

Factors Predicting Bat Detection, Occupancy and Activity across Iowa Landscapes

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ABSTRACT

Bats provide crucial ecosystem services to the midwestern United States. However, many populations are in decline as a result of climate change, habitat fragmentation, wind turbine fatalities, and White-nose syndrome. To protect habitats in an effort to preserve bat species populations, details about their preferred habitat need to be determined. Nine bat species are native to Dubuque County, Iowa, though their current activity in the county is unknown. I set up acoustic detectors at twenty-two sites in the county. Acoustic detectors at each site recorded bat activity for four nights throughout the summer of 2018. I also recorded landscape and weather covariates. Reliable occupancy and detection models were produced for four bat species: *Eptesicus fuscus*, *Lasiurus borealis*, *Myotis lucifugus*, and *Perimyotis subflavus*. The models revealed how bat presence varied over the landscape and how bat detection varied with nightly covariates. Regressions on bat species activity data revealed that activity of seven species was strongly correlated to at least one landscape characteristic. Land cover variables, including urban, forest, and agricultural cover, were common covariates. These predictive factors were generally related to bat species life history and ecology. These revealed habitat preferences can guide management strategies for species vulnerable to population declines in the midwestern United States. Over 400 calls from the Federally Endangered species *Myotis sodalis* were detected in the county, indicating the urgency for proactive management and further study to document the species in this county.

KEYWORDS

Vespertilionidae, presence, modeling, wildlife management, midwestern United States

INTRODUCTION

Bats provide essential ecosystem services globally as a safe and effective form of pest control. They eat a variety of insects, a critical service in agricultural areas because it reduces costs for pesticides, saving the agricultural industry billions of dollars yearly (Cleveland et al. 2006; Boyles et al. 2011). These services are at risk in North America, as bats have been facing massive population declines in recent decades due to wind farms, habitat destruction, and White-nose syndrome (WNS). A recent threat, WNS is a disease caused by the fungal pathogen *Pseudogymnoascus destructans* introduced to the eastern United States in 2006 (Blehert et al. 2009; Arnett and Baerwald 2013). Small, hibernating bats such as *Myotis* were formerly common, abundant, and widespread. However, WNS is especially fatal to these bats, with some colonies losing 30-99% of their population in one year (Frick et al. 2010; Foley et al. 2011). Each bat species specializes on unique agricultural pests, so the loss of one species can be troublesome to the agricultural industry (Cleveland et al. 2006; Kunz et al. 2011). Evaluating the effect of environmental variables on bat species presence and community structures will give a better understanding of how the loss of susceptible bat species may affect these agricultural areas. These results can guide management strategy design and methods for conserving diversity.

Each bat species has unique environmental preferences for roosting and foraging. The activity of bat species in a region is generally a function of microclimate, activity of preferred insects, and resource availability (LaVal et al. 1977; Mager and Nelson 2001). Consistent environmental factors may influence bat species presence such as proximity to water, vegetation, and structural complexity. Although some bats avoid cluttered areas and others avoid open areas, their distributions will frequently converge in regions with water pools (Gehrt and Chelsvig 2003; Wickramasinghe et al. 2003). More variable environmental factors such as temperature, moon phase, and precipitation may influence bat activity on a nightly basis and the effect of these factors can vary between species. Many factors affecting species presence are related to land use, which explains up to 44% of the variation in bat species distribution (Mehr et al. 2011). In changing landscape of the midwestern United States, with substantial agricultural encroachment and urbanization, the relative environmental preferences of bat species are unknown.

Determining how bat species presence varies with different environmental variables is essential to management, conservation, and predicting change. Occupancy modeling is a useful

tool to describe and relate species presence to environmental variables. These models provide insight into the unique environmental preferences of each species and their relative ecological responses to the increasingly human-altered landscape. Applying occupancy models to the community of bats in Dubuque County will determine factors that affect bat presence and identify local interspecific variation in environmental preferences, allowing us to selectively manage to benefit vulnerable species. With the spread of WNS approaching the midwestern United States, it is critical to determine current activity patterns and how environmental factors affect the presence of vulnerable bat species (Frick et al. 2016). At least five of the nine species identified in Dubuque County, Iowa are susceptible to WNS (USFWS 2018). For species vulnerable to WNS, effective management strategies are necessary to protect vital habitat and sustain populations. Understanding how bat species presence varies over a uniquely modified landscape, such as the heavily agricultural and urbanizing midwestern United States, is crucial to designing conservation policies to protect native populations.

To investigate how summer bat activity varies throughout Dubuque County, I describe (1) how bat species occupancy varies over different regions of Dubuque County, (2) how bat detection varies with climatic conditions, and (3) how bat species activity varies with the landscape in Dubuque County. As each species occupies a unique niche, detection, occupancy, and activity patterns are predicted to vary across the landscape by species.

METHODS

Study sites and site selection

The twenty-two study sites are within Dubuque County, Iowa (Figure 1). Nearly 100,000 people live in this county that covers 1600 square kilometers situated on the western banks Mississippi River. Three prominent land use types include urban, agricultural, and forested areas, though the county also had grasslands, wetlands, and riparian habitat (Giglierano 1999). I chose seven agricultural sites, seven forested locations, and eight urban properties for a total of twenty-two sampling sites. The twenty-two sites are evenly spread across the county and represent the diversity of the landscape matrix. The agricultural sites were in or near fields of hay, corn, and/or soybeans. The forested sites were all protected state or county parks; most were oak woodlands

and dominated by deciduous trees. The urban sites were contained within city limits of small towns throughout the county with population density of at least 320 people per square kilometer. Sites were selected based on access to private land and distribution of public land. Sites were chosen by identifying locations within the county that I was able to access on a regular basis and had permission from the property owner. As it is important that each site captures a relatively independent population of bats, no site was within one kilometer of another site. Data were collected from 26 May to 22 July 2018.

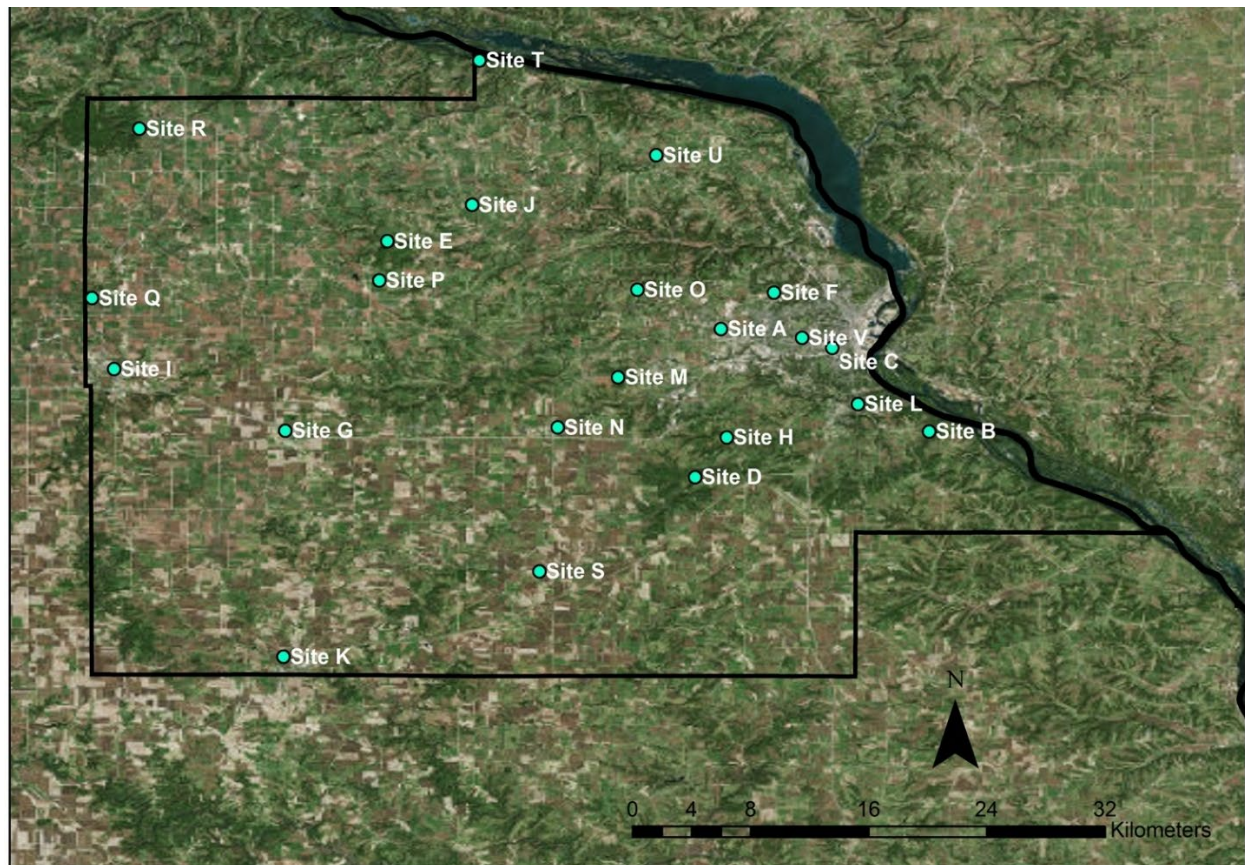


Figure 1. Distribution of the twenty-two sampling sites in Dubuque County. No sampling site was within one kilometer of another sampling site.

Study organisms

To describe the relative environmental preferences of bat species, I included all bat species present in the county during my data collection. Nine species of bat have been identified in Dubuque County, Iowa (Durbin 2009, Table 1). They are all members of the taxonomic family Vespertilionidae. Five of these species hibernate over winter in the county and four of these species migrate through the county. One species (*Myotis septentrionalis*) is Federally Threatened and one species (*Myotis sodalis*) is Federally Endangered, while the remaining species are currently unlisted, though *Perimyotis subflavus* is currently under review (USFWS 2018). All of these bats eat insects, although each species specializes on different insect taxa (Kunz et al. 2011). Each species varies in habitat preference as well; some roost in trees and others roost on buildings or other man-made structures (LaVal et al. 1977). These protection statuses may change as WNS further impacts local bat populations.

Table 1. Ecology of bat species documented to be present in Dubuque County in the last century. Under *Residency type*, “Hibernate” indicates that the bat lives in the area permanently and hibernates over winter, while “Migrate” indicates that the bat only lives in the area during the summer season. Under *WNS risk*, a descriptive measure of disease vulnerability, species listed as “High” are highly affected by the disease and suffer fatalities, while species listed as “Low” are not usually affected by the disease though may carry and transmit the disease to other bats. *Federal listing* indicates status under the Endangered Species Act.

Species ¹	Body mass ² (g)	Residency type	Dietary specialization ³	WNS risk ⁴	Federal listing ⁵
<i>Eptesicus fuscus</i>	17.49	Hibernate	June beetle, Asiatic oak weevil, Click beetle, Leaf hopper, Spotted cucumber beetle, Green stink bug, Brown stink bug	High	Unlisted
<i>Lasionycteris noctivagans</i>	11.02	Migrate	unspecified	Low	Unlisted
<i>Lasiurus borealis</i>	12.33	Migrate	June beetle, Asiatic oak weevil, Green stink bug, Gypsy moth	Low	Unlisted
<i>Lasiurus cinereus</i>	27.06	Migrate	Green stink bug	Unknown	Unlisted
<i>Myotis lucifugus</i>	7.80	Hibernate	Spotted cucumber beetle	High	Unlisted
<i>Myotis septentrionalis</i>	Unknown	Hibernate	June beetle, Brown stink bug	High	Threatened
<i>Myotis sodalis</i>	7.15	Hibernate	Spotted cucumber beetle, Asiatic oak weevil, Leaf hopper, Green stink bug, Mosquito, Hessian fly	High	Endangered
<i>Nycticeius humeralis</i>	9.12	Migrate	Spotted cucumber beetle	Unknown	Unlisted
<i>Perimyotis subflavus</i>	5.74	Hibernate	Leaf hoppers	High	Candidate, under review

1 Durbin 2009. 2 Jones et al. 2009. 3 Kunz et al. 2011. 4 USDA 2015. 5 USFWS 2018.

Acoustic data collection

Data collection began as soon as possible after bat hibernation ended and equipment was acquired. Sampling stopped after each site was sampled for four nights and before most migratory species left the county. Dubuque County is usually warm and humid during this time, resulting in a habitat with abundant insect prey for bats. Beginning May 26, I deployed one to three Wildlife Acoustics SM4FS recorders and U2 microphones on each sampling night, depending on availability and necessity. I set up the detector on a three-meter PVC pole stabilized with a rebar and three ropes. Within sites, I erected detectors in areas with minimal vegetative clutter that may distort the echolocation signal. The pole was accessible, yet out of view by the public when possible, to avoid disturbance and destruction. At each site the unit recorded bat echolocation calls for two consecutive nights. I programmed the units to begin recording one hour before dusk and stop one hour after dawn to include all bat activity during the night. I randomly generated the sequence of sites visited. This schedule was occasionally adjusted for weather events because precipitation, though rare, may have affected bat activity and confounded presence data.

Starting July 1, after all sites were sampled for two nights, I repeated the cycle until each site had a total of four recorded sampling nights. Bat offspring are born in June and begin flying in early July so dividing the samples into two cycles decreased, if not eliminated, the confounding effects of higher activity in July. Using this method and accounting for weather events, the duration of data collection totaled approximately eight weeks.

After the acoustic units recorded bat calls for two consecutive nights, I downloaded the data from the SD cards onto a computer and uploaded calls onto the Kaleidoscope Analysis Software (KAS) program version 1.2.1 (Wildlife Acoustics 2018). KAS displays the frequencies of each recorded call and identifies the call to species based on call metrics, including frequency and duration. Echolocation signatures are unique to each species, though it is difficult for programs to differentiate some species, such as *M. sodalis* and *M. lucifugus*. Although there is high error between these two species, the critical status of *M. sodalis* compelled me to include both species in the analyses separately instead of grouping them together (Britzke 2013; Kaiser and O’Keefe 2015). Species classification, time and day of call, and location were recorded in a call data file to be compared to weather and conditions of each site for each sampling date.

Environmental variable data collection

In addition to land use, other environmental factors are likely to affect bat detection, occupancy, and activity. Site-level variables, including landscape composition and distance to different types of land use, may predict bat occupancy or activity. Sample-level variables, including moon phase, daily high temperature, nightly low temperature, humidity, wind speed, and Julian date may predict bat detection. To determine if any of these variables impact detection, occupancy, or activity, I recorded these factors at each sampling site on each night to incorporate into the analyses. I obtained information on moon phase, temperatures, wind speed, and humidity for every sampling night from records accessible online via the NOAA weather station at the Dubuque Regional Airport (National Weather Service 2018). The landscape data were calculated using ArcGIS version 10.6.1 (ESRI 2016).

Data analysis

I created an occupancy model for each species by first compiling presence at each site on each night using KAS. I input this presence data, along with landscape and weather variables, into Program Presence version 2.12.21 (Hines 2006) and ran single-season occupancy models. I first ran models for each detection parameter and no occupancy parameters. If more than one detection variable fit better than the null model, I ran combinations of those variables to determine which model best fit the species data. Once the proper detection variables were determined, if any, I continued by running each occupancy variable individually with the predetermined detection variable. If more than one occupancy variable fit better than the null model, I ran combinations of those variables until I found the combination of variables that best fit the data.

After predictor variables were determined, I used the logit equation to graph each of the parameters to evaluate their relationship with bat occupancy or detection probability. I graphed the parameters and determined if the relationship was positive or negative based on the direction of the curve (R Core Team 2017).

To determine how each bat species activity varies with landscape variables, I ran correlations between environmental variables with average bat activity levels at each site. The correlations were evaluated and a two-tailed t-test on the data resulted in a matrix of p-values. I

then corrected for these p-values using the Holm-Bonferroni correction. All statistical tests and figures were created in R using package *ggplot2* (R Core Team 2017).

RESULTS

Variation in geography and weather

I found wide variation in land use composition and geographic characteristics among the twenty-two sampling sites. Land use composition data was collected for 100, 500, 1000, and 1500-meter buffer regions, although correlation matrices revealed that data from different buffer scales correlated highly with other buffer scales, such that a single buffer region can be used to predict land use composition at other scales. The majority of the land use correlation matrices revealed statistically significant multicollinearity with the Holm-Bonferroni correction ($p < 0.0001$). Additionally, no site had any river or wetlands within 100 meters, so this buffer region was uninformative for river and wetland land use types. I then chose to include only the 500 meter buffer region so no sites would overlap in their buffer regions. Landscape variables, including distance to land use types and composition of land, also varied greatly between the sites (Table 2). Weather variables also varied over the field season (Table 2).

Table 2. Summary statistics of weather and landscape data incorporated into models. “SD” indicates standard deviation.

Type	Variable	Mean	SD	Minimum	Median	Maximum
Weather	Maximum daily temperature (C)	28.4	3.1	21.1	28.9	33.3
	Minimum nightly temperature (C)	14.5	3.5	8.9	17.2	24.4
	Maximum humidity (%)	87.3	7.9	64.0	90.0	97.0
	Moon illumination (%)	50.9	37.3	0.0	54.0	100.0
	Maximum windspeed (kmh)	15.7	6.4	4.8	16.1	27.4
	Julian date	174	16	146	178	203
Landscape	Forest distance (km)	0.3	0.5	0.0	0.1	1.5
	Agriculture distance (km)	0.4	0.7	0.0	0.2	2.6
	Grassland distance (km)	0.3	0.4	0.0	0.2	1.7
	Urban distance (km)	0.1	0.2	0.0	0.1	0.6
	Wetland distance (km)	1.9	1.3	0.3	1.6	4.1
	River distance (km)	17.1	10.0	2.0	17.0	41.7
	Forest cover (% within 0.5 km)	25.3	29.8	0.0	11.2	90.3
	Agriculture cover (% within 0.5 km)	35.4	31.1	0.0	25.2	94.1
	Grassland cover (% within 0.5 km)	4.4	3.5	0.0	4.8	10.9
	Urban cover (% within 0.5 km)	33.3	39.8	0.0	9.1	99.9
	Wetland cover (% within 0.5 km)	0.4	1.1	0.0	0.0	4.4
	River cover (% within 0.5 km)	1.2	5.0	0.0	0.0	23.7

Bat acoustic detection

All species were detected over the 88 sampling nights and KAS identified 18399 total bat calls (Table 3). Species varied greatly on total number of detections over the field season. *Eptesicus fuscus* was detected most often (6290 total identified calls) and *Myotis septentrionalis* was detected least often (72 total identified calls). *Lasiurus cinereus* was confirmed present with 95% confidence most frequently (84 sampling nights) and *Nycticeius humeralis* was confirmed present with 95% confidence least frequently (1 sampling night).

Table 3. Summary of bat acoustic analysis. Total number of calls is characterized as total activity. Number of confirmed detections out of the 88 sampling nights during the sampling season. Occupancy and detection models were made for species with models labelled as “Yes” because the data were sufficient. Models for species labelled as “No” returned too high standard error to be informative because the species was detected either too rarely or too frequently.

Species	Total Activity	Total Detections	Occupancy Model
<i>Eptesicus fuscus</i>	6290	55	Yes
<i>Lasionycteris noctivagans</i>	417	2	No
<i>Lasiurus borealis</i>	1659	63	Yes
<i>Lasiurus cinereus</i>	4029	84	No
<i>Myotis lucifugus</i>	4115	42	Yes
<i>Myotis septentrionalis</i>	72	4	No
<i>Myotis sodalis</i>	414	15	No
<i>Nycticeius humeralis</i>	469	1	No
<i>Perimyotis subflavus</i>	934	30	Yes
Total	18399	88	

Occupancy and detection modeling

Occupancy models show some similarities in factors affecting occupancy for all species, such as the inclusion of land cover variables in models, while some variables are uniquely impactful to fewer species (Table 4). Plots of variables and detection or occupancy probabilities illustrated sensitivity of species to landscape and weather factors (Figure 2). The occupancy model that best described *Eptesicus fuscus* incorporated data on distance to the river and proportion of agriculture cover near the sampling site. No detection variables predicted detection for this species well. The AIC value for this model is 5.62 points lower than the null model. River distance and agriculture cover positively predicted occupancy probability for *E. fuscus*.

The occupancy model that best described *Lasiurus borealis* incorporated data on distance to wetlands, proportion of forest cover, and proportion of agriculture cover near the sampling site. Moon illumination positively predicted detection for this species well. The AIC value for this model is 6.12 points lower than the null model. I found that wetland distance and agriculture cover both positively predict occupancy probability for *L. borealis*, while forest cover negatively predicted occupancy probability.

The occupancy model that best described *Myotis lucifugus* incorporated data on proportion of forest cover near the sampling site. No detection variables predicted detection for this species

well. Several models that incorporated other variables performed well relative to the null model, though none as well as this model. The AIC value for this model is 4.66 points lower than the null model. Forest cover positively predicted occupancy probability for *M. lucifugus*.

The occupancy model that best described *Perimyotis subflavus* incorporated data on distance to the river and proportion of urban cover near the sampling site. Minimum nightly temperature predicted detection for this species well. The AIC value for this model is 3.64 points lower than the null model. River distance positively predicted occupancy probability for *P. subflavus*, while urban cover negatively predicted occupancy probability. Minimum temperature positively predicted detection probability. All of these models incorporated landscape variables, mainly proportion of forest and agriculture cover.

Table 4. Best fit occupancy and detection models for each bat species. Models are described by parameter type (Ψ : occupancy probability, ρ : detection probability), Akaike's Information Criterion value (AIC), relative model weight (w), and number of incorporated model parameters (K). I tested twelve variables to model occupancy (dFor: distance to forest, dGra: distance to grasslands, dWet: distance to wetlands, dRiv: distance to river, pFor: percent forest cover within 500 meters, pAg: percent agriculture cover within 500 meters, pUrb: percent urban cover within 500 meters, pWR: percent wetlands and river within 500 meters). I tested six variables to model detection probability (minT: minimum nightly temperature, moon: percent illumination of the moon). A period indicates the null model. Only models within 2 AIC of the best model, as well as the null model, are listed.

Species	Model	AIC	Δ AIC	w	K
<i>Eptesicus fuscus</i>	$\Psi(\text{dRiv}, \text{pAg}), \rho(.)$	105.27	0.00	0.541	4
	$\Psi(\text{dRiv}), \rho(.)$	107.10	1.83	0.217	3
	$\Psi(.), \rho(.)$	110.89	5.62	0.033	2
<i>Lasiurus borealis</i>	$\Psi(\text{pFor}, \text{pAg}, \text{dWet}), \rho(\text{moon})$	72.99	0.00	0.312	6
	$\Psi(\text{pAg}, \text{dWet}), \rho(\text{moon})$	74.23	1.24	0.168	5
	$\Psi(.), \rho(.)$	79.11	6.12	0.015	2
<i>Myotis lucifugus</i>	$\Psi(\text{pFor}), \rho(.)$	91.05	0.00	0.227	3
	$\Psi(\text{pFor}, \text{dFor}, \text{pWR}, \text{dGra}), \rho(.)$	91.23	0.18	0.208	6
	$\Psi(\text{pFor}, \text{dFor}, \text{dGra}), \rho(.)$	91.41	0.36	0.190	5
	$\Psi(\text{pFor}, \text{dFor}), \rho(.)$	93.05	2.00	0.084	4
	$\Psi(.), \rho(.)$	95.71	4.66	0.022	2
<i>Perimyotis subflavus</i>	$\Psi(\text{dRiv}, \text{pUrb}), \rho(\text{minT})$	100.04	0.00	0.174	5
	$\Psi(\text{dRiv}), \rho(\text{minT})$	100.17	0.13	0.163	4
	$\Psi(\text{pUrb}), \rho(\text{minT})$	100.49	0.45	0.139	4
	$\Psi(.), \rho(\text{minT})$	101.48	1.44	0.085	3
	$\Psi(\text{pFor}), \rho(\text{minT})$	101.58	1.54	0.080	4
	$\Psi(.), \rho(.)$	103.68	3.64	0.028	2

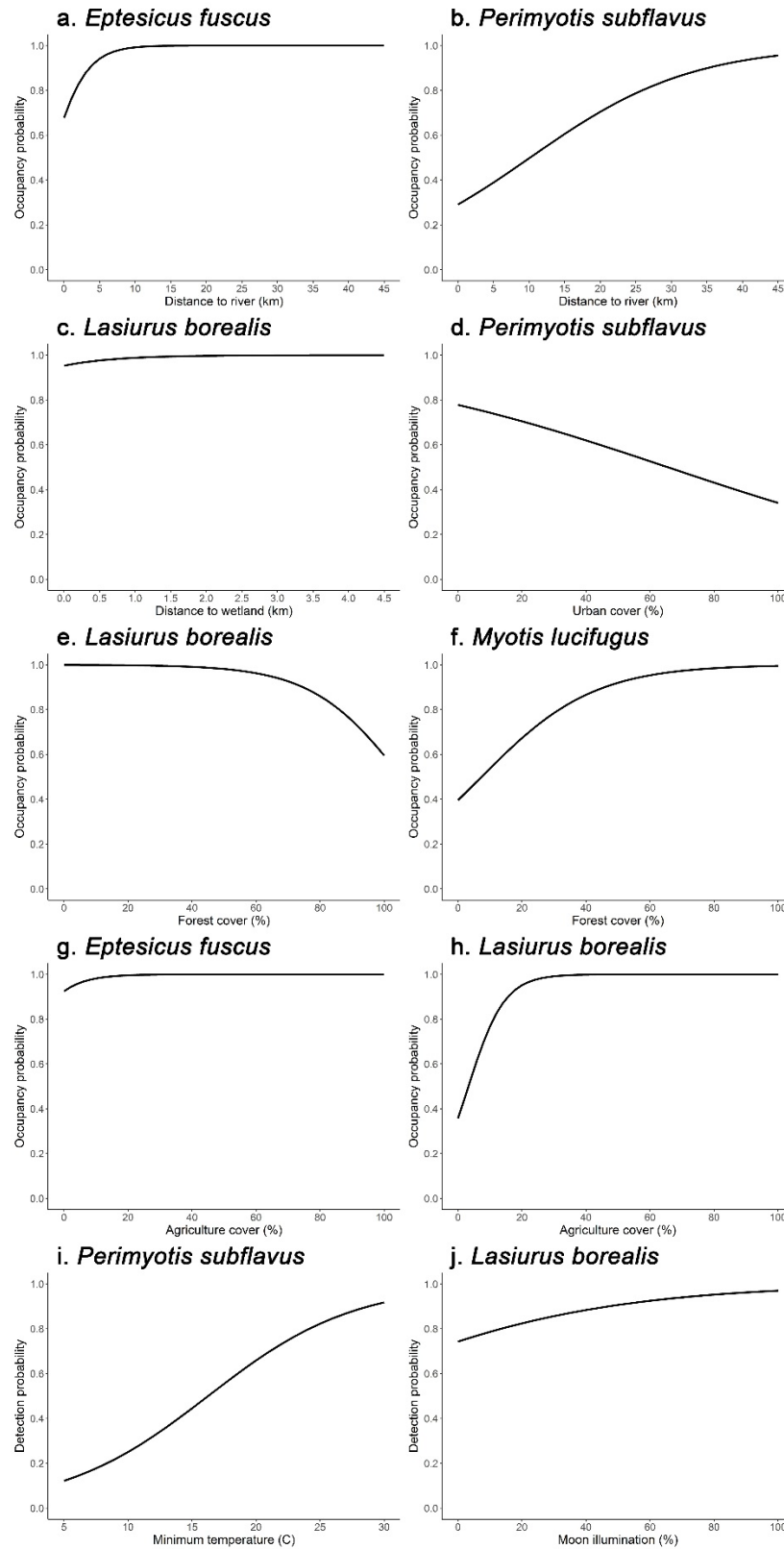


Figure 2. Plots of model covariates illustrate sensitivity of species to landscape (a-h) and weather (i-j) variables.

Relationships between bat activity and landscape variables

Several variables strongly correlate with bat activity on a nightly basis, though each species' activity was correlated to unique covariates (Table 5). No variables correlated strongly to *Eptesicus fuscus* or *Nycticeius humeralis* activity on a nightly basis.

Forest distance, urban cover at 0.5 km, and urban cover at 1.0 km correlated positively with *Lasionycteris noctivagans* activity on a nightly basis, while agriculture cover at 0.5 km negatively correlated with activity. Forest distance correlated positively with *Lasiurus borealis* activity on a nightly basis. Urban distance correlated negatively with *Lasiurus cinereus* activity on a nightly basis.

Agriculture distance correlated positively with *Myotis lucifugus* activity on a nightly basis. Forest cover at 1.0 km correlated positively with *Myotis septentrionalis* activity on a nightly basis, while wetland distance was negatively correlated with activity. Wetland cover at 1.0 km correlated most positively with *Myotis sodalis* activity on a nightly basis, and wetland cover at 0.5 km was also significantly positively correlated with activity.

Forest cover at 0.5 km correlated most strongly with *Perimyotis subflavus* activity on a nightly basis, and forest cover at 1.0 km was also positively correlated with activity. All listed factors are significant using a two-tailed t-test, though insignificant using the Holm-Bonferroni correction. While this correction yields the results statistically insignificant, the factors may still have biological significance to these species.

Table 5. Correlations between bat activity and landscape variables. All p-values are significant using a two-tailed t-test ($p < 0.05$). No factors are significant using the Holm-Bonferroni correction.

Species	Factor	r-value	p-value
<i>Eptesicus fuscus</i>	no effect	no effect	no effect
<i>Lasionycteris noctivagans</i>	Forest distance	0.643	0.001
	Urban cover (0.5 km)	0.589	0.004
	Urban cover (1.0 km)	0.533	0.011
	Agriculture cover (0.5 km)	-0.443	0.039
<i>Lasiurus borealis</i>	Forest distance	0.433	0.044
<i>Lasiurus cinereus</i>	Urban distance	-0.446	0.037
<i>Myotis lucifugus</i>	Agriculture distance	0.505	0.017
<i>Myotis septentrionalis</i>	Forest cover (1.0 km)	0.492	0.020
	Wetland distance	-0.428	0.047
<i>Myotis sodalis</i>	Wetland cover (1.0 km)	0.653	0.001
	Wetland cover (0.5 km)	0.476	0.025
<i>Nycticeius humeralis</i>	no effect	no effect	no effect
<i>Perimyotis subflavus</i>	Forest cover (0.5 km)	0.590	0.004
	Forest cover (1.0 km)	0.560	0.007

DISCUSSION

Land cover type was an important factor in all bat species presence models and is a good predictor of bat presence (Mehr et al. 2011). Additionally, land cover and distance variables are good predictors of bat activity across the county. The unique life histories of bat species can account for variation in models and predictive variables; foraging ecology, roosting ecology, and wing morphology may all impact bat species presence and activity. Species life history is important to consider when issuing management recommendations and interpreting consequences of bat population loss.

Weather factors predicting detection of bat species

Imperfect detection of was explained by weather data in the models of two species, *Lasiurus borealis* and *Perimyotis subflavus*, indicating that there are environmental factors that impact whether they will be detected in areas where they live. All bats emerge and are active at

different times depending on precipitation, long-term climate variables, and insect emergence (Yates and Muzika 2006; Frick et al. 2012). These models show that some species are more sensitive to some weather characteristics than others.

Detection probability of *Lasiurus borealis* was predicted positively by moon illumination. Moon illumination was not a predictive variable in the other three species models. This finding is noteworthy because *L. borealis* is the only migratory species for which models could be made. This may indicate that migratory species like *L. borealis* may use moonlight to navigate the otherwise homogenous midwestern landscape when flying. This species migrates long distances, as much as one thousand km in one direction, to relocate (Holland 2007). The cues bats use to navigate long distances are relatively unknown, though it is assumed that they do not use magnetic fields (Davis 1966). Navigating using moonlight to identify land markers is a reasonable conclusion given what is known about bat navigation and the results identified in this model.

Detection probability of *Perimyotis subflavus* was predicted positively by minimum nightly temperature. This was not a predictive variable in the other three species models. This finding may be attributed to the small size of *P. subflavus*. As it is the smallest bat in the county, it may not have enough energetic reserves to maintain thermoregulation while foraging when it is too cold at night, or perhaps its prey are not active at colder temperatures. Detection probability is less than 20% if the temperature is below 9 degrees centigrade, while detection probability is approximately 50% if the minimum nightly temperature reaches 16 degrees centigrade. In a similar environment with similar weather, Yates and Muzika (2006) also found that *P. subflavus* detection was impacted by minimum temperature. This model shows that *P. subflavus* is more likely to be recorded in areas where it lives on warmer sampling nights than on cooler sampling nights.

Landscape factors predicting occupancy of bat species

Although most species presence models were unique in their incorporated variables, the most commonly relevant variables were forest cover, agricultural cover, and distance to the river. Land use may be particularly impactful on species presence in this region because of the different insect prey communities available (Mehr et al. 2011; Dixon 2012). My conclusions corroborate previous studies, which in addition to land use have found tree cover, elevation, and water proximity to be predictive of species presence (Dixon 2012; Rojas et al. n.d.).

Some variables were more predictive for groups of species. Both *Eptesicus fuscus* and *Perimyotis subflavus* were less present closer to the river. The latter is generally less present with more myotine bats present, so competition with myotine bats may push these species to partition the environment and occupy other habitat (Davis and Mumford 1962).

Agricultural cover was positively predictive of *Lasiurus borealis* and *Eptesicus fuscus* presence, which may be attributed to their similar life histories. Increased occupancy of these species in agricultural areas can likely be attributed to their diet of insect pests and large bodies, which allow them to fly further to exploit resources in otherwise desolate landscapes (Kunz et al. 2011). However, this result is directly contradictory to Starbuck et al. (2015), who concluded that both species occupied areas with greater forest or urban cover.

Forest cover was negatively and positively related to *Lasiurus borealis* and *Myotis lucifugus* occupancy, respectively. This significant difference in presence may be attributed to their different residency statuses in Iowa. While *Myotis lucifugus* is a small bat that roosts in trees and inhabits the county year round, *Lasiurus borealis* is a migratory species that might find flying in cluttered areas more cumbersome (Fenton and Barclay 1980; Dixon 2012). Presence of *Lasiurus borealis* is positively related to agricultural cover and negatively related to forest cover, so environmental complexity may be a large factor in their presence at a site. This wings of this species have a high aspect ratio, allowing these bats to fly exceptionally far and fast (Shump and Shump 1982). Previous studies have found that *Lasiurus borealis* is more likely to be detected over flat landscapes such as agricultural fields (Yates and Muzika 2006).

The only species whose occupancy was predicted by urban cover was *Perimyotis subflavus*. I found that this species did not occupy heavily urban areas, a conclusion that was also reached when this species was studied in Missouri (Starbuck et al. 2015). This contradicts other studies, which have found that urban areas provide artificial roosts, water, and diverse prey for many bats (Gehrt and Chelsvig 2003; Mehr et al. 2011). However, this species generally occupies fringe habitats with trees, which is rare in urban areas of Iowa (Davis and Mumford 1962). Distance of a site to a wetland was positively predictive of *Lasiurus borealis* occupancy, perhaps due to prey availability or covariation between distance to wetland with another factor that impacts occupancy of this species.

Landscape factors predicting activity of bat species

Comparing bat activity between sites can reflect which environmental variables attract bat species for roosting or foraging. A variety of landscape variables predicted bat activity by species. Landscape variables may be particularly impactful on species activity in this region because of the large-scale landscape change that has occurred in the past few centuries. Habitat heterogeneity and distance to edge habitats have also been identified to be related to bat activity in altered landscapes (Gehrt and Chelsvig 2003).

As species' life histories guide how niche space (e.g. habitat or food resources) is partitioned, species of similar ecotypes share similar environmental factors that attract them. For migratory bats, which are a group of taxonomically diverse species, there were no variables that clearly predicted each species' activity. *Lasiurus cinereus* and *Lasionycteris noctivagans* were active near urban areas, perhaps because urban areas are a good source of water for migrating bats (Dixon 2012). *Lasiurus borealis* and *Lasionycteris noctivagans* were less active in forested areas, which may be due to the wing morphology of migrating bats. As they are not well adapted for navigating areas with lots of vegetative clutter, migratory bats tend to fly in more open areas (Fenton and Barclay 1980; Dixon 2012). *Lasionycteris noctivagans* was less active in agricultural areas, directly contradicting the results of the occupancy model for *Lasiurus borealis*. This discrepancy may be due to taxonomic dissimilarity or another aspect of their ecology that impacts their activity over agricultural landscapes.

For the myotine bats, activity was higher in areas with more forest and wetlands and in areas far from agriculture. This may be due to insect prey composition. As myotine bats are much smaller than bats that specialize on larger insects, they are likely to occupy areas where smaller insects are more common. The smallest bat, *Perimyotis subflavus*, was also more active in areas with high forest cover. This is also likely due to its small size and preference for smaller prey that are more abundant near forests and wetlands.

Management implications in Dubuque County

Conservation policies require information on where bats roost and forage. The federally endangered species, *Myotis sodalis*, requires special attention due to its detection on fifteen

sampling nights. Detections of *Myotis sodalis* were relatively frequent and in higher quantity than calls of other species known to reside in the area. This species was identified four hundred and fourteen times by the analysis software, roughly 1.5% of all calls recorded. However, acoustic analysis software commonly mistakes calls of *Myotis sodalis* and *Myotis lucifugus* and mislabels these calls (Dixon 2012; Lemen et al. 2015). No thorough mist-netting efforts have been made in this area for the express reason of finding *Myotis sodalis*, though Dubuque County is at the far northern edge of its predicted range. Additionally, there is no record of *Myotis sodalis* caught in at least five decades. Although we remain skeptical of acoustically confirmed presence of this species, mist-netting is needed to get concrete answers about this species' presence in the county (Kaiser and O'Keefe 2015). Despite doubts regarding analysis software reliability, *Myotis septentrionalis* and *Myotis sodalis* are federally listed species and these findings warrant further investigation into their presence and activity in the region.

Additional acoustic monitoring with manual inspection and targeted mist-netting are critical to confirming this species' presence in the area and when confirmed present, its habitat is protected under federal law. While the occupancy model for *Myotis sodalis* included standard error that was too high to make robust conclusions, the model that best fit occupancy patterns of *Myotis sodalis* included some variables with low enough standard error to be considered: negative association with distance to wetlands, positive association with distance to urban areas, and negative association with wetland or river composition. To manage for the possibility of this species' presence in Dubuque County, I recommend preservation of land areas near wetlands and far from urban areas. A Missouri study from 1977 emphasized the importance of streams for foraging in this species (LaVal et al. 1977). This species was listed as endangered in 1973 and remains in critical condition, especially due to its particular vulnerability to WNS (Thomson 1982). Although it is relatively likely that false positives were recorded by the acoustic analysis software, the possibility of an endangered species within the county certainly warrants further investigation.

The two other myotine species in the county also deserve conservation strategies due to their vulnerability to modern threats such as WNS. These species require [similar/different habitat]. To manage for these confirmed species in the county, I recommend [depends on results]. These precautions may prevent major population losses for myotine bats. Other studies have found that *Myotis septentrionalis* occupancy is higher in areas with low elevation, though Dubuque County has little change in elevation to address (Rojas et al. n.d.) [discuss papers that suggest

management policies] Protecting habitats for summer roosting, foraging, and winter hibernacula is crucial for protecting myotine bats from devastating population losses (Thomson 1982; Barnhart and Gillam 2017).

The other year-round resident bat species of the county, *Perimyotis subflavus* and *Eptesicus fuscus*, may also experience population pressures in the near future, so a proactive management plan could minimize impact. For *Perimyotis subflavus*, I recommend protection of bat habitat far from the river in non-urban areas. For *Eptesicus fuscus*, I recommend maintenance of bat habitat near agricultural areas far from the river, as well as reduced pesticide use. Just like natural populations, management plans are subject to rapid changes and bats must be continually monitored to adjust policies for these changes.

Limitations

Although occupancy models can correct for false-negative and false-positive detections, bat acoustic analysis software detects presence that requires confirmation by further study. More precise and conservative inspection of calls is necessary for complete certainty of call identification. If manual inspection is not feasible, using multiple types of acoustic detectors and analysis software can eliminate possible recording bias (Lemen et al. 2015). A threatened species, *Myotis septentrionalis*, was detected in few locations and populations are believed to have experienced huge losses in recent years. Although there may not be enough detections to make conclusive arguments for the protection of certain land areas, the relatively common presence of *Myotis lucifugus*, a taxonomically and ecologically similar species, may allow us to draw conclusions as to which areas are important for other myotine species (Dixon 2012).

Future directions

Species detected nearly every night (e.g. *Lasiurus cinereus*) and species detected extremely rarely (e.g. *Lasionycteris noctivagans*, *Myotis septentrionalis*, and *Nycticeius humeralis*) may require alternative methods to determine landscape variables that influence their detection, occupancy, and activity. As several species in Dubuque County are migratory (*Lasionycteris noctivagans*, *Lasiurus borealis*, *Lasiurus cinereus*, and *Nycticeius humeralis*), investigating

landscape influences at larger scales can provide insight into the role Dubuque County plays in their migration ecology. Midwestern *Lasiurus* species tend to forage in open areas and pastures, a pattern that may apply to other migratory species (LaVal et al. 1977). Migration may affect detection probability over time and incorporating migration routes and patterns may provide further context to interpret the results.

With bat populations declining, we must act quickly to preserve vulnerable populations. Manual inspection of acoustic analyses can more confidently confirm or reject bat presence in a region. Targeted mist-netting efforts for vulnerable species (e.g. *Myotis septentrionalis* and *Myotis sodalis*) can confirm their presence in the county with absolute certainty, which can be crucial to receiving appropriate conservation status and funding. A thorough study targeted towards myotiline bats in northeastern Iowa should include extensive mist-netting and detailed examination of recorded myotiline bat calls.

Broader implications

These occupancy models provide valuable life history information to reference when creating conservation policies that may conserve vulnerable bat populations. Preservation of crucial hibernacula protect overwintering bat species from disturbance (Barnhart and Gillam 2017). Likewise, maintaining forest corridors and edge habitats may encourage bat roosts and connect vital bat habitats (Hein et al. 2009). In heavily altered landscapes like the midwestern United States, occupancy models can inform management strategies to preserve necessary habitat.

Modeling and analysis techniques can guide management practices for bat populations at risk across the continent. For the bonneted bat in Florida, for example, occupancy models account for climate change and urbanization as factors that may affect future occupancy (Bailey et al. 2017). The ability to estimate changes in vulnerable populations gives conservation efforts an advantage. With further study, we can manage for each species of concern to apply management methods to predict bat habitat preferences and support vulnerable populations.

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