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POPULATION DYNAMICS AND HABITAT USE BY GRAY BATS IN AN ANTHROPOGENICALLY ALTERED LANDSCAPE

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ANTHROPOGENICALLY ALTERED LANDSCAPE

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An Abstract of the Thesis by
Haley Price

Habitat loss resulting from land use change is among the greatest threats to biodiversity. Yet, in some cases imperiled wildlife species may benefit from anthropogenic disturbance. The expansion of urbanization, agriculture, renewable energy, and mining practices impact conservation efforts for threatened and endangered bat species, and particularly species that are affected by white nose syndrome (WNS). The federally endangered gray bat (*Myotis grisescens*) is a cavernicolous species that is susceptible to WNS. Due to their unique roosting and foraging requirements, gray bats inhabit a small portion of the accessible caves within their geographic range. As habitat loss persists, gray bats have been documented using anthropogenic structures in the absence of suitable, naturally occurring roosts. To better understand why gray bats select certain anthropogenic structures, we examined the population dynamics of a gray bat colony and their use of microclimate characteristics inside a stormwater system in southeast Kansas. We described changes in temperature and relative humidity inside the roost and performed capture-mark-recapture surveys to estimate within-season population dynamics. Temperatures within the primary roost sites were on average warmer than outside temperatures, and relative humidity was consistently higher and more stable inside the roost than outside. We also used acoustic surveys and occupancy models to evaluate the effects of landscape composition, vegetation structure, and food availability on gray bat habitat use. The best-supported occupancy models showed a negative

association with percent agriculture cover and distance from the roost site, and a positive association with canopy density, percent developed and forest cover. The stable microclimate inside the stormwater system likely provided the energetic benefits necessary for female gray bats to produce offspring. The anthropogenically altered landscape, including disturbance from surface mining, likely created the roosting and foraging habitat required for gray bats. The value of abandoned mined lands and other disturbed ecosystems should be considered when developing conservation strategies for imperiled species.

KEYWORDS: gray bats, *Myotis grisescens*, microclimate, habitat use, population, white nose syndrome

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CHAPTER I

POPULATION DYNAMICS AND MICROCLIMATE

CHARACTERISTICS OF AN ANTHROPOGENIC GRAY BAT ROOST

ABSTRACT

We estimated colony size and composition of the only known colony of gray bats

in Kansas for an annual cycle to better understand the population structure and reasons

for roost use. From May to August 2022, we performed monthly mark-recapture surveys

to determine sex, age, reproductive status, and abundance of the gray bat colony.

Temperature and relative humidity data were also recorded within the stormwater system

in 2019. We detected significant fluctuations in colony size and sex ratios that were likely

caused by births and the immigration of a bachelor colony in the late summer. Mean

temperatures within the primary maternity roost were warmer than outside temperatures

from May to November, and relative humidity was consistently high. A secondary roost

site showed mean temperatures to be cooler than outside temperatures until September.

The stormwater system served as a maternity colony in the summer, and potentially as a

transitional roost for males and females in the late summer and early fall. We suggest that

anthropogenic structures may play an important role in providing suitable roosting habitat

in the absence of cave systems for gray bats. Documenting seasonal population dynamics

of gray bats may provide useful information to better understand population trends through reproductive periods and give insight regarding the value of anthropogenic roosts for bat conservation.

INTRODUCTION

Bat populations have experienced global declines primarily due to habitat loss and fragmentation resulting from changes in land cover and use (e.g., urbanization), and more recently, from diseases such as white-nose syndrome (Frick et al., 2016, 2020). Challenges posed by urbanization can be particularly detrimental to habitat specialists, whereas habitat generalists may be less affected. However, as habitat loss and fragmentation persist, the availability of anthropogenic roost structures has become increasingly important for many species (Donovan et al., 2005; Russo and Ancillotto, 2015; Thomas and Jung, 2019; Webb et al., 2021). Structures such as buildings, bridges, and tunnels may provide habitat that mimics the structural complexity and microclimate conditions of cave systems or cliffs, but the availability of these structures may not be adequate for species with specific roosting requirements (Russo and Acillotto, 2015). Even if roosting habitat for specialists is available in urban areas, barriers such as urban sprawl may force bats to travel farther to reach foraging habitat (Jung and Threlfall, 2016; Threlfall et al., 2012). Therefore, understanding the use of anthropogenic roosts could inform conservation of bat populations in anthropogenically-altered landscapes.

Gray bats (*Myotis grisescens*) are a federally endangered cavernicolous species found in the limestone karst region of central and eastern North America, with range

corners in Georgia, Illinois, Indiana, Florida, and Kansas. The majority of the population

hibernates in 9 to 15 caves within their geographic range (Fig. 1.1; Hill and Smith, 1984).

Due to the gray bats' selective roosting preferences, they occupy approximately 5.0% of

the available caves within their range (Hill and Smith, 1984; Tuttle, 1979). Roost types

vary depending on purpose and time of year. Reproductive female gray bats in particular

require a narrow range of microclimate conditions to maintain thermo-neutrality with

lower energetic costs (Tuttle, 1976b).

While gray bats are typically associated with cave systems, several colonies have

been documented using human structures with cave-like features including dams (Lamb,

2000; Wyckoff, 2006), stormwater systems (Decher and Choate, 1989; Harvey, 1988;

Hays and Bingham, 1964; Long, 1961), and bridges (Barbour and Davis, 1969; Etchison

and Weber, 2020; Martin, 2007; Sasse, 2019). The use of stormwater systems and other

similar structures has increased as habitat loss continues to increase (Hoye and Spence,

2004). The length, spatial complexity, reduced light, and stable microclimate of these

anthropogenic roosts have created suitable roosting environments for gray bats

(Meierhofer et al., 2019; Katzenmeyer, 2016). These structures may also pose risks to

bats. For example, human disturbance, repeated flooding events, pollution, and predation

may result in high mortality in anthropogenic structures (Fenton et al., 1994; Hoye and

Spence, 2004; Russo and Ancillotto, 2015). However, anthropogenic structures may

provide suitable roosting sites in regions where limited cave systems exist, or where

natural cave systems are positive for the fungal pathogen *Pseudogymnoascus destructans*

(Pd). In some cases, anthropogenic roost structures may expand the geographic range of

bat species into areas with few available cave systems (Ancillotto et al., 2018; McCracken et al., 2018).

In addition to the threats posed by urbanization and other forms of land use change, emergent diseases have caused further declines of bat populations in North America. For instance, white-nose syndrome (WNS), caused by the introduction of Pd to North America in 2006, has led to further declines in bat populations across much of eastern and parts of western North America (Coleman, 2014; Maslo et al., 2015). WNS has affected 13 species of bats, and has inflicted high mortality rates (>90%) in the little brown bat (*Myotis lucifugus*), the northern long-eared bat (*Myotis septentrionalis*), and the tricolored bat (*Perimyotis subflavus*) (Cheng et al., 2021). The tendency of gray bats to hibernate at high densities in a small number of caves may make them more susceptible to WNS (Frick et al., 2017; Langwig et al., 2015). However, while WNS has been documented in gray bats since 2012, they have not experienced mortality rates similar to other Myotis species (Jackson et al., 2022; Powers et al., 2016). It is possible that migrating gray bats have contributed to the spread of Pd among cave systems because their clustering behavior during hibernation may increase bat-to-bat transmission (Boratynski et al., 2015; Boyles et al., 2008; Gilbert et al., 2010; Martínková et al., 2020).

The spread of WNS among gray bats and other cave-roosting bat species may be mitigated by physical conditions within the roost. For example, Pd spores and mycelium cannot persist in air temperatures above 16°C and relative humidity greater thatn 81% (Verant et al., 2012). Summer roosts may provide refugia from Pd if temperatures are consistently above the temperature range for the fungus to grow, allowing bats to recover from infection. Air temperatures reported from gray bat maternity colonies range from 14

to 25°C, which indicates that the fungus is less likely to persist in summer roosts (Tuttle, 1976b; Tuttle and Stevenson, 1978).

This study aimed to examine seasonal population dynamics and roost site characteristics of a gray bat colony in an anthropogenic roost system at the periphery of their geographic range. We estimated bat abundance, age structure, and sex ratios using mark-recapture models and exit counts, and we described seasonal microclimates within the roost. We then compared findings to those reported in naturally occurring cave systems. Anthropogenic structures may serve as alternative roosting habitat for cave-dwelling bats if these structures provide the required narrow range of microclimates and potential protection from Pd exposure.

METHODS

Study Area

Our study focused on a known gray bat colony in southeastern Kansas (Fig. 1.1). The colony was discovered in the 1960s in the Pittsburg, Kansas stormwater system. The stormwater system is a variable network of tunnels that has multiple entrances and three known roosting locations that the colony switches among depending on time of year. A small number of gray bats and tricolored bats (*Perimyotis subflavus*) also use it during winter. The stormwater system is approximately 1.5 to 2 m in height 2 to 2.5 m in width. It is occasionally flooded during heavy rainfall events. The original stormwater system is over 100 years old, but system repairs began in 2003 (City of Pittsburg, 2023). Original sections of the system consist of brick and mortar, but newer sections were made with reinforced concrete. The interior roost and opening adjacent roost sites are approximately 884 m and 152 m, respectively, from the entrance of the stormwater system.

Sampling

We captured bats in 2022 using a single harp trap placed at the entrance of the stormwater system. We captured bats during the early summer (May/June) and late summer (July/August) when juvenile bats were first volant. Sampling periods consisted of four nights each month beginning at sunset and continued for two hours after the first capture. For each capture, we recorded the mass, sex, age (juvenile or adult), and reproductive status, and marked the bat with aluminum bands. We determined age by examining the ossification of the interphalangeal discs of the wings. Bats were considered juveniles when the joints were not yet ossified, and adults when their joints were ossified (Anthony, 1988). Reproductive status was determined based on external morphology. Females were classified as pregnant, lactating, post-lactating, or unknown when none of the characteristics of pregnancy were present. Males were classified as non-reproductive or reproductive based on descended testes (Llaven-Marcias et al., 2021).

Emergence Counts

We performed emergence counts via video recording with infrared lights in 2019 (Thorton, 1991). We recorded emergence videos at both the interior roost and opening adjacent roost sites to document changes in activity and population size throughout the year. Recording started at sunset and ended when either a bat was not seen exiting for 5 minutes, or when bats were entering and exiting in similar numbers (Elliott et al., 2005). Videos were later processed, and estimates were compared to those from mark-recapture models.

Temperature and Relative Humidity

We collected microclimate data within the stormwater system using Thermochron iButtons and HOBO pro series data loggers. These devices were affixed to the ceiling and side walls of the stormwater system at 30-m and 152-m intervals, respectively, in accessible locations that were used by bats for roosting or traveling to and from entrances. To avoid disturbance of the colony, the equipment was placed either at night or during the winter when minimal bats were present. Temperature data were recorded every 210 minutes and later summarized by distance and season for comparison to published data from naturally occurring roosts.

Statistical Analysis

To characterize seasonal population trends throughout the study period, we created encounter histories based on months of the year when individuals were captured. There were four encounter periods in 2022. Using the robust design method, we structured the data into monthly intervals to allow for multiple recapture occasions throughout the summer. The repeated samples within monthly intervals improved estimates of detectability by season (Kendall and Pollock, 1992). Because the colony size increased through births and immigration during the study period, we considered the population to be open. Therefore, we used Jolly-Seber (JS) models to analyze apparent survival (Phi), detection probability (p), super population (N; the total number of individuals available to enter the study), and the probability of new individuals from the super population entering through births and immigration (pent) (Jolly, 1965; Seber, 1965). Since the colony is known to be smaller, and we knew where the bats were emerging each night, we only used time as a covariate when modeling for Phi, p, and

pent. We used the best-supported informative models for estimating total abundance over capture events (Table 1.1). To compare sex and age ratios, we generated two seasonal categories: early summer (May and June), and late summer (July and August). We used $\chi 2$ contingency tables to compare estimated seasonal categories (Green and Robbins, 2020).

RESULTS

We captured 561 bats (379 male, 182 female) in the summer of 2022. The best-supported model for population estimates over time (May – August) included apparent survival over time, constant detection probability, probability of entry over time, and constant superpopulation (Table 1.1). Population estimates increased by 421.14% from early to late summer (Fig. 1.2). We also found differences in sex ratios between early and late summer 2021 and 2022. The proportion of females to males was higher compared to late summer ($\chi^2 = 49.24$, df = 1, $P < 0.001$; Fig. 1.3). Age ratios between early and late summer differed as juveniles became volant in July, but the overall ratio between the two ages did not change ($\chi^2 = 16.67$, df = 1, $P < 0.001$; Fig. 1.4). Adults remained more abundant than juveniles throughout the summer.

Abundance indices from the video exit counts were slightly lower, but similar to estimates from mark-recapture models (Fig. 1.2). Abundance indices increased by 762.73% from early to late summer 2019. Estimates were similar to those from the population estimates from the Jolly-Seber models. We observed a maximum of 1,524 bats exiting the stormwater system by late September. Bats regularly switched roosts between the interior and opening adjacent roost sites during the months of September and October, prior to migrating to winter hibernacula.

Air temperatures within the stormwater system varied spatially and temporally throughout the summer months. Daily roost temperatures at the interior roost site were more stable than outside temperatures collected at the entrance of the stormwater system (Fig. 1.5). Mean outside temperatures from April to November ranged from 7 – 24°C. Interior roost site temperatures reached a maximum of 29°C during the month of July. Mean interior roost temperatures from April to August were on average 3 – 14% warmer than average monthly outside temperatures. Mean roost temperatures from September to November averaged between 5 – 55% warmer than monthly outside temperatures. Relative humidity was consistently high throughout the summer at the roost site as data loggers often recorded maximum saturation (100%; Fig. 1.5). Mean roost temperatures at the opening adjacent roost site from April to August were on average 4 – 11% cooler than outside temperatures, and from September to November the roost site was on average between 5 – 41% warmer (Fig. 1.5). Temperatures at the opening adjacent roost site reached a maximum of 23°C in September and 22.5°C in October when the colony occupied the site.

DISCUSSION

Population estimates of gray bats in the Pittsburg stormwater system showed a large increase in 2022, likely indicating that the colony experiences fluctuations due to seasonal migration (Green and Robbins, 2020; Robertson, 2003; Timmerman and McDaniel, 1992). Population estimates showed a decrease in population during the month of June, which could be an artifact of trap avoidance. Pregnant female gray bats give birth during late May through early June, which could have caused more cautious

behavior to avoid unnecessary energy loss. The stormwater system also had multiple

openings through which bats may enter and exit, causing a lower capture rate.

During the summer of 2022, we saw a male to female ratio of 1:1.47, indicating

that males were also present with the maternity colony. We did not capture any juveniles

during the early summer, so all captured males were adults, born in 2021. One study of

gray bats in Missouri, Oklahoma, Arkansas, and Kansas found that there was never

complete isolation of the sexes, which is consistent with our results (Elder and Gunier,

1978). The sex ratio that we found was slightly more male-skewed compared to Elder

and Gunier (1978), which could be due to the small sample size in May and June, or

perhaps trap avoidance by pregnant and/or lactating females. We also performed capture-

mark-recapture surveys during the latter half of each month, when more immigrating

males may have been present. The large increase in population size during July and

August is consistent with seasonal immigration by a bachelor colony. During this time,

the sex ratio changed from female-skewed to male-skewed (Fig. 1.3). The male-skewed

sex ratio in the late summer may be associated with behavioral factors. Bachelor colonies

may rejoin during August to October prior to transitioning to winter caves to increase

their chances of reproduction (Green and Robbins, 2020). Many bat species exhibit

swarming behaviors for the purposes of reproduction prior to hibernation with males

typically outnumbering females in trapping surveys (Furmankiewicz, 2008; Parsons et

al., 2003; Rivers et al., 2006). Gray bat bachelor colonies are also known to have multiple

roost sites throughout the summer and can roost switch after offspring become volant

(Tuttle, 1979; Tuttle and Stevenson, 1978). The bachelor colony in our study area could

be arriving in late summer to take advantage of the stormwater system's proximity to the

water features created by surface mining within the region (i.e., strip pits) for foraging purposes (Ancillotto et al., 2019; Moore et al., 2017; Chapter II). The observed late-season increase in males could also be associated with migration. The highest abundance of gray bats occurred shortly prior to the colony migrating to winter hibernacula. This pattern could indicate that the stormwater system may serve as a transitional roost between summer and winter caves (Elder and Guneir, 1978; Timmerman and McDaniel, 1992).

Abundance indices may be a suitable alternative to statistical modeling when data are limited or when there are logistical constraints on sampling (McKelvey and Pearson, 2001). Our emergence counts showed a similar trend to the mark-recapture model estimates, with an increase in population size from June to August from births and immigration. Emergence counts were also able to show population trends after our mark-recapture sampling period had concluded in August, including late-season changes in abundance and roost switching between the interior and opening adjacent roost sites. Infrared video recordings are a non-invasive alternative for censusing roosts, though the ability to obtain accurate estimates is variable and dependent upon the size of the colony and sampling effort (Kunz, 2003; McCracken, 2003). Emergence recordings likely worked well for our study because the maximum population is estimated to be maximum less than 2,000 individuals.

The microclimate characteristics in the roost overlapped those of naturally occurring maternity caves. Average primary roost site temperatures during the months of May to August were within or above average temperatures documented in natural maternity caves, and stable compared to outside temperatures (Fig. 1.6; Tuttle 1976b).

Female gray bats select maternity roosts with microclimates that are higher in temperature and relative humidity because maternal body temperature is correlated to fetal development (Racey and Swift, 1981). The stormwater system likely met the temperature requirements necessary to be a viable alternative to natural maternity roosts, and may provide thermoregulatory energy savings during reproductive periods (Sedgeley, 2001; Speakman and Thomas, 2003). Portions of the stormwater system used by the maternity colony included domed areas with a high ceiling located directly below a parking lot. These locations included the warmest temperatures recorded during the study. Thus, artificial conditions resulting from land use change may benefit bats in some cases.

In addition to providing a maternity roost, our results indicate that the stormwater system may also be a suitable transient habitat due to the lack of suitable roosting habitat prior to reaching winter hibernacula. Gray bats become more transient after offspring are volant, and colonies will often using alternate roost sites (Thomas and Best, 2000; Tuttle, 1976a). The gray bats in our study primarily used the opening adjacent roost site after the maternity and bachelor colonies joined and prior to migrating to winter hibernacula. Average roost temperatures at this site were characteristic of transient roost sites reported elsewhere, i.e., cooler than the primary maternity roost site, but warmer than documented winter hibernacula, which may energetically benefit juveniles during migration (Hall, 1982; Neubaum, 2006, 2018; Speakman and Thomas, 2003; Tuttle, 1976b). Unlike gray bat winter hibernacula, the stormwater system is not suitable as a winter roost because the low domed structure of the tunnels prevents large volumes of cold air to accumulate (5 – 11°C; Tuttle, 1979).

High relative humidity has also been considered an important factor in roost selection for reproductive female gray bats. Streams warmed by outside air temperatures that flow through naturally occurring caves contribute to warming cave temperatures, thereby influencing gray bat roost selection (Perry, 2013; Tuttle and Stevenson, 1978). High relative humidity in both summer and winter roosts, in addition to suitable temperature ranges, aid in the reduction of evaporative water loss. Evaporative water loss caused by low relative humidity at roost sites can lead to a loss in body mass over time (Baudinette et al., 2000; Herreid and Schmidt-Nielsen, 1966; Thomas and Cloutier, 1992; Webb et al., 1995). Low relative humidity is especially high risk for reproductive female bats that experience added water loss through lactation (Adams and Hayes, 2008; Jonasson and Willis, 2011). The increased water efflux indicates that higher humidity in maternity roosts and a close proximity to water are likely to help offset water loss for reproductive females (Kurta et al., 1990).

CONCLUSIONS

Gray bats are a federally endangered species whose recovery depends on protection of critical roosting habitat. Anthropogenic structures such as the Pittsburg stormwater system can meet the habitat requirements of gray bats during summer, including for a maternity colony, juveniles, and a transient bachelor colony. The population dynamics of the Pittsburg colony are similar to historical estimates following its discovery in the 1960s (Hays and Bingham, 1964; Decher and Choate, 1988, Robertson, 2003). The warmer and more stable temperatures, high relative humidity, and close proximity to foraging sites have likely allowed gray bats to persist in the region, which is absent of natural caves. To successfully manage bats' increased use of

anthropogenic structures, conservation will likely need to consider species-specific seasonal roost selection. Managers should be aware of the potential benefits the microclimate of anthropogenic structures, such as the Pittsburg stormwater system, provide in lieu of adequate roosting habitat. However, stormwater systems may also expose bats to heightened risks, including disturbance by humans, floods, pollution, and predators. Considering the rarity of gray bats in the region, it may be effective to manage the stormwater system for the gray bat because the success of the maternity colony is dependent upon suitable roosting habitat for producing offspring (Tuttle, 1976b). Future work should continue to document use of anthropogenic structures by gray bats and other imperiled species. Special consideration should be given to the potential for these structures to provide protection from WNS. We also suggest the continuation of capture-mark-recapture surveys in southeast Kansas to create a longer capture history that permits stronger estimates of population size over time. Additional demographic information will provide guidance on protecting the health and persistence of threatened and endangered species like the gray bat. Potential use of anthropogenic structures should be considered when developing recovery plans for bats.

Table 1.1. The number of parameters (K), Akaike's Information Criterion (AIC), delta AIC (ΔAIC), AIC weight (Wt), and cumulative weight (Wt), for candidate models used to estimate population size of the Pittsburg gray bat colony in southeast Kansas, USA, 2022. Models include covariates affecting the probability of apparent survival (Phi), detection probability (p), probability of new individuals from the super population entering at time t (pent), and superpopulation (N).

Model	K	AIC	ΔAIC	Wt
Phi(~time)p(~1)pent(~time)N(~1)	8	220.66	0.00	0.81
Phi(~1)p(~time)pent(~time)N(~1)	9	225.79	5.14	0.06
Phi(~time)p(~time)pent(~time)N(~1)	11	226.17	5.52	0.05
Phi(~1)p(~time)pent(~1)N(~1)	7	226.29	5.63	0.05
Phi(~time)p(~1)pent(~1)N(~1)	6	260.09	39.43	0.00
Phi(~1)p(~1)pent(~time)N(~1)	6	268.31	47.65	0.00
Phi(~1)p(~1)pent(~1)N(~1)	4	313.81	93.16	0.00
Phi(~time)p(~time)pent(~1)N(~1)	9	389.99	169.34	0.00
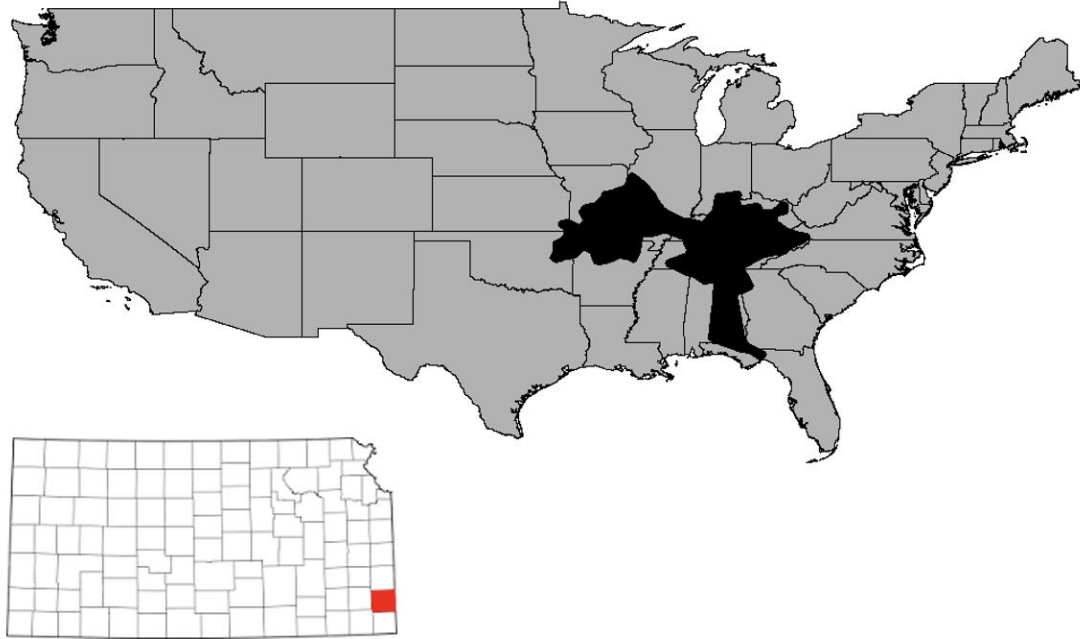
Fig. 1.1. Geographic range of *Myotis grisescens*, occupying the eastern karst regions of states indicated within the boundary (Tennessee Bat Working Group), and the peripheral limits of their range in Crawford county, Kansas (highlighted in red).
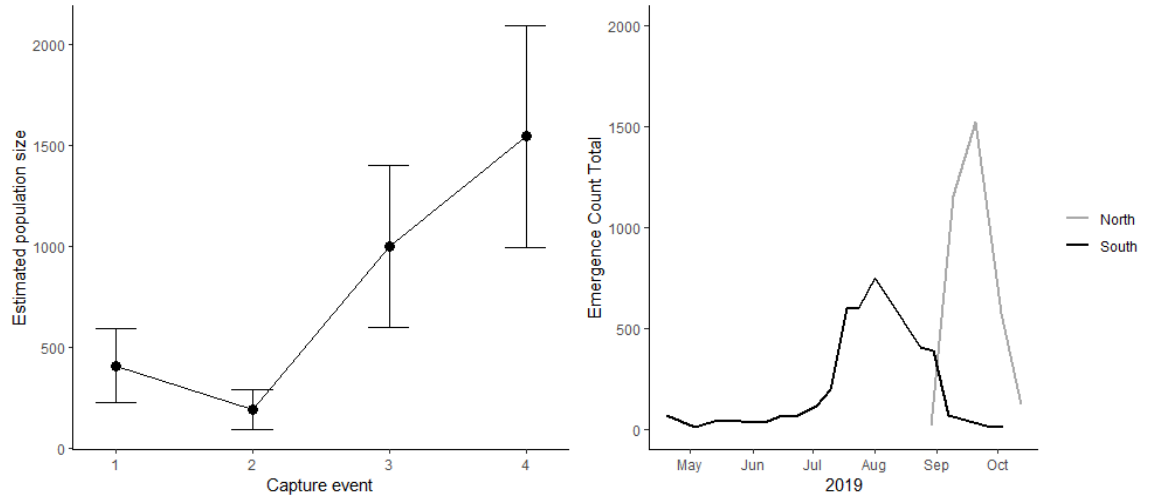
Fig. 1.2. Population estimates over four capture events from May to August 2022 with 95% confidence intervals (left) and emergence counts from April to October 2019 (right).
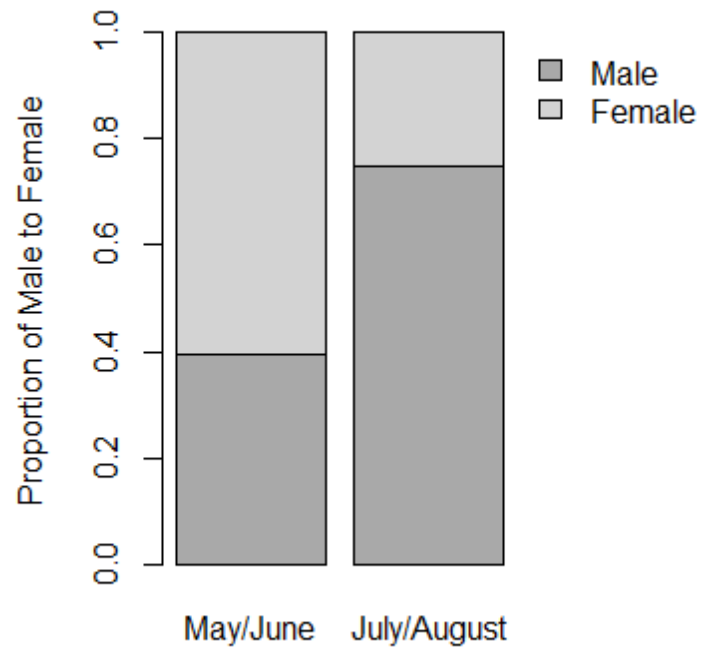
Fig. 1.3. Male (dark gray) to female (light gray) sex ratios of gray bats from May and June to July and August 2022 ($\chi^2 = 49.24$, df = 1, $P < 0.001$).
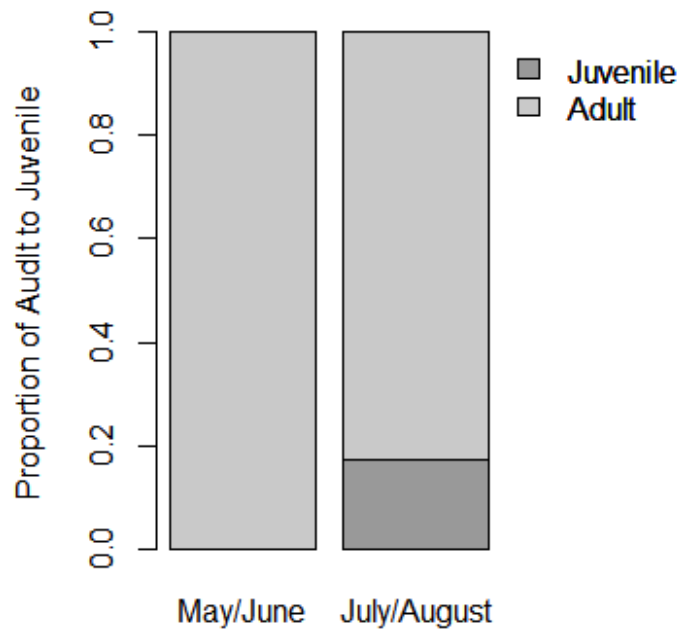
Fig. 1.4. Adult (light gray) to juvenile (dark gray) age ratio of gray bats from May and June to July and August 2022 ($\chi^2 = 16.67$, df = 1, $P < 0.001$).
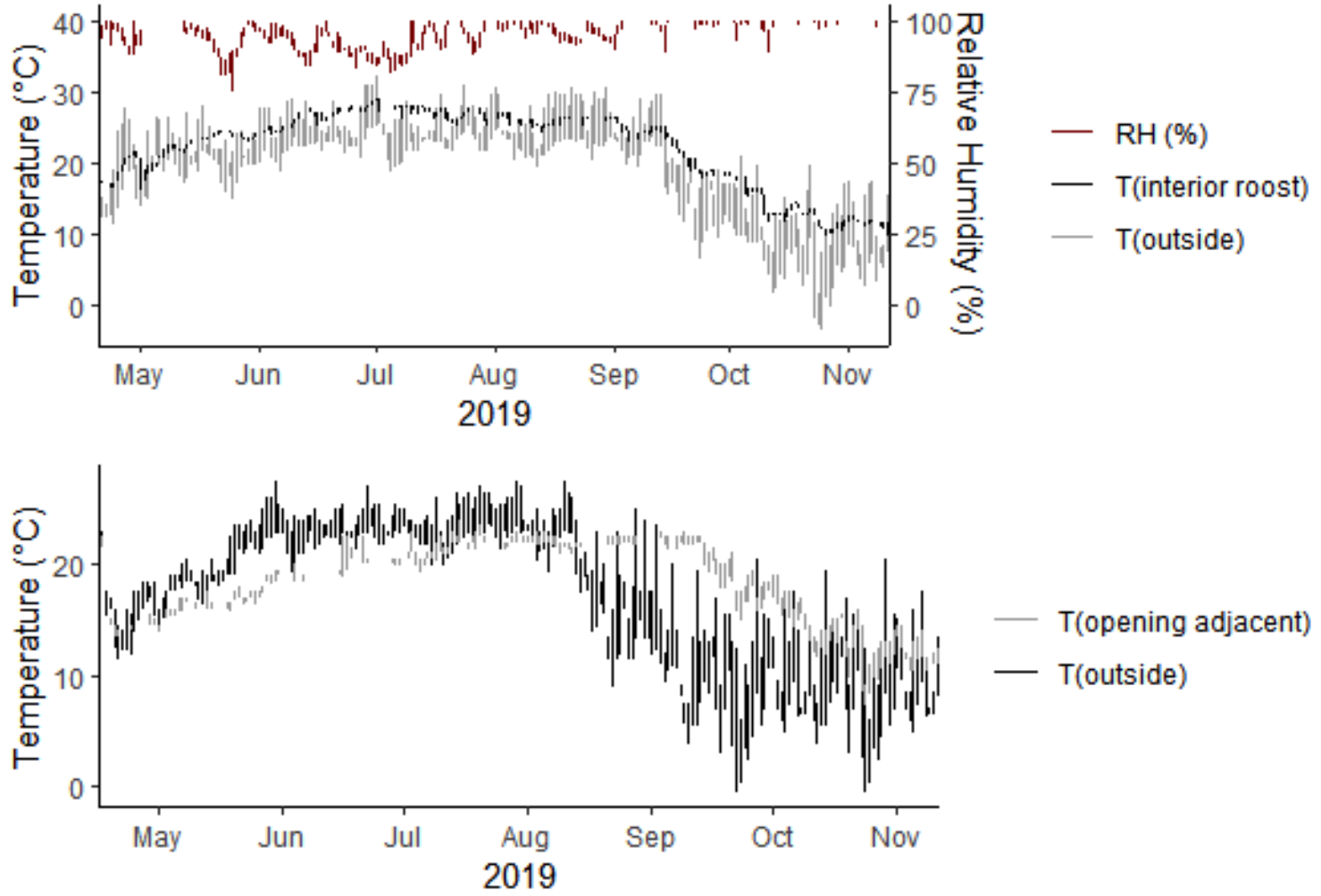
Fig. 1.5. Outside temperature vs. interior roost site temperature (°C) and relative humidity (RH, %) (above), and outside vs. opening adjacent roost site temperatures (°C) in the Pittsburg stormwater system, Crawford County, Kansas.

CHAPTER II

HABITAT USE BY THE GRAY BAT IN AN

ANTHROPOGENICALLLY ALTERED LANDSCAPE

ABSTRACT

Knowledge of habitat use by bats in an anthropogenically altered landscape is vital for effective conservation. Our objective was to examine relationships between gray bat site occupancy, landscape composition, vegetation structure, and food availability in an area that has experienced heavy land use change from its historical native prairies. We used acoustic detectors to survey bats in southeast Kansas during the summers of 2021 and 2022. We fit single-season occupancy models to estimate detection probability and site occupancy at multiple scales. We compared *a priori* hypotheses within an information theoretic approach by evaluating support for candidate models that included landscape and habitat covariates. Site occupancy of gray bats at the landscape scale was negatively associated with agriculture cover and distance from the primary roost site. Site occupancy on the habitat scale was positively associated with canopy density, and negatively associated with distance from the roost site. Models with food availability were not well-supported. We found larger effect sizes for habitat-scale relationships than for landscape-scale relationships. Thus, recovery plans should consider small-scale

patterns in vegetation structure in addition to spatial arrangement of landscape features in proximity to roost habitat.

INTRODUCTION

Habitat loss and fragmentation are among the leading causes of global declines in bat populations. It is therefore important to understand habitat use to inform conservation strategies in rapidly changing landscapes. Most bat species in eastern and central North America rely on forests to meet energy and roosting requirements, and a lack of continuous forest cover can have negative effects on bat presence and abundance (Ford et al., 2005; Krusic et al., 1996; Watling et al., 2020). Land use changes such as urbanization, deforestation, and agricultural development can negatively affect the amount of roosting and foraging habitat that is available, and the expansion of agriculture and urbanization are predicted to continue to negatively impact bat habitat (Blary et al., 2021; Frick et al., 2020). On a finer scale, loss of habitat structure and prey availability via human activity have also negatively affected bat occupancy (Bender et al., 2021; Ellerbrok et al., 2022; Froidevaux et al., 2021). For many species, habitat loss and fragmentation not only decrease the amount and quality of roost sites, but also water sources and insect abundance (Fenton and Bogdanowicz, 2002; Froidevaux et al., 2021; Gallagher et al., 2021; Lacki et al., 2007; Norberg and Rayner, 1987; Ober and Hayes, 2008).

While land use change is generally considered to have negative effects on biodiversity, the response of bats to anthropogenic alterations on the landscape are more nuanced than previously understood (Blary et al., 2021; Henderson et al., 2008; Kalda et al., 2015; Kitzes and Merenlender, 2014; Mena et al., 2022; Olivier et al., 2020). Bat occupancy and activity may vary across a gradient of landcover types with varying degrees of human disturbance (Meramo et al., 2022). Bat occupancy and activity are not considered to be homogenous across human disturbed landscapes and are more dependent on species-specific behavioral and/or morphological characteristics (Jung and Trelfall, 2016, 2018; Meramo et al., 2022; Rodríguez-Aguilar et al., 2017). Urbanization is also widely considered to decrease bat diversity; however, some species increase in abundance near urban areas because buildings may provide the structural complexity necessary for roosting habitat and thermal stability through the urban heat island effect (Coleman and Barclay, 2012; Zhao et al., 2006). Therefore, a species-specific approach may be more appropriate for developing conservation strategies.

Surface mining is a particularly destructive process in which soil is removed by heavy equipment to extract belowground resources such as coal, thereby destroying entire communities. In some cases, surface mined areas are reclaimed, but many historically mined areas were abandoned to natural succession (Bailey and Hooey, 2017; Schneider, 1970; Welch and Hambleton, 1982). Prior to the development and implementation of the Surface Mining Control and Reclamation Act of 1977 (SMCRA), mined land sites were often left abandoned leading to sporadic succession at varying rates (Baily and Hooey, 2017). Multiple reclamation methods were used following the SMCRA, often producing diverse mosaics in formerly mined landscapes. Surface mining practices can lead to

habitat loss, poorer water quality, and decreased prey availability that may negatively affect bat populations (Boccardy et al., 1968; Feng et al., 2019; Schneider et al., 1970; Starnes et al., 1995; Visser et al., 1983; Welch and Hambleton, 1982). However, mining can also have positive effects on bat occupancy and abundance (Frick et al., 2020; Orimoloye et al., 2020; Theobald et al., 2020). For example, more than half of the 45 North American bat species have been documented using abandoned mines in the absence of caves during hibernation (Perry and Jordan, 2020; Tobin et al., 2018; Watkins, 2002). Abandoned mines used by bat populations are typically characterized by greater structural complexity, greater length, and warmer and more stable temperatures compared to other unoccupied mines (Kurta and Smith, 2014). Strip pits, i.e., water-filled trenches of varied depths produced from surface mining, may support aquatic insect populations that serve as a primary food source for bats. Reclamation efforts and natural succession of areas that experienced surface mining have led to afforestation and the creation of wetlands that increased soil quality and reduced erosion, resulting in complex habitats for many bat species and their prey (Hooey and Bailey, 2017; Lituma et al., 2021).

Gray bats are a year-round cave obligate that underwent range-wide population declines in the 1960s primarily caused by human disturbance in caves, though other factors including habitat loss and pesticide use contributed as well (Tuttle, 1979). After they were listed as federally endangered in 1976, a Recovery Plan was published in 1982 to help populations rebound. The use of cave gates reduced disturbance during critical reproductive periods and hibernation. The plan has been viewed as widely successful; population estimates in 2007 indicated that the population had grown from 293,600 in 1976 to 3.4 million gray bats in 2007 (Tuttle 1979; Martin 2007).

Due to gray bats' selective roosting preferences, they are restricted to approximately 5% of the available caves within their range, which makes understanding their habitat use important (Hill and Smith, 1984). Roost types vary depending on purpose and time of year. Gray bat maternity colonies typically roost in caves surrounded by forests and located near prime foraging habitat such as lakes, rivers, and large streams. Gray bats use forests for protection while flying to and from foraging sites. Forest habitat may be especially important to juveniles, which typically use forests during the first week of flight as they forage while their flight muscles develop (Tuttle, 1979). Open water with well-developed riparian vegetation is also known to be an important habitat requirement. Gray bats foraging primarily over open water and occasionally in riparian vegetation (LaVal et al., 1977; Moore et al., 2017; Tuttle, 1979). Juveniles may forage more commonly on coleopterans in forested areas compared to their adult counterparts. On a broader scale, gray bats may be selective feeders that respond to aquatic insect availability (Brack and LaVal, 2006). Foraging areas for gray bats are typically <1 km in length from roost locations and adjacent to heavily wooded areas with only a few individuals observed foraging in open grasslands (LaVal et al., 1977).

Whereas gray bats are typically associated with cave systems throughout their annual cycle, several colonies have also been documented using human structures with cave-like features. Gray bats can fly long distances to reach foraging sites (>70 km; LaVal et al., 1977; Moore et al., 2017), and they usually forage over open water such as rivers or reservoirs. However, the distance that adult females and newly volant young must travel between roosts and foraging areas may result in considerable fitness costs and ultimately determine whether colonies can persist (Rosenburg and McKelvey, 1999).

Thus, landscape composition, and specifically the spatial arrangement of foraging habitat relative to roosts, may affect gray bat occupancy. Gray bats consume a range of aquatic insects, primarily in the orders Coleoptera, Diptera, Ephemeroptera, Lepidoptera, and Trichoptera, so the availability of quality water sources is an important factor for foraging habitat (Best et al., 1997; Brack and LaVal, 2006; Lacki et al, 1995; Mitchell and Martin, 2002). The amount and type of insects consumed varies depending on the time of year as foraging habitat, insect phenology, and short life spans of insects determine species availability. Gray bats are opportunistic foragers that preferentially select moth, beetle, caddisfly, and mayfly species when available (Lacki et al., 1995; Feldhamer et al., 2009).

Our goal was to examine factors that affect the occurrence of gray bats in an anthropogenically disturbed landscape at the periphery of their geographic range. To accomplish this, we modeled site occupancy of gray bats in a region that has been modified by surface mining and agriculture from its historically prairie-dominated landscape. Our specific objectives were to evaluate support for relationships between occupancy and 1) landscape composition, 2) vegetation structure, and 3) prey availability of insect orders typically consumed by gray bats at each site. We predicted that gray bats would use features associated with abandoned mined lands. Specifically, we predicted that site occupancy would be positively related to vegetation structure, forest cover, and open water (LaVal et al. 1977; Moore et al. 2017; Ober and Hayes, 2008; Tuttle, 1976a, 1979). We also predicted that site occupancy would decrease with distance from the roost site early in the season because reproductive female gray bats and their newly volant young are central place foragers with limiting energy requirements (Moore et al., 2017; Rosenberg and McKelvey, 1999; Thomas and Best 2000). Finally, we predicted that site

occupancy would increase with increased biomass of insect orders commonly observed in gray bat diets. The lack of natural caves in our study area suggests that gray bats did not occur in the region historically. Thus, their persistence may depend on the region's mining history, and by proximity to an anthropogenic roost that mimics a cave. The ability of species such as gray bats to benefit from disturbed landscapes and anthropogenic structures may reflect their resilience from threats, such as white nose syndrome (WNS).

<div align="center">METHODS</div>

Study Area and Sites

We studied gray bat occupancy in the Cherokee Lowlands region of southeast Kansas and southwest Missouri (Fig. 2.1). This region is characterized by a flat, erosional topography, and it historically supported temperate prairie grasslands with mixed hardwood forest in riparian areas. Grasslands were dominated by warm-season bunchgrasses including big bluestem (*Andropogon gerardi*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*). Soils were fertile and derived from soft rocks, such as sandstone and shale with coal beds that lie beneath (Bailey and Hooey, 2017; Powell, 1972). Agricultural land was dominant within the study area including monocultures of corn, wheat, soybeans, and hay pasture for livestock (KDA, 2022). Water sources included Cow Creek, East Cow Creek, and the Spring River, and many man-made ponds.

Surface mining for coal began in the late 1800s and continued until the mid 1970s when the SMCRA was implemented. Mining heavily altered the native habitats and left more than 600 hectares of water, including deep, water-filled trenches (i.e. strip pits) and

<div align="center">27</div>

adjacent piles of overburden (soil removed to access coal beds) to a once relatively flat landscape (KDWP, 2023). Sporadic restoration efforts began on a limited number of sites after mining ended and continued to the present day. However, the majority of mined lands in the region were abandoned to be naturally vegetated which has led to a gradient of habitat types such as grasslands, shrublands, and woodlands with varying soil quality (Bailey and Hooey, 2017). Many sites were dominated by exotic shrubs including autumn olive (*Elaeagnus umbellata*), bush honeysuckle (*Lonicera maackii*), sericia lespedeza (*Lespedeza cuneata*), and privet (*Ligustrum spp.*). Common native tree species on revegetated mine lands included shagbark hickory (*Carya ovata*), bitternut hickory (*Carya cordiformis*), bur oak (*Quercus macrocarpa*), pin oak (*Quercus palustris*), and black walnut (*Juglans nigra*) (KDWP, 2023). The study region's topography and soils differ from the limestone karst that characterizes the Ozark Plateau and portions of the Central Hardwood region where the majority of the gray bat populations occurs (Hill and Smith, 1984). The limestone karst region contains numerous sinkholes, underground streams, and caverns created by rainwater that permeates through the limestone and erodes it over time. Naturally occurring caves such as those used by gray bats during summer are largely absent from the Cherokee Lowlands. However, the development of the Pittsburg, KS, stormwater system in the early 20th century, afforestation of abandoned mine lands, and the abundance of water sources (i.e., strip pits, man-made ponds, and the Spring River, etc.) have provided conditions that may mimic habitats preferred by gray bats inside their geographic range (Tuttle, 1976a). We identified 32 study sites with varying mining histories, from intensive mining and restoration to no mining history.

Study sites included habitats that were representative of the study area (e.g., forest edges, riparian, grasslands), and were roughly proportional to the surrounding landscape.

Acoustic Surveys

We surveyed bats with either Wildlife Acoustics Song Meter Bat 3 (SM3) or Song Meter Mini Bat detectors. One sampling period consisted of four nights, and each site was surveyed twice between May and August 2021 and 2022. Song Meter Bat 3 detectors were placed on the ground with the microphone placed atop a 2-m pole. Song Meter Mini Bat detectors were attached to the top the 2-m pole because they were compact and had an internal microphone. Microphones were oriented upward and 45° toward the most open area at each site to exclude as much vegetation clutter and insect noise as possible. We calibrated the sensitivity of each detector to standardize the sample rate, distance sampled, trigger frequency and window, and maximum recording length (Larson and Hayes, 2000; Livengood, 2003; Neece et al., 2018). Recording began 30 minutes before sunset and ended 30 minutes after sunrise. We removed the detectors after 4 nights and processed echolocation calls with Kaleidoscope Pro 5.4.9. We used conservative digital filters to sort outside noise, low-quality sequences, and sequences with <3 pulses. We then manually verified all remaining call sequences. Species were identified using call characteristics such as minimum frequency (minF), characteristic frequency (Fc), characteristic slope (Sc), and duration (dur). We created detection histories for each site by assigning 1 to a sampling period when a species was detected and 0 when a species was not detected (Weller, 2008; Yates and Muzika 2006).

Landscape, Vegetation, and Weather Measurements

To characterize landscape composition, we extracted landcover metrics for each sampling location from the 2019 National Landcover Database (NLCD). We calculated percent area of agriculture, forest, open, and developed landcover within a 1 km buffer around each survey point. Statewide hydrography layers from the National Wetland Inventory (NWI) were also used to determine percent area of wetland and open water (Table 2.1). We determined distance to the roost site by measuring distance in kilometers via Google Earth. To characterize the local vegetation structure at each site, we calculated the density of small stems/ha by counting the trees with a DBH <2.5 cm and 0.5 m tall in a 10-m radius around the survey point. We calculated tree stems/ha of all trees >2.5 cm DBH (Starbuck et al., 2015). We used a 10-factor prism at each site to calculate basal area. We estimated canopy density using a densiometer (Strickler, 1959). Weather data were compiled from Weather Underground (weatherunderground.com) from stations closest to each site. We compiled maximums and minimums of temperatures (°F) and relative humidity (%), and total precipitation (inches) from hourly values during each sampling period.

Food availability

We collected insect samples in congruence with acoustic sampling to determine potential food availability for foraging gray bats. Insect light traps were deployed twice at each site both summers with at minimum 30 days between each sampling. The Bioquip light trap consisted of a battery-powered UV light tube placed above a collection container. Ethyl acetate was used as the killing agent for the insects collected. Traps were placed 50 m away from the acoustic detectors to reduce potential bias from attracting

insects to the detectors. We left the traps out for one night during each acoustic sampling period. Traps were placed at sunset and collected in the early morning (i.e. 0500 – 0700). Insects were identified to family and oven-dried before biomass was measured. We recorded biomass of insect orders previously documented in gray bat diets (Best et al., 1997; Brack and LaVal 2006; Lacki et al., 1995).

Statistical Analysis

We used single-season occupancy models to assess the relationships between site occupancy of gray bats and habitat covariates representing habitat structure, food availability, and landscape composition. We fit competing occupancy models following an information theoretic approach using the package unmarked 1.2.5 in the program R We treated each night as a separate sampling occasion and assumed bat populations to be closed to emigration and immigration during the sampling period because we sampled on consecutive nights during the same sampling period (MacKenzie et al., 2017). We evaluated continuous measures of vegetation structure and prey availability across sites with reclamation efforts from past surface mining, as well as sites with no history of surface mining. Sites with reclamation efforts were included because these areas represent habitat types managed for wildlife and recreation purposes. We included day of year, nightly maximums and minimums of temperatures and relative humidity, precipitation, and year as detection covariates in competing detection models. We evaluated occupancy patterns in two separate analyses addressing both landscape and local scales. The first candidate model set examined the relationships between occupancy and landscape composition derived from NLCD and NWI layers (Table 2.4). The second set examined habitat covariates representing vegetation measurements (Table 2.4). The

16 candidate models assessing the landscape covariates included additive combinations of all predictor variables and represented a priori hypothesis about relationships between gray bats and percent agriculture cover, forest cover, and open water. The 17 candidate models assessing the vegetation covariates included additive combinations of all predictor variables and represented a priori hypothesis about relationships between gray bats and vegetation characteristics and prey availability. Vegetation characteristics included basal area, stems per hectare, saplings per hectare, canopy density, and distance from the roost site. We used AICc to determine the best-supported detection covariates for the gray bat and included these in all subsequent models for estimating occupancy (Tables 2.1, 2.2). All continuous covariates were z-transformed prior to analysis. Correlated covariates ($r > 0.7$) were excluded from the same models. Because temporal replication was limited and we were not interested in turnover rates, we fit single season occupancy models with year as a fixed effect. These models considered occupancy of sites as independent and conditional upon the covariates in said models (Crum et al., 2017; Fuller et al., 2016; Linden and Roloff, 2013; Linden et al., 2017). Inferences were made from the best supported models using Akaike's Information Criteria and model weights. Informative models with ΔAIC <2 were considered supported (Anderson and Burnham, 2002; Arnold, 2010).

RESULTS

We surveyed 31 sites in 2021 and 2022. Two sites were excluded from the landcover analysis due to mechanical or battery failures in the detectors, and four sites were excluded from the habitat analysis due to detector or trap failure (2.2). We recorded 32,752 bat passes in 2021 and 41,774 passes in 2022 from 7 species of bats. We detected

gray bats at 60% of sites across eight nights of recording. Each year, gray bat detection increased in July and August after the immigration of a bachelor colony (Chapter I).

We found support for relationships between landcover and gray bat occupancy. The best-supported model for estimating detection included day of year, precipitation, and year (Tables 2.3, 2.4). There was no evidence for lack of fit in the global model for the landcover analysis ($\hat{c} = 0.9$, $P = 0.492$). The best-supported model for occupancy estimates using the landcover covariates included percent agriculture cover and distance from roost site (Table 2.3). Site occupancy decreased by 53.01% from 0 to 15% agriculture cover, and site occupancy decreased by 61.04% from 0 to 50-km distance from the roost site (Fig. 2.2). A model including percent developed and percent forest cover was marginally within 2 ΔAICc of the best model and showed weak, but positive effects on occupancy (Fig. 2.2). Percent open water cover did not significantly affect the probability of occupancy for gray bats (Table 2.3).

We also found support for relationships between habitat covariates and gray bat occupancy. There was no evidence for lack of fit in the global model for the habitat analysis ($\hat{c} = 1.21$, $P = 0.163$). The best-supported model for occupancy estimates included tree canopy density, (Table 2.4). Site occupancy increased 150% from 33-66% tree canopy density. A model including trees per hectare was within 2 ΔAICc units of the best model, and also showed weak but positive effects (Fig. 2.2). We did not find support for models with food availability, percent open water, or other landscape or vegetation covariates (Tables 2.3, 2.4).

DISCUSSION

Results from our study indicate that habitat use by gray bats is affected by factors at both the landscape and local scales. We documented gray bats using a heavily modified landscape at the periphery of their geographic range. As predicted, occupancy was related to landscape composition and local habitat features that may be shaped by past surface mining activities. We predicted that gray bats would have greater site occupancy at sites with greater cover of forest and open water. Multiple studies have found support for effects of land cover factors associated with forest on site occupancy of insectivorous bat species (Heim et al., 2015; Neece et al., 2018; Starbuck et al., 2015; Treitler et al., 2016). For example, migratory species like hoary bats (*Lasiurus cinereus*), silver-haired bats (*Lasionycteris noctivagans*), big free-tailed bats (*Nyctinomops macrotis*), and spotted bats (*Euderma maculatum*) may have higher rates of occupancy in higher densities of forest during summer months (Starbuck et al., 2022). Moreover, bat occupancy may be positively affected by forest edges at the landscape scale (Hogberg et al., 2002; Jantzen and Fenton, 2013; Kalcounis-Rueppell et al., 2013; Morris et al., 2010). Though weaker than expected, we found a positive relationship between occupancy and increased forest cover compared to previous studies of bat occupancy (Farrow and Broders, 2011; Froidevaux et al., 2021). Gray bat maternity colonies typically inhabit caves or cave-like systems surrounded by forests because trees provide protection for reproductive females while traveling to foraging locations, and for juveniles as they build strength during the first weeks of flight (Brack and LaVal, 2006; Tuttle, 1976b).

We did not find support for relationships between site occupancy and open water. Prior research has shown that gray bats are opportunistic feeders that primarily forage over large water bodies (Moore et al., 2017; Tuttle, 1976b; LaVal et al., 1977). The lack of an apparent association with open water may have resulted from the abundance of water within the study area from large streams and man-made ponds (i.e., strip pits and livestock ponds). Water is an important resource for the persistence of bat populations in urban settings (Ancillotto et al., 2019; Lehrer et al., 2021). The presence of the gray bat colony may be explained in part by the abandoned mined areas that provided increased closed canopy habitat and multiple water sources (strip pits, livestock ponds, artificial wetlands, etc.) for foraging purposes (Snyder, 2022; Stahlschmidt et al., 2012). Although open water did not appear to affect acoustic activity at the scale of our analysis, water is an important habitat factor in the central portion of gray bats' geographic range and should be considered when developing conservation management plans. We also found a weaker relationship between percent urban cover and gray bat occupancy. Site occupancy increased with percent urban landcover, but effects were small and may be attributed to the fact that the roost site is located within the stormwater system beneath the city of Pittsburg.

We found support for a negative relationship between agriculture cover and site occupancy. Gray bat occurrence decreased with percent agriculture cover within a 1 km buffer around points. Bats may avoid row crops because they are homogenous and have less insect abundance and diversity than forested areas (Monck-Whipp et al., 2018; Put et al., 2019). Several studies have found negative effects of the expansion of agricultural landscapes for bat species (Frey-Ehrenbold et al., 2013; Kaiser and o'Keefe, 2015; Neece

et al., 2018; Park, 2015). One such study examining habitat use of pregnant and lactating Indiana bats (*Myotis sodalis*) on multiple scales found that almost half of the tracked individuals selected forest and shrubland cover compared to agriculture cover, despite agricultural land consisting of over 50% of the landscape within 10 km (Womack et al., 2013). Others found that the presence of herbaceous buffers in agricultural land positively affected bat occupancy and abundance by creating an edge effect (Blary et al. 2021; Harris, 1988; Kalcounis-Rueppell et al., 2013; Kalda et al., 2015). Gray bats forage in mature forests near larger water bodies, so the riparian and forested areas associated with mined areas may essentially provide islands of habitat in an agriculture-dominated landscape.

We predicted that gray bats occupancy would decrease as distance from the primary maternity roost site increased. Our top model for the landcover analysis showed a negative relationship between occupancy of gray bats and distance from the roost site. The only known population of gray bats in the study region forms a maternity colony during May and June. A bachelor colony joins the roost later as the season progresses (Chapter I). Because reproductive female gray bats and their newly volant young are central place foragers with unique energy requirements, we expected occupancy to decrease as distance from the roost site increased during the summer months (Moore et al., 2017, Rosenberg and McKelvey, 1999; Thomas and Best 2000). Reproductive females can spend more than half their energy budgets foraging. While large foraging radii have been observed in gray bats, adult reproductive females typically travel between 1–4 km from roosts to foraging sites (LaVal et al., 1977; Rosenberg and McKelvey, 1999; Tuttle, 1976b). Our results support prior research on the foraging radii of gray bats

in the Pittsburg colony. Robertson (2003) estimated mean foraging distances based on sex and age, and found that adult males averaged 8.65 km, adult females averaged 12.35 km, and juveniles averaged 3.07 km (Robertson, 2003). Decher and Choate (1989) similarly found marked gray bats within 14.3 km of roost sites (Decher and Choate, 1989). More recently, an aerial telemetry study from the Ozark Plateau found that reproductive female gray bats have a larger foraging range than previously documented, in some cases >300 km^2 (Moore et al., 2017). The negative relationship between occupancy and distance to roost in our study could also be affected by a combination of several factors including insect abundance and habitat fragmentation through land use change. Female gray bats could be flying longer distances to forage if there is a lack of quality foraging habitat with low insect abundance surrounding maternity roosts, or if foraging habitat is fragmented by urbanization and agriculture (Moore et al., 2017; Olivier et al., 2020).

We found support for relationships between site occupancy and canopy density and trees per hectare. Multiple species, especially species found within the *Myotis* genus, are positively affected by increased canopy closure (Bailey et al., 2019; Ford et al., 2005; Womack et al., 2013). Gray bats in our study occurred primarily at sites with higher canopy density, and closer to the roost, which suggests that they use the closed canopy sites for commuting or foraging purposes. Our data is consistent with previous research on the Pittsburg gray bat colony which showed evidence of gray bats using riparian woodlands as flyways during early summer, and open water and densely vegetated floodplains in late summer (Decher and Choate, 1989). Riparian areas are considered to be important for bats and serve as water sources (Menzel et al., 2005; Racey, 1998). Our

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results also suggest that, similar to prior research on the Pittsburg colony, site occupancy in areas dominated by row crop agriculture and livestock pasture is greater in areas with greater tree density (Decher and Choate, 1989). Bat species in agricultural dominated landscapes benefit from the existence of hedgerows and a proximity to woodland, likely because differences in vegetation structure are also known affect food availability (Blary et al., 2021; Boughey et al., 2011; Carrasco-Rueda and Loiselle, 2020). The natural succession and reclamation efforts on the mined lands within the study area resulted in more closed canopies and greater tree density, providing the vegetation structure necessary for gray bats to forage during summer.

We found no support for relationships between occupancy of gray bats and prey availability. Reclaimed mined can provide new habitat for hundreds of insect species, but the persistence of insect populations is varied and dependent upon the method and quality of reclamation. Soil quality and heterogeneous vegetation structure are specifically important for providing insect habitat (Buchori et al., 2018; Ireland et al., 1994; Sugiarto et al., 2016). The mined lands in our study area were largely abandoned to spontaneous succession but a portion have received some technical restoration that has increased insect biomass that may provide the gray bats with sufficient food. However, we did not find clear relationships between site occupancy and biomass of aquatic insect orders. It is possible that gray bats in our study region may have a more varied diet in the central portion of their geographic ranges, or that insects were sufficiently abundant across the study area to meet their energy requirements.

CONCLUSIONS

Overall, we found landscape-scale effects on gray bat occupancy and provided baseline data which may be used to further evaluate gray bat habitat use and activity patterns at both landscape and habitat scales. The highly modified landscape and creation of a cave-like structure in a historically prairie-dominated landscape likely met the conditions required for a gray bat maternity colony. The strip pits and adjacent successional forests at the periphery of their geographic range may mimic the natural conditions preferred by gray bats in the Central Hardwoods region where they have historically occurred. Restoring areas that have experienced surface mining, either through reclamation efforts or through natural succession, could reduce forest fragmentation and increase habitat that has the structural features bats require for foraging and roosting purposes (Bailey and Hooey, 2017; Lituma et al., 2021). Future studies should further examine gray bat habitat relationships, for example, using radio telemetry to document specific foraging patterns and habitat use based on finer scale habitat measures. This information may facilitate habitat management in anthropogenic landscapes as habitat loss persists. Nevertheless, we provide evidence that a federally endangered bat species is potentially benefitting from a landscape that was heavily disturbed by surface mining. The value of disturbed ecosystems should be considered when developing recovery plans for imperiled species.

Table 2.1. Covariates used to analyze habitat use by gray bats in southeastern Kansas and Missouri, USA.

Covariate	Description
Agriculture	Cultivated land that comprises row crops or close-grown crops, hay fields or pasture use for cattle grazing
Developed	Impervious surfaces (buildings, houses, parking areas, and roads)
Forested	Deciduous or evergreen stands, either mixed or exclusive
Open	Prairie, herbaceous areas, barren land
Open Water	Lotic and lentic features (lakes, ponds, streams, and rivers)
Wetland	Undeveloped, herbaceous areas that are permanently or seasonally flooded
Average total insect biomass	Averaged mass of insect samples
Average trichopteran biomass	Averaged mass of trichopterans
Average lepidopteran biomass	Averaged mass of lepidopterans
Average coleoptera biomass	Averaged mass of coleopterans
Stems per hectare (ha)	Number of trees per hectare
Small stems per hectare (ha)	Number of saplings per hectare
Basal area	Total cross-sectional area of trees at breast height (1.3 m)
Canopy density (%)	Proportion of an area on the ground that is covered by the crown of trees (expressed in percentage)

Table 2.2. List of study sites, ownership, and year(s) sampled in a study of bat occupancy in southeast Kansas and Missouri, 2021–2022 .

Study Site	Ownership	X	Y	Year(s) Sampled
1	KDWP	37.423	-94.762	2021, 2022
3	KDWP	37.391	-94.777	2021, 2022
4	PSU	37.372	-94.781	2021, 2022
5	KDWP	37.321	-94.680	2021, 2022
6	KDWP	37.181	-94.644	2021, 2022
8	KDWP	37.437	-94.627	2021, 2022
11	MDC	37.429	-94.591	2021, 2022
13	MDC	37.459	-94.591	2021, 2022
14	MDC	37.505	-94.576	2021, 2022
15	KDWP	37.474	-94.701	2021, 2022
16	KDWP	37.618	-94.745	2022
17	PSU	37.349	-94.803	2021, 2022
19	MDC	37.451	-94.563	2021, 2022
21	City of Pittsburg	37.403	-94.710	2021, 2022
23	KDWP	37.234	-94.979	2021, 2022
24	KDWP	37.253	-94.824	2021, 2022
25	City of Pittsburg	37.454	-94.711	2021, 2022
26	KDWP	37.266	-94.922	2021, 2022
27	KDWP	37.061	-95.074	2021, 2022
28	KDWP	37.201	-95.048	2021, 2022
29	City of Pittsburg	37.423	-94.710	2021, 2022
30	KDWP	37.287	-94.772	2021, 2022
31	Private	37.357	-94.910	2021, 2022
32	Private	37.405	-94.730	2021, 2022
33	Public High School	37.408	-94.670	2021, 2022
34	City of Galena	37.041	-94.637	2021, 2022
35	Private	37.251	-94.649	2021, 2022
36	Private	37.134	-94.800	2021, 2022
37	City of Pittsburg	37.379	-94.708	2021, 2022
38	City of Arma	37.537	-94.713	2021
39	Private	37.509	-94.986	2021, 2022
40	Private	37.370	-94.590	2021, 2022

Table 2.3. The number of parameters (K), Akaike's Information Criterion (AICc), delta AICc (ΔAICc), AICc weight (AICc Wt), cumulative weight (Wt), and log likelihood (LL) for candidate models used to determine relationships between site occupancy for gray bats and landscape factors in the Kansas and Missouri, USA, 2021–2022. Models are composed of covariates affecting the probability a species occurred at a site (Ψ) and the probability of detecting a species, given it is present at a site (ρ). The detection covariates for all models include night, precipitation, and year.

Model	K	AICc	ΔAICc	AICc Wt	Wt	LL
Ψ (crop, distance)	7	431.56	0.00	1.00	0.16	-207.78
Ψ (crop)	6	431.71	0.15	0.93	0.15	-209.12
Ψ (distance)	6	432.03	0.47	0.79	0.13	-209.28
Ψ (distance, open water),	7	433.17	1.61	0.45	0.07	-208.59
Ψ (developed, forest)	7	433.51	1.95	0.38	0.06	-208.76
Ψ (crop, forest)	7	433.64	2.08	0.35	0.06	-208.82
Ψ (.)	5	433.66	2.10	0.35	0.06	-211.31
Ψ (developed, open water)	7	433.69	2.13	0.34	0.06	-208.85
Ψ (distance, forest)	7	433.97	2.41	0.30	0.05	-208.98
Ψ (crop, forest, distance)	8	433.99	2.43	0.30	0.05	-207.69
Ψ (crop, open water, distance)	8	434.00	2.44	0.30	0.05	-207.69
Ψ (open water, crop)	7	434.12	2.56	0.28	0.05	-209.06
Ψ (forest)	6	435.90	4.34	0.11	0.02	-211.21
Ψ (crop, open water, developed)	8	435.90	4.34	0.11	0.02	-208.64
Ψ (open water)	6	436.03	4.47	0.11	0.02	-211.28
Ψ (global)	11	443.29	11.73	0.00	0.00	-208.10

Table 2.4. The number of parameters (K), Akaike's Information Criterion (AICc) (ΔAICc), AIC weight (AICc Wt), cumulative weight (Wt), and log likelihood (LL) for candidate models used to determine relationships between site occupancy for gray bats and habitat factors in Kansas and Missouri, USA, 2021–2022. Models are composed of covariates affecting the probability a species occurred at a site (Ψ) and the probability of detecting a species, given it is present at a site (ρ). The detection covariates for all models include night, precipitation, and year.

Model	K	AICc	ΔAICc	AICc Wt	Wt	LL
Ψ (canopy)	6	399.39	0.00	0.23	0.23	-192.90
Ψ (canopy, trees/ha)	7	399.96	0.57	0.17	0.40	-191.90
Ψ (trees/ha)	6	400.95	1.57	0.10	0.50	-193.68
Ψ (lepidopteran biomass, canopy)	7	401.04	1.66	0.10	0.60	-192.45
Ψ (coleopteran biomass, canopy)	7	401.59	2.20	0.08	0.67	-192.72
Ψ (total biomass, canopy)	7	401.63	2.25	0.07	0.75	-192.74
Ψ (trichopteran biomass, canopy)	7	401.73	2.35	0.07	0.82	-192.79
Ψ (basal area)	6	401.97	2.59	0.06	0.88	-194.19
Ψ (total biomass, canopy, trees/ha)	8	402.15	2.77	0.06	0.94	-191.66
Ψ (total biomass, canopy, basal area)	8	402.94	3.56	0.04	0.98	-192.06
Ψ (saplings/ha)	6	406.37	6.98	0.01	0.98	-196.39
Ψ (.)	5	406.80	7.42	0.01	0.99	-197.85
Ψ (coleopteran biomass)	6	407.12	7.73	0.00	0.99	-196.77
Ψ (total biomass)	6	408.08	8.69	0.00	1.00	-197.25
Ψ (trichopteran biomass)	6	408.88	9.49	0.00	1.00	-197.65
Ψ (lepidopteran biomass)	6	409.24	9.85	0.00	1.00	-197.83
Ψ (global)	14	413.11	13.72	0.00	1.00	-187.89

Table. 2.5. Coefficients, standard errors (SE), and the upper and lower boundaries for the 95% confidence limits for the best supported occupancy models for the gray bat in Kansas and Missouri, USA, 2021-2022.

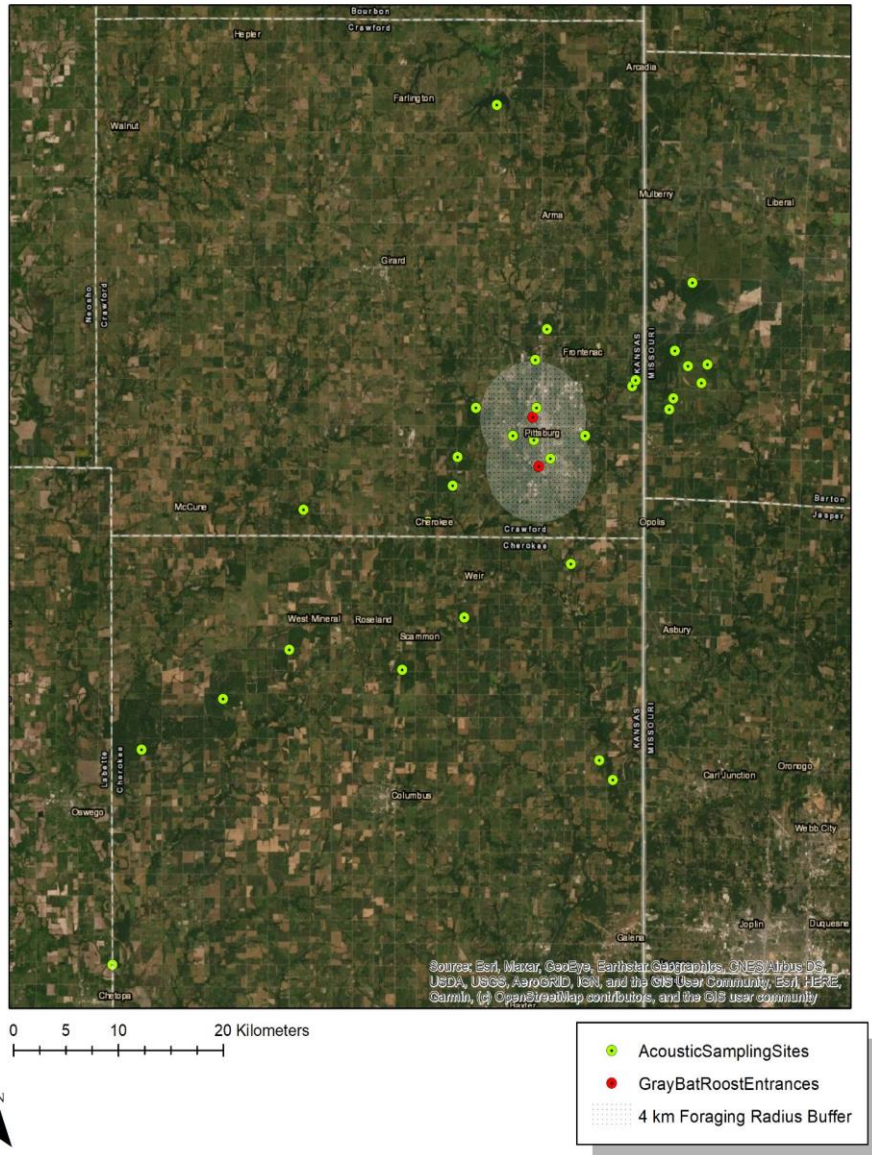| Variables by analysis	Coeff.	SE	Lower CI	Upper CI
Landscape				
Intercept	2.26	0.82	0.05	1.03
% Agriculture	- 0.51	0.31	- 1.12	0.09
Distance from the roost site	- 0.49	0.30	- 1.08	0.11
% Developed	0.83	0.48	- 0.12	1.78
% Forest	0.40	0.32	- 0.23	1.01
Habitat				
Intercept	0.72	0.39	- 0.05	1.48
% Tree canopy density	1.38	0.52	0.36	2.40
Trees per hectare	1.38	0.70	0.01	2.75

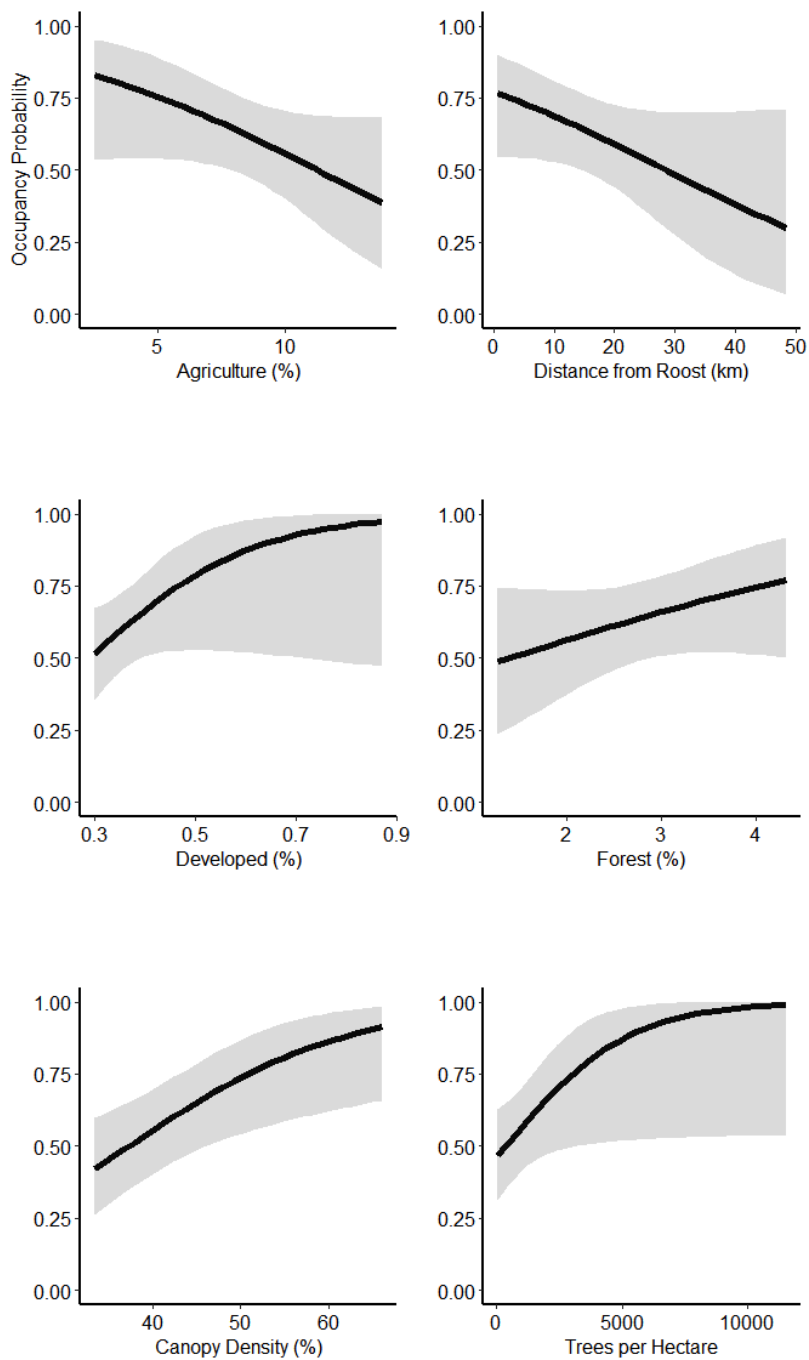**Figure 2.1.** Map of acoustic survey sites across Kansas and Missouri.

Figure 2.2. Predicted probability of occupancy across the range of percent agriculture, developed, and forest cover in a 1 km radius, distance from the roost site, and tree canopy density for the gray bat in the Cherokee Lowlands, USA, 2021-2022. Error bands represent 95% confidence intervals.

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