EVALUATING BAT RESPONSE TO HUMAN-ALTERED LANDSCAPE IN A MIDWESTERN RIVER CORRIDOR: AN ABUNDANCE MODELING ANALYSIS USING BIOACOUSTICS

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Chapter 1. Literature Review

HUMAN-WILDLIFE INTERACTIONS

In the last couple of centuries, human populations have been experiencing a massive boom. The world population is estimated to reach 9.7 billion by 2050 (Mahajan 2020). Much of this growth is occurring in urban areas, where more than 55% of the world's population currently resides (United Nations 2018, Mahajan 2020). As human populations grow, urban and rural areas are expected to expand, which exposes native ecosystems and wildlife in the surrounding landscapes to the effects of anthropogenic activity (Angel et al. 2011). Land development and urbanization are considered primary drivers in the biodiversity crisis. Land development introduces sensory pollutants and chemical toxins to natural environments, alters natural ecosystem processes, and causes habitat fragmentation, alteration, and eradication (Gehrt and Chelsvig 2003, Gehrt and Chelsvig 2004, Newbold et al. 2015, Senzaki et al. 2017). Developed landscapes alter plant and animal community compositions and experience higher rates of species declines, even in species considered to be widespread and adaptable to urbanization (Lintott et al. 2016, Mendes and Srbek-Araujo 2020).

Currently, about 25% of the world's population lives in cities with over one million residents (Korine et al. 2022), but the impacts of urbanization and land development are not limited to major cities. All urban landscapes differ from natural habitats in several ecologically significant ways (Gago et al. 2013, Lehrer et al. 2021). Cities introduce a variety of sensory pollutants like artificial light and anthropogenic noise, which can impact foraging activities, reproductive behavior, health, and sociality (Stone 2009, Bunkley et al. 2015, Shannon et al. 2016, Senzaki et al. 2020, Lehrer et al. 2021). Infrastructure such as roads, buildings, and impervious surfaces supplant natural landscapes and cause fragmentation or eradication of habitat (Senzaki et al. 2017). Fragmented habitats exhibit decreased food availability and limited movement for taxa (Lehrer et al. 2021) and support lower diversity levels of flora and fauna (Haddad et al. 2015, McKinney 2008). Additionally, urban landscapes may alter the physiological responses of various organisms (Korine et al. 2022).

The effect of urbanization on wildlife is dependent on the specific traits of different organisms (McKinney 2006). Certain species of wildlife are highly sensitive to anthropogenic disturbances, which may prompt them to avoid urban areas. Other organisms display tolerance to anthropogenic land alterations and may thrive in urban habitats (Threlfall et al. 2011). The opportunistic nature, and behavioral or ecological adaptability, of an organism, may be tied to their survival and success in urban landscapes (Luniak 2004). For example, specialist organisms, which rely on specific habitats or diets, tend to have lower chances of success in urban environments compared to generalist species (McKinney 2008). An example of an increasingly common urban generalist is a coyote (*Canis latrans*). Their flexible diet and behavioral plasticity (Breck et al. 2019) make them much more successful in urban landscapes than specialists who require a specific diet and habitat that the urban landscape cannot provide. These differences in the adaptability of wildlife in urban landscapes often lead to altered community assemblages that disproportionately reflect their community structure in surrounding natural areas (Shochat et al. 2006). Knowledge about species' adaptability in urban environments, however, is currently limited (Voigt and Kingston 2016).

The urban environment poses unique challenges and opportunities for many wildlife, but few types of animals are as associated with the urban environment as bats (Lintott et al. 2014). While some bats successfully exploit human resources, overall bat species richness and activity levels decrease in urban landscapes (Lane et al. 2006, Lintott et al. 2016). Morphological and

behavioral attributes of different bat species influence their ability to adapt to urban environments (Lintott et al. 2016). Bat response to urbanization likely falls on a spectrum of adaptability and is likely species-specific (Rodriguez-Aguilar et al. 2017). Currently, information is scarce on the species-level responses of bats to human-altered settings. Examining the individual adaptability of bat species to urban landscapes will enable us to recognize which species struggle the most with anthropogenic disturbances and allow us to develop speciesspecific management responses to potentially mitigate conflicts (Linott et al. 2016).

Bats pose a unique challenge when it comes to understanding their response to urbanization. All animals inhabit a three-dimensional world, but most mammals primarily use a horizontal plane. Bats, as aerial mammals, equally use a vertical component (Flores-Abreu et al. 2014). How organisms use space in their environment impacts demography, competition, interspecific relationships, habitat use and selection, and behavior (Cooper et al. 2014) and is understudied in flying vertebrates apart from birds (Flores-Abreu et al. 2014). Mammals that are constrained to a terrestrial surface often have reduced mobility and are more likely to be physically influenced by topography and anthropogenic development (Davies and Asner 2014), but a bat's use of three-dimensional space may alter these impacts. The vertical spatial niche used by bats adds complexity to studying the impacts of urban factors in three-dimensional space (Gamez and Harris 2022). Bats also exhibit a high degree of diversity in-flight behavior, which impacts habitat use and foraging strategies, further impacting the complexity of studying bats in an urban landscape (Mednes and Srbek-Araujo 2020). The spatial ecology of flying animals has fundamental behavioral and ecological implications (Cooper et al. 2014) and the use of threedimensional space by bats in urban settings should be considered in future urban bat research and management.

URBAN FACTORS IMPACTING BAT PRESENCE

Infrastructure

Urban infrastructure replaces natural habitat with anthropogenic land cover (Lehrer et al. 2021). Natural landscapes are modified by replacing natural resources, like forests, with manmade surfaces and structures. The presence of buildings and infrastructure impacts landscapes in both two-dimensional and three-dimensional space. In the two-dimensional space, urbanization replaces natural habitat with impervious surfaces and structural barriers. This alters the habitat availability, spatial configuration, and interconnectedness of the landscape and changes species assemblages (Gibb and Hochuli 2002, McKinney 2002, Geschke et al. 2018, Simkin et al. 2022). In the three-dimensional space, buildings create impervious clutter which may restrict bat movement across a landscape (Lehrer et al. 2021). The presence of buildings, however, may be beneficial for some bat species that use human structures for roosting. Bat use of human-made structures may be dependent on the type and composition of the structures (Lehrer et al. 2021). Other types of infrastructure, such as roads and highways, introduce direct mortal threats and busy roadways may restrict bat movement across landscapes (Abbott et al. 2012). Bridges and man-made tunnels may provide important foraging and roosting habitats for bats, but they can also be a source of disturbance that can impact bat behavior and habitat use (Adam and Hayes 2000).

Artificial Light

The biological world heavily revolves around the natural alterations of night and day, and most organisms have evolved temporal cycles that impact behavior and physiology (Cravens et al. 2017). Artificial light at night (ALAN) is one of the most prominent environmental changes

associated with land development and urbanization as ALAN disrupts nocturnal ecosystems and natural light-associated biological processes in many organisms (Korine et al. 2022). Approximately 23% of the global land surface is exposed to ALAN, making it a substantial threat to the biodiversity crisis (Falchi 2016). The effect of ALAN on bats varies based on the species of bat and the type of light (Haddock 2019, Straka 2019) but has been known to alter behavior (Barre et al. 2021) and increase roost abandonment and spatial avoidance (Cravens et al. 2017). Many species restrict themselves solely to dark areas, but the behaviors and morphology of certain bats may make them more inclined to be "light-tolerant" despite the ecosystem-altering effects of ALAN (Acharya and Fenton 1999, Azam 2018, Haddock 2019). For example, while artificial light is associated with global declines in insect populations, lights can provide a foraging advantage for some bats due to the congregations of insects found around artificial light sources (Acharya and Fenton 1999, Azam 2018). In general, bats that are morphologically favored for fast flight are considered light-tolerant species (Rowse et al. 2016). In terms of prey items, moths are more commonly consumed under artificial light than other prey items, which directs the focus of the research on foraging in artificial lights to fast-flying, mothspecialists like hoary and red bats (Arharya and Fenton 1992, Cravens et al. 2017).

In general, most bats exhibit light-avoidant behaviors. Various myotids demonstrate decreased activity levels during periods when lights are lit and avoid areas of ALAN by up to 50m from the lights, even ones at low luminance (Azam, 2018). Other bat species are known to delay emergence in the presence of ALAN, suggesting light affects a greater range of behaviors than just light avoidance (Stone 2009, Stone 2012). In Costa Rica, both fast and slow-flying bats in urban areas exhibited light avoidance behaviors and decreased activity in the presence of ALAN (Frank 2019). Even bat species considered to be "light-tolerant" may alter their

movements based on the presence of ALAN (Straka 2019). For example, *Pipistrellus pipestrellus* seemingly tolerates lighting in limited amounts, but individuals are more likely to seek tree cover to navigate in cities that are brightly lit (Hale 2015, Pauwels 2019). Solutions to mitigate the effects of artificial light on nocturnal ecosystems are complicated by the need for perceived human safety (Altringham and Kerth 2016). Bat-friendly lighting solutions should balance limiting the spectral intensity and spectra of LEDs at vertical illuminance while providing enough horizontal illuminance to benefit public safety (Altringham and Kerth 2016, Azam 2018).

Anthropogenic soundscapes

Many wildlife taxa are documented to show an aversion to anthropogenic noise (Bunkley et al. 2015). The effects of urban noise on bats are unclear and understudied even though bats primarily rely on auditory perception to experience their surroundings (Nagel 1974, Bunkley et al. 2015). As most bats use ultrasonic frequencies, bats may be tolerant of most urban noise under 15kHz (Hooten et al. 2022), but this has not been thoroughly studied in a city setting. Experimental studies, however, demonstrated that bats limit movement, alter echolocation behavior, and exhibit habitat avoidance in the presence of noise (Bunkley et al. 2015, Lehrer et al. 2021). Anthropogenic sound may mask prey-generated sound that gleaning bats use to hunt, making them unable to discern prey locations. Echolocation may also have a reduced range in the presence of anthropogenic noise (Buckley et al. 2015). Currently, the spatial variation of urban noise is unaccounted for in urban wildlife management (Parris et al. 2018).

Human-altered waterways

Water is a major predictor of bat occupancy (Lehrer et al. 2021), with water availability, food availability and foraging space, and navigation being the primary drivers (Hayes and Loeb 2007, Lehrer et al. 2021). While bat species activity tends to be higher near natural waterways, bats frequent man-made ponds, lakes, and pools in urban parks, golf courses, and residential neighborhoods (Lehrer et al. 2021). Bat's use of man-made ponds and pools, however, is likely limited and having nearby natural waterways is preferential for bats. A close association exists between waterways and insectivorous bat species that prey upon emergent aquatic invertebrates (Kalcounis-Rueppell et al. 2007). Pollution and anthropogenic development alter community structures of invertebrates in waterways, which can impact the abundance and availability of insects for bats and other predators foraging in riparian zones (Bank et al. 2006, Kalcounis-Rueppel et al. 2007). This relationship between anthropogenic impacts on aquatic macroinvertebrate community structure and habitats where bats may forage is extremely understudied (Kalcounis-Rueppell et al. 2007). As top predators that forage in both aquatic and terrestrial zones, bats may be a good model to study how macroinvertebrate community structure, because of anthropogenic activity, may impact higher trophic levels (Ballinger and Lake 2006). Considering the impacts of human alterations of natural waterways may be an essential part of bat management given the effects on drinking behaviors, foraging and navigational corridors, and food availability.

BAT DIVERSITY

With over 1,400 recognized species, bats account for about one-fifth of mammalian diversity. Bats, members of the order Chiroptera, exhibit high ecological and taxonomic diversity

and are the most widely distributed of all land mammals (Frick et al. 2020). There are currently around 20 recognized families of bats (Lei and Dong 2016) and they are found nearly everywhere on Earth except Antarctica and some remote islands (Schmidly 1991). Until recently, the order Chiroptera was split into two suborders, Megachiroptera and Microchiroptera, which were divided based on several noticeable differences between the two groups (Lei and Dong 2016). Bats known to use echolocation in foraging and navigation were placed in the suborder Microchiroptera (Broders et al. 2004, Lei and Dong 2016) and the non-echolocating Megachiropterans, also known as "Old World bats," were named partially for the large body size of some of the species in this group, which can reach a wingspan of up to 1.5 meters (Almeida et al. 2011). Recently, however, researchers proposed an alternative chiropteran classification based on updated morphological, genetic, and behavioral analysis of bats, with the two suborders now being titled Yinpterochiroptera and Yangochiroptera (Lei and Dong 2016). These recent classifications are not based on echolocation but on DNA analysis and the structure of the inner ear (Fenton 2022).

The suborder Yinpterochiroptera consists of seven families of bats that occur in the Old World. This suborder includes the family Pteropodidae, which are the Old-World fruit bats, and six families of echolocating insectivores (Fenton 2022). Of the over 1,400 species of bats worldwide, there are 410 species currently classified as Yinpterochiropterans (Fenton 2022). Apart from genetics, a distinguishing feature of Yinpterochiropterans is the possession of a thickwalled Rosenthal's canal, which is a structure in the inner ear used for carrying nerves between the ear and the brain (Fenton 2022, Sulser et al. 2022). Thick-walled Rosenthal's canals are associated with modern mammals (Fenton 2022) and are found in all other mammals except for Yangochiropteran bats (Sulser et al. 2022). Bats in the suborder Yangochiroptera make up about 80% of all echolocating bat species. There are 938 species in 14 different families and are found on every continent that has bats (Fenton 2022). Given the diversity in this group,

Yangochiropterans exhibit a wide variety of behaviors, diets, habitat preferences, and foraging strategies. Yangochiropterans possess a wall-less Rosenthal's canal, which accommodates more neuronal structures compared to a thick-walled Rosenthal's canal and may coincide with a higher capacity for fine-tuned echolocation (Fenton 2022). For example, most Yangochiropterans utilize a frequency-modulated type of echolocation which uses short pulses of sound between longer intervals of silence (Sulser et al. 2022). While all Yangochiropterans exhibit the wall-less Rosenthal's canal, the features of the spiral ganglion are highly variable across species in the Yangochiropteran suborder (Fenton 2022, Sulser et al. 2022). This variability may be a neuroanatomical evolutionary driver for the distinct lifestyle and echolocating strategies in this suborder (Sulser et al. 2022).

The diversity of bat species differs between temperate and tropical regions. There are over twice as many mammal species in the tropics compared to temperate regions, likely due to the increased variety and availability of food sources (Fleming 1973). As a temperate region, North America exhibits a lower diversity of bats, with roughly 47 species of bats ranging across the United States and Canada (Fleming 1973). The highest diversity of bats found in the United States is in the southwestern states (Schmidly 1991). While overall bat species diversity is low in North America, bats exhibit a wide range of ecological and functional diversity (Stevens and Willig 2002). In the eastern United States, which is frequently delineated by what is east of the Mississippi River, there are roughly 20 species of bats. The state of Indiana has thirteen documented species of bats. All species, except one in the family Molossidae, are in the family Vespertilionidae, which is the largest and most widespread family in the order Chiroptera (Reid

2006). Six of these species are winter hibernators, four species are migratory and are found in Indiana during reproductive season, and three are uncommon species with limited records in the state. The nine most common species in central Indiana are the big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivigans*), evening bat (*Nycticeius humeralis*), tri-colored bat (*Perimyotis subflavus*), little brown bat (*Myotis lucifugus*), Indiana bat (*Myotis sodalis*), and northern longeared bat (*Myotis septentrionalis*). Apart from *Eptesicus fuscus*, all these species are listed as state endangered or of special concern (DNR 2023).

THREATS FACED BY BATS

In the past couple of decades, bats have suffered population declines due to numerous conservation challenges. Currently, the most prominent threats to bats include wind-energy development, the spread of white-nose syndrome, and habitat loss and degradation (Browning et al. 2021). The combination of these threats is causing sudden and simultaneous population declines for insectivorous bats on a scale rivaled by few recorded ecological events (Boyles et al. 2011). The threats faced by bats are particularly urgent due to the unique life history of bats. Most bats produce a single pup each year, exhibit a slow rate of fetal growth, and have a long life span (Nowak 1994). Due to this, bats recover slowly from increased mortality rates (Voigt and Kingston 2016, Schmidly 1991), and the impacts of these losses are predicted to be felt for centuries.

White-nose syndrome (WNS) is an infectious disease caused by a fungus known as *Psuedogymnoascus destructans* and has been the cause of the deaths of over seven million bats in North America since February 2006 (Boyles et al. 2011). *P. destructans* opportunistically infects the skin of bats during hibernation, which triggers frequent arousal and a cascade of physiological disturbances, which can lead to a fatal depletion in energy reserves (Frick et al. 2010, Boyles et al. 2011, Verant et al. 2014). There are about a dozen species of bats known to contract WNS, and five species are exhibiting severe population declines of up to 90% (Auteri and Knowles 2020). Species that roost in mass aggregations are also uniquely vulnerable, due to large percentages of populations being in close proximity (Schmidly 1991).

Wind energy, one of the fast-growing renewable energy sources (Jensen 2018), is a major threat to several species of migratory bats. Bats are being killed at unprecedented rates from direct collisions with wind turbine blades (Boyles et al. 2011, Erickson et al. 2016). At-risk species include tree-dwelling migratory bats, such as *Lasiurus borealis* and *Lasiurus cinereus*, and seasonal hibernacula migrators, such as *Myotis sodalis* (Erickson et al. 2016). Mortalities from wind turbine-related energy have the potential to cause severe population-level impact on migratory bats (Baerwald and Barclay 2011, Hale et al. 2021). For example, current model trends suggest that hoary bat populations could be decimated by 50% by 2028 due to wind energy development (Friedenburg and Frick 2021). A further complication is that the bats most susceptible to growing wind energy threats are often some of the most poorly censused (Cornman et al. 2021).

Bats are essential to the health of a functional ecosystem (Cable et al. 2021). The cumulative loss of millions of bats is not only an ecological disaster but has substantial consequences for humans (Boyles et al. 2011). Bats provide large-scale monetary benefits to the agriculture industry (Voigt and Kingston 2016). It has been estimated that the loss of North American bats alone could lead to up to \$3.7 billion per year in agricultural losses (Boyles et al. 2011). Bats are also the source of important scientific advancements for humans in the medical

industry and in sonar research. Given the importance of bats, worldwide trends in bat decline have massive negative implications for humans and ecosystem balance.

BIOACOUSTICS AND ECHOLOCATION

Properties of echolocation

Sensory systems allow organisms to respond to external stimuli and extract meaningful information from their environment (Corcoran and Moss 2017; Russo et al. 2018). Many bats use an active sensing system known as echolocation that uses self-generated energy. In echolocation, bats generate sounds in the larynx, emit sounds through the mouth or nose, and analyze returning echoes to orient themselves and navigate through environments (Nelson and MacIver 2006). Bat brains are uniquely specialized for analyzing and extracting features of sonar signals that are important for sending and receiving acoustic feedback, as specific neurons can respond selectively to a specific range of pulse-echo delays (Corcoran and Moss 2017).

Echolocation is dynamic and flexible. Over 80% of bats are known to use laryngeal echolocation (Moss and Surlykke 2010, Fenton and Simmons 2014), with frequencies ranging between 8 and >200 kHz (Altringham 2011). There are a main two classifications of echolocation calls, referred to as frequency-modulated (FM) calls and constant-frequency (CF) calls. These call types vary in general shape, duration, and bandwidth of the echolocation pulses (Brtizke et al. 2011). CF-calls are long-duration calls that keep a constant frequency over the span of the echolocation call (Baier and Wiegrebe 2018). FM-calls span a broader range of frequencies, which provides higher resolution information for the bat. The nature of FM echolocation is species-specific and situational (Obrist 1995). FM-bats that are foraging in uncluttered open spaces produce longer signals of narrow bandwidth while FM-bats foraging in

complex, cluttered environments produce shorter, broadband calls (Moss and Surlykke 2010) that sweep a wider range of auditory neurons (Corcoran and Moss 2017) to provide fine-tuned target localization (Moss and Surlykke 2010). FM-modulated bats also systematically change the timing and bandwidth of echolocation pulses when approaching a flying prey target, often utilizing both CF- and FM-type calls. The echolocation pulses become shorter, faster, and steeper as the bat progresses through the search, approach, and terminal-buzz stages of prey pursuit and capture (Corcoran and Moss 2017, Kloepper et al. 2019).

Bats use different types of signals to operate in different ecological niches. Variations in echolocation call structure can be split into two categories: demographic and ecological. Demographic information known to affect the structure of echolocation calls includes age (Jones et al. 1992), size (Guillen et al. 2000), sex (Schuchmann et al. 2012), body size (Fenton and Simmons 2014), geographic location (Gillam and McCracken 2007), and individuality (Betts 1998, Britzke et al. 2011). Ecological and behavioral conditions that impact call variation include the density and complexity of clutter that bats are flying through (Broders et al. 2004, Britzke et al. 2011), presence of conspecifics (Gillam et al. 2007, Corcoran and Moss 2017), sources of noise in the backdrop (Gilliam et al 2007), phase of echolocation (Britzke et al. 2011, Corcoran and Moss 2017), natural light levels (McGowan and Kloepper 2020), and ecological task (Gillam et al. 2007, Kloepper and Pudlo 2019). Acoustic diversity is expressed at a variety of interspecific and intraspecific levels (Russo et al. 2018).

Acoustic studies

Historically, knowledge of bat biology has been obtained from animals captured using mist-nets and tracked with radiotelemetry (O'Farrell and Gannon 1999). Due to changes in

technology and recent declines in bat populations, the monitoring of echolocation calls for identification and behavior studies has grown in popularity (O'Farrell and Gannon 1999). While both physical capture and acoustic monitoring come with inherent bias (O'Farrell and Gannon 1999), acoustic monitoring technology is attractive for several reasons. First, acoustic surveys allow for a more complete inventory of bat species in an area (O'Farrell and Gannon 1999) and acoustics can provide more exact estimates of diversity than physical captures (Dawson and Efford 2009). Having more accurate estimates of species diversity allows for more effective monitoring of changes in species richness over time. Second, the use of acoustic monitors overcomes some of the challenges of working in the nocturnal environment or during conditions when the capture probability would be low (Russo et al. 2018). Third, acoustics research is less invasive to bats and less time-consuming for researchers. Fourth, there is a wide variety of portable and inexpensive bat detectors that are commercially available, making acoustic surveys more affordable and easily accessible. Fifth, acoustic monitoring has allowed researchers to investigate population declines due to white-nose syndrome without the risk of transmitting white-nose syndrome during alternative capture methods (Brooks 2011).

Despite these benefits, there are significant limitations to acoustic monitoring. First, the high levels of interspecific overlap and intraspecific variation in echolocation calls increase the risk of false-positive and false-negative identification of bats. Acoustic ID can be particularly challenging for low-duty call species due to higher levels of intraspecific variability, leading to potential overrepresentation in acoustic surveys (Russo et al. 2018). Additional manual vetting of bat calls or the use of multiple automatic-ID software decreases the risk of Type I and II errors in a dataset, but this can increase the time and cost for the researcher. Second, acoustic monitoring provides limited demographic data since it is impossible to distinguish between individuals in an

acoustic survey. Individuals are known to exhibit variation in their calls based on demographics (Lintott et al. 2014), but research is too limited to be able to decipher demographics from acoustic data. It is also impossible to identify whether calls are coming from multiple bats or the same bat multiple times, which complicates surveys as activity might not equal abundance (Hayes 2000). Third, technological advancements open many doors for research but also introduce new sources of potential error. Acoustic studies are at risk for unnoticed detector malfunctions, low-quality recordings that increase chances of Type I or II error, and user error if not used by highly trained personnel (Chesmore 2004). There is also an absence of well-developed call libraries for researchers to use on analysis (Riede 1998).

To address the limitations of acoustic species identification, researchers often place bats in groups based on call characteristics. Bats are frequently divided into low-frequency, midfrequency, and high-frequency groups. While this doesn't provide data on specific species, groups of bats that share echolocation call characteristics are often adapted for specific types of habitats and prey capture (Fraser et al. 2020). Bats with similar acoustic signatures may also be placed into groups based on their taxonomy. For example, due to acoustic similarity in the echolocation of endangered Myotis species, many researchers focus on the acoustic identification of some Myotis species as a group or a complex (Broders et al. 2004, Britzke et al. 2011). In many cases, geography is the only way to confirm bat species ID. For example, the echolocation calls of the Seminole bat (*Lasiurus seminolus*) and the eastern red bat (*Lasiurus borealis*) are too similar to differentiate using acoustic detectors alone (Perry 2018). Radio telemetry and capture techniques are required to establish presence of Seminoles and eastern red bats in ranges where species overlap.

BAT HABITAT SELECTION

Bats are highly adaptable, and their habitat needs vary by species. In general, bat occupancy in a habitat is due to a combination of forest structure, prey abundance, and the availability of roosts and water sources (Hayes and Loeb 2007), but variation in morphologies and echolocation behavior between bat species plays a large role in their habitat use and selection (Magalhaes de Oliveira et al. 2020). For example, wing shape is highly variable amongst species and impacts the speed and mode of flight used by bats, which impacts their habitat use (Norberg 1994, Magalhaes de Oliveira et al. 2020). Bats with broader wings are better adapted for slower flight with increased maneuverability, making them better suited to forage in cluttered environments (Feldhammer et al. 2009). Bats with narrower, pointed wings tend to be able to achieve faster flight with less maneuverability, making them better suited to foraging in more open, uncluttered environments (Norberg 1994). Dissimilarities in wing morphology also relate to dissimilarities in diet variation, as bats with more pointed wings seem to be more specialized and bats with more rounded wings exhibited a more generalist diet (Malgalhaes de Oliveira et al. 2020). Additionally, the echolocation properties of a bat species will strongly influence habitat selection (Britzke et al. 2011). Different bat species utilize different call characteristics, such as frequency ranges, slope, duration, pulse intervals, and bandwidth (Brtizke et al. 2011). Larger-bodied bats are more likely to use lower frequency calls that are produced less often while smaller-bodied bats use higher frequency calls at higher rates (Fenton 2001). Bats use the frequency of echolocation that is most appropriate for the size of the prey they are catching. For example, lower call frequencies are more commonly used by bats hunting larger insects, as echoes from insect-sized targets are weak when the wavelength is longer than the length of an insect's wing (Houston et al. 2004).

Habitat selection also varies by seasonality. Bats may move to different locations throughout the year due to seasonal changes in food availability, temperature, and other environmental factors. This varies based on whether the bat is a hibernating bat or a migratory bat. In the Midwest, migratory bats utilize forests as habitats throughout the entirety of the year or migrate to warmer regions (Willis and Brigham 2005). To withstand winter temperatures, migratory bats use extended bouts of torpor and possess a furred uropatagium that they use to retain heat (Shump and Shump 1982). The seasonal movements of the three foliage-roosting, migratory species in Central Indiana are poorly understood as these bats tend to be solitary and elusive (Cornman et al. 2021). In summer, these migratory bats utilize a variety of habitats, including tree cavities, dense foliage, tall grass, leaf litter, and even human structure (Clare at al. 2009). The use of overwintering sites is understudied but seems to vary by individuals (Vonhof and Russell 2015).

Habitat selection by hibernating bats is a complex process influenced by factors such as temperature, humidity, and roost availability. During the winter, hibernating bats make regional migrations to hibernacula that have specific temperature and humidity conditions to survive. Due to their stable, above-freezing temperatures and high humidity levels, places like caves, mines, and underground tunnels are attractive places for bats to hibernate (Perry 2013). Unfortunately, *Psuedogymnoascus destructans* thrives in cold and moist settings, putting hibernating bats at high risk for white-nose syndrome (Perry 2013). Both solitary and colonial species of bats are found in hibernacula. For example, *Eptesicus fuscus* roosts singularly in caves while *Myotis sodalis* may roost in tight groups of thousands (Raesly and Gates 1987).

Most hibernating bats in the Midwest use forested habitats throughout the summer months (Silvis et al. 2016). Summer habitats for bats can be categorized into two types: foraging and

roosting habitat. Bats will use a variety of roosting and foraging habitats based on their species, gender, and local conditions. Common habitats for summer roosts are tree cavities, underneath dead bark, hanging in foliage, rock crevices, culverts, bat houses, and urban structures that mimic natural habitats (Kunz 1982). Habitat selection is heavily influenced by reproductive behaviors during the summer months (Menzel et al. 2002, Carter and Feldhammer 2005). Bats exhibit sex-specific behaviors with many bats exhibiting sexual segregation throughout the summer (Istvanko et al. 2016). Commonly, females will form maternity roosts while males are more likely to remain solitary (Kunz et al. 2003). Sexual segregation in roosting may also impact whether males and females are spatially segregated in foraging habitats (Istvanko et al. 2016). Currently, research on spatial segregation of males and females is understudied in many forest-dwelling species. Given the difference in energetic requirements between males and females, foraging habitat selection may be highly impacted by sex (Istvanko et al. 2016).

The conservation of bat habitat is critical given the current challenges faced by bats. The protection of forest habitat is especially important as wooded areas are critical to sustaining bat diversity and abundance by providing roosts and foraging grounds. This is not only important for forest-dependent species. Species that are known to be open-space foragers often rely on the forest edges for increased insect abundance and reduced predation risks (Morris et al. 2010). Even urban species diversity is likely determined to an extent by the surrounding landscape, especially the presence of wooded areas for roosting, foraging, and protection. Bat habitat selection is likely complex along the natural-urban-rural interface, but the protection of forested habitat supports greater bat diversity and abundance in general (Krauel and Lebuhn 2016).

OCCUPANCY AND ABUNDANCE MODELING

Successful management of wildlife populations requires obtaining accurate estimates of species occupancy and abundance. Estimating occupancy and abundance can be a costly and difficult endeavor as ecological data is inherently complex and wildlife species are rarely detected with perfect accuracy (Royle and Link 2006, Scott et al. 2002). During wildlife surveys, non-detection does not equate to species absence unless the probability of detecting the species is 100%. Observed counts are sometimes used as a proxy for true population size, but this would require a perfect detection probability or for the detection probability to be constant across samples. When an individual isn't observed, it can mean one of two things: that the species was present at a site but went undetected or that a species was truly absent. Additionally, an observed count of a species likely misses some species that have gone undetected and does not reflect the true abundance. A further complication is the variability of detection. Detectability may vary due to site detections or survey conditions on a particular day (Lele et al 2012). Due to these variations, detection/non-detection data cannot be analyzed as if it is true presence/absence data and observed count data cannot be analyzed as if it is true abundance data. To address this, models have been developed to solve problems caused by imperfect detectability.

Occupancy modeling is a modeling approach that predicts the presence of species at a location (MacKenzie et al. 2002, Pauli et al. 2017), making it a useful tool in conservation. Occupancy modeling can also be used to incorporate variables of occupancy and detection such as habitat and site characteristics. Occupancy modeling involves the repeated sampling of a set of locations over a period to estimate the probability of species occupancy while accounting for imperfect detection (Pauli et al. 2017). This is useful in two primary ways. First, occupancy modeling is useful for examining the relationship between species distributions and the factors

that influence whether a species exists in that location (Gould et al. 2019). Secondly, occupancy modeling is useful in understanding metapopulation dynamics and how occupancy is related to site characteristics (Hanski 1992). Occupancy models are appropriate for measuring both short-and long-term fluctuations in populations, which is important for monitoring species status (Green 1997).

The assumptions of occupancy models are as follows. One, the state of occupancy must be closed, meaning occupancy cannot change at a site during the sampling season. Two, sites must be independent, meaning that the detection of a species at one sampling site is independent of detecting a species at another sampling site. This limits how closely spaced the sites are to prevent the same individuals from being detected at multiple sites. Three, there can be no unexplained heterogeneity in detectability or occupancy. The probability of occupancy must be the same across sites or explained by site covariates, while differences in detectability must be explained by the characteristics of the site or the survey (Gu and Swihart 2004). If assumptions are violated, estimates of occupancy and detection can experience bias, and inferences from the study may be incorrect (Gu and Swihart 2004). Fortunately, more advanced occupancy models allow for assumption violations, such as occupancy models that relax the closure assumption, allowing for the analysis of an open population (Kendall et al. 2013). For example, Kendall et al. (2013) used an open model during a single-season occupancy modeling analysis to account for the asynchronous arrival and departure of their target amphibian species at a site during breeding season.

Accounting for imperfect detection is essential in bat acoustics research due to the high levels of intra- and interspecific variation in bat calls (Clement et al. 2014, Ferguson et al. 2015, Pauli et al. 2017). This variation leads to a higher risk of type I (false-positive) or type II (false-

negative) errors in identification (Clement et al. 2014). False-negative detection errors occur when a species present at a sampling site is not detected. False-positive detection errors occur when a species is misidentified and therefore considered present when it is not (Clement et al. 2014, Ferguson et al. 2015). To help avoid bias and misestimations from both types of error, bat studies often use occupancy models that account for false-positive and false-negative detection errors (Royle and Link 2006). This is especially important when managing endangered species. Models involving bat acoustic data often utilize two different identification software programs along with manual vetting of echolocation calls by a professional (Clement 2016) or combining the data with mist-netting records (Clement et al. 2014). Additionally, multi-species occupancy modeling is conducive to acoustic surveys as acoustic data are usually collected for many species at once (Pauli et al. 2017).

The role of species in an ecosystem depends not only on their presence but also on their local abundance (Waldock et al. 2022). Estimates of species abundance may be obtained by using abundance modeling such as N-mixture models. N-mixture models estimate the number of individuals of a species at each sampling site based on replicate counts despite imperfect detection. These models account for detection and abundance simultaneously but are sensitive to violations in assumptions. The assumptions of Royle's N-mixture models are as follows. One, animal populations at each location are closed and remain constant. The movement of individual animals is allowed as long as superpopulations remain constant. Two, all individuals in a population have the same probability of detection during each sampling season. Three, individual detection probabilities are independent of one another (Royle and Link 2006).

Generalized Royle models do not assume population closure and account for additions and deletions to site populations. This allows for the Royle model to be applied to open

populations while providing an estimate of population dynamic parameters and estimates of the total abundance (Dail and Madsen 2011). Eliminating the closed population assumption, however, makes the time interval between sampling periods important. In these cases, models for the observed counts should account for any increased potential for movement due to longer time spans existing between the sampling occasions. Incorporating population dynamics like recruitment and population growth allows for a more flexible analysis of population dynamics and abundance, making it a valuable tool for managing complex ecological systems (Dail and Madsen 2011). Dail and Madsen used the generalized model to verify the closure assumption in a Mallard point count analysis and to estimate the population abundance of American robins with point count data in a multi-site, multi-year study. This generalized model may have limitations as there have been biased estimates of survival and recruitment in cases of density dependence (Bellier et al. 2016).

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Chapter 2. Evaluating bat response to human-altered landscape in a midwestern river corridor: an abundance modeling analysis using bioacoustics

ABSTRACT

Bats face numerous conservation challenges across the United States including wind energy development, the spread of white-nose syndrome, and habitat loss. Human alterations to natural environments can impact the presence of bats. How habitat alterations affect different bat species is not clearly known. Our goal is to examine bat use across a gradient of habitats altered by humans. During the 21-22 summer seasons, we used acoustic detectors to survey a variety of sites to examine bat response to the human-altered habitats along the White River corridor in Delaware County, IN. To ensure sampling occurred across a range of habitat types, we created an a priori model categorizing 1-km long sections of habitat into five habitat groups based on habitat structure and human influence. Within each category, we randomly selected six sample sites for a total of 30 sites along the river corridor. Wildlife Acoustics SM4+ echolocation detectors were used to collect acoustic data for three nights for two different times each summer. Habitat and environmental covariates were measured using artificial light measurements, field observation data, and ArcGIS Pro. Calls were analyzed using Kaleidoscope and BCID software along with manual identification based on species rarity and call structure attributes. We conducted a Dail-Madsen N-mixture modeling analysis to estimate call abundance and detection probabilities to evaluate the effects of habitat structure on bat use. The dominant species in the study area were overwhelmingly Eptesicus fuscus, followed by the Myotis sp. group, Lasiurus borealis, Nycticeius humeralis, Lasionycteris noctivagans, and Perimyotis subflavus. Due to low sample size, Lasiurus cinereus were ineligible for this analysis. Species abundance exhibited a wide variety of responses to urban variables. Prominently, Myotis species exhibit an extreme

negative relationship with even low levels of artificial light. Most of our species models, whether a forest-obligate or a generalist species, predicted that higher levels of riverbank canopy percentage yield an increased abundance of bats, suggesting that forests and forest-edges are an essential resource for urban bat communities. Probability of detection was minimally affected by temperature and annual Julian date, except for silver-haired bats whose odds of detection decreased with annual Julian date. Our aim is to gain a better understanding of species-specific habitat requirements for struggling bat populations and aid future management decisions regarding the effects of land development on bats.

INTRODUCTION

Wildlife biodiversity continues to face growing pressures from human influence and development (Gehrt and Chelsvig 2003, Newbold et al. 2015). Land development, a primary driver in the biodiversity crisis, dramatically alters compositions of flora and fauna communities (Gehrt and Chelsvig 2003, Haddad et al. 2015), affects ecosystem processes (Gehrt and Chelsvig 2004), introduces pollutants and toxins to natural environments (Newbold et al. 2015), and results in habitat fragmentation, alteration, and eradication (Gehrt and Chelsvig 2003, Newbold et al. 2015, Senzaki et al. 2017). Land development and urbanization is linked to unprecedented rates of species declines (Mendes and Srbek-Araujo 2020), even in species known to be widespread and tolerant (Lintott et al. 2016).

Currently, approximately a quarter of the global population lives in cities exceeding one million inhabitants (Korine et al. 2022), but the impacts of urbanization are not limited to highly populated cities. All urban areas, even small towns, differ from natural landscapes (Gago et al. 2013). Impacts of urbanization on wildlife are generally considered to be negative, but the effect

of urbanization on an organism depends on its taxon-specific traits (McKinney 2006). Some wildlife are highly sensitive to anthropogenic disturbances and avoid urban areas while other species tolerate or even thrive in anthropogenic settings (Threlfall et al. 2011). The survival of wildlife in urban landscapes may be tied to species opportunism and plasticity in their behavioral and ecological roles (Luniak 2004). For example, specialist organisms are less likely to be successful in urban environments than generalist species (McKinney 2008). Varying levels of adaptability among wildlife often result in community compositions that are dramatically different from those found in natural ecosystems (Shochat et al. 2006).

Though rarely seen due to their cryptic nature, bats are frequently found in urban environments (Lintott et al. 2014). Overall, bat species richness and activity levels decrease in urban landscapes (Lintott et al. 2016), but some species of bats have been known to adapt to developed landscapes and successfully exploit anthropogenic resources (Bergeson et al. 2020). For example, buildings create impervious clutter which may restrict bat movement across a landscape (Lehrer et al. 2021), but the presence of buildings may be beneficial for species like *Eptesicus fuscus* that frequently use man-made structures for roosting (Kurta and Baker 1990). Additionally, urbanized settings are highly correlated with the presence of artificial light at night (ALAN) (Korine et al. 2022). In general, bats exhibit light-avoidant behaviors (Stone 2009, Schoeman 2016), such as roost abandonment (Stone et al. 2015) and spatial avoidance of highlylit areas (Stone et al. 2015, Rowse et al. 2016a, Cravens et al. 2017), but lights can provide a foraging advantage for some faster-flying bat species like *Lasiurus borealis* due to the congregations of insects found around artificial light sources (Acharya and Fenton 1999, Schoeman 2016, Azam 2018). These types of morphological and behavioral characteristics can influence the ability of bats species to adapt to urban settings, and morphological traits of bats

are becoming used as a predictor of urban tolerance for certain species (Lintott et al. 2016). Due to the wide-variety of morphologies and strategies used by bats, there is likely a taxon-specific spectrum of adaptability to urban landscapes (Rodriguez-Aguilar et al. 2017).

Many species of bats in North America rely on forest habitats for foraging and roosting. Forests are key for supporting biodiversity and anthropogenic development negatively influences distributions of bats by reducing or fragmenting foraging and roosting habitats (Buchholz et al. 2021), causing many forest-dependent species to suffer significant population declines. In addition to threats from land development, bats are facing unprecedented population declines due to the fungal disease white-nose syndrome (WNS) and mortality from wind energy generation (Frick et al. 2010, Erickson et al. 2016, Browning et al. 2021). As urban areas continue to expand, the loss of forested areas may decrease species diversity and available habitat for struggling bat populations. Identifying factors that promote or decrease bat activity in urban areas is an essential part of developing management strategies that support Midwestern bat species and facilitate species diversity.

To investigate the impact of urbanization on bat abundance and habitat selection, we conducted a bioacoustics survey across a variety of human-altered riverine environments in a Midwestern river corridor. Limiting site selection to a river corridor ensures some environmental constants and provides insight into how urbanization affects bat presence along a water source, as distance to water is one of the main predictors of bat presence in urban landscapes (Pauli et al. 2015, Cable et al. 2021, Lehrer et al. 2021). We hypothesize that 1) bat abundance and species richness will be higher in areas of higher forest cover and lower in urbanized, human-altered areas, and 2) that there will be a negative effect of urbanization on species abundance, but responses will be species-specific depending on urban tolerance level.

METHODS

Location

Data were collected during two summers along the White River corridor in Delaware Country, IN. Delaware County is located in east-central Indiana, approximately 48km west from the border of Ohio and 80km northeast of Indianapolis (Figure 1). The county is approximately 1,025.4 km² with about 112,000 residents (average population density of 116 people/ km²). The primary incorporated city of Delaware County is Muncie (approximately 65,000 residents, average population density of 995 people/ km²). The White River runs westward through the central part of the county through downtown Muncie (Delaware.in.us, 2023).

Study Site Selection

We used a stratified random sampling approach for acoustic monitor placement. Using ArcGIS Pro, we placed a point along every km of the White River for the span of Delaware County. We categorized these sites into urbanization groups based on forest percentage in a 1-km buffer, riverbank characteristics, and land dwellings data. Sites were categorized into five groups, each representing a gradient of urbanization ranging from natural forested habitat to downtown urban. Six sites from each of the five groups were randomly selected for a total of thirty sampling sites (Figure 1). At each site, the surrounding environment was assessed for suitability of acoustic recording. Suitable acoustic locations provide ample distance from clutter and avoid reflective surfaces like asphalt, structural surfaces, and open water (Frick 2013). Our microphones were positioned at least 5m from vegetative clutter, 10m from structural surfaces, and 5m from the riverbank. If a site was deemed unsuitable for collection, a direction of up or down river was randomly selected, and the acoustic monitor was placed at the closest suitable

acoustic environment. All selected monitoring sites were within 0.25 km of the original ArcGISselected monitoring location.

Acoustic Collection

From May 25-August 12 in 2021 and 2022, we acoustically sampled for a total of 360 detector nights. Each night, bats emerged from summer roosts to forage around 2100 and returned in the early hours of the morning between 0200-0600. At each location, an ultrasonic recorder (Wildlife Acoustics SM4Bat with calibrated SMM-U1 microphone, Maynard, MA, U.S.A.) was deployed for acoustic collection (sampling rate: 192 kHz, gain: 36 dB, dig HPF: fs/12, dig LPF: Off, trigger level: 18 SNR, trigger win: 2.0 s, div ratio: 16). Echolocation calls were collected in full spectrum. Each microphone was fixed to the top of a 10ft tall PVC pipe to prevent acoustic haze due to ground reflections from the bat calls. At each site, the microphones recorded at 256 kHz overnight from 2030-0900. We recorded calls over a span of three consecutive nights at each site twice per summer for a total of twelve sampling nights at each location. We allowed for six nights of recording per site each year to account for night-to-night variation in echolocation activity (Hayes 1997). We sampled sites in opposite order during the second year to account for seasonal variation in bat activity.

Habitat Data

To evaluate species abundance based on habitat data, we measured habitat characteristics in the monitoring sites using a combination of GIS analysis, on-site data, and collaborative data. We summarized the forest cover in a 1-km buffer around each monitoring site using the Delaware County tree canopy map layer by McCreary and Berland (2020) and recorded the proportional tree cover as a percentage. We assessed riverbank canopy cover by evaluating river

lines to be canopy or non-canopy and recorded the proportional riverbank canopy cover as a percentage in the 1-km around the monitoring site. Both forest cover percentage and riverbank canopy percentage serve as a measurement of habitat availability and protected edge habitat for navigating the river corridor. We measured the distance from the nearest bridge to each monitoring point and recorded the distance in meters. Bridges introduce potential sound pollution from vehicles into the river corridor, and distance from nearest bridge serves as a measurement of avoidance for potential anthropogenic sound sources that wildlife may prefer to avoid (Bunkley et al. 2015).

Artificial light measurements were collected on site during August 2022 after 2100 when artificial lights were lit. We developed an a priori lighting index using the quantity, intensity, and distance of visible light sources from the monitoring site. Artificial light introduces sensory pollutants for nocturnal organisms and is known to alter the behavior of various nocturnal organisms (Cravens et al. 2017, Barre et al. 2021, Korine et al. 2022). To measure this, we counted the visible lights sources at the monitoring site and 30m up and down river along the riverbank for three measurement points per site. We mapped each visible light source and used Google Earth to measure the distance of each light source from the monitoring site and assigned an intensity rating ranging from 1-3 for each source of light based on visible effect in the surrounding environment. The distance of each light source was divided by its respective intensity rating and the resulting values were added together to calculate an artificial light value for the three measurement points at the site. The three measurement points were then added together to give a single artificial light score for the site. The scores ranged from 0.0 to 0.4.

Lastly, MIBI (Benthic Macroinvertebrate Index of Biotic Integrity) data was obtained from the Muncie Bureau of Sanitation (Holloway and Gradel, 2022). Land alteration can impact

the abundance and availability of insects for bats and other predators foraging in riparian zones (Bank et al. 2006, Kalcounis-Rueppel et al. 2007), and MIBI scores provide an assessment of overall abundance and diversity of macroinvertebrate insects in an area. As indicator species, macroinvertebrate data also provides insight into the overall quality of aquatic habitats (Carter et al. 2017). MIBI scores were collected along the White River from the years of 2020-2021, and we used MIBI score from the closest macroinvertebrate sampling site to our monitoring sites. The majority of the MIBI sites were within 0.5 km from the closest monitoring site, but MIBI sites at the ends of the county were up to 2.5 km away from the closest monitoring site.

Acoustic Analysis

We classified bat echolocation calls to species using Wildlife Acoustics Kaleidoscope Pro 5.4.8 bat call analysis software (Wildlife Acoustics, Inc; Concord, Massachusetts, U.S.A) and Bat Call ID version 2.8b (BCID) (Allen, 2012) to identify calls to species and construct detection histories. We programmed Kaleidoscope Pro and BCID to limit identifications by requiring call sequences to contain a minimum of five pulses with 70% minimum pulse agreement for species level identification. Calls were classified to nine common species based on known species ranges. In Kaleidoscope Pro 5.4.8, we restricted species selection using The Bats of North America 4.3.0 filter on the default setting. In BCID, species selection was restricted to nine common Indiana species based off historic capture data: *Eptesicus fuscus, Lasiurus borealis, Lasiurus cinereus, Lasionycterius noctivagans, Nycticieus humeralis, Perimyotis subflavus, Myotis lucifugus, Myotis sodalis,* and *Myotis septentrionalis*. Due to the overlap in the echolocation calls in the genus *Myotis* (Britzke et al. 2011), all Myotis calls were pooled into a single *Myotis* sp. group to avoid identification error. We manually vetted a subset of calls from each recording night to check for species misidentification and ensure that false identifications of

non-bat calls were not prominent in the dataset. Calls classified to species level were only included in the final dataset if there was species-level agreement between both automatic identification software.

Statistical Analysis

We intended to conduct an occupancy modeling analysis using a method developed by Royle and Link (2006) to estimate bat presence and detection probabilities. This method, developed by Royle and Link (2006), accounts for instances of false-negative and false-positive detections that may occur due to the inherent bias of acoustic measurement (Clement et al. 2014). Due to high bat species presence in the data, however, our dataset was ineligible for an occupancy modeling analysis. As our sampling took place along the river corridor, we predict that the presence of water biased bat presence in our dataset as water is a known predictor for bat occupancy (Lehrer et al. 2021). Four species (*Eptesicus fuscus, Lasiurus borealis, Lasionycterius noctivagans*, and *Nycticeus humeralis*) were present at all thirty sampling sites on at least one night.

Instead, we conducted a Dail-Madsen N-mixture modeling analysis to estimate bat call abundance and detection probabilities (Dail and Madsen 2011, Caldwell et al. 2019). The Dail-Madsen model is an extension to the Royle (2004) N-mixture model but relaxes the closure assumption of the model to allow estimates of abundance for an open population. The generalized Dail-Madsen N-mixture model used is:

 $N_{it} \sim \text{Poisson} (\lambda, \alpha)$ $G_{it} \mid N_{it-1} \sim \text{Poisson} (\gamma * N_{it-1})$ $S_{it} \mid N_{it-1} \sim \text{Binomial}(N_{it-1}, \omega)$ $N_{it-1} = G_{it} + S_{it}$ $\gamma_{it} \sim \text{Binomial} (N_{it}, P)$

with the unobserved abundance at site *i* at time *t* (*N*_{*it*}), expected abundance (λ), dispersion parameter (α), number of individuals gained by immigration during one night at site *i* since time *t* (G_{*it*}), number of individuals that survived since time *t*-1 at site *i* at time t (S_{*it*}), arrival rate of individuals (γ), apparent survival probability of individuals (ω), detection probability (*P*), and observed number of bat calls at site *i* at time *t* (γ_{it}).

Our habitat covariates for each monitoring site were forest canopy coverage in a 1-km buffer, riverbank canopy coverage in a 1-km buffer, artificial light level values, the distance to the nearest bridge, and the MIBI score. Our environmental detection data were annual Julian date, average nightly temperature, and year. We conducted Spearman's correlation tests on habitat covariates to avoid redundancy in the variables. Variables were retained if their correlation was less than 0.60, which removed forest canopy coverage as a variable due to high correlation with artificial light. All possible combinations of covariates of abundance were evaluated for each species using Akaike's Information Criterion (AIC) value (Burnham and Anderson 2001). All models within two AIC-units of each other were considered equally plausible. The final set of top models were averaged for a single global model (Mazerolle 2023) (Table 1). The models were fit using the unmarked package in R version 4.3.2 (Fiske and Chandler 2011), using acoustic data to predict call abundance as substitute for bat activity. In the model, we compared 95% confidence intervals of call abundance between the habitat covariates for all nine species. We used the models to create predictions of abundance for each habitat covariate with the others held constant at their mean.

RESULTS

Acoustic Monitoring

We sampled 30 sites over 360 survey nights across the two summers, which yielded a total of 206,798 detector recordings. Of these, 157,986 were identifiable bats calls per Kaleidoscope Pro, with many of the rest being insect noise or unknowns. Of the identifiable bat calls, Kaleidoscope Pro and BCID agreed on species level assignments for 87,964 calls. We manually vetted subsets of this dataset to confirm the presence of all expected species for Delaware County. The dominant species in the study area were overwhelmingly big brown bats, followed by the *Myotis* sp. group, eastern red bats, evening bats, silver-haired bats, and tricolored bats. Due to low sample size, hoary bats were ineligible for this analysis.

Environmental variables

We used riverbank canopy cover (%, 1-km buffer), artificial light index value, distance to nearest bridge, and MIBI scores as the environmental predictors in our final abundance models. We removed total forest cover (%, 1-km buffer) as a predictor due to high correlation to artificial light levels (rho = 0.68).

Species models

Big brown bat: Big brown bats were our most detected species and accounted for 77.3% classified to species in 2021 and 2022. We detected big brown bats at 100% of sites on every survey night. Riverbank canopy coverage and distance to nearest bridge were positively related to big brown bat abundance, with big brown bat abundance increasing by 350 bats between 0.0 and 0.8 riverbank canopy coverage (Table 2, Figure 2) and 140 bats between 0 and 3000 m distance from the nearest bridge (Figure 3). Artificial light levels and MIBI scores were

negatively related to big brown bat abundance, with big brown bat abundance decreasing by 415 bats between the lowest and highest artificial light levels (Figure 4) and 450 bats between MIBI scores of 32 to 48 (Figure 5). Probability of detection for big brown bats was related to annual Julian date and temperature, with probability of detection decreasing by 2.5% between day 140 and 220 (Figure 6) and increasing by 10% between 45- and 80-degrees Fahrenheit (Figure 7).

Myotis sp. group (little brown bat, Indiana bat, northern long-eared bat): Myotis species accounted for 8.9% of calls classified to species in 2021 and 2022. We detected Myotis species at 70% of the sites and on 50.5% of the survey nights. Myotis species exhibit a significant negative relationship with artificial light (Table 2, Figure 8), with *Myotis* sp. abundance decreasing from 125 bats to 0 at even minor artificial light levels. Riverbank canopy coverage, distance to nearest bridge, and MIBI scores were positively related to *Myotis* sp. abundance. *Myotis* sp. abundance increased by eight bats between 0.0 and 0.8 riverbank canopy coverage (Figure 9), six bats between 0 and 3000 m distance from the nearest bridge (Figure 10), and by 25 bats between MIBI scores of 32 to 48 (Figure 11). Probability of detection for the Myotis species was related to annual Julian date, with probability of detection increasing by 15% between day 140 and 220 (Figure 12). Probability of detection for the Myotis species was related to average nightly temperature, with probability of detection for the Myotis species was related to average Sahrenheit (Figure 13). Probability of detection for the Myotis species was related to year, with probability of detection increasing by 14% between 2021 and 2022 (Figure 14).

Eastern red bat: Eastern red bats accounted for 4.9% of calls classified to species in 2021 and 2022. We detected eastern red bats at 100% of the sites and on 93.9% of the survey nights. Riverbank canopy coverage was negatively related to eastern red bat abundance, with eastern red bat abundance decreasing by nine bats between 0.0 and 0.8 riverbank canopy coverage (Table 2,

Figure 15). Eastern red bat abundance was positively related to artificial light levels and distance to the nearest bridge, with eastern red abundance increasing by seven bats between the lowest and highest artificial light levels (Figure 16), and by 38 bats between 0 and 3000 m distance from the nearest bridge (Figure 17). MIBI score had no impact on eastern red bat abundance (Figure 18). Probability of detection for the eastern red bat was not affected by annual Julian date (Figure 19). Probability of detection for the eastern red bat was related to average nightly temperature, with probability of detection decreasing 48% between 75- and 80-degrees Fahrenheit (Figure 20).

Evening bat: Evening bats accounted for 4.6% of calls classified to species in 2021 and 2022. We detected evening bats at 100% of the sites and on 84.1% of the survey nights. Riverbank canopy coverage and distance to nearest bridge were positively related to evening bat abundance, with evening bat abundance increasing by 70 bats between 0.0 and 0.8 riverbank canopy coverage (Table 2, Figure 21) and 10 bats between 0 and 3000 m distance from the nearest bridge (Figure 22). Artificial light levels and MIBI score had no impact on evening bat abundance (Figures 23, 24). Probability of detection for big brown bats was related to annual Julian date and temperature, with probability of detection increasing by 14% between day 140 and 220 (Figure 25) and increasing by 22% between 45- and 80-degrees Fahrenheit (Figure 26).

Silver-haired bat: Silver-haired bats accounted for 3.3% of calls classified to species in 2021 and 2022. We detected silver-haired bats at 100% of the sites and on 77.5% of the survey nights. Silver-haired bat abundance was negatively related to riverbank canopy coverage and artificial light levels, with silver-haired abundance decreasing by 32 bats between 0.0 and 0.8 riverbank canopy coverage (Table 2, Figure 27) and 15 bats between the lowest and highest artificial light levels (Figure 28). Distance to nearest bridge and MIBI scores had no impact on

silver-haired bat abundance (Figures 29, 30). Probability of detection for the silver-haired bat was related to annual Julian date, with probability of detection decreasing by 90% between day 140 and 220 (Figure 31). Probability of detection for the silver-haired bat was related to average nightly temperature, with probability of detection increasing 75% between 45- and 80-degrees Fahrenheit (Figure 32). Probability of detection for the silver-haired bat was related to year, with probability of detection increasing by 22% between 2021 and 2022 (Figure 33).

Tricolored bat: Tricolored bats accounted for 1% of calls classified to species in 2021 and 2022. We detected tricolored bats at 76.7% of the sites and on 44.2% of the survey nights. Tricolored bat abundance was positively related to riverbank canopy cover (Table 2, Figure 34), with tricolored bat abundance increasing from 0 to 27 bats between 0.4 and 0.8 riverbank canopy. Tricolored bat abundance was negatively related to artificial light levels and distance to the nearest bridge, with tricolored abundance decreasing by 8 bats between the lowest and highest artificial light levels (Figure 35) and by 4 bats between 0 and 3000 m distance from the nearest bridge (Figure 36). MIBI scores had no impact on tricolored bat abundance (Figure 37). Probability of detection for the tricolored bat was related to annual Julian date, with probability of detection increasing by 17% between day 140 and 220 (Figure 31). Probability of detection increasing 10% between 45- and 80-degrees Fahrenheit (Figure 32). Probability of detection for the tricolore bat was related to year, with probability of detection increasing by 1.2% between 2021 and 2022 (Figure 33).

DISCUSSION

Our results show some support for our hypotheses. Species richness was higher in more forested, riparian sites with all six species groups detected at our most natural sites and only four species groups detected at our most well-lit, urban site. Specifically, our Myotis species group and tricolored bats exhibited a significant decrease in presence as sites became more urban. Our model predictions show some support for our second hypothesis that urbanization will have a negative effect on predicted species abundance, but that this effect will vary by bat species tolerance. In general, we see a negative effect of urbanization on bat species abundance, however, the level of response varied by species. Many species exhibited similar trends in response to the covariates, but in some cases, we saw minimal or positive effects to urbanization.

Most of our models predicted that increased riverbank canopy percentage yields increased abundance of bats. Big brown bats, Myotis species bats, evening bats, and tricolored bats all exhibited a positive relationship between riverbank canopy percentage and bat abundance, despite some of these species being known as urban-tolerant species or species known to forage in open clearings. Big browns, in particular, are known to be urban generalists that successfully roost and forage in urban areas (Agosta 2002). This suggests that even for urban-tolerant species or species that are adapted to foraging in open areas, trees offer important fitness benefits and are critical to the health and survival of many bat species (Bergeson 2021, Kunz et al. 2003). Our results add to a developing body of research supporting that forested habitat and forest-edges are an essential resource for urban bat communities (Gehrt and Chelsvig 2008).

Big brown bats were our most successful species, with big browns present at every site on every recording night. While our models predict an increased abundance of big brown bats at

decreased light levels and increased riverbank canopy percentage, this species' overwhelming abundance at all sites further supports that big brown bats are urban-tolerant generalists. Known to have flexibility in habitat use and roost selection (Agosta 2002, Neubaum et al. 2007), our study further confirms big brown bat's generalist ability to take advantage of both urban and natural habitat. Our models, however, predict that big brown bats do exhibit some level of preference for more forested areas. For example, our models predicted the presence of 600 big browns at sites with 80% riverbank canopy percentage on any given night while only predicting 250 big brown bats at a site with 0% riverbank canopy percentage. While this demonstrates a substantial decrease in big brown bat abundance at decreased riverbank canopy percentage, having 250 bats at a site with no canopy coverage is substantial on its own. This suggests that while big brown bats may be successful in highly altered and urbanized habitats, these urban big brown bats will better thrive in conditions of decreased artificial light levels and increased forest cover availability. Similar studies (Cravens and Boyles 2019, Seewagon and Adams 2021) found that big brown bats actively avoid LED lights but have been known to exploit insects around mercury or sodium vapor lights, suggesting the spectral composition of light sources may impact big brown response to light-polluted habitats.

Interestingly, big brown bats exhibited a mild decrease in predicted abundance along areas of the river with higher MIBI scores. This could be due to a couple of phenomena. First, our MIBI scores, a proxy for insect abundance and diversity, were highest in the most heavily forested, riparian sections of the river. As big brown bats are urban generalists, they may be taking advantage of prey availability in more urbanized sections of the river where other bats are less abundant. Therefore, their ideal foraging situation may be dimly-lit urban edge-habitats where there is decreased competition with other bats. Second, big brown bats can cross large

stretches of urban habitat to reach ideal foraging habitat and food resources (Duchamp et al. 2004, Schimpp et al. 2018), and big brown bats may travel up to 11 km to forage (Starbuck et al. 2014). Big brown bats, a beetle specialist (Whittaker 1972, Burke 2002, Agosta and Morton 2003, Whitaker 2004, Feldhammer et al. 2009), may be covering vast expanses of the White River, meaning they may not need to prioritize areas with potentially greater prey diversity if a constant source of their specialized prey is available.

Myotis species were the second most abundant group after big brown bats. Out of all our species, our model with strongest impact is the relationship between Myotis species abundance and artificial light. Myotis abundance exhibited a strong negative relationship with artificial light with our predicted Myotis abundance dropping quickly to zero in the presence of even small levels of artificial light. While Myotis species were detected at two-thirds of our sites, the sites with Myotis presence ranged from forested-riparian to forested-residential. In these sites, the brightest available light sources were usually from distant porch lights or streetlights, with leaves and vegetation often further obstructing the view of the light source from the river corridor. This suggests that light tolerance for Myotis species may be limited to gentle, distant sources of artificial light near forested habitat. This supports previous research that found Myotis avoid areas of ALAN (McGuire and Fenton 2010, Cravens and Boyles 2019, Seewagon and Adams 2021) by up to 50m from the lights (Azam 2018), even lights that are at low luminance. Due to their light-aversion, Myotis species are likely to experience decreased foraging habitat availability compared to other bats that are more tolerant to light-polluted environments (Seewagon and Adams 2021). Interestingly, little brown bats (Myotis lucifugus) are known to roost in manmade structures (Kurta 2008, Johnson et al. 2019) suggesting that the benefits to

roosting in buildings for some little brown bats outweigh potential exposure to artificial light sources when leaving manmade roosts.

While artificial light levels had the greatest impact on Myotis species abundance in this study, the Myotis species group also exhibited a positive relationship with riverbank canopy percentage and mild positive relationships with distance to nearest bridge and higher MIBI scores. Previous research supports the fact that Myotis activity is highest in forests or riparian habitats (Henderson and Broders 2008). The aversion of Myotis species to our urban monitoring sites suggests they may have strict habitat requirements along with their intolerance to artificial light. These requirements likely include ample forest cover, adequate distance to anthropogenic sensory pollution, and prey abundance availability. Landscapes dominated by agriculture and urban development would not meet these requirements. As all three Myotis species in this study are State Endangered in Indiana, a thorough understanding of the species-specific requirements of this forest-dwelling species should be a focal point for future urban bat research.

Eastern red bats were our third most detected species. Given their widespread abundance, we detected fewer eastern red bats than anticipated. There is current speculation that eastern red bats may be experiencing a substantial decline although they are not currently listed by the U.S. Fish and Wildlife. Eastern red bats are known to be moderately tolerant of urbanization (Parkins et al. 2016), although they do not exhibit the same roost flexibility in urban areas that big brown bats possess. Our results reflected eastern red bat's tolerance for urbanized areas. Our models showed that eastern red bats preferred lower percentages of riverbank canopy percentage and exhibited a slight increase in abundance at higher artificial light levels. Like other bat species that are adapted for faster flight, red bats are generally considered to be a light-tolerant species (Rowse et al. 2016, Cravens and Boyles 2019). Faster flight also predisposes them for foraging

in uncluttered, open habitats (Elmore et al. 2005). Our data is consistent with other studies that detected red bats frequenting open, non-forested habitat (Hickey and Fenton 1990, Hickey et al. 1996, McCracken et al. 1997) and streetlights (Mager and Nelson 2001).

While red bats exhibit tolerance for a range of habitat conditions and urban influence, red bats are forest-dwelling bats that rely heavily on forest availability for roosting (Monarchio et al. 2020). Other studies found that red bats commute across distances to open foraging grounds (Mager and Nelson 2001, Elmore et al. 2005), but the maximum distance they travel from their day roost may be less than 10 kilometers (Hutchinson and Lacki 1999). This implies that the proximity of forested habitat may influence whether a red bat utilizes an open area for foraging. A permanent water source in the vicinity is also important for red bats (McCracken et al. 1997, Hutchinson and Lacki 1999), suggesting that red bats may tolerate urban settings for commuting and foraging, but they select landscape-level habitat that provides nearby access to a water source and forested roosting habitat. This further reiterates that access to trees and forested habitat is essential, even for bats that are more adapted to urban environments.

To our knowledge, this is the first-time evening bats have been recorded in Delaware County. The evening bat, endangered in the state of Indiana, is a common species in the southeastern United States but has been experiencing expansions in its range for the past six years (Andersen et al. 2017; Kaarakka et al. 2018, Rolland et al. 2022). Recent studies in Michigan, Wisconsin, and Minnesota show that evening bats are becoming increasingly common in northern regions of the Midwest (Kaarakka et al. 2018). Evening bats were our fourth-most detected species in our study, further supporting the idea that evening bats are expanding their range northward.

Evening bats are known to prefer roosting in trees and foraging in areas that are less developed (Duchamp et al. 2004), but they have been known to roost in man-made structures (Rolland et al. 2022) and to forage near urban areas (Schimpp et al. 2018). Our results showed that evening bat abundance increases with riverbank canopy percentages, but the response of evening bats to artificial light and MIBI scores was relatively neutral. These results complement previous research that suggest evening bats rely heavily on forest ecosystems and prefer to forage along forest edges, riparian zones, or open fields near roosting habitat (Morris et al. 2011). Evening bats were detected at every site in our study, but almost a third of the detected calls came from three adjacent monitoring sites in highly forested habitat with complete canopy on both sides of the river near a few low-traffic bridges. Given the high abundance of localized bats and the fact that evening bats prefer to forage within two miles of their roost (Kurta 2008), this may be the site of a roosting colony. Evening bats are also known to prefer mature trees close to water sources as the site of their maternity colonies (Munzer et al. 2023). Additionally, evening bat abundance in our study increased as distance to bridges decreased, but this relationship may be influenced by the proximity between the three primary evening bat sites and two dimly lit, low-traffic bridges.

Silver-haired bat abundance exhibited a negative relationship with riverbank canopy percentage and artificial light levels but was not impacted by bridge distance or MIBI scores. Silver-haired bats are highly dependent on forests for roosting, but they are known to feed predominantly in open clearings or along roads and waterways adjacent to forested areas (Reimer et al. 2010). Unlike other species that forage in open habitats, silver-haired bats are not adapted for faster flight (Cryan 2003), estimating average foraging speeds of only 4.8-5.0 m/s (Best and Hunt 2020). Odds of detection for silver-haired bats were also influenced by annual

Julian date, with silver-haired bat detection probability decreasing significantly after early/mid-June. Silver-haired bats are migratory bats that are known to be absent in mid-summer in the Lake Michigan region and surrounding states (Kurta et al. 2018). Previous research found that most of the silver-haired bats in the Midwest region may be summering in northern Michigan and Wisconsin and into Ontario (Kurta 2017, Kurta et al. 2018). This suggests that silver-haired bat presence in Delaware County may be occurring during late spring migration, with silverhaired bat presence decreasing significantly during the month of June. The combination of these factors indicates that silver-haired activity in Delaware County is highest during late May/early June in dimly-lit clearings near open stretches of river.

Our results reflected the tricolored bat's status as a riparian specialist (Veilleux et al. 2003, Ford et al. 2005, Gaulke et al. 2023). Our models demonstrated a strong positive relationship between riverbank canopy percentage and tricolored abundance, with no individuals being predicted unless riverbank canopy percentage was at least 40%. Tricolored bats in our study area also exhibited a strong negative relationship with artificial light levels, although this relationship was not as extreme as the response of Myotis to artificial light. Tricolored bats are known to rely heavily on forested habitat for both roosting and foraging (Veilleux et al. 2003, Perry and Thill 2007) and their wing morphology combined with their acoustic behavior makes them morphologically adapted to forage in high clutter areas (Menzel et al. 2005, Lacki et al. 2007). Historically, tricolored bats have been associated with edge habitats and waterways (Fujita and Kunz 1984, Shute et al. 2021, Gaulke et al. 2023), which complements our results that tricolored bat abundance exhibits a positive relationship with increased amounts of riverbank coverage. Unlike our Myotis species, tricolored bats were present at one urban site close to the downtown section of the city of Muncie. This site was comprised of both sides of the riverbank

having coverage, low light-levels, and mid-level MIBI score. Spans of forest coverage blocked anthropogenic pollutants like light and sound coming from the surrounding industrial buildings and residences. Forested areas in the vicinity likely acted as barriers, mitigating the effects of anthropogenic pollutants like light and sound from the adjacent streets, industrial zone, and residences. This implies that some tricolored bats may exhibit degrees of urban tolerance provided they have access to even minute amounts of forested habitat, forest edges, and a water source.

The extent to which bats can thrive in human-altered environments relies on their taxonspecific characteristics and the specific conditions of an urban environment. Forest-obligate species are the most constrained in their ability to adapt to human-altered habitat because they rely more heavily on continuous forest expanses, which are declining across all landscapes. Nevertheless, urban-generalists and those adapted to forage in open environments also have varying degrees of dependence on forests for roosting for foraging habitat. Thus, forest availability is likely required for maintain high levels of bat diversity in urbanized areas. In addition to evaluating forest availability in developing areas, it is essential for land managers to consider the unique requirements of each species, such as the extreme limited tolerance that endangered Myotis species exhibit towards artificial light. Our results suggest forested availability and artificial light levels along waterways are important management considerations for all bat habitats.

Future studies should also consider means of decreasing the anthropocentric methods used when assessing urban variables. ALAN, for example, is often measured in terms of human sensitivity and perception to light but can be greatly altered by the distance to and angle from artificial light sources (Owens and Lewis 2018). This is especially true for nocturnal organisms

that occupy 3D-space that may be experiencing sources of ALAN from above, at high speeds, or from unique microhabitats.

CONCLUSIONS

Species abundance for most of our detected species (big brown, Myotis species, evening, and tricolored) increased with higher percentages of riverbank canopy. Even red bats and silverhaired bats, which exhibited an increased abundance in response to some urban variables, rely heavily on trees as critical sources for roost habitat. This reiterates that availability of forested habitats is an essential resource for urban bats, whether a forest-obligate or urban-tolerant species. Myotis species (little brown bat, Indiana bat, northern long-eared bat) and tricolored bats demonstrated aversion to urban sites, with Myotis species exhibiting a strong intolerance to artificial light and tricolored bats exhibiting a preference for higher riverbank canopy coverage. Our results suggest that urban forest availability and artificial light exposure should be considerations in future management decisions regarding habitat protection and the effects of land development on bats, particularly near urban waterways. Future research should focus on impacts of bridge type, developing more comprehensive measurements of prey availability for bats, and improving the anthropocentric methods used when measuring urban variables.

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TABLES & FIGURES

Table 1. Dail-Madsen model results with the lowest Akaike's Information Criterion values (\triangle AIC <2). Abundance (λ), recruitment (γ), survivorship (ω), and detection probability (P) are included in model descriptions along with covariates: RB%: Riverbank canopy %; BR: Distance to nearest the bridge; AL: Artificial light level; MIBI: Benthic macroinvertebrate index of biotic integrity river score; day: annual Julian date; temp: average nightly temperature between 11 p.m. and 5 a.m.; year: 2021 vs. 2022; and a period for no covariate effects. Species names are big brown bat (*Eptesicus fuscus*), Myotis sp. group (*Myotis lucifugus/sodalist/septentrionalis*), eastern red bat (*Lasiurus borealis*), evening bat (*Nycticius humeralis*), silver-haired bat (*Lasionycterius noctivagans*), and tricolored bat (*Perimyotis subflavus*).

Species	Model	$\triangle AIC$	K
Big brown	λ (RB%+BR+AL+MIBI) γ (.) ω (.) p (day + temp)	0	10
Myotis Sp.	λ (RB%+BR+AL+MIBI) γ (.) ω (.) p (day + temp + year)	0	10
Eastern Red	λ (RB%+BR+AL+MIBI) γ (.) ω (.) p (day + temp)	0	10
Evening	λ (RB%+BR+AL) γ (.) ω (.) p (day + temp)	0	9
	λ (RB%+BR) γ (.) ω (.) p (day + temp)	0.02	8
	λ (RB%+BR+AL+MIBI) γ (.) ω (.) p (day + temp)	1.99	10
	λ (RB%+BR+MIBI) γ (.) ω (.) p (day + temp)	1.49	9
Silver-haired	λ (RB%+BR+AL) γ (.) ω (.) p (day + temp + year)	0	10
	λ (RB%+AL) γ (.) ω (.) p (day + temp + year)	0.49	9
	λ (RB%+AL+MIBI) γ (.) ω (.) p (day + temp + year)	0.63	10
	λ (RB%+BR+AL+MIBI) γ (.) ω (.) p (day + temp + year)	0.95	11
Tricolored	λ (RB%+BR) γ (.) ω (.) p (day + temp + year)	0	9
	λ (RB%+BR+MIBI) γ (.) ω (.) p (day + temp + year)	1.68	10
	λ (RB%+BR+AL) γ (.) ω (.) p (day + temp + year)	1.86	10

Table 2. Model-averaged coefficients and 95% confidence intervals across all abundance models. Species names are big brown bat (*Eptesicus fuscus*), Myotis sp. group (*Myotis lucifugus/sodalist/ septentrionalis*), eastern red bat (*Lasiurus borealis*), evening bat (*Nycticius humeralis*), silver-haired bat (*Lasionycterius noctivagans*), and tricolored bat (*Perimyotis subflavus*).

Species	Parameter	Coefficient.	95% C.I.
Big brown	Intercept	6.09	6.04, 6.14
C	Riverbank Canopy	0.27	0.21, 0.31
	Artificial Light	-0.28	-0.34, -0.21
	Bridge Distance	0.07	0.03, 0.10
	MIBI Score	-0.27	-0.32, -0.23
Myotis Sp.	Intercept	2.14	1.91, 2.36
•	Riverbank Canopy	0.28	0.16, 0.41
	Artificial Light	-3.73	-4.16, -3.31
	Bridge Distance	0.17	0.14, 0.20
	MIBI Score	0.78	0.69, 0.87
Eastern red	Intercept	2.49	2.29, 2.70
	Riverbank Canopy	-0.20	-0.37, -0.02
	Artificial Light	-0.28	-0.51, -0.04
	Bridge Distance	0.40	0.28, 0.50
	MIBI Score	0.01	-0.17, 0.18
Evening	Intercept	3.43	3.18, 3.68
-	Riverbank Canopy	0.81	0.67, 0.95
	Artificial Light	-0.04	-0.24, 0.15
	Bridge Distance	0.07	0, 0.15
	MIBI Score	-0.03	-0.13, 0.08
Silver-haired	Intercept	2.65	2.52, 2.78
	Riverbank Canopy	-0.46	-0.6, -0.32
	Artificial Light	-0.5	-0.69, -0.31
	Bridge Distance	0.1	-0.02, 0.22
	MIBI Score	0.1	-0.05, 0.24
Tricolored	Intercept	1.2	0.57, 1.82
	Riverbank Canopy	1.84	1.32, 2.37
	Artificial Light	-1.36	-2.25, -0.47
	Bridge Distance	-0.55	-0.79, -0.31
	MIBI Score	-0.12	-0.34, 0.10



Figure 1. Thirty acoustic monitoring sites along the White River in Delaware County, IN from May-August in 2021-2022. Monitoring sites span through Daleville, Yorktown, Muncie, Smithfield, and Windsor.



Figure 2. Model predicted big brown bat (*Eptesicus fuscus*; EPFU) abundance based on a gradient of riverbank canopy cover in a 1-km buffer. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 3. Model predicted big brown bat (*Eptesicus fuscus*; EPFU) abundance based on the distance to closest bridge from the monitoring site. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 4. Model predicted big brown bat (*Eptesicus fuscus*; EPFU) abundance based on a gradient of artificial light levels at the monitoring site. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 5. Model predicted big brown bat (*Eptesicus fuscus*; EPFU) abundance based on MIBI scores. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 6. Relationship between the annual Julian day and the probability of detection of big brown bats (*Eptesicus fuscus*; EPFU) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 7. Relationship between the average nightly temperature and the probability of detection of big brown bats (*Eptesicus fuscus*; EPFU) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 8. Model predicted *Myotis* sp. group (*Myotis lucifugus/sodalist/septentrionalis*) abundance based on levels of artificial light. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 9. Model predicted *Myotis* sp. group (*Myotis lucifugus/sodalist/septentrionalis*) abundance based on a gradient of riverbank canopy cover in a 1-km buffer. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 10. Model predicted *Myotis* sp. group (*Myotis lucifugus/sodalist/septentrionalis*) abundance based on the distance to closest bridge from the monitoring site. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 11. Model predicted *Myotis* sp. group (*Myotis lucifugus/sodalist/septentrionalis*) abundance based on MIBI scores. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 12. Relationship between the annual Julian day and the probability of detection of the *Myotis* sp. group (*Myotis lucifugus/sodalist/septentrionalis*) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 13. Relationship between the average nightly temperature and the probability of detection of the *Myotis* sp. group (*Myotis lucifugus/sodalist/septentrionalis*) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 14. Relationship between 2021 vs. 2022 and the probability of detection of the *Myotis* sp. group (*Myotis lucifugus/sodalist/septentrionalis*) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 15. Model predicted eastern red bat (*Lasiurus borealis*, LABO) abundance based on a gradient of riverbank canopy cover in a 1-km buffer. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 16. Model predicted eastern red bat (*Lasiurus borealis*, LABO) abundance based on levels of artificial light. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 17. Model predicted eastern red bat (*Lasiurus borealis*, LABO) abundance based on the distance to closest bridge from the monitoring site. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 18. Model predicted eastern red bat (*Lasiurus borealis*, LABO) abundance based on MIBI scores. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 19. Relationship between the annual Julian day and the probability of detection of eastern red bats (*Lasiurus borealis*, LABO) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 20. Relationship between the average nightly temperature and the probability of detection of eastern red bats (*Lasiurus borealis*, LABO) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 21. Model predicted evening bat (*Nyctecius humeralis*, NYHU) abundance based on a gradient of riverbank canopy cover in a 1-km buffer. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 22. Model predicted evening bat (*Nyctecius humeralis*, NYHU) abundance based on the distance to closest bridge from the monitoring site. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 23. Model predicted evening bat (*Nyctecius humeralis*, NYHU) abundance based on levels of artificial light. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 24. Model predicted evening bat (*Nyctecius humeralis*, NYHU) abundance based on MIBI scores. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 25. Relationship between the annual Julian date and the probability of detection of evening bats (*Nyctecius humeralis*, NYHU) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 26. Relationship between the average nightly temperature and the probability of detection of evening bats (*Nyctecius humeralis*, NYHU) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 27. Model predicted silver-haired bat (*Lasionycterius noctivagans*; LANO) abundance based on a gradient of riverbank canopy cover in a 1-km buffer. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 28. Model predicted silver-haired bat (*Lasionycterius noctivagans*; LANO) abundance based on levels of artificial light. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 29. Model predicted silver-haired bat (*Lasionycterius noctivagans*; LANO) abundance based on the distance to closest bridge from the monitoring site. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.


Figure 30. Model predicted silver-haired bat (*Lasionycterius noctivagans*; LANO) abundance based on MIBI scores. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 31. Relationship between the annual Julian date and the probability of detection of silverhaired bats (*Lasionycterius noctivagans*; LANO) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 32. Relationship between the average nightly temperature and the probability of detection of silver-haired bats (*Lasionycterius noctivagans*; LANO) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 33. Relationship between 2021 vs. 2022 and the probability of detection of silver-haired bats (*Lasionycterius noctivagans*; LANO) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 34. Model predicted tricolored bat (*Perimyotis subflavus*, PESU) abundance based on a gradient of riverbank canopy cover in a 1-km buffer. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 35. Model predicted tricolored bat (*Perimyotis subflavus*, PESU) abundance based on levels of artificial light. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 36. Model predicted tricolored bat (*Perimyotis subflavus*, PESU) abundance based on the distance to closest bridge from the monitoring site. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 37. Model predicted tricolored bat (*Perimyotis subflavus*, PESU) abundance based on MIBI scores. All other model covariates were held constant at their mean. Data collected on May-August, 2021 and 2022 from the White River in Delaware County, IN. Solid line represents the mean predicted abundance and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 38. Relationship between the annual Julian date and the probability of detection of tricolored bats (*Perimyotis subflavus*, PESU) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 39. Relationship between the average nightly temperature and the probability of detection of tricolored bats (*Perimyotis subflavus*, PESU) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.



Figure 40. Relationship between 2021 vs. 2022 and the probability of detection of tricolored bats (*Perimyotis subflavus*, PESU) in Delaware County, IN in May-August, 2021 and 2022. All other model predictors were held constant at their mean. Solid line represents the mean probability and shaded ribbon is the bounds of the 95% Prediction Intervals.