

Identifying Factors Across Multiple Scales That Impact Bat Activity and Species Richness in a Fragmented Landscape

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Abstract

Context

The high amount of spatial variation in bat data and lack of multi-scale studies on how human land use impacts bats creates a need for more information on how these habitat impact bats at different scales. This is the most widespread road survey done in the Oak Openings Region, a biodiverse mixed land use region in Northwest Ohio. There is also a lack of prior hotspot analysis using bat acoustic activity.

Objectives

The main objective of this study was to determine what habitat factors impact bat activity and species diversity along road transects at multiple scales. Another objective was to identify the areas of highest bat activity in the region with hotspot analysis.

Methods

The Bat data was collected using acoustic monitoring along road transects. Bat activity and species richness were compared to local scale characteristics collected in the field and landscape scale characteristics collected in ArcGIS and FRAGSTATS to determine the most important habitat characteristics. Hotspots of bat activity were calculated in ArcGIS.

Results

At the local scale, bat activity and/or species richness were positively associated with canopy height, clutter from 0–3 meters (m), humidity, natural habitat, canopy cover, months water present, and temperature and negatively associated with clutter from 3-6.5 m. At the landscape scale, activity and/or richness had positive associations with number of habitat types, m of roads, percent savanna, ponds, upland prairie, and total forest cover. Activity and/or species richness were negatively associated with percent conifer forest, floodplain forest, and cropland at the landscape scale. Hot spots were consistent between years and clustered in the northern part of the region, especially near protected areas. Cold spots were less consistent between years but generally located in the southern part of the region near agricultural areas.

Conclusions

When managing bat habitat along roads, it would be advantageous to decrease clutter at medium height levels, vary habitat types, increase open natural habitats such as savanna and upland prairie, avoid excessive conifer and floodplain forest or cropland cover, plant tall trees, and provide water sources. This

study shows that combining acoustic road surveys with habitat at multiple scales are an effective way to examine the most important habitat factors influencing bat activity and species richness.

Introduction

While insectivorous bats are critically important for controlling insects, their populations are declining worldwide due to threats such as habitat loss, disease, and energy development (Boyles et al. 2011; Frick et al. 2019; Kunz et al. 2011). It is necessary to monitor bat populations and determine what habitat characteristics contribute to their survival. Acoustic monitoring has been an increasingly popular and reliable technique for monitoring bat activity (D'Acunto et al. 2017; Fisher-Phelps et al. 2017; Lacoeuilhe et al. 2014; Medinas et al. 2019). Acoustic monitoring has the benefits of being non-invasive, allowing for collection of large amounts of data across a wider spatial and temporal range than mist nets, omnidirectional, and capturing a wider range of species than mist nets (Gibb et al. 2019; O'Farrell et al. 1999).

Acoustic surveys can be conducted at stationary points or moving (walking or in a vehicle). Moving surveys from vehicles have the advantage of covering a larger area in less time compared to stationary transects (Fisher-Phelps et al. 2017; D'Acunto et al. 2017). A major disadvantage is that vehicular surveys can only be conducted on roads, which eliminates bat species that avoid roads from surveys (D'Acuto et al 2017; Zurcher et al. 2010). However, this also means that vehicular surveys can be used to see what factors are most important in improving bat habitat along roads. Another advantage to road surveys is that they can cover a wider spatial area than stationary ones, allowing a larger area to be surveyed. Road surveys are especially useful for surveying fragmented areas when in a grid pattern, since this pattern maximizes the connectivity between and accessibility of roads for vehicles, such as in the Oak Openings Region of Northwest Ohio (Freter 2020; Sreelekha et al. 2012).

Roads have a variable impact on bats. One negative impact of roads is collisions with vehicles, which can cause bats to avoid crossing roads (Fensome and Matthews 2016; Zurcher et al. 2010). The avoidance of roads by some bats causes roads to fragment the landscape, which prevents these bats from accessing resources (Russo and Ancillotto 2014). Bats may also mistake roads from water sources from above, which could be energetically costly (Russo and Ancillotto 2014; Russo et al 2012). Traffic noise may also make prey detection more difficult and bats appear to avoid areas with higher noise pollution (Schaub et al. 2008). In addition to this noise pollution, chemical pollution from vehicles can harm bats as well as their insect prey (Altringham and Kerth 2016). Bats may avoid areas with more light pollution caused by streetlights too, due to increased predation risk (Stone et al. 2015). However, lights can also attract some bat species because the insects they feed on congregate around them (Longcore and Rich 2004). Some bat species will also forage along the habitat edges created by roads (Longcore and Rich 2004). Roadside habitats also often have higher arthropod species richness and higher abundance of some types of arthropods, especially when they are sandy or exposed to the sun, which could mean more prey for bats there (Bernes et al. 2017; Rotholz and Madelik 2013).

Bat species that are rare, specialists, forest foraging, and low-flying, such as *Myotis* spp., tend to avoid roads (Zurcher et al. 2010). Species that forage in open areas, common, generalists, and high-flying are more likely to forage on roads (Altringham and Kerth 2016; Fensome and Matthews 2016; Fuentes-Montemayor et al. 2013; Lacoelhe et al. 2014; Longcore and Rich 2004; Stone et al. 2015). Eastern red bats and hoary bats are species that may have higher activity along roads (Amelon et al. 2014; Barclay 1985;). Even when bats prefer foraging along roads they may function as ecological traps, which are habitats that are low quality and cannot sustain a population but are preferred over higher quality habitats (Russo and Ancillotto 2014). Roads can function as ecological traps due to the risk of collisions with vehicles for bats foraging there (Medinas et al. 2019).

While some research exists on what habitat is most important for bats along road transects, more data is still needed and most existing studies are single scale and looked at a small number of variables at once. Bat activity along roads tends to be lower where the amount of residential and agricultural areas is higher (Medinas et al. 2019; Pourshoushtari et al 2018) and higher near water (Medinas et al. 2013). Habitat type around roads can also impact the risk to bats, as risk of collision is higher near preferred bat habitat such as woodlands, probably due to the increased road crossings there (Fensome and Matthews 2016; Medinas et al. 2021). In some cases the presence of native forest can decrease collisions though, since it may decrease the need to cross the road to find suitable habitat (Secco et al. 2017). Since communities of bats are distinct from those in the overall landscape, there is some need to determine the habitat composition most beneficial to bats. It is also necessary to use multiple scales for this analysis since bat habitat use is scale-dependent (Gallo et al. 2017). A lack of multiple year studies also fails to account for differences between years in bat activity due to changes in weather or traffic volume (Medinas et al. 2021). Most studies on bats and roads also focus on high-traffic roads, even though low-medium traffic rural and suburban roads can also negatively impact bat populations (Medinas et al. 2019).

An avenue that has not been explored is the use of hotspot analysis for examining the areas of the highest bat activity along road transects. Hotspots are specific areas within a larger region with particularly high concentrations of individuals or species (Sussman et al. 2019). They can also be defined as areas where a metric exceeds a specific threshold, for example being in the top 5 percent of all sites for activity (Sussman et al. 2019). Hotspot analysis is useful for studying highly mobile wildlife such as bats due to high variability in their distributions (Sussman et al. 2019). Previous research has looked at hotspots of roadkill bats (Medinas et al. 2021), but none have attempted to find bat activity hotspots using acoustic monitors. It would be advantageous for management to find the areas of highest activity for live bats along roads, not just where collisions with vehicles are occurring.

This study looks at what habitat factors are associated with bat activity and species richness along road transects in a mixed-use landscape in Northwest Ohio. Hotspot maps were also created to visualize areas of highest bat activity along the transects. We predict that bat activity will not be evenly distributed across the study site and that hotspots will exist. These are more likely to occur in areas with more natural habitat, especially forest cover.

Methods

Study Area

The Oak Openings Region is a mixed-use area providing key bat habitat. It is a 47600 ha area in Northwest Ohio containing a wide variety of habitat types (Buckman-Sewald et al. 2014). About 12% of the region is protected preserve, but the rest is open to development (Abella et al. 2017; Martin and Root 2020). The region has experienced major habitat changes since 2009, with a decrease in forests, wet prairie and cropland, and an increase in built-up areas, upland prairie and savanna (Martin and Root 2020). It has undergone large amounts of fragmentation due to an increase in urbanization on the Toledo/Detroit corridor and includes a major airport (Becker et al. 2013; Higgins 2003). Road density in the region is an estimated average of around 5 km/km² within a 1 km buffer (Adams 2014). Despite this development, the area is a biodiversity hot spot and contains over a quarter of the oak savanna habitat in the world (Becker et al. 2013; Higgins 2003). Eight insectivorous bat species can be found in the region. These species are the big brown (*Eptesicus fuscus*), little brown (*Myotis lucifugus*), northern long-eared (*Myotis septentrionalis*), tri-colored bat (*Perimyotis subflavus*), evening (*Nycticeius humeralis*), hoary (*Lasiurus cinereus*), eastern red (*Lasiurus borealis*), and silver-haired bats (*Lasionycteris noctivagans*) (Buckman-Sewald et al. 2014). Previous studies in the region have mainly focused on protected parks and the regions around them, so this will be the first to cover the whole region.

Acoustic Monitoring

Road surveys started 30 minutes after sunset and end 3 hours after sunset, which is the timeframe during which bat activity peaks (Hayes 1997; Buckman-Sewald et al. 2014). Road transects were surveyed actively by driving along them at 32 km/hr twice a month and continuously recording using an Anabat SD2 monitor and an attached GPS unit fixed on a paint pole with bungee cords and rubber bands. Sites surveyed within the same night were more than 1 km apart, so that they are not within the same Anabat reception area (Livengood 2003). Transects were chosen that covered as many different habitat types as possible (e.g. a mix of forested, residential, and savanna areas) and had annual average traffic volume of less than 4000. Transects in 2019 were 1–2 km long and were changed to 5 km transects in 2020 for more efficient sampling.

Local Scale Habitat Data

Local scale variables were measured in the field. Canopy cover, vegetation density, canopy height, and understory vegetation height were measured 15 m away from the road on both sides of it every 500 m (changed to every 1 km in 2020). Percent canopy cover was measured once a month using photos in HabitApp (version 1.1). Canopy height (m) was measured once a year during peak growing season (late June-early July) using a Nikon Prostaff 3 laser rangefinder and understory vegetation height was measured once a month (once a season in 2019) measured with a tape measure. Amount of clutter was measured once a month by counting the number of uncovered squares on a 6.5 m cloth scatter board and subtracting that from the total number of squares at the 0–3 m level, 3-6.5 m level, and total board.

The number of saplings, which were defined as trees with diameters between 1–5 inches (Northern Research Station Forest Service 2017) within the 15 m radius was counted starting in 2020. If local scale characteristics could not be surveyed at transect points due to being on private land, they were estimated visually. Illumination was measured during nighttime transect surveys using a light meter. Distance to light (measured using rangefinder), and whether streetlights or ditches were present were also recorded at transect measuring points once a year. Habitat on each side of the road was characterized as natural, agricultural, or residential every 500 m (1 km in 2020) along road transects once a year. Land use was in one of 6 categories, with 1 being both sides of the road residential, 2 being one side residential and one agricultural, 3 being both sides agricultural, 4 having one side residential and the other natural, 5 having one side agricultural and the other natural, and 6 being when both sides were natural.

NOAA historic weather data for temperature (°C), humidity (%), wind speed (km/hr) and barometric pressure (inHg) was obtained from Weather Underground (www.wunderground.com) for the survey night during the peak activity period (30 minutes to 3 hours after sunset) in 2019. Brunton ADC Pro Handheld Weather Stations used to measure the same variables before each survey in 2020–2021 to get more precise measurements. Moon phase and percent illumination by the moon was determined through MoonGiant (<http://www.moongiant.com/phase/today/>). The average, maximum, and minimum for each variable measured at least once a month was calculated for each field season. Weather variables were counted as local scale because they were measured in the field most years.

Landscape Scale Habitat Data

Landscape scale habitat characteristics were analyzed in ArcMap 10 (ESRI, Redlands, California, USA) and FRAGSTATS. In ArcMap 10, the percent of each land cover type (cropland, dense urban, residential, floodplain forest, swamp forest, upland deciduous forest, upland coniferous forest, upland savanna, upland prairie, perennial ponds, and wet prairie) was measured in a 100 m and 500 m buffer (250 m buffers were used around transects in 2019 but were changed to 500 m because 250 m buffer data was overly correlated with 100 m buffer data. It was determined that buffer size did not cause bias in total percentage) around each data collection point along road transects using a land cover type map for the Oak Openings region (Martin and Root 2020) (Fig. 1). The distances to the nearest forested, residential, water source and agricultural were measured using the land cover map and ArcGIS distance tools for stationary points in 2019 (this was cut in 2020 due to lack of significant results) was measured.

Kilometers of roads in each size buffer was determined using previously obtained local road data, Google Earth (US Census Bureau 2018), and ArcGIS distance tools. Defense Meteorological Satellite Program (DMSP) Operational Linescan System (OLS) imagery (NOAA 2013) was used to measure large scale light pollution.

FRAGSTATS (McGarigal and Marks 1995) with no sampling was used to measure cohesion index, SIDI, and contagion index for each land cover type. The number of habitat types in each size buffer was also counted (shown to be comparable for 250 and 500 m buffers).

Data Analysis

Identifications of calls were made from sonograms in Analook by comparing to existing call libraries (Buckman-Sewald 2014). Species identifications are made based on time and frequency. Number of total calls was used as a measure of relative bat activity.

A correlation matrix was used to determine if variables were overly correlated with each other (> 0.8). All but one of each set that are highly correlated with each other was removed from further analysis. We used forward stepwise regression tables using AICc in JMP to examine relationships between activity and species richness and the local and landscape habitat variables. For each individual year, models were created for each set of variables with all weather, vegetation structure, land cover in large buffers (500 or 250 m), small buffers (100 m) and FRAGSTATS/light pollution variables tested as separate groups. Final models were created using any variables that made the final models for each of these sets to see which impacted bat activity and species richness the most. If residuals were non-normal or had unequal variance, the dependent variable (activity or species richness) was transformed using a log-normal distribution. All variables measured both years were used in a final model using both years of data to see what variables were most important across both years.

Hotspot analysis

Hotspot analysis was conducted in ArcMap 10 ArcMap using the Getis-Ord Gi* statistic (Ord and Getis 1992) to find the major areas of bat activity along transects for each year to examine bat spatial distribution in study areas and see how it changes over time.

Results

The variables of wet prairie, residential, cropland, and total forest in 100 m buffers, maximum and minimum of both clutter levels and canopy cover, contagion index, maximum light, minimum moon illumination and average of temperature, humidity, and barometric pressure were eliminated from final models, as they were overly correlated with other variables. Wet prairie, residential, cropland, and total forest in 100 m buffers were overly correlated with their respective habitat types in larger size buffers, maximum and minimums of clutter and canopy cover were overly correlated with the average of their respective variables and each other, averages of weather variables were overly correlated with the maximum and minimum of their respective variables, minimum mood illumination was overly correlated with maximum and average moon illuminated, maximum light was overly correlated with minimum and average light, and contagion index was overly correlated with cohesion index.

Local Scale Habitat Data

Local scale habitat variables in the best model for species richness (Table I) were canopy height, habitat type, months water present, and average clutter at both height levels. Weather variables in the best fitting species richness model were minimum and maximum barometric pressure and minimum temperature. For habitat type, points with one side residential and other natural had significantly higher species richness (tested using Wilcoxon each-pair tests) than any habitat types with no natural types of habitat

on either side of the road, points with one side natural had significantly higher species richness than points with one side agricultural and the other residential or both sides agricultural, and points with one side natural and the other agricultural had significantly higher activity than those with both sides agricultural. Canopy height, months of water present, clutter at the 0–3 m height level, minimum temperature, and maximum barometric pressure were positively associated with species richness. Percent clutter at 3-6.5 m and minimum barometric pressure were negatively associated with bat species richness.

Local scale variables in the best fitting final model for bat activity (Table II) included clutter at both height levels, habitat type, and average canopy cover. Weather variables in the best fitting activity model were maximum temperature, humidity, and barometric pressure. Wilcoxon each-pair tests revealed that activity was significantly higher at points with one side of the road residential and the other natural or both sides of the road natural compared to any of the habitat types without natural habitat on either side of the road. Points with agriculture on both sides of the road had significantly lower activity with those with agriculture on one side and natural on the other or residential on both sides of the road. Maximum temperature, humidity, and barometric pressure, percent canopy cover, and average percent clutter at 0–3 m were positively associated with bat activity. Average percent clutter at 3-6.5 m was negatively associated with average bat activity.

Landscape Scale Habitat Data

The landscape scale variables in the best model for species richness (Table I) included savanna, conifer forest, and cropland in larger sized buffers, ponds and upland prairie in smaller sized buffers, and the number of habitat types in larger size buffers. Average percent savanna and number of habitat types in larger size buffers and percent ponds and upland prairie in smaller size buffers were positively associated with species richness. Percent upland conifer forest and cropland in larger size buffers were negatively associated with bat species richness.

The landscape scale variables in the best-fitting model for bat activity (Table II) included percent upland conifer forest, total forest, floodplain forest and cropland and m of road and number of habitat types in larger size buffers. Meters of road, number of habitat types, and percent total forest and savanna in larger size buffers were positively associated with bat activity. Cropland, upland conifer forest, and floodplain forest in larger size buffers were negatively associated with average bat activity.

Hotspot analysis

Bat activity was not distributed evenly across the region, although there was some clustering near protected areas. In 2019 there were 18 hotspots and 2 cold spots (Fig. 2a), in 2020 there were 13 hotspots and 2 cold spots (Fig. 2b), and in 2021 there were 16 hot spots and 16 cold spots (Fig. 2c). Cold spots were areas statistically less likely to have bat activity and hot spots were areas statistically likelier to have high bat activity using Getis-Ord Gi. Hotspot analysis revealed consistently high bat activity in the northern part of the survey area near Secor Metropark, which was one of the smaller protected areas in

the study region. Cold spots were less consistent, although they were usually in the southern part of the region if present.

Discussion

Results were complex and illustrate that bat activity and species diversity are impacted by a wide variety of factors, with structural and contextual characteristics having the greatest impact. Best fitting models also mainly consisted of many variables with each one making a small contribution instead of one variable contributing the most. These models successfully show the habitat variables at multiple scales that are most associated with bat species richness and average activity. The species richness models had a higher AICc and lower R^2 than the activity model, so the activity models may be better predictors of what makes high quality bat habitat, although both are worth considering when managing for bats.

Scale was one factor causing variability in results. Variables that were important at one scale were often not important at another. For instance, variables that were strongly associated with bat activity or species richness at 100 m were often not associated with it at 500/250 m (e. g. perennial ponds), and vice versa. This supports previous findings that it is important to use multiple spatial scales (Gallo et al. 2017).

There were consistent hotspots of bat activity along transects between years. These hotspots were mainly located near Metroparks, which indicates the importance of protected parks. It is unclear why so many were clustered in the northern region, but this may be related to the northern region having less cropland cover. Cold spots with no activity, while not consistent between years, were located in the southern region where there was heavy cropland cover. If cropland avoidance is influencing the location of hot and cold spots of activity, it is consistent with other findings along transects. Hotspot analysis was shown to be a reliable method for determining areas of highest activity across years.

Bats avoided areas with higher amounts of cropland along transects. Species richness and activity were lower when at least one side of the road had agricultural habitat unless the other side was natural and cropland was negatively associated with bat activity and species richness along transects. Previous studies also found that bats generally avoided areas with high agricultural cover (Blakey et al. 2017; Put et al. 2019). Most of the agriculture in the region consists of large row crop monocultures. Previous research shows that increasing farmland heterogeneity or using organic farming methods is beneficial to bat activity and diversity, so if possible, encouraging local farms to diversify their crops, plant tree rows, or use organic methods could help bats (Monck-Whipp 2018; Wickramasinghe et al. 2003).

While activity and species richness were lower when there was agricultural habitat on one side of the road, they were higher with natural habitat on one side of the road compared to points with only agricultural or residential habitat. Points with natural habitat on both sides did not have significantly higher activity or richness than those with natural habitat on only one side. Retaining natural field or forest habitat alongside the road on at least one side would be beneficial in managing for ideal bat habitat. It is worth noting that the number of bats killed by cars is also higher in these areas of high-

quality habitat, so they could serve as ecological traps unless high speed traffic is limited in areas of especially high bat activity (Medinas et al. 2012; Russo and Ancillotto 2015). Also, landscape scale results showed that types of natural habitat didn't impact bats equally.

Open habitats such as savanna and upland prairie were positively associated with activity and/or species along transects. Savanna was positively associated with both species richness and activity at transect points. Buckman-Sewald (2014) found higher activity of hoary bats, one of the most common species along transects, in savanna habitats. This may be contributing to higher activity in areas of more savanna cover along transects. The lack of clutter from tall trees in shrubs in these habitats likely make them easier for bats to forage in, especially for open adapted species such as hoary bats. While savanna habitats have increased in cover in recent years due to restoration efforts (Martin and Root 2020), additional restoration may be beneficial to bats.

Floodplain forests in larger size buffers was negatively associated with activity along transects. However, Blakey et al. (2017) found higher bat activity in floodplain forest. This could mean that the impact of floodplain forests is somewhat variable. Higher percent conifers in larger size buffers were also associated with lower activity and species richness at transect points. Previous studies have found that bats utilized conifer stands less or not at all (Yoshikura et al 2011). Many of the conifer forests in the Oak Openings region are non-native commercial pine stands that generally less diverse than surrounding forests (Abella 2010; Abella et al. 2017). Previous studies have found increased plant and wildlife diversity when removing or thinning these pine stands in the region, with additional efforts to remove and convert this land to early successional cover underway (Abella 2010; Abella et al. 2017; Martin and Root 2020). My results suggest that removing or thinning these pine stands could be beneficial for bats, as they generally avoid areas with large blocks of this habitat type. While forest cover is usually positively associated with bat activity, the presence of these specific types seems to be detrimental for bats. This could be related to low forest quality for these types or that the most common bats around road transects are open-foraging species.

Total percent forest was positively associated with activity along transects. This indicates that while specific forest types were detrimental to bats, overall forest cover still seems to have a positive impact along roads. Previous studies also found a significant positive impact of total forest cover along roads and developed areas, although there is some variability based on species (Evelyn et al. 2004; Medinas et al. 2019). There was a positive association between canopy height and species richness and between average percent canopy cover and total activity. Previous studies have also found positive associations between canopy height and cover and bat activity, especially along roads (Bader et al. 2015; Bailey et al. 2019; Jung et al. 2012; Russell et al. 2009). This combined with the forest cover results indicates that planting trees along roads could be beneficial for bats. Other structural variables, such as clutter, were also important.

For clutter, whether the impact was positive or negative depended on the height level. There were negative associations between clutter at 3-6.5 m and species richness and activity along transects. This supports

previous findings that bats avoid areas of higher vegetation clutter and taller understory cover (Adams et al. 2009; Campbell et al. 1996; Lintott et al. 2015; Rainho et al. 2010). However, there were positive associations with clutter 0–3 m for the open guild at stationary points and for species richness and activity along transects. This is likely because most open habitats had higher clutter at the lower height level and less clutter at the higher height level, which is ideal for open foraging species, the most common group along transects. These results suggest that it would be advantageous for open foraging bats for land managers to reduce clutter at the 3-6.5 m level, while increasing low level vegetation along roads.

Water is another resource that should be increased along roads. Higher percent of ponds in 100 m buffers was significantly correlated with higher species richness along transects. Combined with the positive association between months water observed at transect and species richness, this indicates that water is especially important to a diverse bat community along roads. It is worth noting that number of months where water was recorded was only recorded in 2021, while previous years whether ditches were present was only noted once a season (if ditches were present once, they were noted as present all month for those years), so that may have impacted results. This is consistent with past findings (Gaisler et al. 1998).

Meters of roads were positively associated with bat activity along transects, indicating that roads and fragmentation can have a positive impact on bat activity rather than negative, albeit only for open-foraging species that forage along habitat edges. The importance of forest, water, and roads along roads was consistent with past findings (Gaisler et al. 1998; Myczko et al. 2017). The number of habitat types was positively associated with species richness and activity along roads, which indicates that fragmentation and habitat heterogeneity is positively associated with bat activity along roads. This may be because bat species foraging along roads tend to be more fragmentation tolerant and prefer to forage along habitat edges.

Northern long-eared bats were never found along transects and little-brown bats and tri-colored bats very rarely were. These species were located more frequently, although they were still rarer than other species, during surveys in protected parks in the same region during the same period (Russo-Petrick 2022). All three of these species are of conservation concern, so this indicates that roadside habitats are not preferred by these species. While some variables were consistently important, the variety in results and that no one variable had an especially large contribution to models shows how complicated the question of what habitat factors impact bats is and how much results can vary when multiple scales are considered.

Conclusions And Management Recommendations

Based on our findings, future studies of how landscape variables affect bats should use multiple scales, since impacts differed depending on the scale measured. For instance, even within the landscape scale, habitat variables important in one size buffer were not important in the other size buffer. Certain variables at both local and landscape scales were consistently important. For instance, at the point-level scale

clutter at the 0–3 m level, canopy height and canopy cover were consistently positively associated with bat activity and/or species richness, while clutter at the 3-6.5 m level had a negative association. Land managers should increase tall tree cover and avoid mid-height shrub cover along roads to improve bat habitat there. The importance of ponds and months water in models also indicates that increasing water sources such as ditches along roads may help bats. At the larger scale, the activity and species richness of foraging species that forage along roads were positively associated with habitat heterogeneity and fragmentation by roads although this may not hold for all species in all areas. Other large-scale habitat characteristics that appear to be beneficial for bats along roads include percent savanna, upland prairie, total forest cover, while bat activity and/or species richness were lower with more upland conifer, floodplain forest, and cropland cover. Avoiding adding more cropland or conifer cover near roads and increasing savanna and upland prairie cover may also help bats. Finally, these results show how road surveys can be a useful method for monitoring bat activity and species richness across multiple scales.

Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

All authors contributed to study conception and design. Data collection and analysis were performed by and the first draft of the manuscript was written by Kelly Russo-Petrick All authors commented on subsequent drafts of the manuscript and read and approved the final manuscript.

Data Availability

The datasets generated during and/or analyzed during this study are available from the corresponding author upon request.

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Tables

Table I: Final stepwise regression models for bat species richness transect points. The amount of contribution by each variable (parameter estimate) is written next to it in parentheses, as is the scale the variable was measured at (point- or landscape scale). The best fitting variables from 500 m radius land cover, 100 m radius land cover, fragmentation and light pollution, weather, and vegetation structure models were used to create these. Lower AICc values show a stronger fit.

Variables	AICc	R ²
Canopy height m (0.0115)	1315.089	0.3326
% savanna in 250/500 m (3.5352, landscape scale)		
% conifer forest in 250/500 m (-2.1997, landscape scale)		
% cropland in 500/250 m (-0.6962 landscape scale)		
% ponds in 100 m (9.2928, landscape scale)		
% upland prairie in 100 m (0.9315, landscape scale)		
# of habitat types in 500/250 m (0.0654, landscape scale)		
Avg. % clutter 0-3 m (0.007, local scale)		
Avg. % clutter 3-6.5 (-0.0042, local scale)		
Months water present (0.0435, local scale)		
Min. barometric pressure in (-2.0506, local scale)		
Max. barometric pressure (1.7551, local scale)		
Min. temperature (0.04225, local scale)		

Table II: Final stepwise regression models for total bat activity at transect points. The amount of contribution by each variable (parameter estimate) is written next to it in parentheses, as is the scale the variable was measured at (point- or landscape scale). The best fitting variables from 500 m radius land cover, 100 m radius land cover, fragmentation and light pollution, weather, and vegetation structure models were used to create these. Lower AICc values show a stronger fit.

Variables	AICc	R ²
% upland conifer forest in 500/250 m (-0.5987, landscape scale)	-35.6885	0.2883
% total forest in 500/250 m (0.2034, landscape scale)		
% floodplain forest in 500/250 m (-0.8982), % cropland in 500/250 m (-0.1587, landscape scale)		
M. of road in 500/250 m (<0.0001, landscape scale)		
Number of habitat types in 500/250 m (0.0064, landscape scale)		
Avg. % clutter 0-3 m (0.0020, local scale)		
Avg % clutter 3-6.5 m (-0.0013, local scale)		
Max. temperature °F (0.0093, local scale)		
Max. humidity % (0.0037 Avg. % clutter 0-3 m (0.0020, local scale)		
Max. barometric pressure in. (0.2822, local scale)		
Habitat type (0.0147, local scale)		
Avg. % canopy cover (0.0011, local scale)		

Figures

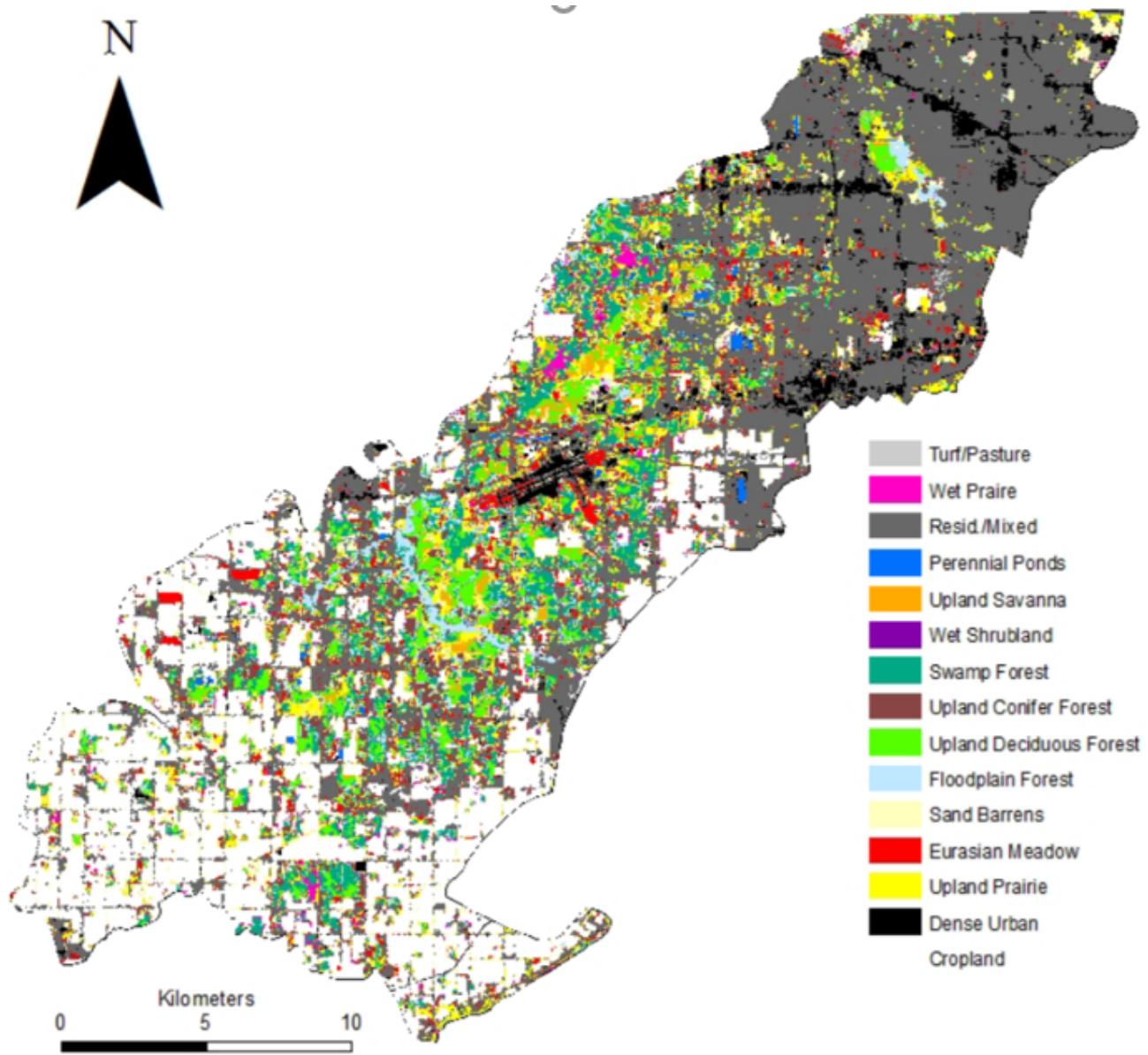


Figure 1

The Oak Openings Region land cover map of northwestern Ohio using the Brewer-Vankat boundary (Martin and Root 2020).

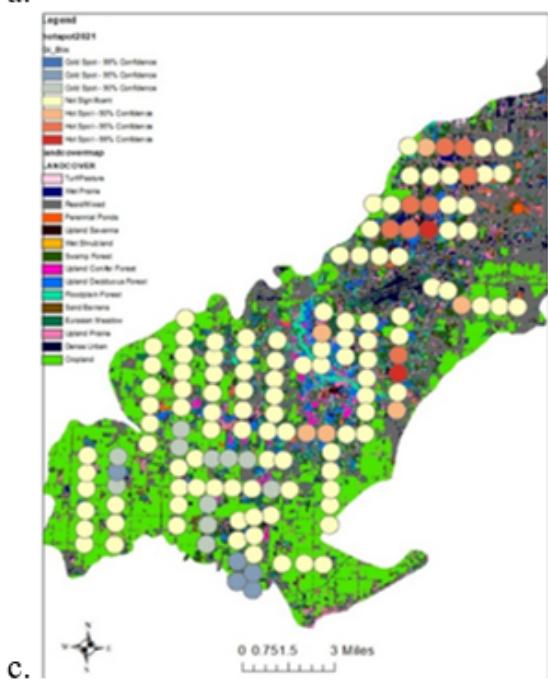
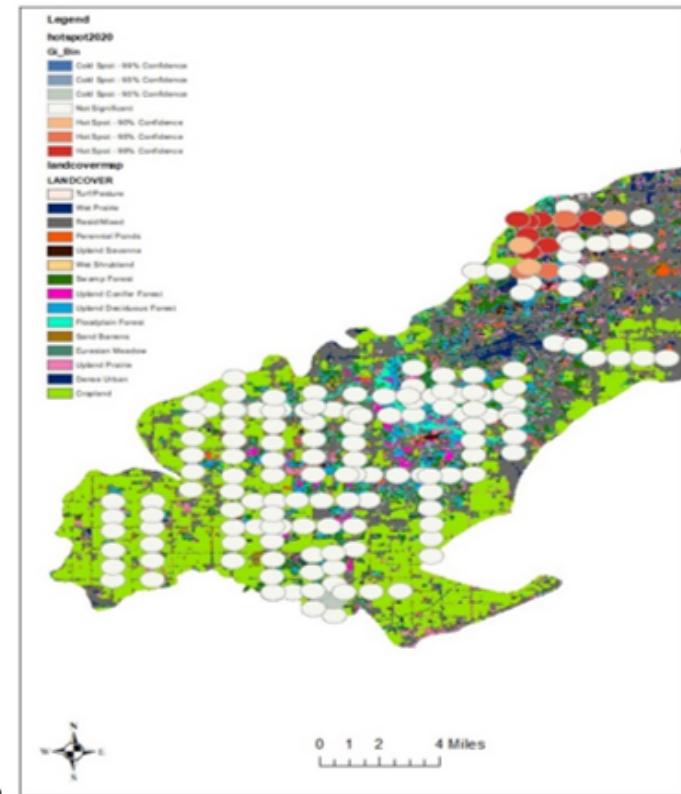
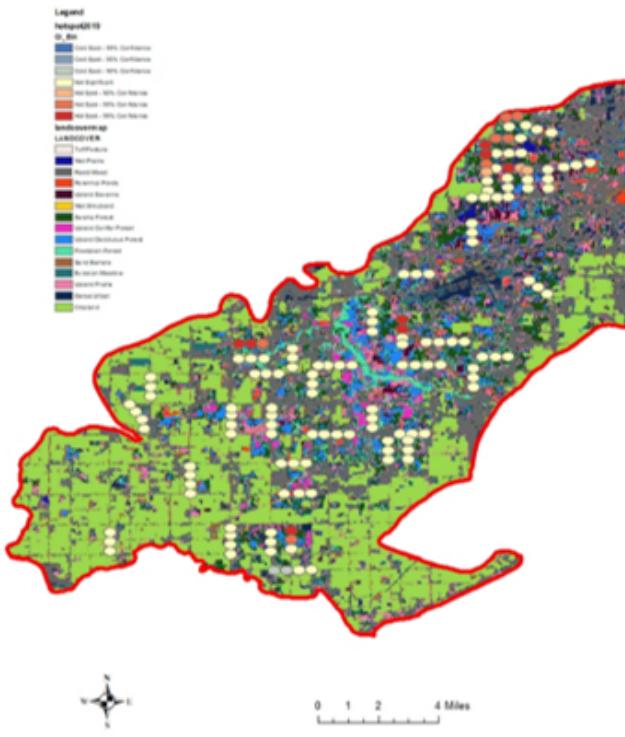


Figure 2

Hotspot maps from a. 2019, b. 2020, and c 2021

Supplementary Files

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- Appendix1.docx