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

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# Abstract

Roads have variable impacts on wildlife, including bats. Bat habitat preferences along roads vary across spatial scales, creating the need for multi-scale habitat studies. The main objective of this study was to determine what habitat factors impact bat activity and species richness along road transects at local and landscape scales and to identify areas of highest bat activity in the Oak Openings Region of Northwest Ohio using acoustic monitoring. At the local scale, bat activity and/or species richness were positively associated with canopy height, clutter at 0-3 meters, humidity, natural habitat, canopy cover, months water present, and temperature, and were negatively associated with clutter at 3-6.5 meters. At the landscape scale, activity and/or richness had positive associations with habitat heterogeneity, roads, open natural habitats, ponds, upland prairie, and overall forest cover, and had negative associations with conifers and cropland. High activity areas were consistent between years and clustered in the northern part of the region, especially near protected areas and low activity areas were typically located in the southern part of the region near agricultural areas. When managing bat habitat along roads, it would be advantageous to decrease mid-level clutter, vary habitat types, increase savanna and upland prairie cover, avoid excessive conifer or cropland cover, plant tall trees, and provide water sources. This study shows that combining acoustic road surveys with habitat analyses at multiple scales can be used to examine the most important habitat factors influencing bat activity and species richness.


# Introduction

Roads are ubiquitous across the landscape. They cover over 21 million km and are expected to increase 25% in length by 2050 (Meijer et al. 2018). Additionally, many of the habitat patches in the world that are roadless are highly fragmented by surrounding roads, with more than half the roadless land in patches smaller than 1 $km^2$ (Ibisch et al. 2016).

The ubiquitous nature of roads increases the need to know their impacts on wildlife. Roads adversely affect wildlife by increasing mortality, reducing habitat connectivity, size, and quality, and altering behavior through noise and light pollution (Dean et al. 2019; Ramp et al. 2006; Riley et al. 2014). However, some wildlife gain advantages from roadside habitats. For instance, some species, especially predators, use the edges created by roads as movement and vegetation by roadsides can provide food and shelter, especially in highly developed areas (Bennett 1991; Ramp et al. 2006; Riley et al. 2014). Highly-mobile flying species are more likely to suffer negative impacts from roads because they interact with them more (Rytwinski and Fahrig 2012). Among highly-mobile species, those with low reproductive rates and small body size are most vulnerable to negative impacts from roads (Rytwinski and Fahrig 2012). Still, the impacts on flying species are overall variable for the same reasons that road impacts on wildlife are variable in general, as they are also negatively impacted by mortality, decreases in habitat quality and connectivity, and noise and light pollution from roads, but use road edges for movement and some animals such as bats forage on insects gathered around roadside lights (Ethier and Fahrig 2011; Stone et al. 2015).

Bats are one highly-mobile flying group that is variably impacted by roads. For example, some bats may avoid roads due to risk of collisions with vehicles, high traffic noise making prey detection difficult, higher chemical pollution that can harm bats and their insect prey, and increase predation risk from light pollution (Altringham and Kerth 2016; Fensome and Matthews 2016; Schaub et al. 2008; Stone et al. 2015; Zurcher et al. 2010). This avoidance can cause a reduction in habitat connectivity as roads fragment the landscape, which prevents bats from accessing resources (Russo and Ancillotto 2014). Despite these negative impacts, roads can have some positive effects and attract some bat species, such as the hoary bat (Barclay 1985). For instance, streetlights and roadsides in general can attract some bat species because the insects they feed on congregate around there and roads also create habitat edges for open-foraging bat species (Bernes et al. 2017; Dean et al. 2019; Ethier and Fahrig 2011; Longcore and Rich 2004; Rotholz and Madelik 2013). Bat species that are rare, specialists, forest foraging, and low-flying, such as *Myotis* spp., tend to avoid roads, while species that forage in open areas, common, generalists, and high-flying are more likely to forage on roads (Altringhman and Kerth 2016; Fensome and Matthews 2016; Fuentes-Montemayor et al. 2013; Lacoeuilhe et al. 2014; Longcore and Rich 2004; Stone et al. 2015; Zurcher et al. 2010).

Previous research has found that bat activity along roads tends to be lower where the amount of residential and agricultural areas are 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 vehicular collision may be 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, however, the presence of native forest can decrease collisions since it may decrease the need to cross the road to find suitable habitat (Secco et al. 2017).

While some research exists on what roadside habitat is most important for bats, more data is needed, as most existing studies are single scale and examine a small number of variables at once (Medinas et al. 2013; Medinas et al. 2019; Pourshoushtari et al 2018). It is important to use multiple scales for this analysis, since bat habitat use is scale-dependent (Gallo et al. 2018). 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).

This study examines what habitat factors are associated with bat activity and species richness along road transects in a mixed-use landscape in Northwest Ohio during 2019–2021. 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 some areas, called “hotspots,” will have significantly higher activity. We also predict that areas of higher residential and agricultural cover will have less bat activity and species richness than natural habitats.

# 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 kilometers (km)/km$^2$ within a 1 km buffer (Adams 2014). Despite the heavy 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, including the big brown (*Eptesicus fuscus*), little brown (*Myotis lucifugus*), northern long-eared (*Myotis septentrionalis*), tri-colored (*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 areas around them (Hollen 2017; Turner 2018), so this will be the most spatially widespread dataset to date.

# Acoustic Monitoring

Acoustic monitoring has been an increasingly popular and reliable technique for observing activity of wildlife, including bats (D'Acunto et al. 2017; Fisher-Phelps et al. 2017; Lacoeuilhe et al. 2014; Medinas et al. 2019). Acoustic monitoring is useful, because it is non-invasive, allows for collection of large amounts of data across a wider spatial and temporal range than mist nets, is omnidirectional, and captures a wider range of species than mist nets (Gibb et al. 2019; O'Farrell et al. 1999). Road transects were surveyed by driving along them at 32 km/hour (h) twice a month from May-September 2019–2021. Bat activity was continuously recorded using an Anabat SD2 monitor and an attached GPS unit fixed on a paint pole with bungee cords and rubber bands. Road surveys started 30 minutes after sunset and ended 3 hours after sunset, which is the timeframe during which bat activity peaks (Hayes 1997; Buckman-Sewald et al. 2014). Detection distance of monitors varies but is typically around 30–40 m (Hollen 2017, Loeb et al. 2019). 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). A total of 74 1–5 km transects were surveyed across 3 years. We chose transects that covered as many different habitats and land use types as possible (e.g. a mix of forested, residential, agricultural, and savanna areas) and had annual average traffic volume of less than 4000 (Ohio Department of Transportation).

# Local Scale Habitat Data

Local scale variables were measured in the field, and visually estimated if transect points were located on private land (Appendix 1). Canopy cover, vegetation density, canopy height, and understory vegetation height were measured 15 m away from the road on both sides at set points 500–1000 m away. The 15 m distance and sampling protocol was based on prior roadside habitat surveys and is about half the average range of the Anabat detector (Hollen 2017; Turner 2018). 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 tall cloth scatter board and subtracting that from the total number of squares at the 0–3 m level and 3-6.5 m levels. The number of saplings, which were defined as trees with diameters between 2.5–12.7 centimeters (cm) (Crocker 2017) within the 15 m radius was counted starting in 2020. Illumination (in lux) was measured during nighttime transect surveys using a light meter at the same transect points from the road. Distance to light, measured using a rangefinder, and whether streetlights or ditches were present were also recorded at transect measuring points once a year from the road. Habitat on each side of the road was characterized as natural, agricultural, or residential at every survey point along road transects once a year. We classified land use in 1 of 6 categories, with 1 both sides of the road residential, 2 one side residential and one side agricultural, 3 both sides agricultural, 4 one side residential and one side residential, 5 one side agricultural and the other side natural, and 6 both sides natural.

NOAA historic weather data for temperature (°C), humidity (%), wind speed (km/h) and barometric pressure (inHg) were 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 were used to measure the same variables before each survey in 2020–2021 to get more precise measurements. Results were shown to be very similar between both years using either method by checking Weather Underground for the same sites in 2020–2021 and running a correlation analysis (correlation > 0.8). 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 classified as local scale because they were measured in the field.

# Landscape Scale Habitat Data

Landscape scale habitat characteristics were analyzed in ArcMap 10 (ESRI, Redlands, California, USA) and FRAGSTATS 4.2 (McGarigal and Marks 1995) (Appendix 1). 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. In 2019 250 m buffers were used around transect sampling points but were changed to 500 m in 2020 and 2021 because 250 m buffer data was overly correlated with 100 m buffer data (> 0.8). It was determined that the buffer size change from 250 to 500 m did not cause bias in total percentage using multivariate comparisons in JMP because variables taken in 250 m buffers were over 80% correlated with the same variables in 500 m buffers around the same points. When 250 and 500 m buffer data were combined, they were no longer consistently overly correlated with 100 m buffer data. Percent of each land cover type was measured 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 length of roads in meters (m) 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 4.2 with no sampling was used to measure cohesion index, Simpson's Diversity Index (SIDI), and contagion index for all land cover types. The number of habitat types in each size buffer was also counted.

# Data Analysis

Identifications of bat calls were made in Analook by comparing sonograms to existing call libraries (Buckman-Sewald 2014). Species identifications were made based on time and frequency. An automated identification program (BCID) was also used when possible. Number of total calls was used as a measure of relative bat activity. Bat calls were counted as being at whichever sampling point was closest. Total calls were summed for all months for each year and then averaged before final analysis.

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 (Appendix 2). We used forward stepwise regression tables using Akaike information criterion ($AIC_c$) in JMP to examine relationships between activity and species richness and the local and landscape habitat variables. This method was used because of the massive number of potential variable combinations, since it let us explore all possible combinations in an automated manner (Pauli et al. 2015). 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. Combined models were created using any variables that made the best fitting 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.

# Hotspot analysis

Hotspots are specific areas within a larger region with particularly high concentrations of individuals or species or 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). 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. Hotspot analysis was conducted in ArcMap 10 using the Getis-Ord Gi* statistic (Ord and Getis 2001) to find the major areas of bat activity along transects for each year to examine how bat spatial distribution changed over time. We used the larger size buffer radius (i.e. 500 m) around each survey point. The Getis-Ord Gi* statistic finds areas that have significantly higher than average values (hot spots) and lower than average values (cold spots) of clustering within a 90% confidence interval (Ord and Getis 2001). All bat occurrence points across May-September 2019–2021 were used to calculate hotspots based on total activity for each year.

# Results

## Acoustic Monitoring

All calls were able to be identified to species. A total of 3383 calls were recorded across 3 years (Table 1). Activity per transect point across all 5 months ranged from 0 to 31 calls, with an average of 5.63 calls. Species richness per individual transect point ranged from 0 to 6, with an average of 2.84 species. Of the eight species known to be found in the area, seven were detected along transects, with the northern long-eared bat the only local species not found on transects.

Table 1
Bat species identified with total number of acoustic calls along road transects per year 2019–2021. Months represented by number: May (5), June (6), July (7), August (8), and September (9). Northern long-eared bats were omitted due to not being detected on transects

| **Species** | **2019** | **2020** | **2021** | **Total** |
| --- | --- | --- | --- | --- |
| Big Brown (*Eptesicus fuscus*) | 260 | 365 | 455 | 1080 |
| Little Brown (*Myotis lucifugus*) | 3 | 0 | 6 | 9 |
| Tri-colored (*Peromyotis subflavus*) | 2 | 0 | 3 | 5 |
| Evening (*Nycticeius humeralis*) | 21 | 8 | 14 | 43 |
| Hoary (*Lasiurus cinereus*) | 92 | 359 | 492 | 943 |
| Eastern red (*Lasiurus borealis*) | 15 | 149 | 152 | 316 |
| Silver-haired (*Lasionycteris noctivagans*) | 171 | 236 | 234 | 641 |
| Total | 564 | 1117 | 1356 | 3037 |

## Local Scale Habitat Data

Local scale habitat variables in the best model for species richness (Table 2) 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. 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. Average percent clutter at 3-6.5 m and minimum barometric pressure were negatively associated with bat species richness.

Table 2
Variables in best fitting stepwise regression model for bat species richness along transect points (AICc = 1315.089, $R^2$ = 0.3326). The scale, coefficient, and upper and lower 95% confidence intervals are listed by each variable. The best fitting variables from 250/500 m radius land cover (larger size buffer), 100 m radius land cover (smaller size buffer), fragmentation and light pollution, weather, and vegetation structure models were used to create these

| Variables | Scale | Coefficient | Upper 95% | Lower 95% |
|---|---|---|---|---|
| Percent savanna in larger size buffer | Landscape | 3.5352 | 5.9309 | 1.3953 |
| Percent conifer forest in larger size buffer | Landscape | -2.1997 | -0.1158 | -4.2836 |
| Percent cropland in larger size buffer | Landscape | -0.6962 | -0.1627 | -1.2296 |
| Percent ponds in smaller size buffer | Landscape | 9.2928 | 20.0457 | -1.4600 |
| Percent upland prairie in smaller size buffer | Landscape | 0.9315 | 1.9677 | -0.1047 |
| Number of habitat types in larger size buffer | Landscape | 0.0654 | 0.1270 | 0.0038 |
| Average percent clutter 0–3 meters | Local | 0.0070 | 0.0129 | 0.0018 |
| Average percent clutter 3-6.5 meters | Local | -0.0042 | -0.0003 | -0.0081 |
| Canopy height (meters) | Local | 0.0115 | 0.0244 | -0.0013 |
| Habitat type | Local | 0.0500 | 0.1146 | -0.0147 |
| Months water present | Local | 0.0435 | 0.1020 | -0.0150 |
| Minimum barometric pressure (inches) | Local | -2.0506 | -0.0680 | -4.0331 |
| Maximum barometric pressure (inches) | Local | 1.7551 | 3.4551 | 0.0551 |
| Minimum temperature (ºF) | Local | -0.0423 | 0.0650 | 0.0195 |

Local scale variables in the best fitting final model for bat activity (Table 2) 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 one side natural and the other agricultural had significantly higher activity than those with both sides agricultural. 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, 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 2) included savanna, conifer forest, cropland and the number of habitat types in larger sized buffers, ponds and upland prairie in smaller sized 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 3) included percent upland conifer forest, total forest, cropland, 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 and upland conifer forest in larger size buffers were negatively associated with average bat activity.

Table 3

Final stepwise regression models for total bat activity at transect points(AICc= -36.1388, $R^2$ = 0.2856). The scale, coefficient, and upper and lower 95% confidence intervals are listed by each variable. The best fitting variables from 500/250 m. radius land cover (larger size buffer), 100 m. radius land cover (smaller size buffer), fragmentation and light pollution, weather, and vegetation structure models were used to create these.

| Variables | Scale | Coefficient | Upper 95% | Lower 95% |
|---|---|---|---|---|
| Percent upland conifer forest in larger size buffer | Landscape | -0.6240 | -0.0005 | -1.0600 |
| Percent total forest in larger size buffer | Landscape | 0.1996 | 0.3698 | 0.0294 |
| Percent cropland in larger size buffer | Landscape | -0.1397 | -0.0212 | -0.2582 |
| Meters of road in larger size buffer | Landscape | < 0.0001 | < 0.0001 | < 0.0001 |
| Number of habitat types in larger size buffer | Landscape | 0.0125 | 0.0252 | -0.0001 |
| Average percent clutter 0–3 meters | Local | 0.0020 | 0.0034 | 0.0007 |
| Avg percent clutter 3-6.5 meters | Local | -0.0013 | -0.0005 | -0.0021 |
| Average percent canopy cover | Local | 0.0011 | 0.0024 | -0.0002 |
| Habitat type | Local | 0.0142 | 0.0282 | 0.0002 |
| Maximum temperature (ºF) | Local | 0.0090 | 0.0157 | 0.0023 |
| Maximum humidity (percent) | Local | 0.2307 | 0.0069 | 0.0002 |
| Maximum barometric pressure (inches) | Local | 0.2937 | 0.6178 | -0.0303 |

# 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, especially near protected areas. 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 richness are impacted by a wide variety of factors, with structural and contextual characteristics, such as clutter and habitat type, 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. While our models are large for best fitting regression models, they had lower $AIC_c$ and higher $R^2$ values than all alternate models with less variables. Our models show the habitat variables most associated with bat species richness and activity at multiple scales. While similar results from other studies imply these factors in our best-fitting models are likely important in multiple areas (Adams et al. 2009; Bader et al. 2015; Bailey et al. 2019; Blakey et al. 2017; Buckman-Sewald 2014; Campbell et al. 1996; Evelyn et al. 2004; Gaisler et al. 1998, Hollen 2017; Jung et al. 2012; Lintott et al. 2015; Medinas et al. 2019; Put et al. 2019; Rainho et al. 2010, Yoshikura et al. 2011), our results may not apply to all areas, so more research is needed to confirm generalizability, especially since no specific variable contributed a particularly large amount any one model.

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 by Gallo et al. (2018), who found that different variables were important at 50 m, 500 m, and 1 km scales. There may be a difference between 100 m and 250/500 m buffers but not 250 and 500 m buffers because 100 m buffers are closer to local scale than 250 and 500 m ones. For instance, number of habitat types was important in 250/500 m buffers but not 100 m ones. The number of habitat types was positively associated with species richness and activity along roads, which indicates that habitat heterogeneity is positively associated with bat activity along roads. This may be because bat species found foraging along roads tend to be more fragmentation tolerant and prefer to forage along habitat edges, such as hoary bats (Barclay 1985, Hollen 2017). This variable being more important at only larger size buffers implies a more large scale effect of this variable.

Bat activity was also not evenly distributed across the region. Survey points with agricultural habitat on at least one side of the road tended to have lower bat activity and species richness than those without agricultural cover and points with natural habitat on at least one side of the road generally had higher activity and species richness than those without natural habitat. Furthermore, spots of the least bat activity were clustered in the part of the region with the most agriculture. 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, but previous research showed that increasing farmland heterogeneity or using organic farming methods is beneficial to bat activity and diversity. 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) and retaining natural field or forest habitat alongside the road on at least one side would also be beneficial in managing for ideal bat habitat. Both natural open and forested habitats were beneficial for bats, although the type of forest mattered to some extent.

Open habitats such as savanna and upland prairie and total forest were positively associated with activity and/or species along transects. While savanna habitats have increased in cover in recent years due to restoration efforts (Martin and Root 2020), additional restoration may be beneficial. 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, as the lack of clutter from tall woody vegetation in these habitats likely make them easier for open-adapted bat species to forage in. 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). Conifers were the only type of forest that was negatively associated with bat activity, which may be because most conifer cover in the area is farmed monotypic stands (Abella 2010, Abella et al. 2017). The finding that higher percent conifers was associated with lower activity and species richness is consistent with previous studies (Buckman-Sewald 2014, Hollen 2017, Yoshikura et al. 2011). Natural habitat with diverse vegetation appears to be most beneficial for bats.

For clutter, whether the impact was positive or negative depended on the height level. Both species richness and bat activity were negatively associated with clutter at 3-6.5 m 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 with species richness and activity along transects. This is likely because open habitats associated with higher bat activity and species richness, such as savanna and upland prairie 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 if land managers reduce clutter at the 3-6.5 m level and increased low level vegetation along roads. Other structural variables, such as clutter, were also important.

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 indicates that planting tall trees along roads potentially could be beneficial for bats.

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 could be important to a diverse bat community along roads. This is consistent with past findings (Gaisler et al. 1998). 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 every month for those years), so that may have impacted results.

Some species foraged along roads more than others. Northern long-eared bats were never found along transects and little-brown bats and tri-colored bats very rarely were. These three 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. This may be because we examined all species together, and responses are species specific or differ between forest and open habitat specialist guilds. Comparing results between open and forest specialist guilds at stationary points revealed differences in habitat preferences between the groups and less variables were used in those models, but forest specialist activity along transects was too low compared to open specialists to do similar models for transects (Russo-Petrick 2022). Because of the complicated nature of bat community responses, looking at guild or species-specific responses may be beneficial in the future if there are enough calls to do so.

# Conclusions And Management Recommendations

Based on our findings, future studies of how habitat variables affect bats should use multiple scales, since we found varying impacts both temporally and spatially. Even within the landscape scale, habitat variables important in one size buffer were not important in the other. While caution should be applied when attempting to generalize these results, certain variables at both local and landscape scales were consistently important. For instance, at the local-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 landscape scale, bat activity and species richness 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 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. Kelly Russo-Petrick did data collection and analysis and wrote the first draft of the manuscript. Karen Root helped with project design and editing the manuscript. 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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# Figures

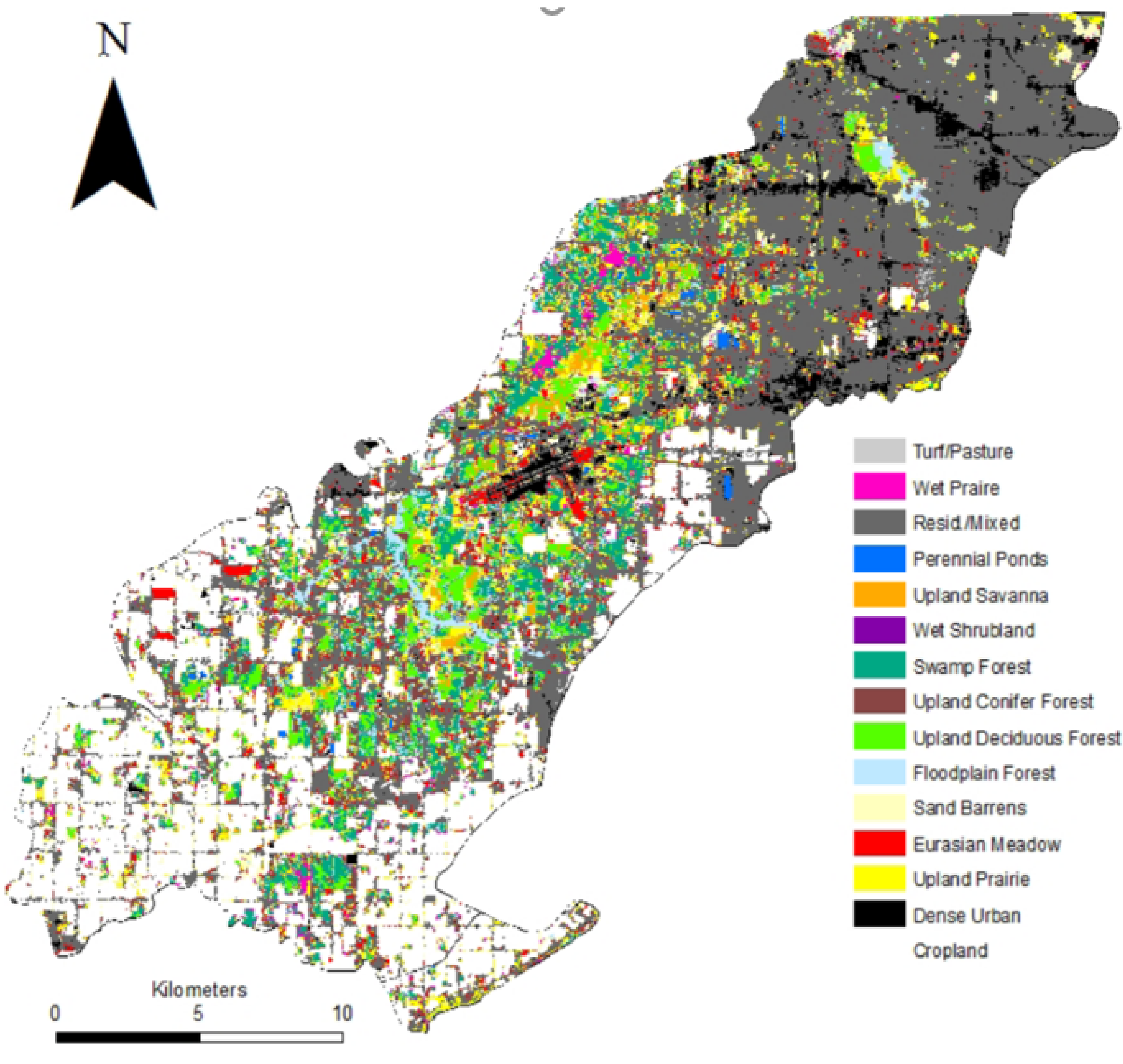
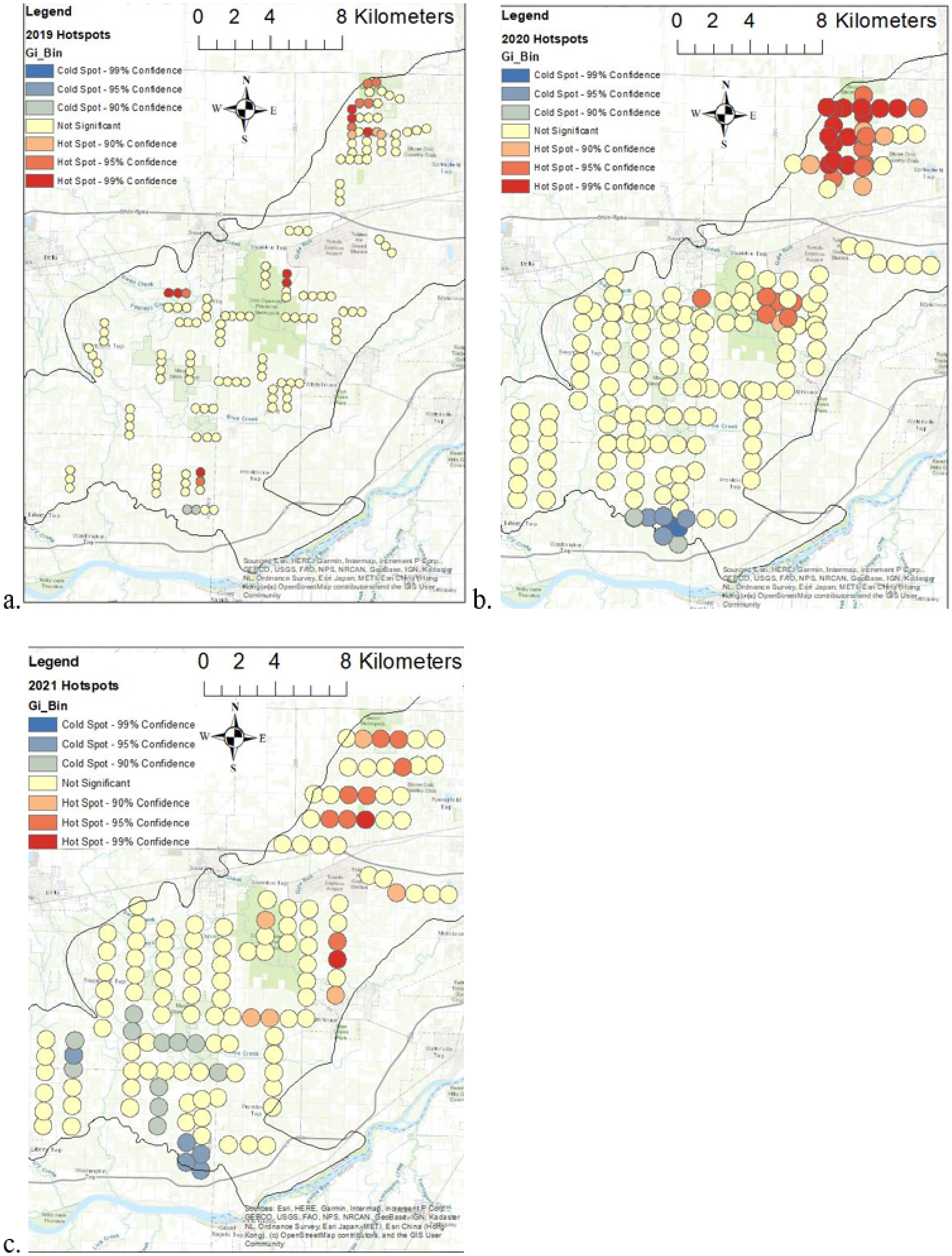



**Figure 1**

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




## Figure 2

Hotspot maps from a. 2019, b. 2020, and c 2021. Hot spots (>90% confidence interval of significantly high clustering of bat activity) are in red and cold spots (>90% confidence interval of significantly low clustering of bat activity) are in blue

# Supplementary Files

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- Appendix.docx