

COMMUNITY DYNAMICS AND OCCUPANCY FOR BAT SPECIES WITHIN THE
GREAT LAKES REGION FOLLOWING WHITE-NOSE SYNDROME EXPOSURE

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ABSTRACT

North American bats are threatened by several factors including timber harvest, wind energy development, and white-nose syndrome (WNS). We used 5 long-term bat monitoring stations (LTBMS) to monitor the presence of bats in Wisconsin and determine changes in occupancy and detection probabilities from 2007 to 2017. We automatically classified calls to species using Kaleidoscope Pro (Wildlife Acoustics Inc., Maynard, MA), performed manual vetting, and generated an occurrence dataset for each year. We used multi-species occupancy models in a Bayesian framework to compare community dynamics of bats temporally by year before and after the arrival of WNS in the state. Occupancy probability for all species of bats excluding hoary bats (*Lasirurus cinereus*) declined over the survey period (i.e. 95% CI were <0 for all estimate coefficients) and following the detection of WNS. Big brown bats (*Eptesicus fuscus*) declined the least in occupancy probability overall. We observed larger declines in occupancy probabilities for the remaining cave-dwelling species, (little brown bats (*Myotis lucifugus*), tri-colored bats (*Perimyotis subflavus*), and northern long-eared bats (*Myotis septentrionalis*)) than other species of bats. Occupancy probabilities of eastern red bats (*Lasirurus borealis*) and silver-haired bats (*Lasionycteris noctivagans*) declined over the 11-year period. Detection probability fluctuated across all species and years with cave-dwelling species ranging in the lowest values overall. Our results indicate that LTBMS are successful in documenting long-term changes in the occupancy probabilities of bat species. Managers with similar objectives could use our methodology or results as a means of comparison or prediction to changes in the bat community across North America.

Several species of bats in North American are of conservation concern due to multiple factors including habitat degradation, incidental take, and the devastating fungal disease white-nose syndrome. The impact of these factors varies across species, resulting in the need for bat research on the community scale. The Western Great Lakes Region (WGLR; Minnesota, Wisconsin and the northern peninsula of Michigan) is an area where all of these threats are present. During the summers of 2015-2017, we surveyed 14 sites in the WGLR using an array of 20 SMZC echolocation recorders (Wildlife Acoustics Inc. Maynard, MA)

randomly stratified between riparian and upland habitats. We used Kaleidoscope Pro (Wildlife Acoustics) and Echoclass (Eric Britzke, U.S. Army Engineer Research and Development Center, Vicksburg, MS, USA) software to identify recorded bat calls to species. Over 3 years and 2,624 recorder nights, 207,171 audio recordings were collected and from these, 74,267 bat calls were identified. We used multi-species occupancy modeling to determine the influence of covariates including, the co-detection of other bat species, distance to road, distance to water, elevation, canopy stage, and year. Our models identified important co-detection relationships across the community; big brown bats (*Eptesicus fuscus*) influenced the occupancy of eastern red bats (*Lasirurus borealis*), and northern long-eared bats (*Myotis septentrionalis*); the co-detection of little brown bats (*Myotis lucifugus*) influenced the occupancy of big brown bats; and the co-detection of northern long-eared bats influenced the occupancy of little brown bats. Year of survey was the only variable that influenced the occupancy of hoary bats (*Lasirurus cinereus*), silver-haired bats (*Lasionycteris noctivagans*), and tri-colored bats (*Perimyotis subflavus*). Our results indicate that the analytical method, multi-species occupancy modeling is a logical application for bat echolocation acoustic data and can help address research needs on community dynamics and species interactions. Managers can use our results throughout the WGLR to guide research on species interactions and niche ecology across the bat community on a fine-scale to determine temporal niche partitioning.

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CHAPTER 1

LITERATURE REVIEW OF THE BAT COMMUNITY IN THE WESTERN GREAT LAKES REGION

Importance of Bats

Bats and their taxonomic order Chiroptera consist of over 1,200 species and are the second most diverse mammalian group after rodents. Bats in North America belong to the suborder Microchiroptera (microbats). Microbats are a diverse group that exhibits small body size, the use of echolocation, and typically are generalist insectivores. Some species, however, specialize and feed on specific insects, nectar, fish, frogs, fruit, or blood (Altringham 2011). Bats prey on pest species including corn earworms (*Helicoverpa zea*) and mosquitos (*Culex spp.*) (Reiskind and Wund 2009, Maine and Boyles 2015). Bats provide an ecological service to the agricultural industry valued at \$658 million in Wisconsin and between \$3.7 and \$53 billion in the United States (Boyles et al. 2011).

Insectivorous bats are voracious predators and frequently consume half their body weight in prey nightly (Harvey et al. 2011). This large amount of food fuels a rapid metabolism. Heart rates of bats in flight have been recorded up to 800 beats per minute (Altringham 2011). As autumn transitions towards winter, bats accelerate their feeding rates and increase their body mass by up to 32% in fat reserves (Kunz et al. 1998, Reynolds and Kunz 2000, Reeder et al. 2012), which are depleted over the winter months during hibernation. Hibernation is a prolonged state of torpor with bouts of lowered metabolic rate and body temperature (Altringham 2011). During torpor, the heart rate of some bat species can decrease to 5 to 20 beats per minute (Ransome 1990).

Despite their small size and varied metabolism, bats generally are long-lived: in 2015 one banded little brown bat (*Myotis lucifugus*) in Wisconsin lived at least 33 years (White 2016). Many species of bats couple this long lifespan with a low reproductive rate, making them particularly vulnerable to population declines (Jones et al. 2009, Harvey et al. 2011).

Threats to Bats

White-nose syndrome (WNS) is a disease of bats in North America caused by an invasive fungal pathogen *Pseudogymnoascus destructans* (*Pd*) that is believed to have come from Europe in the early 2000s (Leopardi et al. 2015). This disease is named after the characteristic white fuzzy fungus that develops on the nose and muzzle of host bats in the late stages of infection (Warnecke et al. 2013, Verant et al. 2014). Infections of *Pd* increase metabolic activity in bats and cause a higher frequency of arousal from hibernation, reducing typical bouts of torpor by nearly half (Reeder et al. 2012). Mortality is attributed to emaciation, dehydration, and respiratory acidosis due to the increase in metabolic activity from these arousals (Lorch et al. 2015). This disease has been progressing westward since its discovery in New York in 2006 and is particularly detrimental to colonial, cave-hibernating bats, including little brown bats and northern long-eared bats (*Myotis septentrionalis*) (Langwig et al. 2012). Ninety-nine percent of all colonial bats in WNS-affected hibernacula have succumbed with an estimated 6 million mortalities (Alves et al. 2014). Susceptibility to WNS, however, varies across species and has resulted in changes in the composition of bat communities where WNS has become endemic (Jachowski et al. 2014). The disease spread westward across North America in the early 2000s, with the leading edge currently stretching from Manitoba to central Texas and incidental occurrences recorded in Washington (Fig. 1, Hopkins and Soileau 2018). The WNS-affected area includes the Western Great Lakes Region (WGLR), consisting of Minnesota, Wisconsin, and the upper peninsula of Michigan, in which the disease has been present since 2013. The recent onset of WNS within the WGLR renders this area as a prime candidate for determining the effects of WNS on the bat community.

Susceptibility to WNS has not been observed in migratory tree bats, but they still are of conservation concern due to their low reproductive rates, susceptibility to direct and indirect effects of pesticides, and vulnerability to collisions with wind turbines during their migration (Arnett et al. 2008, Rollins et al. 2012). Although wind turbines cause mortalities in cave-hibernating bats, they disproportionately affect their migratory counterparts (Kunz et al. 2007).

Bat Community of WGLR

The WGLR has 4 species of cave-hibernating bats: big brown bats (*Eptesicus fuscus*), little brown bats, northern long-eared bats, and tri-colored bats (*Perimyotis subflavus*). Tri-colored bats are the only members of the genus *Perimyotis* in the United States and Canada (Harvey et al. 2011). The species was formerly of the genus *Pipistrellus* and individuals often still are referred to as “pips” or “eastern pipistrels” (Hooper et al. 2006, Harvey et al. 2011). All of these species are impacted by WNS (Blehert et al. 2009).

Big brown bats are one of the most common species in the WGLR and typically are found in proximity to humans and their structures (Harvey et al. 2011). Although they are susceptible to WNS, big brown bats have shown resistance to the disease, which is attributed to their larger body mass and fat reserves (Frank et al. 2014). Little brown bats once were considered among the most abundant and widespread of bat species in North America. Since the occurrence of WNS, however, populations have rapidly declined (Frick et al. 2010). Survivorship is estimated to be <1.5% for this species (Russell et al. 2015).

Approximately 80% of the remaining population of little brown bats reside in the upper Midwest near the Great Lakes (Russell et al. 2014). Northern long-eared bats were listed as federally threatened and protected under the United States Endangered Species Act in 2015, due to its rapid population declines from WNS (90%-100% in affected areas) (USFWS 2016). Both little brown bats and northern long-eared bats typically have one pup per year whereas the other species in the WGLR typically have twins, but litter sizes can range from 1 to 4 (Harvey et al. 2011). Tri-colored bats tend to hibernate singly or in small clustered groups, which is hypothesized to make them more susceptible to mortality during this period (Schwartz and Schwartz 2001, Briggler and Prather 2003, Hoyt et al. 2018). Tri-colored bats have been observed migrating seasonally prior to hibernation (Fraser et al. 2012).

The other 4 species of bats in the WGLR are migratory tree bats, including the eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivagans*), and evening bat (*Nycticeius humeralis*). These species reside in the WGLR during summer months but migrate to southern states in winter and hibernate within tree cavities or bark (Altringham 2011). Evening bats recently were

discovered in the WGLR in 2016 and little is known about their wintering habitat (Harvey et al. 2011, Holtan and Street 2016). Eastern red bats and silver-haired bats have been detected with *Pd*, but show no clinical signs of WNS (Bernard et al. 2015). Transmission between these migratory species and their cave-hibernating counterparts has not been observed but demands further study.

Community Dynamics of Bats

The diversity within the community of insectivorous bats is driven by competition (Arlettaz and Hausser 1997, Patterson et al. 2003, Ashrafi et al. 2011). These species have developed an assortment of unique jaw, sensory organ, and wing morphologies in response to this inter-specific competition for habitat and prey-base (Aldridge and Rautenbach 1987, Barclay and Brigham 1991, Siemers and Schnitzler 2004, Siemers and Swift 2006). Bats that echolocate at similar call bandwidth, frequency, and call structure experience competition from either the “jamming” of calls in high-traffic areas, which could lead to bats dispersing elsewhere (Habersetzer 1981, Ratcliffe et al. 2004, Necknig and Zahn 2011) or by drawing additional species in to high-quality habitat through “eavesdropping” behavior (Fenton 2003, Gillam 2007, Dechmann et al. 2009, Furmankiewicz et al. 2011, Übernickel et al. 2013, Jachowski et al. 2014).

To limit inter-specific competition, niche partitioning among bat species occurs primarily on spatial and temporal scales (Jachowski et al. 2014). Temporal partitioning over the course of a night typically is observed in bat species that use the same limited resource simultaneously, such as water features in arid environments (Kunz 1973, Reith 1980, Castro-Arellano et al. 2009, Hall et al. 2016). Spatial partitioning has been observed in fine scale for insectivorous species of bats, where specific characteristics of foraging habitat are exploited (Arlettaz 1999, Arlettaz et al. 2000, Patterson et al. 2003, Nicholls and Racey 2006, Razgour et al. 2011, Hall et al. 2016). The effects of rapid population decline of bats on the factors that cause niche partitioning are understudied, but Jachowski et al. (2014) observed cascading indirect effects on community structure attributed to declines of populations of little brown bats after the occurrence of WNS.

Acoustic Sampling

Acoustic sampling is one of the most effective methods for monitoring the presence of bats (O'Farrell and Gannon 1999, Loeb et al. 2015). Acoustic Recorders are devices that record sounds within the echolocation frequencies of bats. These sounds are saved as digital files on the device and can be analyzed to identify species. Software programs and packages facilitate the identification process. To reduce the likelihood of false-positives, however, manual identification procedures often are used concurrently (Fritsch and Bruckner 2014). Two primary methods are used for the identification of species using echolocation data (Brigham et al. 2004). Zero-cross analysis breaks down the complexity of bat echolocation by measuring the duration of each call cycle, which then can be used to calculate frequency; making this approach less demanding on recording equipment in terms of power and data storage, but less sensitive than full-spectrum analysis (Corben 2004). Full-spectrum analysis includes harmonics and amplitude in the characteristics of echolocation calls, increasing identification sensitivity but requiring robust recording equipment (Corben 2004, Szewczak 2004). Acoustic sampling allows for non-invasive data collection compared to mist netting or hibernacula counts (Loeb et al. 2015). A priority of current research is the long-term acoustic monitoring programs to document bat population levels related to WNS (Ford et al. 2011). In the WGLR, Wisconsin is unique, having established a permanent bat monitoring program 7 years prior to the arrival of *Pd* (WIATRI 2012a-e).

Bayesian Analysis

Bayesian statistical analysis is rising in popularity with ecologists (Ellison 2004). Although its application in natural resource sciences is a recent development, this method of analysis is over 250 years old (Kéry 2010). The process is built upon Bayes' theorem, which is the calculation of the probability of 2 events by multiplying the probability of the first $p(A)$ by the conditional probability of the second $p(B)$ (McKillup 2012).

$$p(A|B) = \frac{p(B|A) * p(A)}{p(B)}$$

Similar to its more common frequentist statistics counterpart, Bayesian methods view data as the observed realization of stochastic systems. Bayesian statisticians, however, consider parameters, the values used to describe random processes, as part of a larger unobserved stochastic system (Kéry 2010). In execution, this perspective takes the form of a prior distribution, a population of potential parameter values that then provide a probabilistic characterization of the influence of these parameters (Mackenzie et al. 2018). This approach generates probability distributions and their level of uncertainty. For ecologists, these results can be simple to understand, directly show their biological significance, and allow for easy comparison with other models (Mills 2013).

Multiple Species Occupancy Modeling

A quantitative method that lends itself to Bayesian statistical analysis is occupancy modeling. Occupancy, defined as a proportion of sample units that are occupied, is a measure of a species' presence (and therefore absence) adjusting for the probability of non-detection. In ecology, this modeling process is applied to monitor a species' geographic range, resource selection, and meta-population dynamics among others (Mackenzie et al. 2018). The initial occupancy state of the m^{th} species at location i is:

$$Z_{m,l,i} | \omega_m, \Psi_{m,l,i} \sim \text{Bernoulli}(\omega_m \Psi_{m,l,i})$$

where $\Psi_{m,l,i} = PR (Z_{m,l,i} = 1 | \omega_m = 1)$ is the probability that species m is present at location i during season 1 (Mackenzie et al. 2018). Data augmentation variables are represented by ω_m (Mackenzie et al. 2018). The true presence or absence of species m at location i during season 1 is denoted as $Z_{m,l,i}$ and is considered as a latent random variable as it is not directly observable (Mackenzie et al. 2018).

Occupancy modeling has been implemented as an analytical method for several bat species on an individual basis (Yates and Muzika 2006, Duchamp and Swihart 2008, Weller and Baldwin 2012,

Coleman et al. 2014), but current literature on multi-species site occupancy modeling of bats is very limited (Pauli et al. 2017). The results of these multi-species models share information among species, therefore allowing for the estimation of parameters for rare as well as common species (Dorazio and Royle 2005, Dorazio et al. 2006, Kéry and Royle 2009, Zipkin et al. 2009) which can address conservation concerns across a community (Pauli et al. 2017). Multi-species occupancy modeling is a logical application for bat acoustic data given that calls for multiple species can be recorded simultaneously (Pauli et al. 2017). Our study is only the second multi-species occupancy analysis used to model bat species (Pauli et al. 2017).

GOALS AND OBJECTIVES

Our goal was to describe the community dynamics of bats in the WGLR following exposure of the WGLR to WNS. The objectives were to 1) determine the long-term occupancy of bats in Wisconsin from 2007 to present in relation to WNS exposure and 2) determine the current occupancy of bats within the WGLR in relation to habitat covariates and the co-detection of other species.

CHAPTER 2

RH: Meyer et al. • Multi-species Bat Occupancy

Long-term Changes in Occupancy of the Bat Community in Wisconsin Including the Arrival of White-nose Syndrome

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ABSTRACT

North American bats are threatened by several factors including timber harvest, wind energy development, and white-nose syndrome (WNS). We used 5 long-term bat monitoring stations (LTBMS) to monitor the presence of bats in Wisconsin and determine changes in occupancy and detection

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probabilities from 2007 to 2017. We automatically classified calls to species using Kaleidoscope Pro (Wildlife Acoustics Inc., Maynard, MA), performed manual vetting, and generated an occurrence dataset for each year. We used multi-species occupancy models in a Bayesian framework to compare community dynamics of bats by year before and after the arrival of WNS in the state. Occupancy probability for all species of bats excluding hoary bats (*Lasirurus cinereus*) declined over the survey period (i.e. 95% CI were <0 for all estimate coefficients) and following the detection of WNS. Big brown bats (*Eptesicus fuscus*) declined the least in occupancy probability overall. We observed larger declines in occupancy probabilities for the remaining cave-dwelling species, (little brown bats (*Myotis lucifugus*), tri-colored bats (*Perimyotis subflavus*), and northern long-eared bats (*Myotis septentrionalis*)) than other species of bats. Occupancy probabilities of eastern red bats (*Lasirurus borealis*) and silver-haired bats (*Lasionycteris noctivagans*) declined over the 11-year period. Detection probability fluctuated across all species and years with cave-dwelling species ranging in the lowest values overall. Our results indicate that LTBMS are successful in documenting long-term changes in the occupancy probabilities of bat species. Managers with similar objectives could use our methodology or results as a means of comparing or predicting changes in the bat community across North America.

KEY WORDS acoustic, Bayesian, bat, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Lasiurus*, long-term bat monitoring station, multi-species occupancy modeling, *Myotis*, *Perimyotis subflavus*, Wisconsin.

White-nose syndrome (WNS) is a disease of bats in North America caused by an invasive fungal pathogen *Pseudogymnoascus destructans* (*Pd*) that is believed to have come from Europe in the early 2000s (Leopardi et al. 2015). Infections of *Pd* increases metabolic activity in bats and causes a higher frequency of arousal from hibernation, reducing typical bouts of torpor by nearly half (Reeder et al. 2012). Mortality is attributed to emaciation, dehydration, and respiratory acidosis due to the increase in metabolic activity from these arousals and is particularly detrimental to colonial, cave-hibernating bats, including little brown bats (*Myotis lucifugus*) and northern long-eared bats (*Myotis septentrionalis*)

(Langwig et al. 2012, Verant et al. 2014, Lorch et al. 2015). Ninety-nine percent of all colonial bats in WNS-affected hibernacula have succumbed with an estimated 6 million mortalities (Alves et al. 2014). Susceptibility to WNS, however, varies across species and has resulted in changes to the composition of bat communities where WNS has become endemic. The disease spread westward since its discovery in New York in 2006 with its leading edge currently stretching from Manitoba to central Texas and incidental occurrences recorded in Washington (Hopkins and Soileau 2018). The WNS-affected area includes Wisconsin where the disease has been present since 2013. The recent onset of WNS within Wisconsin renders this area as a prime candidate for determining the effects of WNS on the bat community.

Wisconsin has 4 species of cave-hibernating bats: big brown bats (*Eptesicus fuscus*), little brown bats, northern long-eared bats, and tri-colored bats (*Perimyotis subflavus*). All of these species are impacted by WNS (Blehert et al. 2009). Big brown bats are 1 of the most common species in Wisconsin and have been observed to be less susceptible than other species to the disease (Frank et al. 2014). Little brown bats once were considered among the most abundant and widespread of bat species in North America. Since the occurrence of WNS, however, populations have rapidly declined (Frick et al. 2010). Survivorship is estimated to be <1.5% for this species (Russell et al. 2015). Approximately 80% of the remaining population of little brown bats reside in the upper Midwest near the Great Lakes (Russell et al. 2014). Northern long-eared bats were listed as federally threatened and protected under the United States Endangered Species Act in 2015, due to its rapid population declines from WNS (90%-100% in affected areas) (USFWS 2016). Tri-colored bats tend to hibernate singly or in small clustered groups, which is hypothesized to make them more susceptible to mortality during this period (Schwartz and Schwartz 2001, Briggler and Prather 2003, Hoyt et al. 2018). The other 4 species of bats in Wisconsin are migratory tree bats, including the eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivagans*), and evening bat (*Nycticeius humeralis*). These species reside in Wisconsin during summer months but migrate to southern states in winter and hibernate within tree

cavities or bark (Altringham 2011). Evening bats recently were discovered in Wisconsin in 2016 and little is known about their wintering habitat (Harvey et al. 2011, Holtan and Street 2016). Eastern red bats and silver-haired bats have been detected with *Pd*, but show no clinical signs of WNS in other parts of their range (Bernard et al. 2015). Transmission between these migratory species and their cave-hibernating counterparts has not been observed but demands further study.

All of Wisconsin's species of bats are voracious insectivorous predators and frequently consume half their body weight in prey nightly (Harvey et al. 2011) (Reiskind and Wund 2009, Maine and Boyles 2015). Bats that feed on crop and livestock pests provide an ecological service to the agricultural industry valued at \$658 million in Wisconsin and between \$3.7 and \$53 billion in the United States (Boyles et al. 2011). Many species of bats couple this long lifespan with a low reproductive rate, making them particularly vulnerable to population declines (Jones et al. 2009, Harvey et al. 2011).

Acoustic sampling is one of the most effective methods for monitoring the presence of bats (O'Farrell and Gannon 1999, Loeb et al. 2015). Acoustic recorders are devices that record sounds within the echolocation frequencies of bats. These sounds are saved as digital files on the device and can be analyzed to identify species. Software programs and packages facilitate the identification process. To reduce the likelihood of false-positives, however, manual identification procedures often are used concurrently (Fritsch and Bruckner 2014). Acoustic sampling allows for non-invasive data collection compared to mist netting or hibernacula counts (Loeb et al. 2015). Long-term acoustic monitoring programs to document bat population levels related to WNS is a priority of current research (Ford et al. 2011). Wisconsin is unique, having established a permanent bat monitoring program 7 years prior to the arrival of *Pd* (WIATRI 2012a-e).

A logical application for bat acoustic data is multi-species occupancy modeling, given that calls for multiple species can be recorded simultaneously (Pauli et al. 2017). Occupancy, defined as a proportion of sample units that are occupied, is a measure of a species' presence (and therefore absence) adjusting

for the probability of non-detection. In ecology, this modeling process is applied to monitor a species' geographic range, resource selection, and meta-population dynamics among others (Mackenzie et al. 2018). Presence and absence of a species are considered as a latent random variable because a true absence is not observable in nature (Mackenzie et al. 2018). What is observable, however, is the result of the survey's detection probability, which is the notion that all observations are the result of an ecological process occurring and are conditional based on the success of the observation process (Royle and Dorazio 2006, 2008).

Occupancy modeling has been implemented as an analytical method for several bat species on an individual basis (Yates and Muzika 2006, Duchamp and Swihart 2008, Weller 2008, Weller and Baldwin 2012, Coleman et al. 2014), but current literature on modeling of multi-species site occupancy of bats is very limited (Pauli et al. 2017). The results of these multi-species models share information among species, therefore allowing for the estimation of parameters for both rare and common species (Dorazio and Royle 2005, Dorazio et al. 2006, Kéry and Royle 2009, Zipkin et al. 2009) which can address ecological concerns across a community (Pauli et al. 2017). Our study is only the second multi-species occupancy analysis used to model bat species (Pauli et al. 2017).

Our objective was to describe the changes in the long-term occupancy of bats in Wisconsin before (2007-2013) and after (2014-2017) exposure to WNS.

STUDY AREA

We conducted the study at 5 long-term bat monitoring stations (LTBMS) located within public natural resource areas across Wisconsin (Fig. 1). Cofrin Arboretum (CA) consisted of 1.1 km² of oak (*Quercus spp.*) forests, prairies, creeks, and ponds. The LTBMS was adjacent to the University of Wisconsin-Green Bay campus and is located within 125 m of Lake Michigan (WIATRI 2012). Schmeckle Reserve (SR) consisted of 1.13 km² of mixed forest birch (*Betula spp.*), oak, white pine (*Pinus strobus*), restored prairie, and wetlands, including a 0.12 km² human-made lake. The LTBMS was adjacent to a visitor

center and a 0.016 km² restored prairie (WIATRI 2012). Kemp Natural Resource Station (KNRS) consisted of 0.95 km² of old growth forest of hemlock (*Tsuga canadensis*), pine (*Pinus spp.*), and mixed hardwood secondary succession (WIATRI 2012). The LTBMS was located on the edge of a naturally disturbed blowdown that occurred in 2000. The Urban Ecology Center (UEC) consisted of a 0.06 km² wooded park and was located in Milwaukee 2.41 km west of Lake Michigan. The LTBMS was located in a 0.06 km² restored prairie and oak savannah inside Riverside Park (WIATRI 2012). The University of Wisconsin-Madison Arboretum (UWMA) consisted of 4.9 km² of restored woodlands, prairie, public areas, marshlands, and Lake Wingra. The LTBMS was located in 0.243-km² Curtis Prairie, the world's oldest restored prairie (WIATRI 2012).

METHODS

Data Collection and Management

Each LTBMS consisted of a single cement-fixed 3-m tower that holds a top-mounted weather-resistant microphone enclosure and reflector plate. Within each was an AnaBat SD2 detector (Titley Scientific, Columbia, MO) with compact flash storage drive, powered by a 10-w solar panel and 12-v battery and charge controller (EME Systems, Berkley, CA) within a weather-proof locked case. After their initial launch in 2007, recordings began at 30 min before sunset and concluded 30 min after sunrise, throughout the year. We downloaded recorded data saved in a zero-cross format (Corben 2004) from compact flash memory cards using the program CFCRead (Titley Scientific, Columbia, MO).

We processed acoustic files using the software program Kaleidoscope Pro versions 4.0.0 and 4.5.4 (Wildlife Acoustics Inc., Maynard, MA). Data were verified manually by Dr. W. Mark Ford and researchers of the Virginia Cooperative Fish and Wildlife Research Unit and R. Paul White and staff of the Wisconsin Department of Natural Resources Bat Program. Kaleidoscope estimated an associated maximum likelihood estimator (MLE) regarding accurate species identification within a range of 0 to 1 (0-no misidentification, 1-certain misidentification). We used identifications with an MLE value of ≤ 0.05 to

determine if a site was occupied for that night (Clement et al. 2014). We constructed a temporal dataset that contained nights of occurrence by month and year per site. Detections occurring outside the typical active months of March through October were disregarded (White 2018a). As part of the binary nature of occupancy data, each month was reduced to having either a 0 or 1 for each species in which a “0” indicated the LTBMS did not detect that species that month and a “1” indicated the LTBMS detected that species that month and the site was designated as occupied for that month (Mackenzie et al. 2018).

Analytical Methods

We used a dynamic multi-species occupancy methodology to develop models that described and predicted bat occupancy and detection probability at the LTBMS sites across Wisconsin (Kéry and Schaub 2012). For each model, we treated months as repetitions within the survey periods of each year and all priors as uninformed. In the first model, we included year of study in the equation

$$\text{logit}(\Psi_{year,species,site}) = \phi_{species} + \beta_{species} * year_{year} \text{ with } \beta_{species} \text{ as a random effect using a}$$

normal distribution and $year_y$ as a continuous covariate (1-11). In the second model, we treated all years before 2014 as “Pre-WNS” (0) and all years including and after 2014 as “WNS Present” (1) in the

equation $\text{logit}(\Psi_{year,species,site}) = \phi_{species} + \beta_{species} * WNS_{year}$ with WNS_{year} as a random effect binomial covariate using a Bernoulli distribution. We calculated the changes in detection probability over time by repeating the year of survey model while treating $year_{year}$ as a fixed effect. We determined if the

beta coefficients of year or WNS presence had an effect on occupancy probability based on if the 95% credible interval (CI) contained 0 (Pauli et al. 2017). Omitting 0 restricted the beta coefficients to

influence occupancy probability in either a positive or negative relationship (Kruschke 2015, Mackenzie et al. 2018). For all models, year of survey and species were considered as alpha coefficients for

calculating detection probability $\text{logit}(p_{year,species}) = p_{year} + p_{species}$ with p_{year} and $p_{species}$ using

normal distributions for prior distributions of each. We ran each model as 3 independent chains of 50,000 iterations, discarded an initial 10,000 iterations as burn-in and retained every fourth iteration for a total of

15,000 iterations per model. We analyzed the data using Program R, RStudio, and JAGS via the rjags package (Plummer 2003, 2017, Kruschke 2015, R Core Team 2016, RStudio Team 2016).

RESULTS

From 2007 to 2018, 554,512 acoustic files were recorded by the 5 LTBMS, including UEC (252,731), UWMA(115,765), SR (83,744), KNRS (67,943), and CA (34,329). Following 2011, the LTBMS at CA went offline and did not contribute further data. Of the total files, 186,169 (33.57%) were manually vetted by experts within the Virginia Fish and Wildlife Research Unit and the Wisconsin Bat Program and agreed with 64.83% of the Kaleidoscope automatic identification designation. This agreement was regardless of the MLE designation for accuracy provided by the automatic identification process and supports our conservative approach of using automatic identifications designated by Kaleidoscope of an MLE value of ≤ 0.05 (Clement et al. 2014, Reichert et al. 2018). All bat species were detected at each LTBMS at least once. All species were detected each year of the survey except northern long-eared bats in 2017. All species were detected at least once each month throughout the study, except little brown bats were not detected in March of any year.

Occupancy probability for all species of bats declined from 2007 to 2017 (Fig 2). The year of survey model indicated that all species excluding Hoary bats declined in occupancy over the survey period (i.e., 95% CI were < 0 for all estimate coefficients) (Table 1). The order of species from least decline in occupancy probability to most are big brown bats (0.990 to 0.458), silver-haired bats (0.986 to 0.439), eastern red bats (0.986 to 0.431), little brown bats (0.982 to 0.356), tri-colored bats (0.972 to 0.270), and northern long-eared bats (0.978 to 0.237) (Fig. 2). When the 97.5% and 2.5% quantile values were evaluated through a linear model across years, the rate of decline also was representative of this order of decline in occupancy probability (Table 2).

In the WNS detection model, occupancy of species impacted by WNS declined in a similar manner to the previous model, with big brown bats declining the least and northern long-eared bats declining the most

overall (Table 2). The occupancy probability of big brown bats declined (0.985 to 0.552), little brown bats declined (0.967 to 0.499), tri-colored bats declined (0.946 to 0.405), and northern long-eared bats declined (0.958 to 0.349) (Fig. 3). When the 97.5% and 2.5% quantile values of the WNS detection model were evaluated through a linear model, the rate of decline also was representative of this order of decline in occupancy probability (Table 2).

Across years, detection probability fluctuated, peaking in the first year (2007) and was at its lowest in 2016 for all species (Fig. 4). Although the fluctuations of detection probability increase and decrease across years in a similar manner for all species (Fig. 4), the ranges of values differ among species.

Average detection probability for the migratory species was highest overall with the mean 97.5% quantile for eastern red bats and silver-haired bats at 0.808 and 0.743 and their mean 2.5% quantile at 0.638 and 0.557 respectively. The order of highest to least average detection probability for cave-hibernating species was big brown bats with their 97.5% and 2.5% quantiles averaging at 0.6912 and 0.497, little brown bats at 0.618 and 0.413, tri-colored bats at 0.555 and 0.344, and northern long-eared bats at 0.418 and 0.220. Processing these quantile values through a linear model resulted in negative slopes for all species, showing declines in detection probability over time (Table 2).

DISCUSSION

Our results show substantial declines in occupancy probabilities of all but 1 species of bats, suggesting large-scale declines in their populations across Wisconsin. Occupancy modeling has been frequently sought as a solution to predicting the dynamic processes of populations that were either too cryptic or too broadly distributed across a landscape to effectively use traditional mark-recapture methods (Mackenzie et al. 2018). One criticism of this method is that occupancy probability is not sensitive to change derived from declining populations due to survival, colonization, and extinction rates persisting at typical ranges despite decreasing population size (van Strein et al. 2011, Conner et al. 2016, Mackenzie et al. 2018). Given this lack of sensitivity, our results are supported by the known decreases in populations of bats in

Wisconsin from the documented decline in hibernacula counts and summer surveys (Grotsky et al. 2012, Hyzy 2017, Hoyt et al. 2018, Kaarakka 2018, Langwig 2018, White 2018b). Due to the consistent observation process of the LTBMS, our differences in detection probability ranges for these species also is indicative of changes within the bat community at these sites.

We observed large declines in occupancy probabilities for species impacted by WNS (little brown bats, tri-colored bats, and northern long-eared bats). Our results are reinforced by decreases in summer roost counts and declining capture success of mist net surveys statewide (Hyzy 2017, Kaarakka 2018). Our observed decline in occupancy probability coincide with hibernacula counts across the state that recently indicated population declines of at least 90% for little brown bats, northern long-eared bats, and tri-colored bats; with Grant County, the original infection point for WNS in Wisconsin, declining 98.4% overall (Langwig 2018, White 2018b). Occupancy probabilities of big brown bats declined the least for all species in both our models. These results may be attributed to the observed biological resistance of big brown bats to *Pd* due to their relatively large size and fat reserves (Frank et al. 2014). Although this resistance often is associated with the frequency in which big brown bats hibernate in buildings (Whitaker and Gummer 1992, 2000), recent research indicates the occurrence of sub- and pre-clinical WNS on big brown bats roosting in heated buildings (McAlpine et al. 2016).

Occupancy probabilities of eastern red bats and silver-haired bats declined over the 11-year period. While our methodology was sensitive to long-term differences across the years, it was not sensitive to fine-scale temporal detection and non-detection over the course of a night (Jachowski et al. 2014, Neece et al. 2018). A fine-scale approach could have discerned transient migratory species passing by an LTBMS from those that were consistently foraging in the area through an application of more accurate turnover rates and detection probabilities (Neece et al. 2018). By increasing the fine-scale temporal sensitivity of the models, we might bring the occupancy probability estimations for hoary bat into significance, as this species flies at higher altitudes and are infrequent echolocators, which causes this species to experience lower detection probabilities in other studies (Kalcounis et al. 1999, Corcoran and Weller 2018, Neece et

al. 2018). Susceptibility to WNS has not been observed in migratory tree bats, but they still are of conservation concern due to their low reproductive rates, timber harvest, susceptibility to direct and indirect effects of pesticides, and vulnerability to collisions with wind turbines during their migration (Arnett et al. 2008, Rollins et al. 2012). Although wind turbines cause mortalities in cave-hibernating bats, they disproportionately affect their migratory counterparts (Kunz et al. 2007).

Wind energy development in Wisconsin could be associated with our results indicating declines in occupancy, however further analysis regarding the proximity of wind energy facilities to these LTBMS and the dates of their operation is needed (Ford et al. 2011, Weller and Baldwin 2012, Clement et al. 2014, Diffendorfer et al. 2015). , Nearly 68% of an estimated 4,454 bat mortalities were associated with wind turbines in southeastern Wisconsin, and these were all migratory species (Grotsky et al. 2012). Although wind energy developments have been in Wisconsin since 1998, the growth of the industry has been limited due to economic considerations, compared to neighboring states (Oteri et al. 2018).

Our results are the novel presentation of data collected by fixed LTBMS across a state prior to and following the detection of WNS within the survey area. Other areas in the United States including Indiana, Maine, the mid-Atlantic states, and the Great Lakes states have since adopted similar programs based on comparable LTBMS or stations deployed on offshore structures InDNR n.d., Peterson et al. 2016) Our ongoing survey period of 11 years makes this study among the longest acoustic datasets collected by the research community in North American (Ford et al. 2011, Jachowski et al. 2014). Furthermore, our study is just the second to apply multi-species occupancy modeling to the North American bat community and the first to incorporate data collected on both cave-hibernating and migratory species (Pauli et al. 2017).

MANAGEMENT IMPLICATIONS

Our results indicate that LTBMS are successful in documenting long-term changes in the occupancy probabilities of bat species. Managers with similar objectives could implement our methods as a means of

acoustic monitoring that requires minimal upkeep and maintenance. By observing declines in occupancy probability or detection probability for bats at LTBMS, researchers could use our results to infer that potential population declines may be occurring. Managers in other regions whose bat community may be facing different levels of habitat fragmentation, WNS proliferation, or mortality associated with wind energy development could integrate their occupancy results with our study to observe potential differences in long-term changes. Furthermore, the continuation of our long-term study can track the changes of occupancy probability and attribute site-specific features and conditions to these sources of bat mortality.

CHAPTER 3

RH: Meyer et al. • Multi-species Bat Occupancy

Multi-species Occupancy of Bats in the Western Great Lakes Region

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ABSTRACT

Several species of bats in North American are of conservation concern due to multiple factors including habitat degradation, incidental take, and the devastating fungal disease white-nose syndrome. The impact of these factors varies across species, resulting in the need for bat research on the community scale. The Western Great Lakes Region (WGLR; Minnesota, Wisconsin and the northern peninsula of Michigan) is

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an area where all of these threats are present. During the summers of 2015-2017, we surveyed 14 sites in the WGLR using an array of 20 SMZC echolocation recorders (Wildlife Acoustics Inc. Maynard, MA) randomly stratified between riparian and upland habitats. We used Kaleidoscope Pro (Wildlife Acoustics) and Echoclass (Eric Britzke, U.S. Army Engineer Research and Development Center, Vicksburg, MS, USA) software to identify recorded bat calls to species. Over 3 years and 2,624 recorder nights, 207,171 audio recordings were collected and from these, 74,267 bat calls were identified. We used multi-species occupancy modeling to determine the influence of covariates including, the co-detection of other bat species, distance to road, distance to water, elevation, canopy stage, and year. Our models identified important co-detection relationships across the community; big brown bats (*Eptesicus fuscus*) influenced the occupancy of eastern red bats (*Lasirurus borealis*), and northern long-eared bats (*Myotis septentrionalis*); the co-detection of little brown bats (*Myotis lucifugus*) influenced the occupancy of big brown bats; and the co-detection of northern long-eared bats influenced the occupancy of little brown bats. Year of survey was the only variable that influenced the occupancy of hoary bats (*Lasirurus cinereus*), silver-haired bats (*Lasionycteris noctivagans*), and tri-colored bats (*Perimyotis subflavus*). Our results indicate that the analytical method, multi-species occupancy modeling is a logical application for bat echolocation acoustic data and can help address research needs on community dynamics and species interactions. Managers can use our results throughout the WGLR to guide research on species interactions and niche ecology across the bat community on a fine-scale to determine temporal niche partitioning.

KEY WORDS acoustic, Bayesian, *Eptesicus fuscus*, Great Lakes, hoary bat, *Lasionycteris noctivagans*, *Lasiurus*, Michigan, Minnesota, multi-species occupancy modeling, *Myotis*, *Perimyotis subflavus*, Wisconsin.

Bats throughout North America currently are facing many threats to their survival and existence. White-nose syndrome (WNS) is a disease of bats caused by an invasive fungal pathogen *Pseudogymnoascus destructans* (*Pd*). Infections of *Pd* increases metabolic activity in bats and causes a higher frequency of arousal from hibernation, reducing typical bouts of torpor by nearly half (Reeder et al. 2012). Mortality is attributed to emaciation, dehydration, and respiratory acidosis due to the increase in metabolic activity from these arousals and is particularly detrimental to colonial, cave-hibernating bats, including little brown bats (*Myotis lucifugus*) and northern long-eared bats (*Myotis septentrionalis*) (Langwig et al. 2012, Verant et al. 2014, Lorch et al. 2015). Ninety-nine percent of all colonial bats in WNS-affected hibernacula have succumbed with an estimated 6 million mortalities (Alves et al. 2014). Susceptibility to WNS, however, varies across species and has resulted in changes to the composition of bat communities where WNS has become endemic (Jachowski et al. 2014). The disease spread westward since its discovery in New York in 2006 with its leading edge currently stretches from Manitoba to central Texas and incidental occurrences recorded in Washington (Hopkins and Soileau 2018). The WNS affected area includes the Western Great Lakes Region (WGLR), consisting of Minnesota, Wisconsin, and the northern peninsula of Michigan, in which the disease has been present since 2013. The recent onset of WNS within the WGLR renders this area as a prime candidate for determining the effects of WNS on the bat community. Even though susceptibility to WNS in migratory tree bats has not been documented, they still are of conservation concern due to their low reproductive rates, susceptibility to direct and indirect effects of pesticides, and vulnerability to collisions with wind turbines during their migration periods (Arnett et al. 2008, Rollins et al. 2012).

The WGLR has 4 species of cave-hibernating bats: big brown bats (*Eptesicus fuscus*), little brown bats, northern long-eared bats, and tri-colored bats (*Perimyotis subflavus*). Tri-colored bats are the only members of the genus *Perimyotis* in the United States and Canada (Harvey et al. 2011). All of these species are impacted by WNS (Blehert et al. 2009). Big brown bats are 1 of the most common species in the WGLR and typically are found in proximity to humans and their structures (Harvey et al. 2011). Little

brown bats once were considered among the most abundant and widespread of bat species in North America. Since the occurrence of WNS however, populations have rapidly declined (Frick et al. 2010). Survivorship is estimated to be <1.5% for this species (Russell et al. 2015). Approximately 80% of the remaining population of little brown bats reside in the upper Midwest near the Great Lakes (Russell et al. 2014). Northern long-eared bats were listed as federally threatened and protected under the United States Endangered Species Act in 2015, due to its rapid population declines from WNS (90%-100% in affected areas) (USFWS 2016). Tri-colored bats tend to hibernate singly or in small clustering groups, which is hypothesized to make them more susceptible to mortality during this period (Schwartz and Schwartz 2001, Briggler and Prather 2003, Hoyt et al. 2018). Tri-colored bats have been observed migrating seasonally prior to hibernation (Fraser et al. 2012). The other 4 species of bats in the WGLR are migratory tree bats: eastern red bats (*Lasiurus borealis*), hoary bats (*Lasiurus cinereus*), silver-haired bats (*Lasionycteris noctivagans*), and evening bats (*Nycticeius humeralis*). These species reside in this region during summer months but migrate to southern states in winter and hibernate within tree cavities or bark (Altringham 2011). Evening bats recently were discovered in the WGLR during the course of this study (2016) and much is still unknown regarding their wintering habitat (Harvey et al. 2011, Holtan and Street 2016). Eastern red bats and silver-haired bats have been detected with *Pd*, but show no clinical signs of WNS in other parts of their range (Bernard et al. 2015). The possibility of transmission between these migratory species and their cave-hibernating counterparts still is unknown and awaits further study.

The diversity within the community of insectivorous bats is driven by competition (Arlettaz and Hausser 1997, Patterson et al. 2003, Ashrafi et al. 2011). These species have developed an assortment of the unique jaw, sensory organ, and wing morphologies in response to this inter-specific competition for habitat and prey-base (Aldridge and Rautenbach 1987, Barclay and Brigham 1991, Siemers and Schnitzler 2004, Siemers and Swift 2006). Bats that echolocate at similar call bandwidth, frequency, and call structure may experience competition from either the “jamming” of calls in high-traffic areas, which could result in bats dispersing to elsewhere (Habersetzer 1981, Ratcliffe et al. 2004, Necknig and Zahn

2011) or “eavesdropping” behavior, which could result in bats being drawn to high-quality habitat (Fenton 2003, Gillam 2007, Dechmann et al. 2009, Furmankiewicz et al. 2011, Übernickel et al. 2013, Jachowski et al. 2014).

To limit inter-specific competition, niche partitioning among bat species occurs primarily on spatial and temporal scales (Jachowski et al. 2014). Temporal partitioning over the course of a night typically is observed in bats that use the same limited resource simultaneously, such as water features in arid environments (Kunz 1973, Reith 1980, Castro-Arellano et al. 2009, Hall et al. 2016). Spatial partitioning has been observed in fine scale for insectivorous bat species, where specific foraging habitat characteristics, such as prey habitat requirements or artificial light sources, are exploited (Arlettaz 1999, Arlettaz et al. 2000, Patterson et al. 2003, Nicholls and Racey 2006, Razgour et al. 2011, Hall et al. 2016). The effects of rapid population decline of bats on factors that cause niche partitioning are understudied, but Jachowski et al. (2014) observed cascading indirect effects on community structure attributed to population declines of little brown bats after the occurrence of WNS.

Acoustic sampling is one of the most effective methods for monitoring the presence of bats (O’Farrell and Gannon 1999, Loeb et al. 2015). Acoustic recorders are devices that record sounds within the echolocation frequencies of bats. These sounds are saved as digital files on the device and can be analyzed to identify species. Software programs and packages facilitate the identification process. To reduce the likelihood of false-positives, however, manual identification procedures often are used concurrently (Fritsch and Bruckner 2014). Acoustic sampling allows for non-invasive data collection compared to mist netting or hibernacula counts (Loeb et al. 2015). A logical application for bat acoustic data is multi-species occupancy modeling, given that calls for multiple species can be recorded simultaneously (Pauli et al. 2017). Occupancy, defined as a proportion of sample units that are occupied, is a measure of a species’ presence (and therefore absence) adjusting for the probability of non-detection. In ecology, this modeling process is applied to monitor a species’ geographic range, resource selection, and meta-population dynamics among others (Mackenzie et al. 2018). Presence and absence of a species

are considered as a latent random variable because a true absence is not observable in nature (Mackenzie et al. 2018). What is observable, however, is the result of the survey's detection probability, which is the notion that all observations are the result of an ecological process occurring and are conditional based on the observation process' success (Royle and Dorazio 2006, 2008).

Occupancy modeling has been implemented as an analytical method for several bat species on an individual basis (Yates and Muzika 2006, Duchamp and Swihart 2008, Weller 2008, Weller and Baldwin 2012, Coleman et al. 2014), but current literature on multi-species site occupancy modeling of bats is very limited (Pauli et al. 2017). The results of these multi-species models share information among species, therefore allowing for the estimation of parameters for rare, as well as common species (Dorazio and Royle 2005, Dorazio et al. 2006, Kéry and Royle 2009, Zipkin et al. 2009) which can address ecological concerns across a community (Pauli et al. 2017). Our study is only the second multi-species occupancy analysis used to model bat species (Pauli et al. 2017).

Our objectives were to determine the current occupancy of bats within the WGLR in relation to habitat covariates and the co-detection of other species.

STUDY AREA

In 2015, we conducted acoustic surveys for bats in the following sites in Wisconsin: Black River Falls State Forest (BRFSF), Brule River State Forest (BRSF), Chequamegon-Nicolet National Forest (CNNF), Governor Dodge State Park (GDSP), Sandhill Wildlife Area (SWA), and on private land accessed by The Forestland Group (TFG) near Pelican Lake. We also surveyed the L'Anse and Porcupine Mountain properties of TFG in the western and central Upper Peninsula (UP) of Michigan (Hyzy 2017).

In 2016, we surveyed the following sites in Wisconsin: BRFSF, BRSF, GDSP, SWA, and Necedah National Wildlife Refuge (NNWR) (Hyzy 2017).

In 2017, we surveyed SWA, 3 NWRs in eastern Minnesota, including: Minnesota Valley (MNWR), Rice Lake (RLNWR), and Upper Mississippi River National Wildlife and Fish Refuge (UMRNWFR), and 2 privately owned properties in the northeastern UP, including the: TFG Wolverine Property and Curtis Compartment of the Great Lakes New Market Tax Credit (GL-NMTC) property (Fig. 5).

Wisconsin Sites

The BRFSF included 275.2 km² of forestland and 19.31 km of contiguous river. The mixed forest consisted of jack pine (*Pinus banksiana*), oak (*Quercus spp.*), and aspen (*Populus spp.*). The area also contained unique communities of white pine-red maple swamps (*Pinus strobus* and *Acer rubrum*) and pine-oak barrens (WDNR 2018a).

The BRSF included the 70.8 km Brule River drainage that fed into Lake Superior, dropping 128 m in elevation. The mixed northern forest consisted of 56.7 km² of aspen, 5.7 km² of white birch (*Betula papyrifera*), 40.5 km² of red (*Pinus resinosa*), jack, or white pine, 9.3 km² of swamp conifers, 4.05 km² of upland hardwoods, and 4.45 km² of swamp hardwoods (WDNR 2015).

The CNNF included 6070.3 km² of mixed northern forest (USDA 2018a). This area contains large timber production units and over 80.9 km² of wilderness and old growth areas (USDA 2018b). The forest predominately was young northern hardwoods consisting of sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), red maple, basswood (*Tilia americana*), white ash (*Fraxinus americana*), red oak (*Quercus rubra*), quaking aspen (*Populus tremuloides*), yellow birch (*Betula alleghaniensis*), and eastern hemlock (*Tsuga canadensis*). Additional species include white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), northern white cedar (*Thuja occidentalis*), tamarack (*Larix laricina*), quaking and big-tooth aspen (*Populus grandidentata*), and paper birch (Donner et al. 2013).

The GDSP included over 20.2 km² of eastern deciduous forest dedicated to public recreation. The forest component consisted of oak, aspen, hickory (*Carya spp*), and mixed pine (WDNR 1984, Hyzy 2017).

The NNWR consisted of 72.8 km² of wetland, tallgrass prairie, and over 12.1 km² of restored oak savanna/barrens. Forest species included jack pine, red pine, and northern pin oak (*Quercus palustris*) (USFWS 2013).

Pelican Lake in Oneida County Wisconsin was part of the 38.93-km² TFG Chippewa East property, which was scattered across the north-central region of the state. These properties are in proximity to the CNNF and contained similar species (TFG Operations 2018a).

The SWA was a 37-km² area composed of mixed forest (primarily aspen, pine, and oak), grassland, and wetlands. The proliferation of oak wilt (*Ceratocystis fagacearum*) over the last half-century has produced an abundance of oak snags in the area. (Hyzy 2017, WDNR 2018b)

UP Sites

The Curtis Compartment of the GL-NMTC property - was 75.7 km² of aspen, lowland conifer, and pine plantations in Mackinaw County near Curtis and Gould City, Michigan. Forest regeneration was limited due to heavy browsing by white-tailed deer (*Odocoileus virginianus*) (TFG Operations 2018b).

The Wolverine Property is the easternmost site in this study, located in central Chippewa County, and consisted of 1 parcel surrounding and 1 within the East Unit of the Hiawatha National Forest. The combined 58.2 km² consisted of varied stands of hardwoods and conifers, including tamarack, red pine and aspen, and plantations of European larch (*Larix decidua*) (TFG Operations 2018c).

The L'Anse/Marquette and Porcupine Mountain properties were dispersed across Ontonagon, Baraga, and Alger counties in Michigan. These properties, as with the GL-NMTC and Wolverine properties, were privately owned by The Forestland Group and had similar forest management strategies (Hyzy 2017).

Minnesota Sites

The MVNWR stretched for 112.66 km along the Minnesota River and was a public use area for Minneapolis and St. Paul, Minnesota. The refuge contained over 56.7 km² of varied forested, grassland, and savannah dispersed across several independent units surrounded by residential development (USFWS 2018*a*).

The RLNWR was located in Aitkin County near the town of McGregor. The refuge surrounded its namesake 14.6 km² lake and consisted of woodland and wetland habitats (USFWS 2018*b*).

The La Crosse District of the UMRNWR- consisted of land on both sides of the southern Minnesota and Wisconsin border. The district contained varied landscapes including, grasslands, towhead islands, upland and lowland forests, and wetlands (USFWS 2017*a*).

METHODS

Data Collection and Management

At each site, we mounted 20 Song Meter SMZC acoustic recorders (Wildlife Acoustics Inc., Maynard, MA) on trees 1.5-2.0 m aboveground. Units were placed at least 200 m apart to minimize multiple detections of the same individual bats (Coleman et al. 2014). To maximize the likelihood of capturing the entire present community, we distributed recorders evenly between upland and riparian zones (Loeb et al. 2015). Upland zones were defined as areas a minimum of 200 m away from a water body including lakes, marshes, rivers, streams, and wetlands. We randomly generated 30 deployment locations within these diversified zones using ArcMap (Esri Inc.) and selected from them based on access and logistic feasibility. The only exception to this deployment methodology was at NNWR, where recorders were placed in selected transects to address the objectives of the Refuge staff (Hyzy 2017). Acoustic recorders began recording 30 min before sunset and finished 30 minutes before sunrise. Recordings were saved onto a secure digital card in a zero-cross format (Corben 2004).

We identified bat species from recordings using Kaleidoscope series software version 4.3.2 (Wildlife Acoustics Inc., Maynard, MA) and Echoclass version 3.1 (Eric Britzke, U.S. Army Engineer Research and Development Center, Vicksburg, MS, USA). Both programs were approved for automatic classification by the United States Fish and Wildlife Service (USFWS 2017*b*). We used an identification maximum likelihood estimator value (MLE) of ≤ 0.05 from either program to determine if a recorder night was designated as occupied (Clement et al. 2014).

Habitat Covariates

For each recorder, we considered the habitat covariates of distance to roads, distance to water, elevation, and a forest canopy designation (early versus late). The covariates were chosen based on their varied influence across the bat community present in the WGLR (Ford et al. 2005, Pauli et al. 2017, Neece et al. 2018). At each recorder deployment site, we recorded GPS coordinates and the following site-level habitat characteristics: distance (m) and canopy class of the 4 closest neighboring trees in each cardinal direction, elevation, basal area, and a brief site description (Ford et al. 2006, Hyzy 2017). We averaged the canopy class designations (1 – Emergent, 2 – Dominant, 3 – Mid-story, 4 – Suppressed) for each neighboring tree per recorder to a single value and reduced each to a binary early (emergent and dominant) or late stage (mid-story and suppressed) forest designation due to sample small size across the original 4 designations. We determined co-detection of species by the agreement of the programs Echoclass and Kaleidoscope Pro on the identifications of detected species (Lemen et al. 2015). We considered an agreement as both programs independently identifying the same species for a recorder-night within the MLE value of ≤ 0.05 . We calculated distances to roads and water features for each recorder using ArcMap and publicly accessible shapefiles from the United States Census Bureau (<https://www.census.gov/data.html>).

Analytical Methods

We used a dynamic occupancy modeling approach described by Kéry and Schaub (2012) as a foundation to produce a global occupancy model of multiple bat species across an array of recorders over the 3-year period. For our analysis, we treated recorder nights as repetitions within the survey periods of each year and all priors as uninformed. We considered effect by year as fixed, but all other covariates were modeled as random effects (with species as the random effect). We modeled occupancy probability across all species as $logit(\Psi_{year,species,site,recorder}) = \phi_{species} + \beta_{species,1} * year_{year} + \beta_{species,2:8} * Codetections_{site,recorder,year} + \beta_{species,9:12} * Habitat_{site,recorder,year}$ with *Codetections* consisting of the binary presence or absence of an agreed upon species identification by the 2 software programs of all species excluding the 1 being modeled for at each recorder, and *Habitat* consisting of the habitat covariates of distance to road, distance to water, elevation, and early-stage designation for each recorder. To reduced error caused by non-contributing covariates, we constructed a reduced model of selected variables whose 95% CI did not span 0 (Pauli et al. 2017). This approach restricted the covariates to influence occupancy probability either in a negative or positive relationship (Kruschke 2015, Kéry and Royle 2016, Mackenzie et al. 2018). With the results of our reduced model, we again only considered variables whose 95% CI did not span 0 and calculated odds ratios for each the occupancy probability of each selected covariate (Kühlmann-Berenzon and Hjorth 2007). Odds ratios represent the constant effect of the covariates on the probability of occupancy. For all models, species was considered as the alpha coefficient for calculating detection probability using the equation $logit(p_{year,species}) = p_{sp}$ with p_{sp} having a normal prior distribution. We ran each model as 3 independent chains of 50,000 iterations, discarded an initial 10,000 iterations as burn-in and retained every 4th iteration for a total of 15,000 iterations per model. We analyzed the data using Program R, RStudio, and JAGS via the rjags package (Plummer 2003, 2017, Kruschke 2015, R Core Team 2016, RStudio Team 2016).

RESULTS

Over 3 years and 2,624 recorder nights, 207,171 audio recordings were collected and from these, 74,267 bat calls were identified within our conservative application of the MLE value of ≤ 0.05 . The remaining files were disregarded as either noise files or not identifiable. The identified calls contributed to 4,709 detection nights (Table 3) of hoary bats (1,520), eastern red bats (862), little brown bats (776), silver-haired bats (605), northern long-eared bats (498), big brown bats (342), and tri-colored bats (106). Recorder nights differed across sites and years due to logistic challenges including battery depletion, flood conditions, storm damage, and technical malfunctions (Table 3).

Our models indicated covariates that only possessed positive correlations with occupancy probability for all species. For big brown bats, the top covariate was the co-detection of little brown bats, while co-detection of eastern red bats and year of survey also were indicated (Table 4). For eastern red bats, the top covariate was the co-detection of big brown bats, while co-detection of little brown bats, co-detection of northern long-eared bats, and year also were indicated (Table 5). For little brown bats, the top covariate was the co-detection of northern long-eared bats, while co-detection of silver-haired bats and year also were indicated (Table 8). For northern long-eared bats, the top covariate was the co-detection of big brown bats, while co-detection of eastern red bats and year also were indicated (Table 9). Year of survey was the only indicated variable for hoary bats, silver-haired bats, and tri-colored bats (Tables 8, 9, and 10).

Detection probability differed across species. Hoary bats possessed the highest detection probability overall with a 95% CI ranging from 0.585 to 0.624 (Table 11). For the other migratory tree bats, eastern red bats had the highest detection probability (0.519 to 0.569) and silver-haired bats had the lowest (0.340 to 0.388) (Table 11). For the cave hibernating species, little brown bats had the highest detection probability (0.550 to 0.604), and tri-colored bats had the lowest (0.122 to 0.2) (Table 11).

DISCUSSION

We generated over 4,700 detection nights of bats in the WGLR using acoustic recorders during 2015-2017. Hoary bats were by far the most frequently detected, and 2 of the remaining top 4 detected species were the other migratory bats, eastern red bats, and silver-haired bats. This could be indicative of these species relative abundance compared to the cave-hibernating species recent population declines due to WNS proliferation in the WGLR(White 2018). While our methodology was sensitive to differences across nights of our survey, it was not sensitive to fine-scale temporal detection and non-detection over the course of a night (Jachowski et al. 2014, Neece et al. 2018). A fine-scale approach could have discerned transient migratory species passing by a recorder from those that were consistently foraging in the area through an application of more accurate turnover rates and detection probabilities (Neece et al. 2018). Little brown bats accounted for most of our detections from the cave hibernating species, which is indicative of their relative abundance in the WGLR (Russell et al. 2014, 2015).

The co-detection of big brown bats had a far greater influence on the odds ratios of occupancy for eastern red bats and northern long-eared bats (by orders of magnitude) than other covariates in the model (Tables 5 and 9) despite possessing a lower detection probability than either species (Table 11). Big brown bats are a common species throughout North America, yet direct associations among them and specific habitat types are limited to factors that influence foraging behavior (standing water, riparian zones, roads, and urbanization) (Agosta 2002). Eastern red bats have been documented using a variety of roost tree and foraging sites with selection towards riparian forests with limited urban development (Limpert et al. 2007, O’Keefe et al. 2009, Ethier and Lenore 2011, Amelon et al. 2014). Northern long-eared bats, have been documented selecting for mature contiguous forest interiors and are directly associated with snag retention management practices (Menzel et al. 2002, Timpone et al. 2010, Silvis et al. 2015, Hyzy 2017, Pauli et al. 2017). Our results suggest the presence of a strong relationship between these species, yet the cause of this association is unknown and requires further research.

The co-detection of little brown bats was the largest influence on odds ratios of occupancy for big brown bats. This result could potentially be confounded given the relatively high detection probability for little brown bats in this study. Both big brown bats and little brown bats, however, are associated with habitat containing human development (Whitaker and Gummer 1992, 2000, Coleman and Barclay 2011).

The presence of little brown bats was most affected by the co-detection of northern long-eared bats. These 2 species have been observed partitioning the same foraging habitat (Jachowski et al. 2014) and may be selecting for covariates found significant in other studies including the proportion of forest and forest edge or stream length (Pauli et al. 2017).

For every species in our study, we observed a positive relationship between occupancy and the year of survey. Although this variable had the only influence on occupancy probability for hoary bats, silver-haired bats, and tri-colored bats, their ranges were comparable to the rest of the community, of which year was the least influential variable. The positive distribution of these results was unexpected, given the community-wide decrease in bat activity being observed throughout the range of bats where WNS has been observed (Ford et al. 2011). One possible explanation could be due to a spatially unbalanced survey on a landscape and temporal scale (Rodhouse et al. 2011). We surveyed sites in Wisconsin in all 3 years, but only surveyed sites in the UP in 2015 and 2017 and in Minnesota only in 2017 (Table 4). For all years, Wisconsin sites were surveyed starting in May and the sites within Minnesota and the UP were surveyed from July to September. This later sampling draws close to the autumn swarm, a period of social and mating behavior of bats prior to hibernation, which may occur at earlier times in the year at higher latitudes (Van Schaik et al. 2015).

MANAGEMENT IMPLICATIONS

Our results indicate that multi-species occupancy modeling is a logical application for bat echolocation acoustic data and can help address research needs on community dynamics and species interactions (Pauli et al. 2017). Managers can use our results throughout the WGLR to guide research on species interactions

and niche ecology on a fine-scale to determine temporal niche partitioning over the course of a night (Jachowski et al. 2014). Using our co-detection results, managers can interpret the presence of common species such as big brown bats or little brown bats as a potential indicator of more rare species such as northern long-eared bats.

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Table 1. Parameter estimates of occupancy probability (including mean, standard deviation, and 95% credible interval) for bats in Wisconsin before (2007-2013) and after (2014-2017) white-nose syndrome

Species	Mean for Year	SD	95% CI	Mean for WNS	SD	95% CI
Big brown bat	-0.243	0.079	-0.411, -0.098	-1.66	0.687	-3.280, -0.501
Eastern red bat	-0.236	0.075	-0.388, -0.090	-1.297	0.587	-2.425, -0.134
Hoary bat	-0.161	0.109	-0.344, 0.076	-0.148	1.354	-1.892, 3.486
Silver-haired bat	-0.236	0.075	-0.394, -0.093	-1.288	0.59	-2.417, -0.110
Little brown bat	-0.249	0.074	-0.404, -0.114	-1.506	0.583	-2.754, -0.406
Northern long-eared bat	-0.264	0.078	-0.430, -0.120	-1.724	0.643	-3.113, -0.587
Tri-colored bat	-0.245	0.075	-0.400, -0.100	-1.445	0.58	-2.617, -0.311

Table 2. Slopes of 95% CI quantile values (97.5%, 2.5%) across all models for bats in Wisconsin, (2007-2017)

Species	$\Psi(\text{Year of Survey})$	$\Psi(\text{WNS Presence})$	Detection Probability
All Species	-5.121e ⁻³ , -0.0544	-0.107, -0.362	-0.0125, -0.0194
Big brown bat	-0.0116, -0.0432	-0.0909, -0.315	-0.0154, -0.0236
Eastern red bat	-0.0140, -0.0447	-	-0.0154, -0.0236
Silver-haired bat	-0.0138, -0.0439	-	-0.0139, -0.0227
Little brown bat	-0.0176, -0.051)	-0.106, -0.323	-0.0173, -0.0237
Northern long-eared bat	-0.0224, -0.0600	-0.147, -0.412	-0.0189, -0.0183
Tri-colored bat	-0.0235, -0.0547	-0.131, -0.327	-0.187, -0.0224

Table 3. Frequency of occurrence of bats and number of recorder nights per site and year (- indicates none deployed) during acoustic surveys in the Western Great Lakes Region, 2015-2017.

Site	Occurrence 2015	Recorder Nights 2015	Occurrence 2016	Recorder Nights 2016	Occurrence 2017	Recorder Nights 2017
Black River Falls State Forest	139	168	185	121	-	-
Brule River State Forest	488	256	392	137	-	-
Chequamegon-Nicolet National Forest	140	173	-	-	-	-
Governor Dodge State Park	259	158	353	149	-	-
Great Lakes New Market Tax Credit Property	-	-	-	-	33	37
L'Anse/Marquette Properties	135	111	-	-	-	-
Minnesota Valley National Wildlife Refuge	-	-	-	-	237	73
Necedah National Wildlife Refuge	-	-	377	137	-	-
Pelican Lake Property	118	168	-	-	-	-
Rice Lake National Wildlife Refuge	-	-	-	-	109	66
Sandhill Wildlife Area	567	261	408	144	212	166
Upper Mississippi National Fish and Wildlife Refuge - La Crosse District	-	-	-	-	449	118
Porcupine Mountain Property	60	109	-	-	-	-
Wolverine Property	-	-	-	-	48	72
Total	1906	1404	1715	688	1088	532

Table 4. Parameter estimates and odds ratios of covariates for occupancy probability (including mean, standard deviation, and 95% credible interval) of big brown bats in the Western Great Lakes Region, 2015-2017. The grey background indicates variables that were selected based on the 95% credible interval not including 0. We present only odds ratios from the reduced model with 95% confidence intervals of beta estimates

Variable	Beta Coefficient			Beta Reduced Model			Odds Ratio		
	Mean	SD	95% CI	Mean	SD	95%CI	Mean	Median	95% CI
Year of survey	0.926	0.153	0.624, 1.237	0.824	0.122	0.611, 0.892	2.472	2.353	1.866, 3.197
CD ¹ eastern red bat	1.05	0.456	0.223, 2.029	1.303	.478	0.366, 0.980	5.372	3.972	1.561, 10.582
CD ¹ hoary bat	0.247	0.275	-0.358, 0.748	-	-	-	-	-	-
CD ¹ silver-haired bat	0.79	0.408	0.030, 1.658	1.152	8.178	-16.86, 4.938	-	-	-
CD ¹ little brown bat	1.617	0.641	0.463, 2.995	1.700	.690	0.463, 2.118	10.585	5.802	1.941, 24.014
CD ¹ northern long-eared bat	0.749	0.398	-0.062, 1.523	-	-	-	-	-	-
CD ¹ tri-colored bat	1.618	3.663	-1.796, 12.500	-	-	-	-	-	-
Distance to roads	0.067	3.434	-8.033, 9.661	-	-	-	-	-	-
Distance to water	0.4	4.636	-9.471, 11.618	-	-	-	-	-	-
Elevation	2.48	4.35	-0.028, 14.425	-	-	-	-	-	-
Canopy type	-0.191	0.259	-0.649, 0.387	-	-	-	-	-	-

¹.Co-detection

Table 5. Parameter estimates and odds ratios of covariates for occupancy probability (including mean, standard deviation and 95% credible interval) of eastern red bats in the Western Great Lakes Region, 2015-2017. The grey background indicates variables that were selected based on the 95% credible interval not including zero. We present only odds ratios from the reduced model with 95% confidence intervals of beta estimates.

Variable	Beta Coefficient			Beta Reduced Model			Odds Ratio		
	Mean	SD	95% CI	Mean	SD	95%CI	Mean	Median	95% CI
Year of survey	1.012	0.182	0.711, 1.437	0.8342	0.125	0.611, 0.902	2.570	2.397	1.912, 3.402
CD ¹ big brown bat	2.789	2.534	0.372, 9.709	51.002	67.344	0.848, 91.779	2.493e+93	2.680e+24	10.382, 7.480e+93
CD ¹ hoary bat	0.338	0.264	-0.20, 0.869	-	-	-	-	-	-
CD ¹ silver-haired bat	0.805	0.411	0.041, 1.692	1.126	8.194	-16.76, 4.865	-	-	-
CD ¹ little brown bat	2.121	1.48	0.470, 5.770	4.086	3.967	0.571, 4.937	126.445	6.742	1.775, 370.818
CD ¹ northern long-eared bat	1.579	0.562	0.633, 2.821	1.808	0.547	0.849, 2.144	11.126	6.820	2.668, 23.890
CD ¹ tri-colored bat	5.95	5.432	-0.60, 20.26	-	-	-	-	-	-
Distance to roads	2.737	5.961	-2.17, 19.51	-	-	-	-	-	-
Distance to water	0.648	4.538	-9.54, 12.22	-	-	-	-	-	-
Elevation	1.288	3.135	-0.98, 10.41	-	-	-	-	-	-
Canopy type	-0.302	0.235	-0.76, 0.183	-	-	-	-	-	-

¹.Co-detection

Table 6. Parameter estimates and odds ratios of covariates for occupancy probability (including mean, standard deviation and 95% credible interval) of little brown bats in the Western Great Lakes Region, 2015-2017. The grey background indicates variables that were selected based on the 95% credible interval not including zero. We present only odds ratios from the reduced model with 95% confidence intervals of beta estimates.

Variable	Beta Coefficient			Beta Reduced Model			Odds Ratio		
	Mean	SD	95% CI	Mean	SD	95%CI	Mean	Median	95% CI
Year of survey	0.961	0.155	0.675, 1.298	0.817	0.116	0.609, 0.790	2.446	2.341	1.877, 3.121
CD ¹ big brown bat	0.65	0.552	-0.43, 1.755	-	-	-	-	-	-
CD ¹ eastern red bat	0.512	0.488	-0.53, 1.359	-	-	-	-	-	-
CD ¹ hoary bat	0.343	0.252	-0.17, 0.858	-	-	-	-	-	-
CD ¹ silver-haired bat	0.993	0.427	0.246, 1.906	1.212	0.421	0.401, 1.493	4.312	3.386	1.703, 7.847
CD ¹ northern long-eared bat	1.154	0.404	0.412, 2.009	1.309	0.396	0.537, 1.571	5.378	4.337	1.964, 9.832
CD ¹ tri-colored bat	6.105	5.432	-0.28, 20.301	-	-	-	-	-	-
Distance to roads	2.675	6.095	-2.53, 20.682	-	-	-	-	-	-
Distance to water	0.145	5.101	-12.7, 11.891	-	-	-	-	-	-
Elevation	0.643	2.166	-2.58, 5.964	-	-	-	-	-	-
Canopy type	-0.385	0.231	-0.88, 0.044	-	-	-	-	-	-

¹.Co-detection

Table 7. Parameter estimates and odds ratios of covariates for occupancy probability (including mean, standard deviation and 95% credible interval) of northern long-eared bats in the Western Great Lakes Region, 2015-2017. The grey background indicates variables that were selected based on the 95% credible interval not including zero. We present only odds ratios from the reduced model with 95% confidence intervals of beta estimates.

Variable	Beta Coefficient			Beta Reduced Model			Odds Ratio		
	Mean	SD	95% CI	Mean	SD	95% CI	Mean	Median	95% CI
Year of survey	0.884	0.162	0.541, 1.201	0.766	0.114	0.529, 0.842	2.188	2.182	1.636, 2.747
CD ¹ big brown bat	2.256	1.828	0.481, 5.691	50.493	67.609	0.794, 92.519	1.053e+94	2.669e+24	4.431, 3.158e+94
CD ¹ eastern red bat	1.215	0.53	0.327, 2.413	1.280	4.547	0.195, 1.654	6.277	3.849	1.282, 13.699
CD ¹ hoary bat	0.511	0.299	0.018, 1.199	0.581	0.337	-0.077, 0.811	-	-	-
CD ¹ silver-haired bat	0.129	0.483	-0.88, 0.958	-	-	-	-	-	-
CD ¹ little brown bat	1.784	0.923	0.439, 3.813	1.540	1.358	-0.228, 2.048	-	-	-
CD ¹ tri-colored bat	3.179	5.581	-2.83, 18.270	-	-	-	-	-	-
Distance to roads	1.073	3.767	-3.93, 12.680	-	-	-	-	-	-
Distance to water	-0.32	5.283	-16.3, 9.841	-	-	-	-	-	-
Elevation	2.568	4.528	-0.05, 15.384	-	-	-	-	-	-
Canopy type	-0.369	0.237	-0.88, 0.086	-	-	-	-	-	-

¹.Co-detection

Table 8. Parameter estimates and odds ratios of covariates for occupancy probability (including mean, standard deviation and 95% credible interval) of hoary bats in the Western Great Lakes Region, 2015-2017. The grey background indicates variables that were selected based on the 95% credible interval not including zero. We present only odds ratios from the reduced model with 95% confidence intervals of beta estimates.

Variable	Beta Coefficient			Beta Reduced Model			Odds Ratio		
	Mean	SD	95% CI	Mean	SD	95%CI	Mean	Median	95% CI
Year of survey	1.172	0.67	0.639, 3.509	0.706	0.183	0.243, 0.817	4.278	2.400	1.781, 8.653
CD ¹ big brown bat	2.084	2.778	-0.94, 9.459	-	-	-	-	-	-
CD ¹ eastern red bat	1.12	0.975	-0.31, 3.615	-	-	-	-	-	-
CD ¹ silver-haired bat	0.608	0.636	-0.67, 1.983	-	-	-	-	-	-
CD ¹ little brown bat	1.807	1.395	-0.34, 5.082	-	-	-	-	-	-
CD ¹ northern long-eared bat	1.509	1.421	-0.03, 4.580	-	-	-	-	-	-
CD ¹ tri-colored bat	4.546	5.966	-3.16, 19.798	-	-	-	-	-	-
Distance to roads	0.001	0.01	-0.02, 0.022	-	-	-	-	-	-
Distance to water	0.001	0.009	-0.02, 0.020	-	-	-	-	-	-
Elevation	-0.002	0.009	-0.02, 0.016	-	-	-	-	-	-
Canopy type	-0.325	0.309	-0.97, 0.314	-	-	-	-	-	-

¹.Co-detection

Table 9. Parameter estimates and odds ratios of covariates for occupancy probability (including mean, standard deviation and 95% credible interval) of silver-haired bats in the Western Great Lakes Region, 2015-2017. The grey background indicates variables that were selected based on the 95% credible interval not including zero. We present only odds ratios from the reduced model with 95% confidence intervals of beta estimates.

Variable	Beta Coefficient			Beta Reduced Model			Odds Ratio		
	Mean	SD	95% CI	Mean	SD	95%CI	Mean	Median	95% CI
Year of survey	0.828	0.178	0.430, 1.145	0.694	0.138	0.377, 0.790	2.089	2.104	1.488, 2.675
CD ¹ big brown bat	0.099	0.664	-1.20, 1.379	-	-	-	-	-	-
CD ¹ eastern red bat	0.812	0.47	-0.13, 1.794	-	-	-	-	-	-
CD ¹ hoary bat	0.354	0.247	-0.13, 0.853	-	-	-	-	-	-
CD ¹ little brown bat	1.516	0.816	0.094, 3.194	2.413	4.728	-6.695, 3.553	-	-	-
CD ¹ northern long-eared bat	0.347	0.46	-0.57, 1.192	-	-	-	-	-	-
CD ¹ tri-colored bat	-2.797	2.075	-6.40, 1.273	-	-	-	-	-	-
Distance to roads	0.769	3.593	-5.18, 11.004	-	-	-	-	-	-
Distance to water	1.965	4.821	-2.34, 16.780	-	-	-	-	-	-
Elevation	0.083	3.588	-7.33, 12.029	-	-	-	-	-	-
Canopy type	-0.231	0.235	-0.67, 0.281	-	-	-	-	-	-

¹.Co-detection

Table 10. Parameter estimates for occupancy probability (including mean, standard deviation and 95% credible interval) of tri-colored bats in the Western Great Lakes Region, 2015-2017. The grey background indicates variables that were selected based on the 95% credible interval not including zero. We present only odds ratios from the reduced model with 95% confidence intervals of beta estimates.

Variable	Beta Coefficient			Beta Reduced Model			Odds Ratio		
	Mean	SD	95% CI	Mean	SD	95% CI	Mean	Median	95% CI
Year of survey	0.856	0.18	0.452, 1.179	0.770	0.120	0.517, 0.842	2.195	2.185	1.577, 2.825
CD ¹ big brown bat	0.435	0.609	-0.81, 1.616	-	-	-	-	-	-
CD ¹ eastern red bat	0.581	0.502	-0.52, 1.460	-	-	-	-	-	-
CD ¹ hoary bat	0.189	0.327	-0.59, 0.725	-	-	-	-	-	-
CD ¹ silver-haired bat	0.442	0.466	-0.55, 1.303	-	-	-	-	-	-
CD ¹ little brown bat	1.382	0.661	0.049, 2.708	2.461	4.673	-6.606, 3.647	-	-	-
CD ¹ northern long-eared bat	0.706	0.461	-0.27, 1.571	-	-	-	-	-	-
Distance to roads	-0.985	2.984	-10.1, 2.319	-	-	-	-	-	-
Distance to water	1.452	4.549	-2.93, 16.399	-	-	-	-	-	-
Elevation	1.469	3.85	-1.27, 13.836	-	-	-	-	-	-
Canopy type	-0.514	0.314	-1.28, -0.018	-1.780	8.163	-19.39, 1.884	-	-	-

¹.Co-detection

Table 11. Detection probability estimates for species of bats in the Western Great Lakes Region, 2015-2017.

Variable	Mean	Median	95% CI
Big brown bat	0.358	0.359	0.320, 0.393
Eastern red bat	0.544	0.545	0.519, 0.569
Hoary bat	0.605	0.605	0.585, 0.624
Silver-haired bat	0.364	0.364	0.340, 0.388
Little brown bat	0.577	0.577	0.550, 0.604
Northern long-eared bat	0.399	0.399	0.371, 0.427
Tri-colored bat	0.160	0.160	0.122, 0.200

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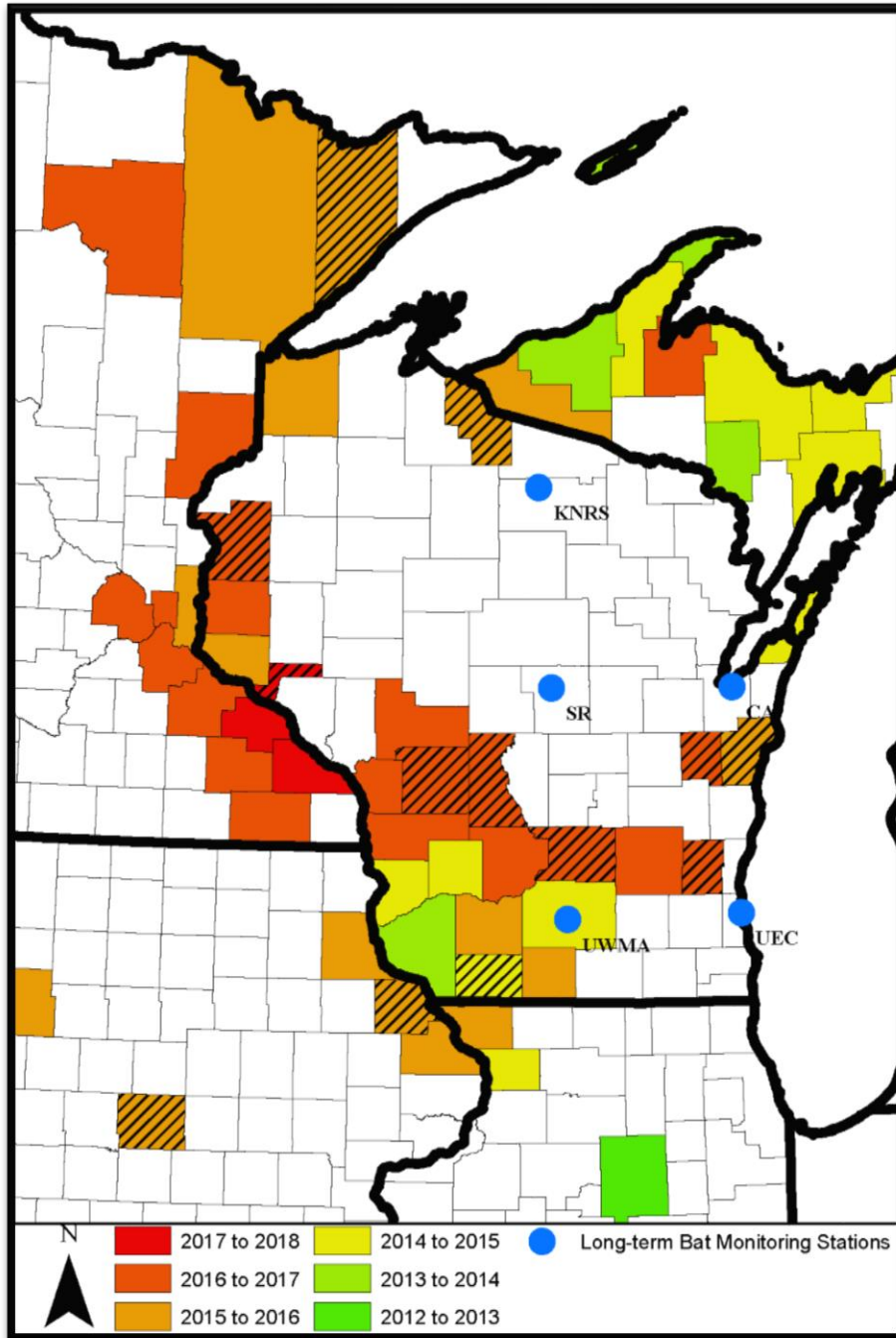


Figure 1. Distribution of long-term bat monitoring stations across Wisconsin and counties that contain bat hibernacula and their corresponding status of white-nose syndrome presence (White 2018b). Long-term bat monitoring stations include: Kemp Natural Resource Station (KNRS), Schmeckle Reserve (SR), Cofrin Arboretum (CA), University of Wisconsin-Madison Arboretum (UWMA), and Urban Ecology Center (UEC).

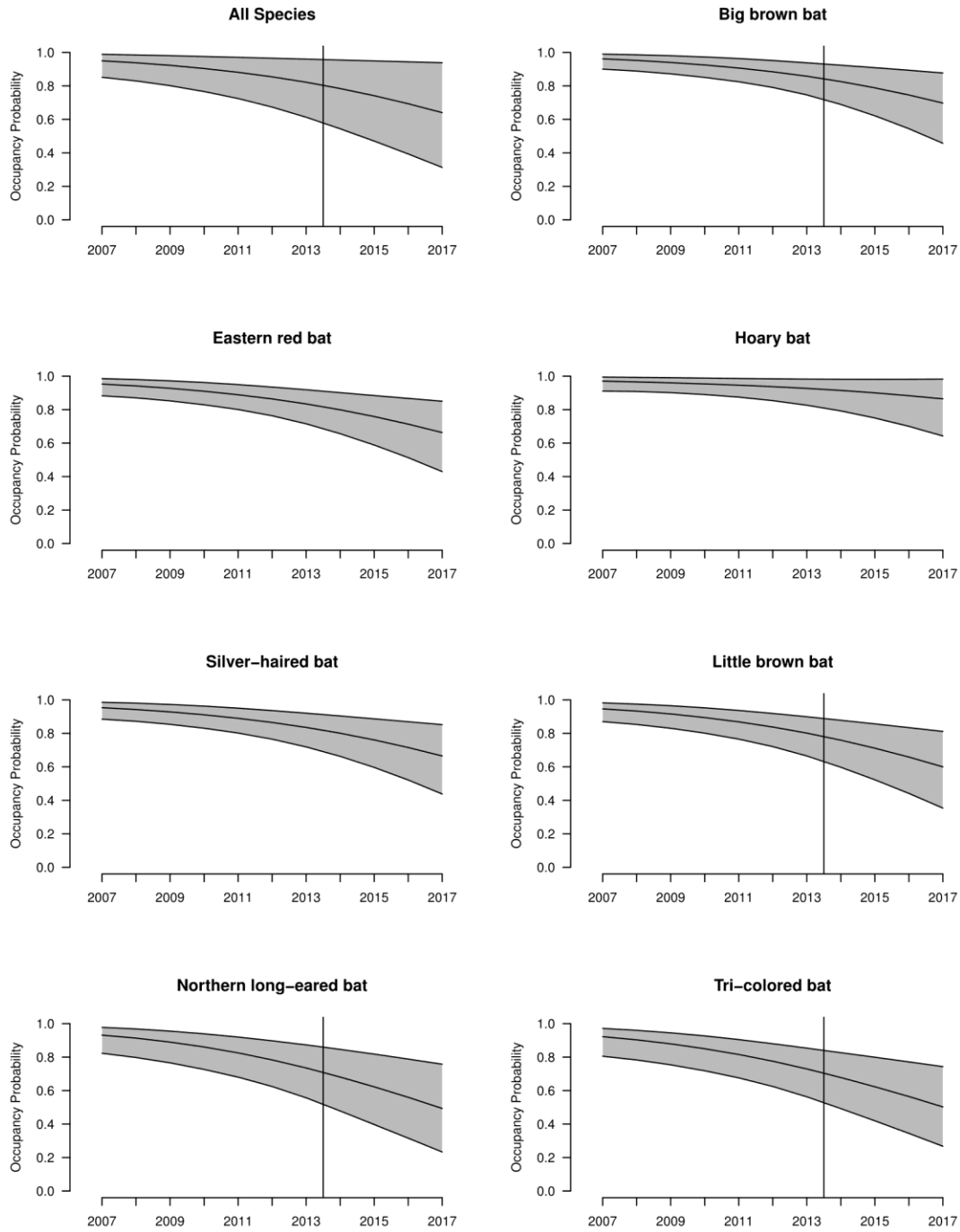


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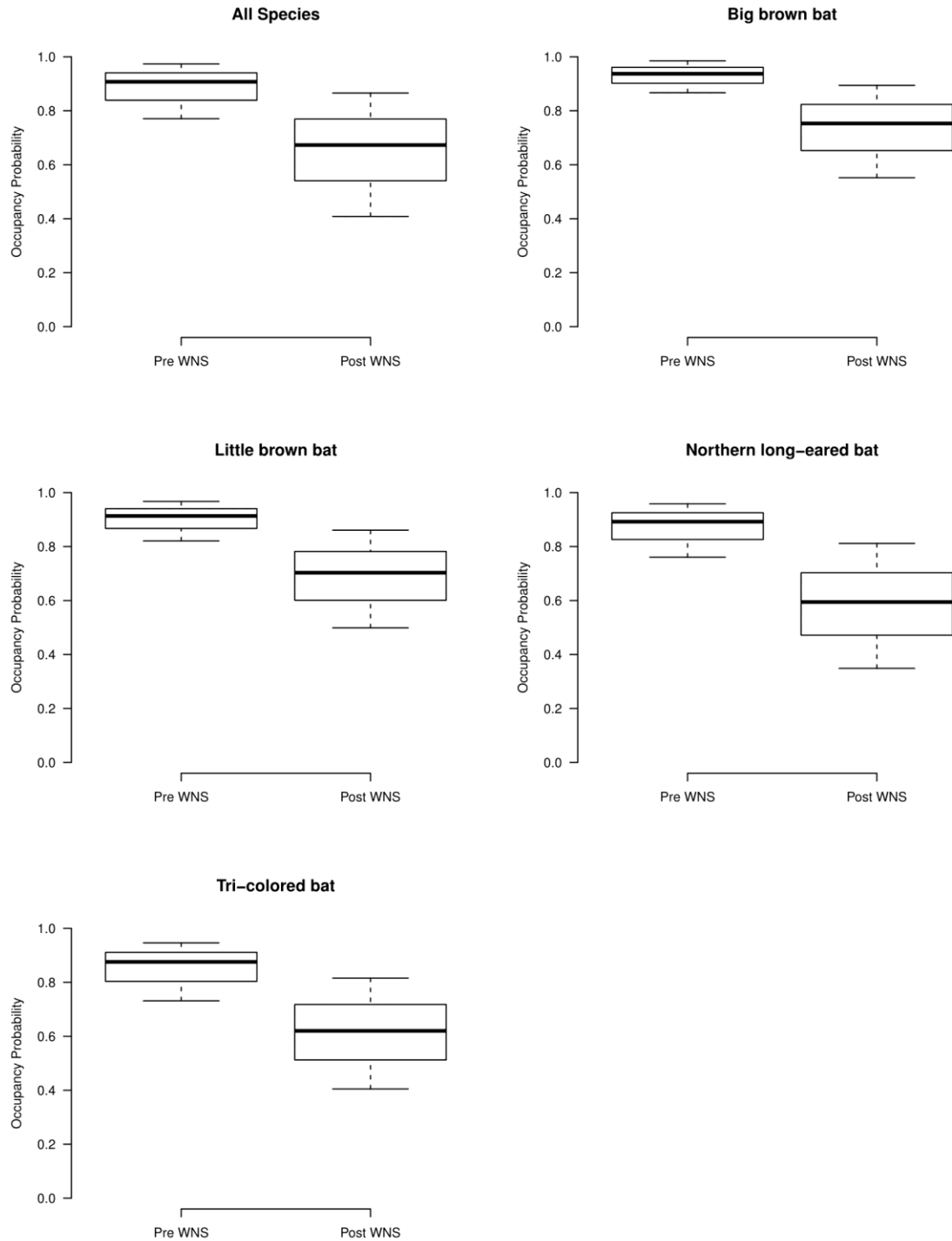


Figure 3. Occupancy probability of species of bats susceptible to white-nose syndrome (WNS) species before (2007 to 2013) and after (2014 to 2017) the discovery of *Pseudogymnoascus destructans* in Wisconsin. The grey areas denote the 95% confidence interval for estimates

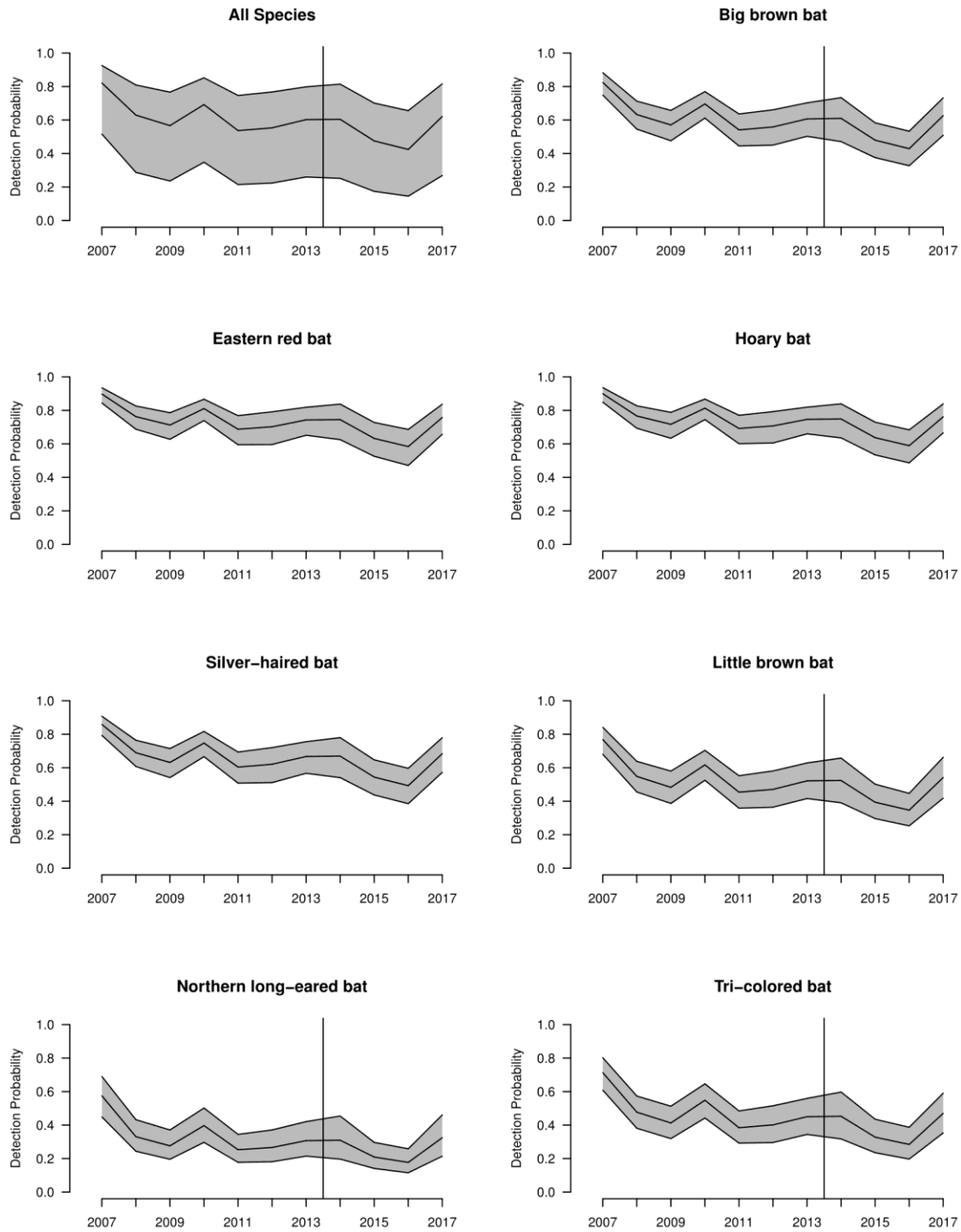


Figure 4. Detection probability for species of bats in Wisconsin, 2007-2017. The grey areas denote the 95% credible interval for estimates. The vertical line designates the detection of white-nose syndrome in Wisconsin for species impacted by the disease.



Figure 5. Distribution of acoustic survey sites in the Western Great Lakes Region, 2015-2017, including: The Forestland Group (TFG), National Wildlife and Fish Refuges (NWFR), and National Wildlife Refuges (NWR)

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Appendix 1

University of Wisconsin – Stevens Point Final Report

NCASI Project Code EW-EWG-2134

This report concerns the work regarding project proposal: “Assessing the Impacts of White-nose Syndrome on Bat Community Dynamics”, as completed by graduate students Brenna Hyzy (recently graduated) and Jordan Meyer. Previous project reports have been completed by Dr. Kevin Russell, whose duties are being assumed by Dr. Scott Hygnstrom and Jordan Meyer.

Work Completed

All species occupancy assessment

In 2017, Jordan Meyer surveyed six sites using passive acoustic sampling techniques. These sites were Sandhill Wildlife Area near Babcock, WI, Upper Mississippi National Wildlife Refuge (hereafter: NWR) – LaCrosse District on the Wisconsin/Minnesota border, Minnesota Valley NWR near Bloomington, MN, Rice Lake NWR near McGregor, MN, and the GL-NMTC and Wolverine properties of the Forestland Group near Newberry, MI. Each site’s survey consisted of 20 Wildlife Acoustics Inc. brand Song Meters that were deployed in a stratified random sample with 10 being placed in forest upland habitat and the other 10 placed in riparian zones. This data collected will be combined with the results Brenna Hyzy collected in 2015 and 2016 in Wisconsin: Black River Falls State Forest, Brule River State Forest, Chequamegon National Forest, Governor Dodge State Park, Sandhill Wildlife Area, and one site on private land accessed via The Forestland Group in Pelican Lake, WI. In addition, Brenna surveyed two sites owned by the Forestland Group in the areas of Marquette and Porcupine Mountain.

Acoustic Identification

All acoustic data from the aforementioned survey sites will be processed by two automatic identification programs: Kaleidoscope (Wildlife Acoustics Inc.) and Echoclass (Eric Britzke, ERDC). Both programs are recommended by the United States Fish and Wildlife Service as providing acceptable presence /probable absence results. In addition, samples of calls from each site will be manually vetted in order to ensure certainty of automatic identifications.

Mist Netting for MYSE

Nightly bat surveys using mist nets were conducted to capture female northern long-eared bats (MYSE) during their maternity period of May and July in Wisconsin. During her portion of the study in 2015 and 2016, Brenna Hyzy caught 40 adult female bats in Governor Dodge State Park, Sandhill Wildlife Area, and Black River Falls State Forest. Of those 23 were pregnant or lactating and 17 were non-reproductive at the time of capture. In 2016 MYSE were not captured at Governor Dodge State Park or Black River Falls State Forest. During Jordan Meyer's contribution to the 2017 season, netting efforts were focused solely at Sandhill Wildlife Area, due to the apparent decrease in netting success at the other sites. In his survey season, Jordan was able to capture 3 adult female MYSE, all of which were pregnant or lactating.

Affixing Radio Transmitters

All female northern long-eared bats that were captured via mist netting were affixed with a radio transmitter (Holohill LB-2X) and tracked for a week on average. Of all captures, 31 transmitters were successful in determining roost trees. Total number of tagged bats found occupying the same tree at one time ranged from 1-7. When emergence counts could be conducted, anywhere from 1-30 bats were observed exiting a roost tree, and with an average of 12 bats sharing one tree at a given time. Some females roosted in different trees every day, while others returned to the same day roost for up to 4 days in a row. On average, females switched roosts every 1.45 days. At each confirmed roost tree, vegetative data collection based on the methods found in Silvis et al. (2012), included roost tree species, diameter at breast height, total tree height, roost entrance height, decay classification, canopy classification, percent

canopy cover, percent bark remaining, and basal area. As well, neighboring trees undergone the same vegetative data collection in order to determine habitat selection characteristics of MYSE.

Presentations

Brenna Hyzy presented her research in the Student Research In Progress Poster Session at the 23rd Annual Conference of The Wildlife Society in Raleigh, North Carolina and in symposia at the Midwest Bat Working Group Conference in Madison, Wisconsin. Jordan Meyer presented at the Student Research in Progress Poster Session at the 24th Annual Conference of The Wildlife Society in Albuquerque, New Mexico.

Work In Progress

Statistical Analysis

Brenna Hyzy used species occupancy data produced by the passive acoustic sampling surveys to generate a model to determine occupancy probabilities of MYSE with certain habitat covariates. Her results suggested a positive correlation with forest density, distance to roads, and higher elevations. Jordan Meyer will expand this modeling process to produce a multiple species bat community perspective. This will allow to determine possible relationships between various species of bats and the habitat conditions that they select for.

The MYSE radio telemetry study was able to produce a model that the odds of a tree being utilized as a roost increased with its diameter at breast height and decay stage, but decreased with canopy class. These results support results found elsewhere in the country.

Future Presentations

Jordan Meyer will be presenting his research in symposia at the Midwest Fish and Wildlife Conference in Milwaukee, Wisconsin and has applied to present at the Joint Bat Working Group Meeting & 28th Annual Colloquium on the Conservation of Mammals in the Southeastern U.S. in Roanoke, Virginia.

Publication

Brenna Hyzy completed her thesis and graduated in May 2017. She continues to refine her statistical analysis with the help of her graduate committee and intends to publish manuscripts shortly. Jordan Meyer is set to complete his Master's program by May 2018 with publications to follow.

Site Occupancy of the Bat Community within the Western Great Lakes Region

Interim Report
To Upper Mississippi National Wildlife & Fish Refuge –
La Crosse District
December 2017

Jordan James Meyer
University of Wisconsin - Stevens Point
College of Natural Resources

Introduction

White-nose syndrome (hereafter WNS) is a disease in North American bats caused by an invasive fungal pathogen *Pseudogymnoascus destructans* (hereafter *Pd*). This disease has been progressing westward since its discovery in New York in 2006 and is particularly detrimental for colonial, cave-hibernating bats, including little brown bat (*Myotis lucifugus*), and northern long eared bat (*Myotis septentrionalis*) (Langwig et al. 2012). Of all colonial bats 99% have succumbed to WNS in infected areas, with an estimated 6 million mortalities (Alves et al. 2014). Susceptibility to WNS, however, varies across species, and has resulted in changes in the composition of bat communities where WNS has become endemic (Jachowski et al. 2014). The current leading edge of WNS stretches across North America from Ontario, Canada to central Texas (Fig. 1). Within this area is the western portion of the Great Lakes Region, consisting of Minnesota, Wisconsin, and the northern peninsula of Michigan, (hereafter referred to as the WGLR) in which WNS has been present only since 2013 (whitenosesyndrome.org). This recent onset of WNS within this region designates the WGLR as a prime candidate for assessing the disease's effects on the bat community.

Bat Community of WGLR

All cave bat species in the WGLR are currently known to be impacted by WNS. These species are the big brown bat, little brown bat, northern long-eared bat, and tri-colored bat (*Perimyotis subflavus*) (Blehert et al. 2009). Big brown bat (*Eptesicus fuscus*) is one of the most common species of bat in the WGLR and is typically found in close proximity to humans and their structures (Harvey et al. 2011). Although they are susceptible to WNS, big brown bats have shown resistance to the disease attributed to their larger body mass and fat reserves (Frank et al. 2014). Little brown bat were once considered among the most abundant and widespread of bat species in North America however, since the occurrence of WNS, populations have rapidly declined (Frick et al. 2010). Survivorship is estimated to be <1.5% for this species (Russell et al. 2015). Approximately 80% of the remaining population of little brown bats

reside in the upper Midwest region near the Great Lakes (Russell et al. 2014). Northern long-eared bat was listed as federally threatened and protected under the United States Endangered Species Act in 2015. The focus of current research for northern long-eared bat is to develop region-specific datasets describing their summer roosting habitats (Silvis et al. 2015). Tri-colored bat are the only members of the genus *Perimyotis* in the United States and Canada (Harvey et al. 2011). The species was formerly of the genus *Pipistrellus* and is often still referred to as “pips” (Hooper et al. 2006, Harvey et al. 2011). Tricolored bats tend to hibernate singly or in small clustering groups (Briggler and Prather 2003). This behavior makes individuals of this species more susceptible to mortality during hibernation and some individuals exhibit migratory behavior as a possible adaptation (Fraser et al. 2012).

Another group of bats in the WGLR are migratory tree bats. These species reside in this region during summer months but migrate to southern territories in winter (Altringham 2011). The migratory tree bats of the WGLR are the eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivagans*), and evening bat (*Nycticeius humeralis*). Evening bat was recently discovered in the WGLR (2016) and much is still unknown regarding its wintering habitat (Harvey et al. 2011, Holtan and Street 2016). Eastern red bat and silver-haired bat have been detected with *Pd*, but show no clinical signs of WNS in other parts of their range (Bernard et al. 2015). The possibility of transmission between these species potentially unaffected by WNS and their more vulnerable counterparts is still unknown and awaits further study.

Acoustic Sampling

Acoustic sampling is one of the most effective methods in monitoring bat species presence. Acoustic Recorders are devices that record sounds that are within the echolocation frequencies of bats. These sounds are saved as digital files on the device and can be analyzed to identify species. There are software programs and packages that facilitate the identification process however, to reduce the likelihood of false-positives, manual identification procedures are still utilized concurrently (Fritsch and Bruckner 2014). This sampling technique does not require any direct handling or firsthand witnessing which

minimizes potential disturbances to bats compared to mist netting or hibernacula counts (Loeb et al. 2015).

Community Dynamics

Prior to the discovery of WNS, literature regarding bat community dynamics was focused primarily on foraging competition and echolocation deviation studies (Kunz 1973, Ratcliffe et al. 2004). Due to the variable impact of WNS across bat species (Frank et al. 2014), researchers have mobilized to ascertain the impacts of the disease on the community level. Analytical methods such as occupancy modeling (Mackenzie et al. 2002) have been implemented on a number of bat species on an individual basis (Yates and Muzika 2006, Duchamp and Swihart 2008, Weller and Baldwin 2012, Coleman et al. 2014). However, current literature on multi-species occupancy of bats is very limited (Pauli et al. 2017).

Objective

This study's objective is to determine site occupancy probabilities of the bat community within the WGLR. Specific to this report, Upper Mississippi National Wildlife and Fish (UMNWFR) refuge served as one of my field sites and was surveyed July 2nd to 17th, 2017.

Methods

At UMNWFR, I mounted 20 Song Meter SMZC's (Wildlife Acoustics) equipped with SMM-U1 ultrasonic microphones, onto trees approximately 1.5-2 meters off the ground. Units were placed at a minimum of 200 meters apart from each other to minimize multiple detections of the same individual bats (Coleman et al. 2014). To maximize the likelihood of capturing the entire present community, I dispersed Recorders evenly between upland and riparian zones (Loeb et al. 2015). Upland zones were defined as areas that were a minimum of 200 meters away from a water feature. Deployment locations were determined in excess randomly within these diversified zones using ArcMap (Esri Inc.) and then chosen based on their accessibility. Recorders began recording 30 minutes prior to sunset and finish 30 minutes

prior to sunrise. Recordings were saved onto a secure digital card in a zero-cross format. At each detector deployment site, I recorded GPS coordinates along with the following site-level habitat characteristics: distance (m) and canopy class of the four closest neighboring trees in each cardinal direction, elevation, basal area, and a brief site description (Ford et al. 2006).

Sample Processing

I used the Kaleidoscope series software (Wildlife Acoustics) set to automatically identify the aforementioned bat species of the WGLR. All other settings for the program were kept at default levels: Signal Parameters were 8-120 kHz, 2-500 ms, 500 Maximum inter-syllable gap (ms), and the minimum number of pulses were 2. For my statistical analysis I will consider a species present if its p-value is $p \leq 0.05$ (Clement et al. 2014).

Results

Over the course of the survey period, 36,907 total audio files were recorded. Of these, 12,491 calls were identified to species (Table 1). All species except for eastern red bat were considered present detected??? by at least one detector (Table 2).

Future Plans

To address potential species identification uncertainty, I will use Echoclass (version 3.1, Eric Britzke, ERDC) in conjunction with Kaleidoscope. Both of these programs are deemed federally-approved automatic classifiers by the United States Fish & Wildlife Service (United States Department of the Interior Fish and Wildlife Service [USFWS] 2017*b*). Each detector will be assigned occupancy based on whether or not the two programs agreed on species identification (2 – Certain), disagreed (1 – uncertain), or there was no detection at all (0) (Royle and Link 2006, Miller et al. 2011).

At this stage of my study, no data have been analyzed statistically. I plan on using a Bayesian multi-species occupancy model (Dorazio et al. 2006, Kéry et al. 2009). This occupancy modeling

approach will define an occupied site as one used at least once by a species (Mackenzie et al. 2002, Lele et al. 2013, Pauli et al. 2017). By determining co-occurrence probabilities with habitat features, detection results from one species could potentially inform on other more rare species accurately (Kéry and Royle 2008, Zipkin et al. 2010).

Presence P-Values:								
Detector	EPTFUS	LASBOR	LASCIN	LASNOC	MYOLUC	MYOSEP	NYCHUM	PERSUB
1	0	1	0	1	0	1	0.00723	0
2	0	1	0	1	0	0.00001	0.455214	0
3	0	1	0	0.060805	0	0.000561	0.997453	1
4	1	1	1	1	1	1	1	1
5	0	1	0	0.083707	0	1	0.428641	0.001792
6	1	1	0	0.100252	5.74E-05	1	1	1
7	0	1	0.000004	0	0	1	1	0
8	0	1	0.000591	0.725939	0	1	1	0.002165
10	0	1	0	1	0	0.308827	1	1
11	0.648168	1	0	0.023613	0	0.690304	1	1
12	1	1	0	0	0	0	1	0.000647
14	1	1	0	0.002264	0	1.5E-06	1	0.405534
16	0	1	0	1.6E-06	0	0	1	0.083132
18	1	1	1	1	1	1	1	1
19	1	1	1	1	1	1	1	1
20	1	1	1	1	1	1	1	1
21	0	1	0	0	0	0	0.293101	0.005643
23	1	0.777118	0	1	3E-07	0.436867	1	1
24	1	1	1	1	1	1	1	1
25	0	0.138297	0	0	0	1	0.444851	4.7E-06

Table 2: The Kaleidoscope output for probability confidence in the form of a p-value of each detector consolidated. The column headings are as follows: “EPTFUS” – big brown bats (*Eptesicus fuscus*), “LASBOR” – eastern red bat (*Lasiurus borealis*), “LASCIN” – hoary bat (*Lasiurus cinereus*), “LASNOC” – silver-haired bat (*Lasionycteris noctivagans*), “MYOLUC” – little brown bat (*Myotis lucifugus*), “MYOSEP” – northern long-eared bat (*Myotis septentrionalis*), “NYCHUM” – evening bat (*Nycticeius humeralis*), “PERSUB” – tri-colored bat (*Perimyotis subflavus*).

KALEIDOSCOPE 4.3.2		Bats of North America 4.3.0 S/A: 0									
Detector	EPTFUS	LASBOR	LASCIN	LASNOC	MYOLUC	MYOSEP	NYCHUM	PERSUB	NOID	NOISE	
1	67	2	301	32	179	2	11	39	179	1619	
2	462	1	577	69	140	14	5	23	517	557	
3	33	2	36	18	81	9	1	0	142	856	
4	0	0	0	0	0	0	0	0	0	0	
5	55	0	62	26	48	0	2	4	105	2703	
6	1	0	9	5	5	0	0	0	24	184	
7	146	29	27	90	5769	58	3	524	1830	4341	
8	245	0	25	40	49	1	0	4	141	380	
10	194	1	413	51	219	8	2	2	355	661	
11	5	0	27	12	18	1	0	0	38	143	
12	13	2	156	78	257	33	0	9	219	1171	
14	3	1	30	15	25	8	0	1	44	375	
16	48	2	25	32	219	31	0	5	230	1032	
18	0	0	0	0	0	0	0	0	0	0	
19	0	0	0	0	0	0	0	0	0	0	
20	0	0	0	0	0	0	0	0	0	0	
21	112	2	133	170	165	25	5	6	517	2994	
23	2	1	40	5	9	1	0	0	10	68	
24	0	0	0	0	0	0	0	0	0	0	
25	99	3	262	143	16	0	4	6	366	2615	

Table 1: The Kaleidoscope output for call identifications of each detector consolidated. The column headings are as follows: “EPTFUS” – big brown bats (*Eptesicus fuscus*), “LASBOR” – eastern red bat (*Lasiurus borealis*), “LASCIN” – hoary bat (*Lasiurus cinereus*), “LASNOC” – silver-haired bat (*Lasionycteris noctivagans*), “MYOLUC” – little brown bat (*Myotis lucifugus*), “MYOSEP” – northern long-eared bat (*Myotis septentrionalis*), “NYCHUM” – evening bat (*Nycticeius humeralis*), “PERSUB” – tri-colored bat (*Perimyotis subflavus*), “NOID” – calls that were not designated to a species, “NOISE” – audio files that were disregarded

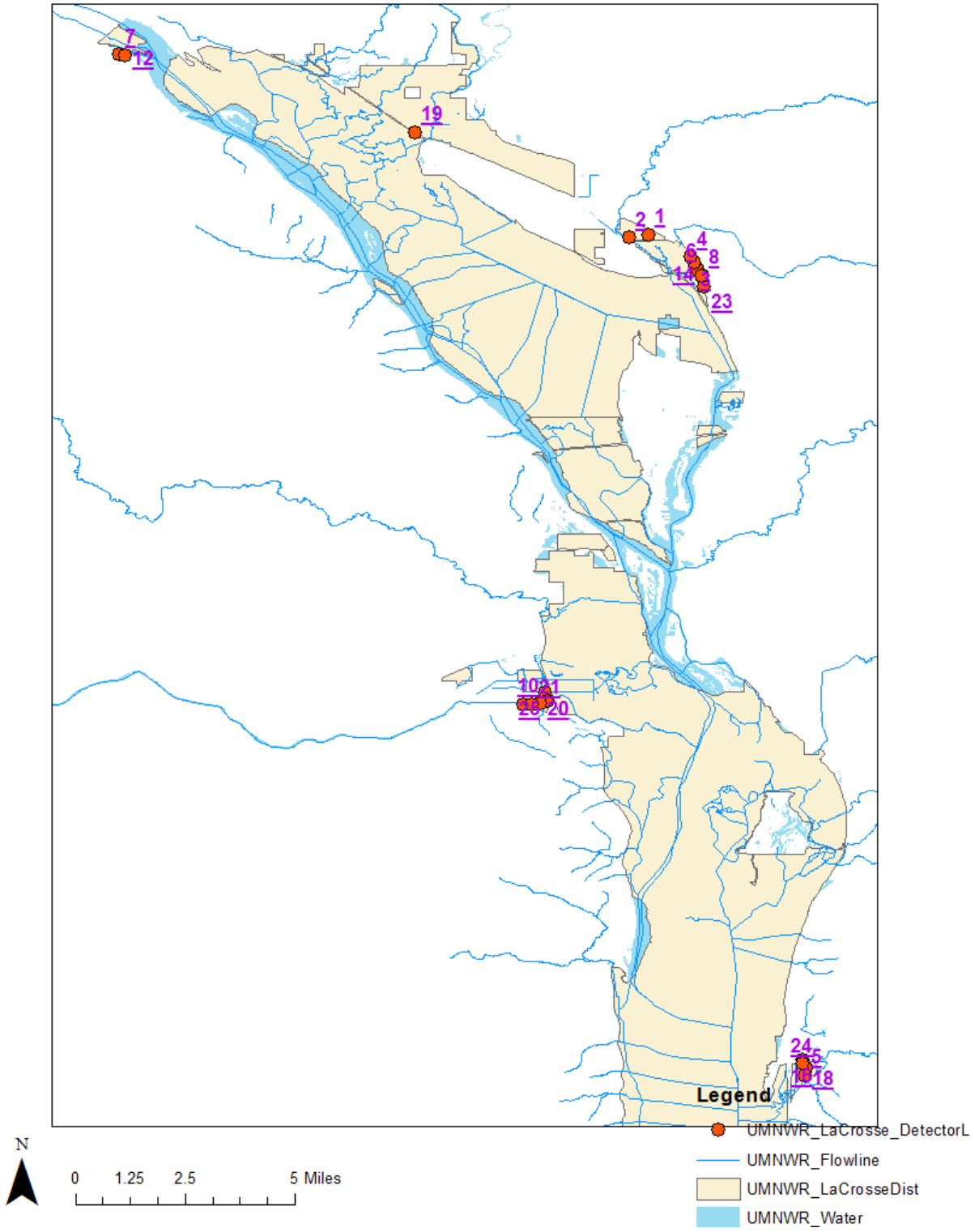


Figure 1: The overall distribution of acoustic recorders across UMNWFR.

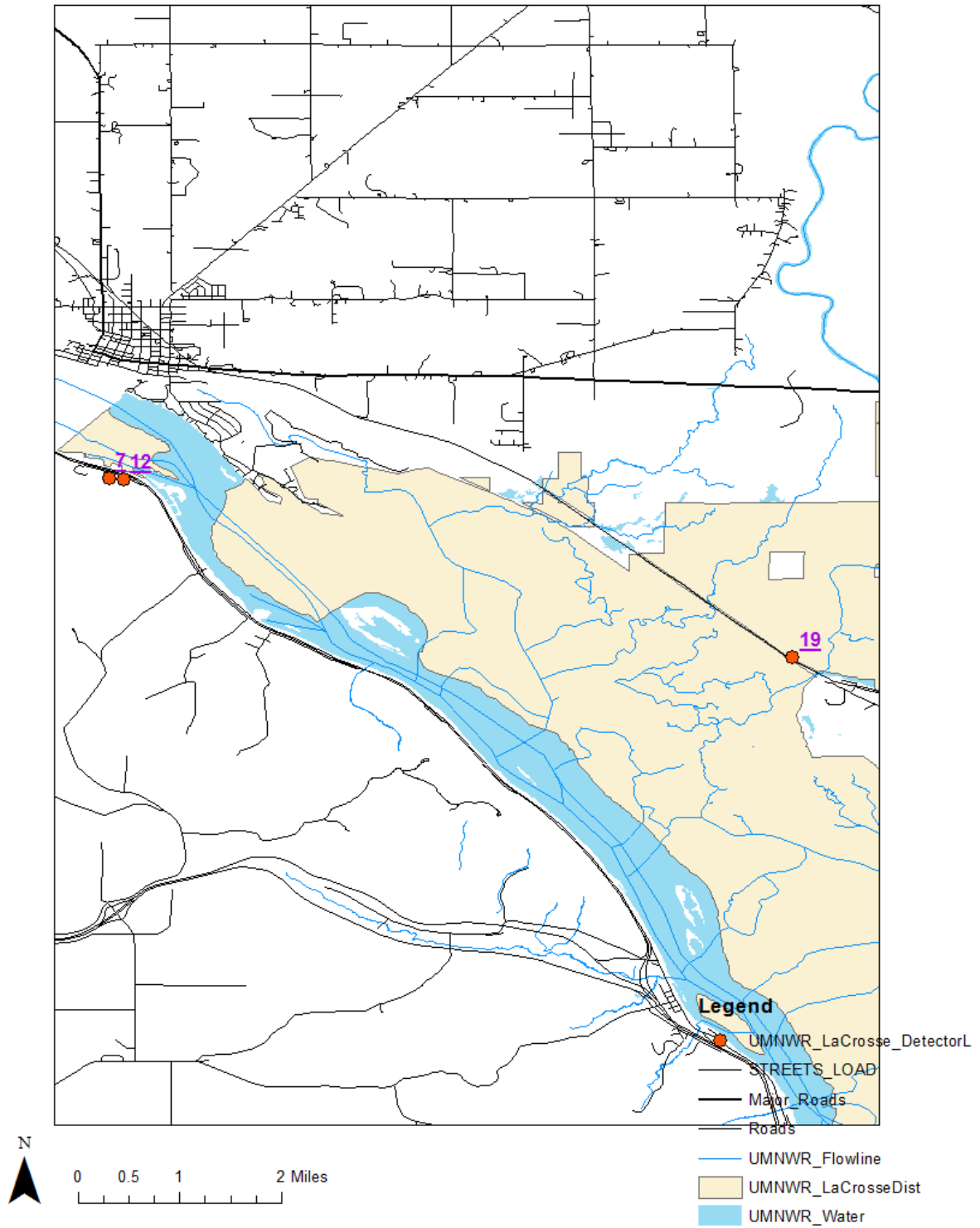


Figure 2: The northeastern-most portion of acoustic recorders deployed at UMNWFR.

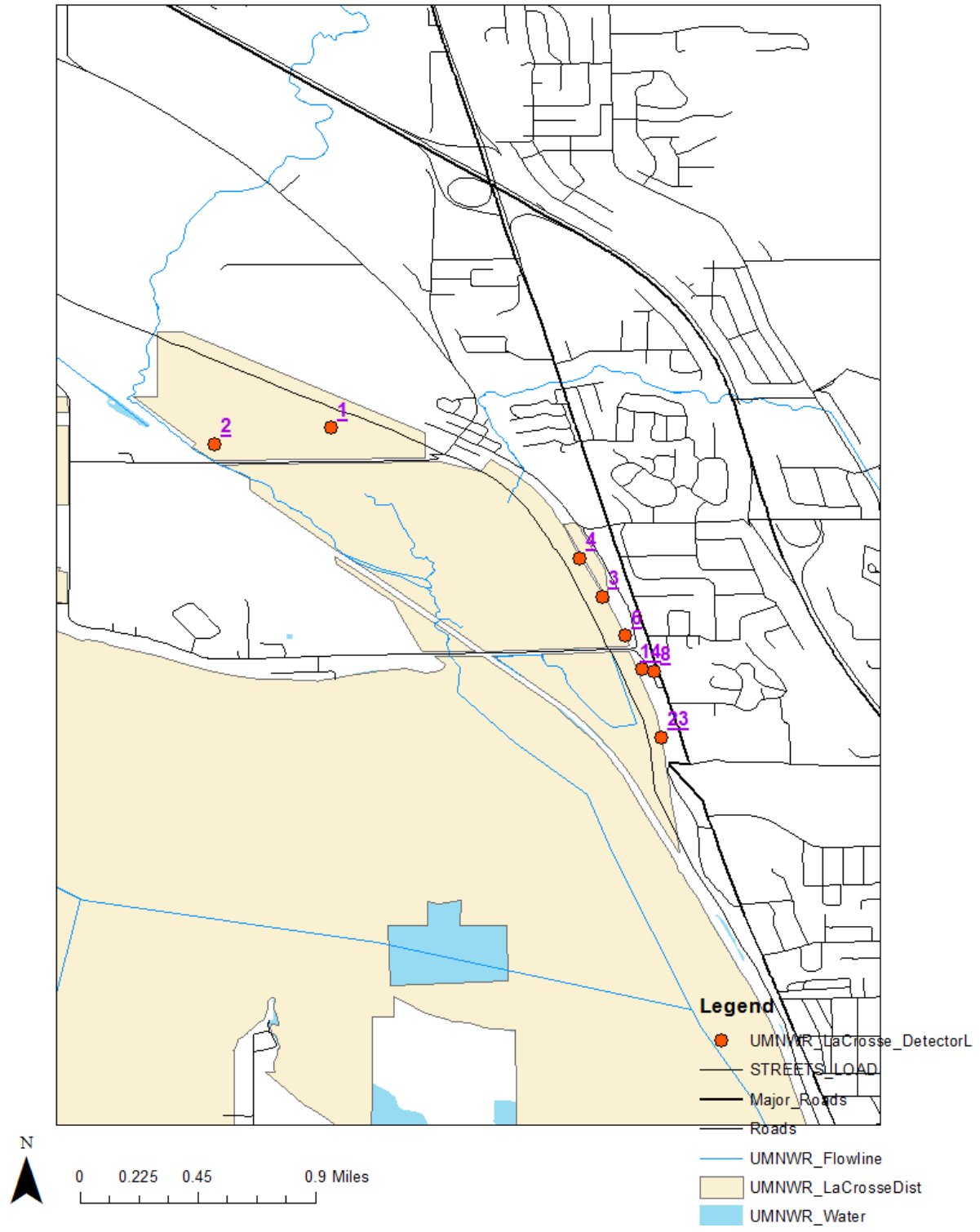


Figure 3: The northwestern-most portion of acoustic recorders deployed at UMNWFR.

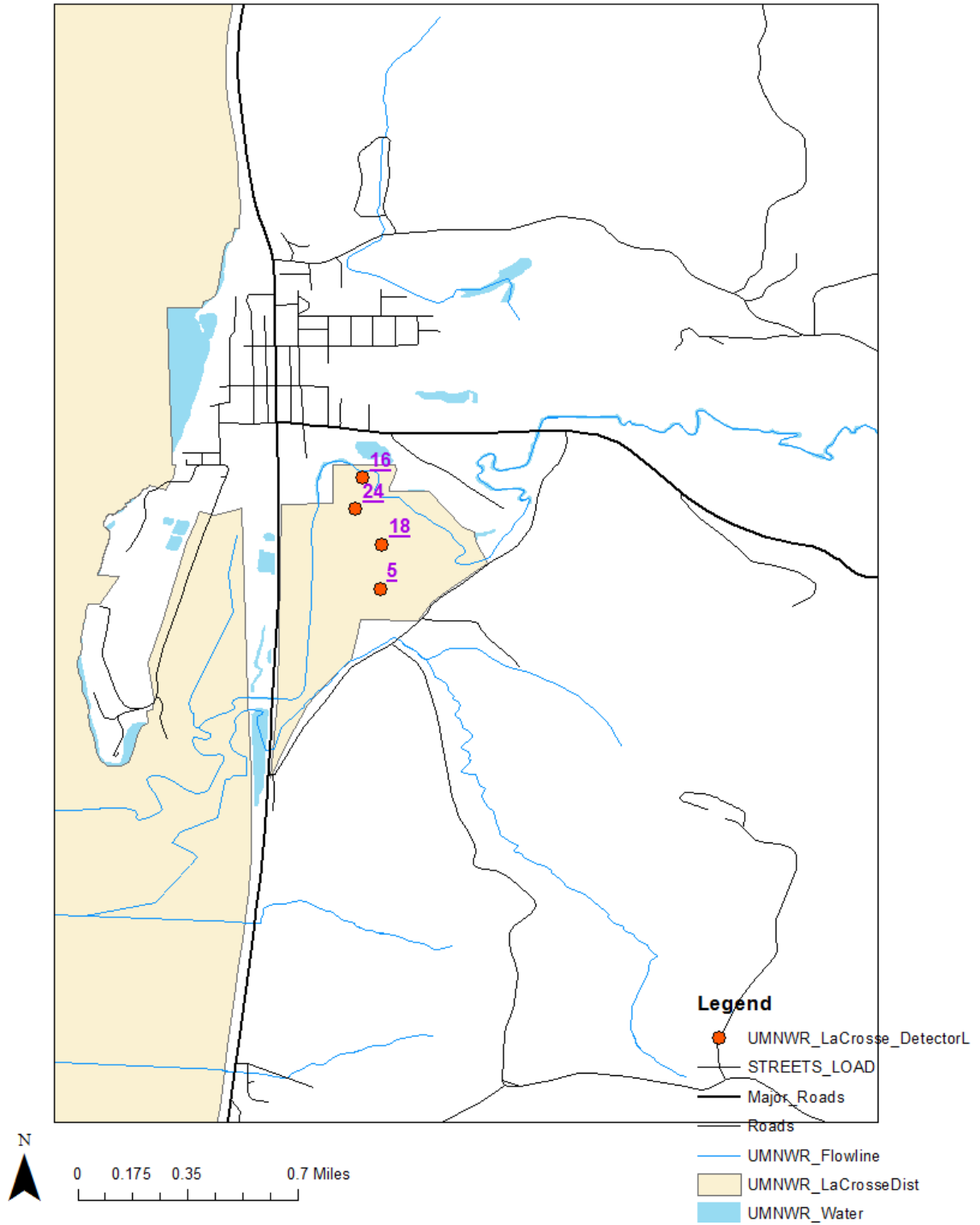


Figure 4: The southeastern-most portion of acoustic recorders deployed at UMNWFR.

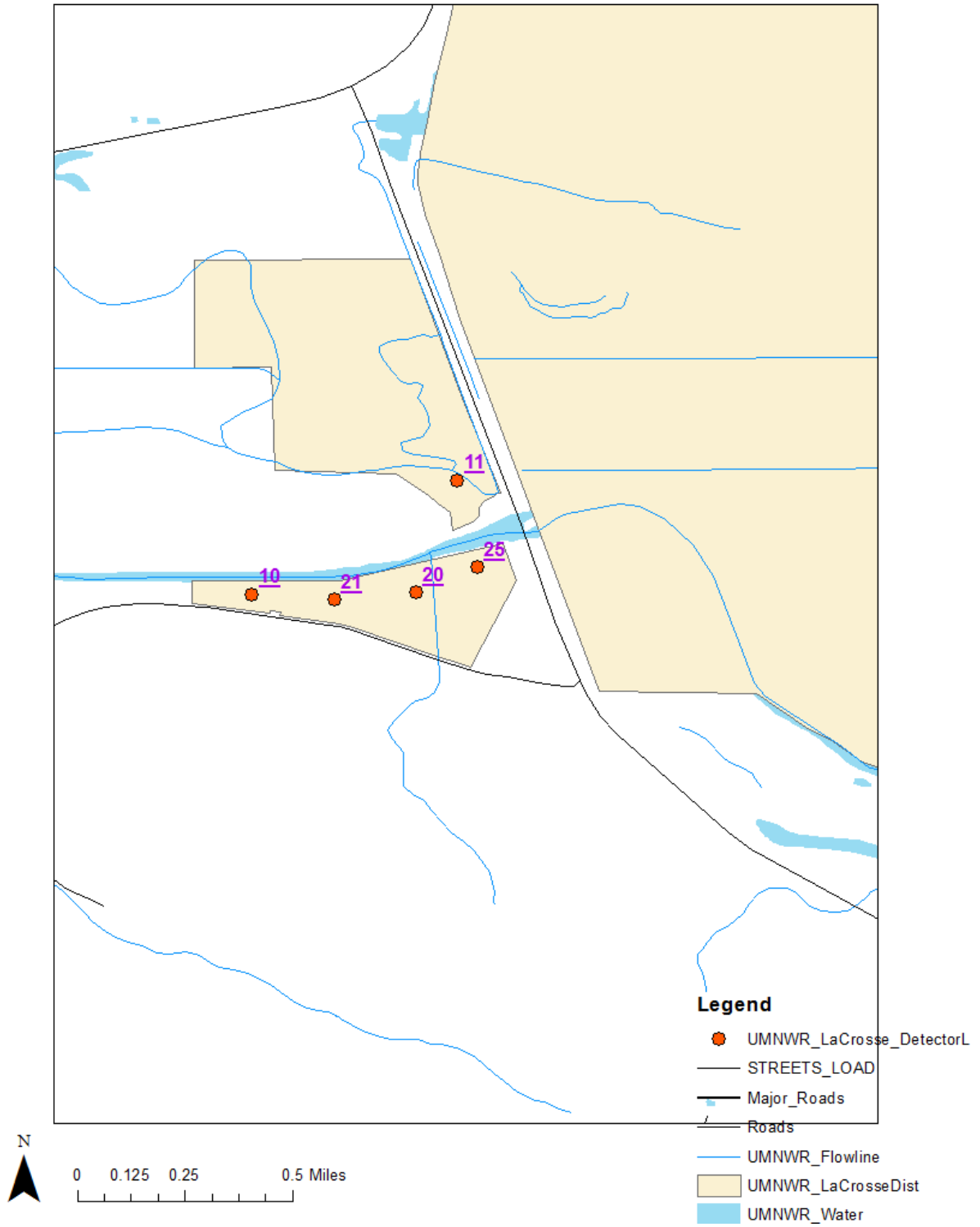


Figure 5: The southwestern-most portion of acoustic recorders deployed at UMNWFR.