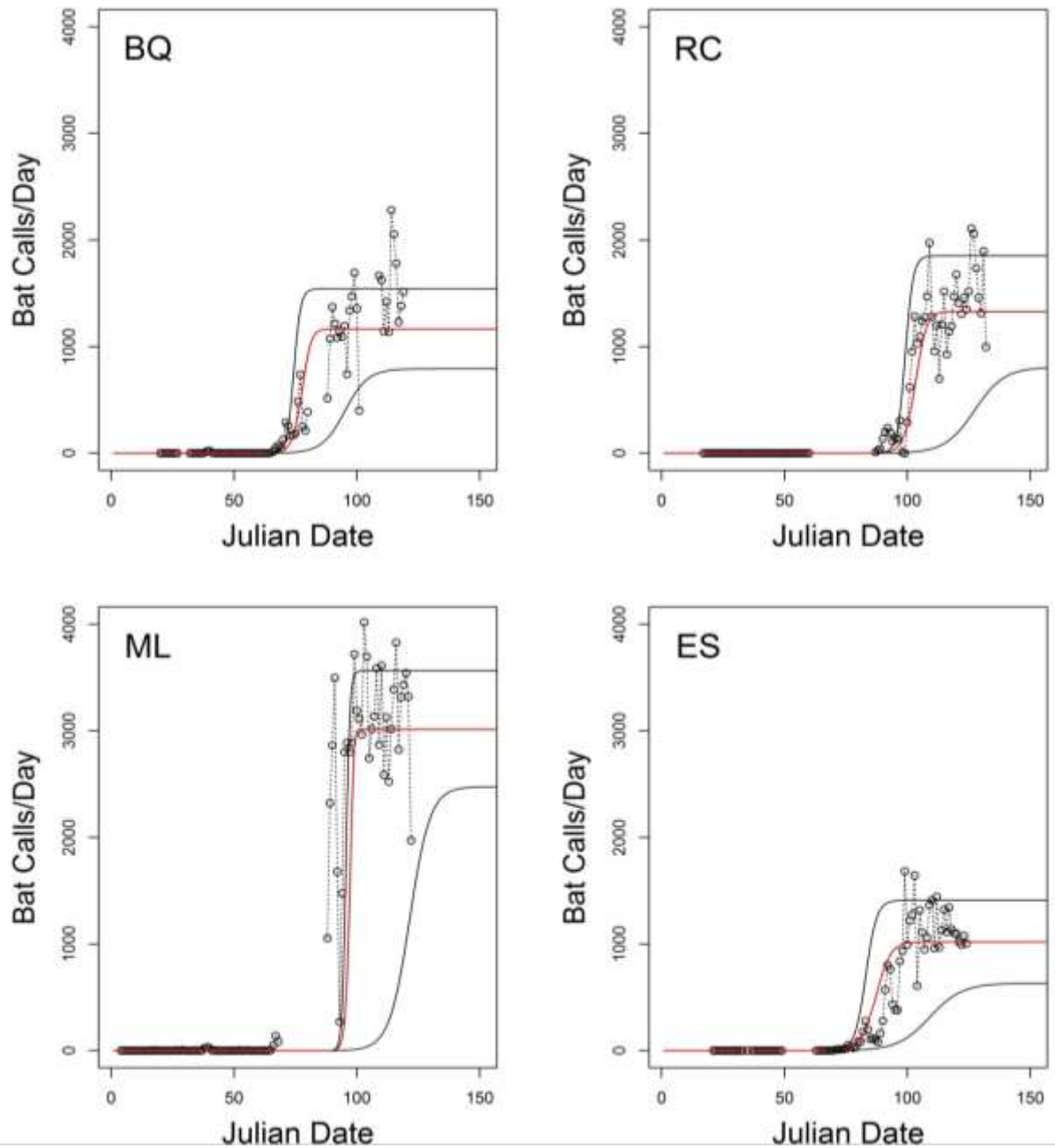


Figure 4. Logistic models accounting for detection error, generated from package PVAClone in R, shown in red. Black lines represent 95% confidence interval.

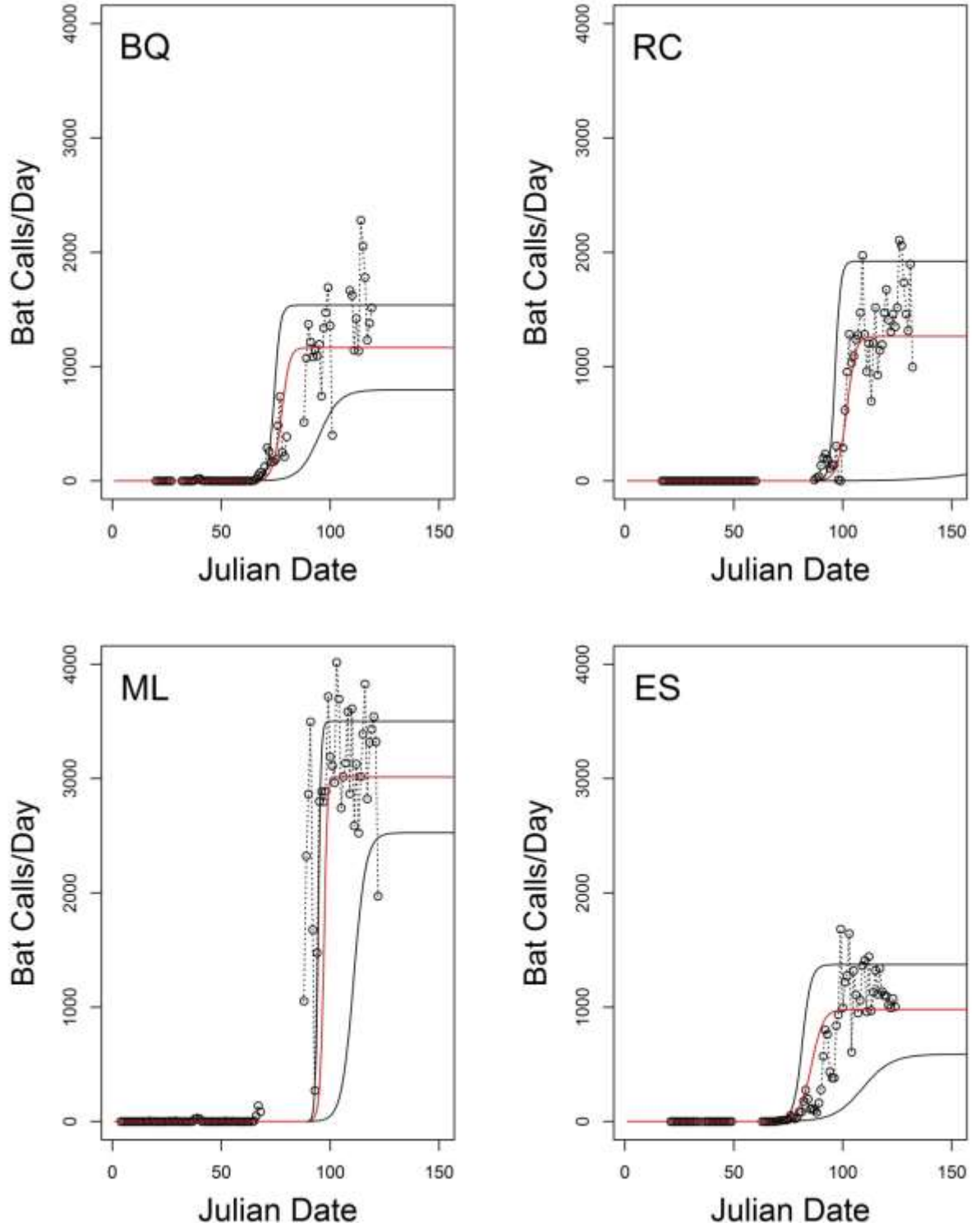


Figure 5. Logistic models not accounting for detection error, generated from package PVAClone in R, shown in red. Black lines represent 95% confidence interval.

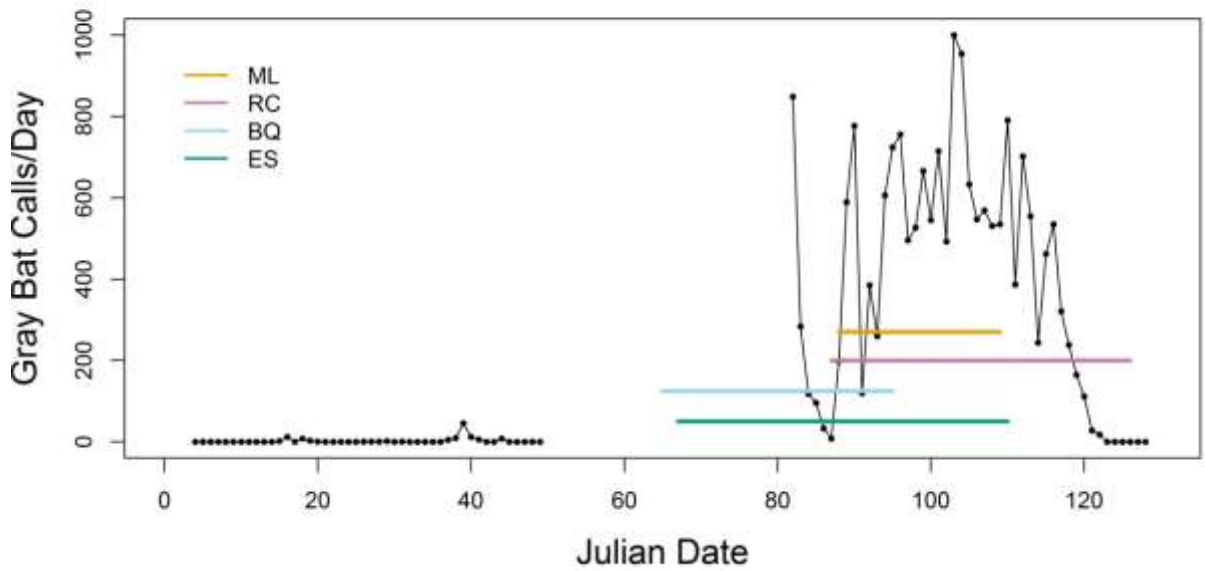


Figure 6. Gray bat calls per day at hibernacula site CC, with comparison to the migratory timing at maternity caves (colored bars). The migratory period of a maternity site was defined as the time between the PVAClone model starting date and the day that the data had a value equal to the site’s carrying capacity.

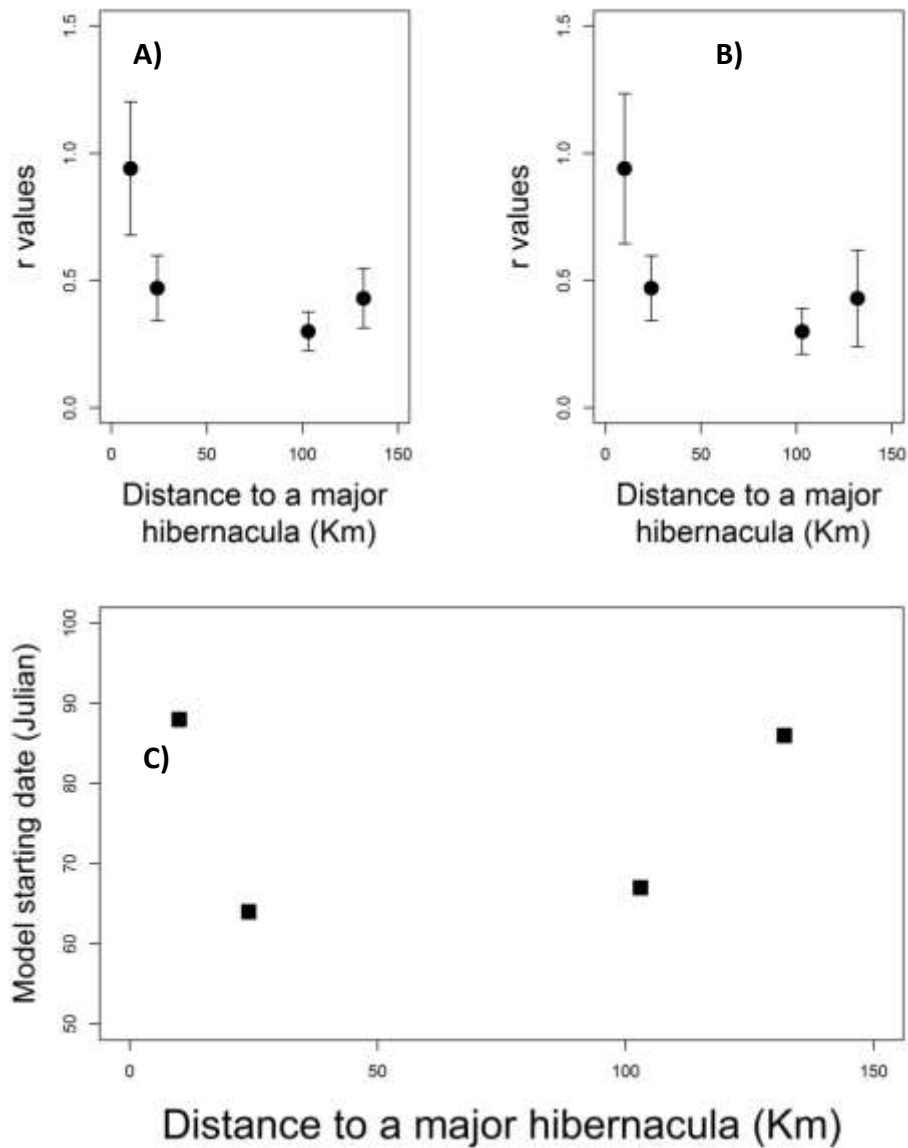


Figure 7. A) The effects of distance between maternity caves and a major hibernacula on the rate of gray bat arrival based on logistic growth models with observation error B) The effects of distance between maternity caves and a major hibernacula on the rate of gray bat arrival based on logistic growth models without observation error. C) The effects of distance between maternity caves and a major hibernaculum on the rate of gray bat arrival based on the PVAClone logistic model starting date.

USING BAT BANDING TO DOCUMENT CONNECTIONS BETWEEN GRAY BAT CAVES

Introduction

Bat banding has historically been used to study many life history traits of bats. Bat banding has been used to study seasonal movements, longevity, site fidelity, and population dynamics (Humphrey and Oli 2015). Several studies on gray bats have revealed migratory trends in Missouri, Kentucky, and Tennessee (Gunier and Elder 1971; Laval and Laval 1980; Holliday et al. 2010). This chapter presents newly documented movements of in Missouri based on band returns.

Recaptures of banded bats, especially of endangered species, are typically quite rare (Ellison 2008). For one group of bats captured and banded on forest landscapes, 1.6% of bats were recaptured over the course of 716 net nights over 160 summer nights between 2000 and 2008 (Perry 2011). One study on have yielded a return rate of approximately 0.06 in big brown bats (*Eptesicus fuscus*) banded in caves and later recaptured in mist nets (Beer 1955). Records from the Bat Banding Program suggested that in 1970, 16,273 bands were reported as applied to bats, and 1238 bands were reported as returns (Ellison 2008). During 2011 there were 10 gray bat band returns reported to the Missouri Department of Conservation (MDC), though only 4 were able to be identified as originating at a certain site. The following year only 1 band return from a gray bat was reported. (MDC, unpublished data). These numbers are small, and methodologies and survey efforts for banding and netting vary wildly across studies, making it difficult to calculate band return rates in many areas.

Bat movements documented by band returns can be described as either local or foreign movements, where local movements occur when a bat is recaptured in the same place it was banded after a suspected migration event, and foreign movements are when a bat is recaptured in new location (Ellison 2008).

Methods

Bat capture. Bats were captured using mist nets and harp traps near cave entrances as approved by the Missouri Department of Conservation and USFWS. Gray bats were banded and biometric data such as forearm length and mass, as well as demographic data such as sex, age class, and reproductive status. Gray bats were banded and released at the site of capture. Surveys were conducted from the fall of 2013 to the fall of 2015.

Banding efforts. Captured *Myotis* spp. were banded with 2.9 mm aluminum bat bands, with most gray bats receiving modified colored bands. Colored bands were made by bead blasting aluminum bands to create a rough surface, and applying fluorescent colored spray paint (Ace Glow Fluorescent™) being careful not to obscure the band numbers. The bands were colored coded to site, and fluoresced under blacklight. Our purpose behind color coding bands was to increase visibility of banded bats within caves, and make it possible for cave surveyors to determine where the bat was banded, even if they could not handle the bat to read the band number. This had been a problem in the past, especially in locations where cave ceilings were very high (pers. communication Missouri Dept. of Conservation 2013).

Gray bats were banded at 9 sites, 7 of which were at cave openings and 2 of which were captures that occurred on the landscape as the bats were foraging (Table 3). Bands were recovered during regular winter hibernacula surveys performed by the Missouri Department of Conservation, Arkansas Game and Fish Commission, and Missouri Bat Census. Individuals from these organizations entered caves during the winter hibernation period and documented the band numbers of any tagged individuals, which allowed identification.

Results

A total of 1136 gray bats were captured and banded during 2013-2015 by researchers at Missouri State University (Figure 8). Winter hibernacula surveys across Missouri and Arkansas led to the recovery of 18 bat bands from these banding efforts, giving a return rate of 1.4%. The department also received a total of 8 band returns on gray bats tagged during the 2013-2015 timeframe by other organizations. Band returns from MSU tagging efforts were mostly found during winter WNS and population monitoring studies performed by state agencies, though 1 occurred when a previously tagged bat was captured during trapping near the mouth of a hibernaculum.

The largest amount of band returns (12) were found inside hibernaculum CC, the largest gray bat wintering site in the state. There was 1 local band return at hibernaculum site CC in addition to 11 foreign returns, which connected site CC with maternity sites BQ (4 returns), ES (1 return), SC (5 returns), and PK (1 return). There were also two bats that had been originally banded at Coffin Cave that were later recovered at site LK. All of the connected cave sites are located in Missouri with the exception of site PK, located in

eastern Kansas and site CM, located in northwestern Arkansas. Of the movements documented in this study, all but 1 (PK to CC) represent previously undocumented connections between caves.

Two individuals banded on the landscape during summer were later found in nearby caves MP and MC. They were originally banded at the Echo Bluffs State Park site during an Endangered Species Act mandated preconstruction survey, and were found in the two caves about 1.5 and 21 km away respectively.

Discussion

The tagging of over 1,000 gray bats represents one of the largest efforts to mark these animals in decades and ideally banded bats from this study will be recaptured for several years. The year 2015 had 35 gray bat band returns reported to the Missouri Department of Conservation, 32 of which were identifiable to the site of banding. Of these, 20 were banded by MSU and 16 were banded during our study period. The overall number of band returns in 2015 was greater than the number of band returns during 2011-2012 in terms of acquiring band returns. The combined total of banded gray bats reported to MDC during the 2 years preceding the study was only 11.

The caves connected by gray bat movements documented in this study create a network that has many linkages (Figure 9). Each node or cave site has a path to all other nodes, though some paths have a longer distance. There are not enough band returns to quantify what this well connected cave network might mean for white nose syndrome spread, but it is possible that movement along such an inclusive network could contribute to WNS spreading between and among caves with ease.

Caves with many connections, those caves that are very central to the network, might contribute more to the spread of White-nose Syndrome than those with fewer connections to other caves. Networks with higher connectivity have more potential pathways for WNS to travel. Future studies on Missouri's cave network should focus on combining historic and recent band return data and determining how the features of the network might affect WNS syndrome spread.

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Table 3. Bat banding site details

Site	Bats Banded	Location Type	Location Use
PK	100	Storm Drain	Maternity colony
ES	228	Storm Drain	Maternity colony
BQ	99	Abandoned Quarry	Maternity colony
ZT	61	Forest	Summer foraging
CR	14	Forest	Summer foraging
BS	31	Cave	Hibernaculum/Maternity colony
WC	3	Forest	Summer foraging
KM	11	Forest	Summer foraging
TD	23	Cave	Maternity colony
CC	246	Cave	Hibernaculum
SC	319	Cave	Transient Cave
CB	1	Forest	Summer foraging

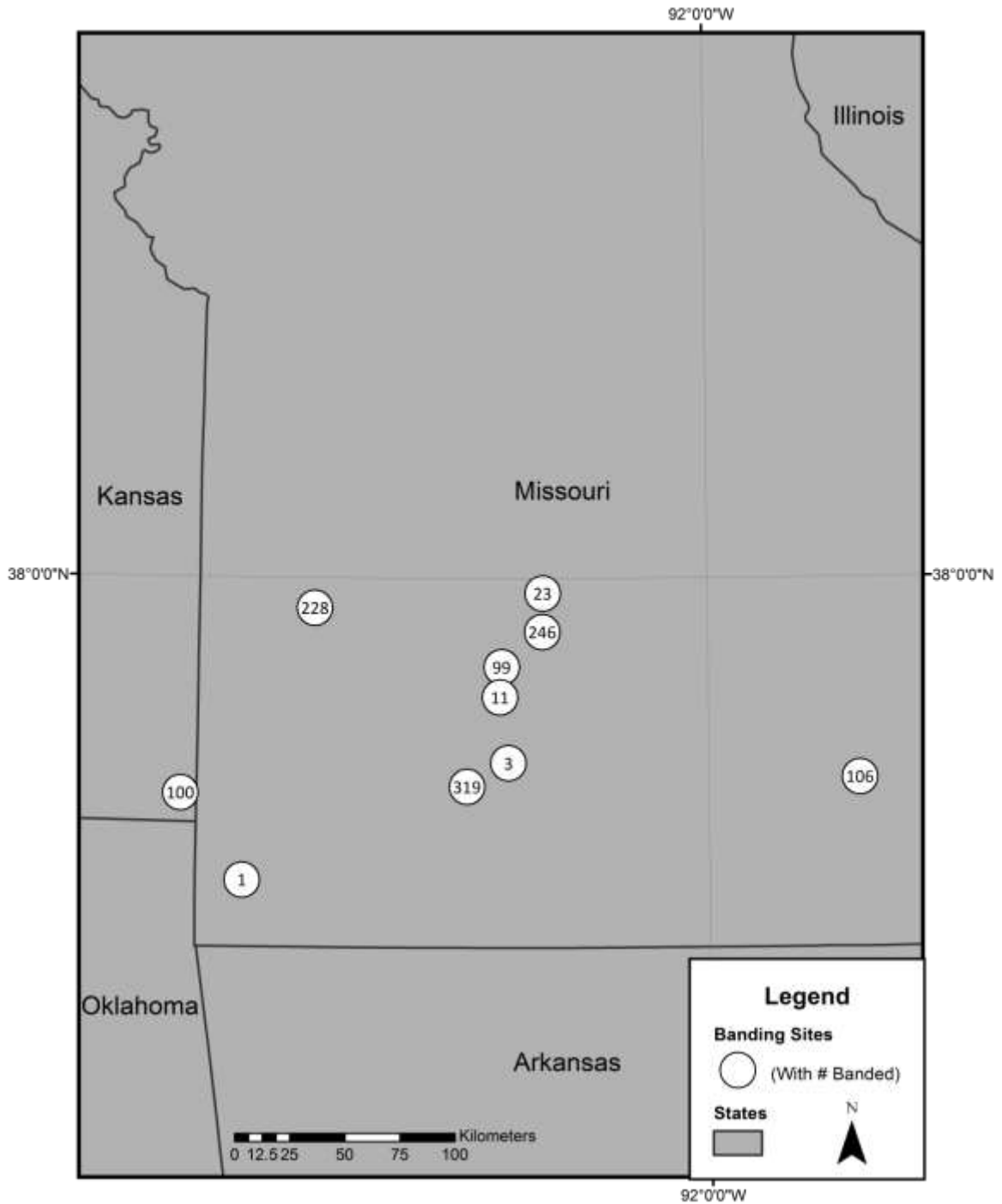


Figure 8. Map of gray bat banding efforts by Missouri State University between 2013 and 2015. Where banding sites were less than 5 km apart, the numbers are aggregated.

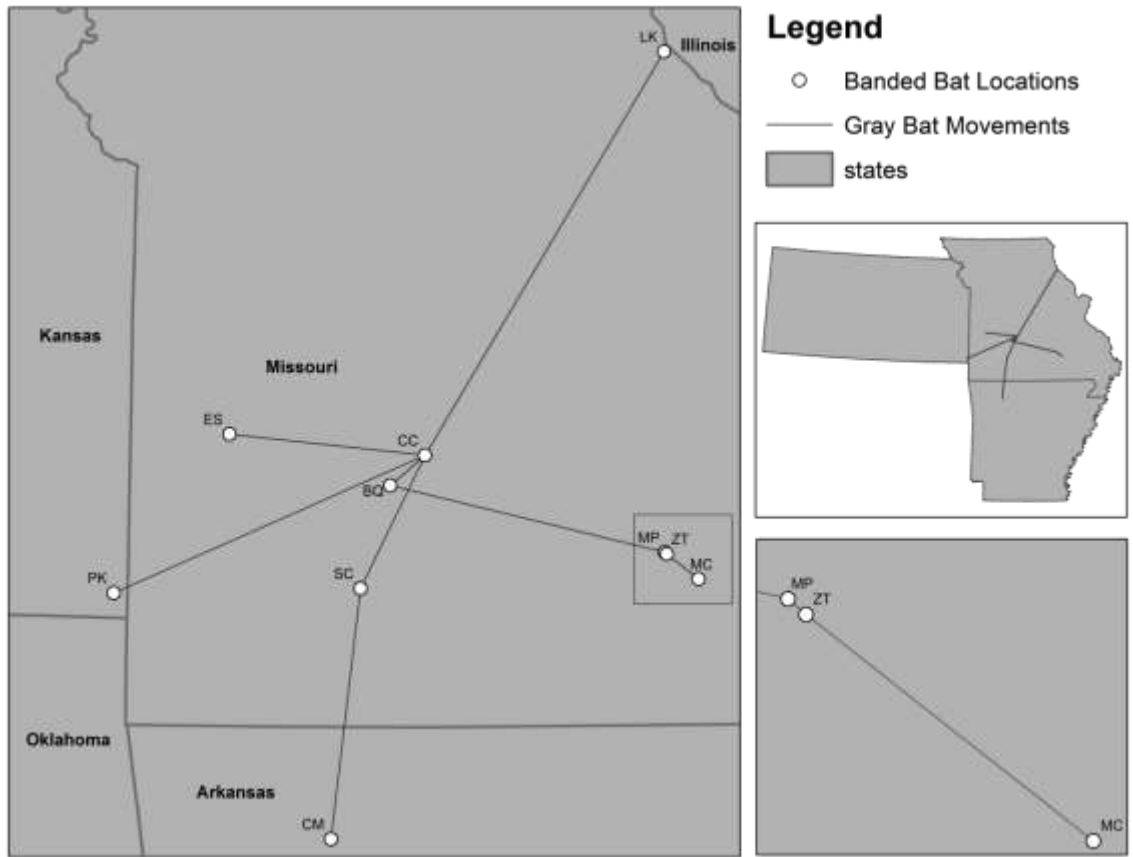


Figure 9. Map of gray bat band returns from bats banded 2013 – 2015 by Missouri State University

CONCLUSIONS

This thesis sought to gather an updated portrait of gray bat migration in Missouri, revisiting what was already known about the timing and locations of their movements and expanding upon it. To my knowledge, it is the first study to do so in over 20 years. I approached the topic from the perspective of individual gray bat caves that were connected by seasonal gray bat movement. Using acoustics, I documented the activity of bat populations at a major hibernaculum and several associated maternity caves, and used that activity as an index of population size over the migration season. Simultaneously, I used bat banding to document connections between seasonal caves. My data represent new observations of seasonal gray bat activity and movement in Missouri. The thesis also represents a new way of using acoustic data and logistic growth models to measure the timing of migratory activity and compare activity over multiple years. This method can be applied to future studies on cave bats and could also be applied to other systems.

These new data and new monitoring methods have applications for White-nose Syndrome (WNS) research. In the future, the acoustic methods and data analysis used in this thesis could be used to compare migratory activity before and after WNS infection at individual caves, something that could be useful to local management agencies that are responsible for hibernacula and maternity sites. The newly documented gray bat movements, discovered through bat banding, also have applications for studying WNS, since the disease is likely spread from cave to cave via bat movement. The new banding data represent an expansion of what is known about the gray bat cave network in the state. Any future studies focusing on caves as a network through which WNS can spread

will be improved with the addition of these data. Accurate estimates of the network connectivity and cave vertex centrality require accurate inputs about the network itself.

Future work studying bat migration should take advantage of the many remote monitoring methods that are available. Bat detectors are an efficient way to compare activities over time, and advances in radio telemetry technology now allow for remote monitoring of the movements of individual bats tagged with transmitters. There are also promising reports of using NEXRAD weather radar to study bat movements. Some species of bats, such as the Brazilian free-tailed bat, are regularly picked up on weather radar due to their large colonies and rapid emergences at sunset. At least 1 major gray bat maternity cave was discovered due to bat activity at emergence that was picked up on weather radar. Using remote sensing techniques and available NEXRAD data, we could gain inexpensive and practical knowledge about seasonal bat activity and migratory patterns. Using reflectance values from radar sites could be another method, like acoustic monitoring, for monitoring the shift in activity at cave sites due to migration. A combination of these methods, along with more traditional bat banding and hibernacula surveys, could create in-depth snapshots of yearly migration.

Gray bat migration is a complex subject and studying it requires addressing multiple spatial scales, from the individual banded bat, to the arrival of populations at each maternity cave, to the landscape of connected seasonal sites. I attempted to address this complex phenomenon with these spatial scales in mind, so that my data would add to and update the body of knowledge about the topic in Missouri and across the species' geographic range. Overall, this thesis asks the questions “when” and “where” gray bat migration happens. I developed a methodology so that in the future another question can

be addressed, the larger question of how gray bat movement affects bat conservation as a whole – how gray bat movement affects the spread of WNS, and how WNS affects gray bat migration.

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