**Bat activity on golf courses influenced by landscape context in northeastern U.S.**

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**0. Abstract**

As golf grows in popularity, golf courses’ potential as wildlife habitat becomes increasingly relevant. Golf courses frequently contain similar features such as rows of trees, ponds, and grasses mowed to various lengths. They vary in their surrounding landscape matrix, as some golf courses may be surrounded by highly-urban or highly forested-areas. Bats may make frequent use of golf courses depending on the environment that surrounds it. We surveyed bats on 11 New Jersey golf courses in 2019 and 2020 to investigate at what point golf courses become important for bats. We measured landscape features within a 2km radius of the course, and we compared them to bat activity at each course using generalized linear mixed models. We recorded over 33,000 bat echolocation signatures in total. Depending on species-specific preferences, bats tended to be more active on golf courses when there were more roosting habitats and/or less foraging habitats nearby. This suggests that bats may be using golf courses as an escape from a less suitable environment. For example, our models agree with the existing body of literature that *Lasiurus borealis* tends to avoid urban areas, and they prefer to forage over streams and fields. Roosting habitat was most important for *Eptesicus fuscus*, as they were more active on golf courses when the surrounding area contained more suburban areas (their preferred roosting sites). Golf courses in the temperate zones of the United States represent strictly maintained green spaces in an increasingly developed landscape. Though there may be no replacing the natural habitat that is lost, golf courses may provide a refuge for bats with fewer nearby alternatives.

**1. Background**

Golf courses are generally common in developed areas, and they are likely to become more numerous as golf grows in popularity. As of 2019, there were 38,864 golf courses in the world, and more are being planned and constructed every year (R&A 2019). Globally, there are 209 countries that have at least one active golf course. The United States accounts for 16,752 golf courses (~43% of the world’s courses), making it the number one golfing country in the world by a wide margin. They are controversial for their environmental impacts, and protests from the general public have been violent in some cases (Briassoulis 2010). Depending on the resources available in the surrounding landscape, building and maintaining a golf course could severely disturb the ecosystem (Palmer 2004, Wheeler and Nauright 2006). That being said, context matters. A golf course in a dry climate may be ill-suited to support lush grasses, and sustaining playable conditions may require unnatural amounts of water and nutrients to be introduced to the ecosystem. However, golf courses located amidst temperate forests are much more sustainable, and they are likely to include natural elements like streams and large trees as obstacles for play. In our study, we turn our attention to the temperate zone and the golf courses that reside within it. The northeastern United States is located within the eastern temperate forest eco-region (EPA 2010, Omernik and Griffith 2014), and golf courses (both public and private) are common.

Depending on landscape context, golf courses represent an urban green space that can support biodiversity in much the same way as a park (Petrosillo et al. 2019). By very nature of the sport, golf courses are generally quiet places with a consistent suite of features. Open fields, wooded corridors, unmowed patches of grass, ponds, and large native trees are all familiar sights on virtually any golf course. The standardized template of most golf courses could be attributed to what golfers refer to as “Augusta National Syndrome”, named after what is considered the biggest event in modern golf. Golfers who watch this televised event expect to find similar features on their local golf courses, and the local golf courses are pressured to supply that standard experience (Millington and Wilson 2016). Thus, the consumer market guides golf courses towards a convergent form. For better or worse, their consistency lends itself well to scientific research.

Additionally, there is a vested interest in making golf courses more eco-friendly. There are incentives for courses that adhere to regulations and make active efforts to improve their potential as wildlife habitat. The Audubon Society has its own certification program for golf courses called the Audubon Cooperative Sanctuary Program (Dodson and Selkirk 2002). Most wildlife studies on golf courses focus on birds and/or insects (Petrosillo et al. 2019). Birds are charismatic animals that add to the ambiance and atmosphere of the course when they sing and fly by, so most golf courses encourage bird activity. Birds also help manage the insect populations, and thus provide the golf course a cleaner alternative to pesticides (Evenden 1995, Gámez‐Virués et al. 2007, Ndang’ang’a et al. 2013). The diverse microhabitats present on golf courses provides much of what the bird may need in daily life; water, shelter, foraging habitat, security (Gillihan 2000, Merola‐Zwartjes and DeLong 2005).

The same qualities that make golf courses attractive for birds also make them attractive for bats, but much fewer studies have explored the bat communities that may make use of golf courses. Because golf courses are relatively similar to each other, and because bats are frequently reported to make use of comparable habitats, bats may live on, or frequently visit, golf courses to feed or roost (Gitzen et al. 2001, Burgin and Wotherspoon 2009). Bats have suffered severe population declines in North America due to fungal pathogens (Lorch et al. 2011, Warnecke et al. 2012) and wind energy facilities (Arnett and Baerwald 2013, Hayes 2013, Smallwood 2013), so investigating potential habitat is a crucial conservation objective.

We used generalized linear mixed-effects models to investigate landscape characteristics that influence how bats use golf courses. We compared bat observations and foraging activity to landscape metrics associated with each golf course in our study. Assuming that most golf courses contain a relatively consistent suite of features, significant trends in bat usage at each site can be attributed to differences in the landscape matrix in which the golf course resides.

**2. Methods**

*2.1. Study Area*

Our study takes place on 11 different golf courses and country clubs distributed throughout the state of New Jersey. Sites were selected so that no more than one golf course per county per year was surveyed.

* Atlantis Golf Course, Little Egg Harbor Township (2020 only)
* Avalon Golf Club, Middle Township
* Cream Ridge Golf Course, Upper Freehold
* Eastlyn Golf Course, Vineland
* Harbor Pines Golf Club, Egg Harbor Township
* High Point Golf Club, Montague Township
* Neshanic Valley Golf Course, Branchburg
* Overpeck Golf Course, Teaneck
* Rutgers Golf Course, Piscataway
* Sea Oaks Country Club, Little Egg Harbor Township (2019 only)
* Stanton Ridge Golf & Country Club, Readington Township

Due to closure of Sea Oaks Country Club mid-way through the study, Sea Oaks was replaced with the nearby Atlantis Golf Course for the 2020 dataset.

*2.2. Survey Protocol*

We deployed two Pettersson D500X microphones per golf course (at least 200m apart from one another) for a total of eight detector nights in both 2019 and 2020 (for system settings, see Appendix 1). Surveys took place between late May and late August on nights that had little/no precipitation in the forecast. Directional microphones were placed at least 10m away from vegetation. Microphones were mounted at least 3m above the ground on collapsible flagpoles near bodies of water and near forest edges. On occasion, we consulted groundskeeper(s) regarding which locations on the golf courses they see the most bats and/or bugs.

*2.3. Species Classification*

We classified recorded bat pulses to the species-level, when possible, using SonoBat version 4 (www.sonobat.com) and the northeastern North America regional library. Classifications had an acceptable call quality threshold of 0.80, a species decision threshold of 0.90, and a maximum of 32 calls considered per file. Manual corrections were made when a species was identified outside of its natural range. For example, *Corynorhinus rafinesquii* does not appear in New Jersey (BatConservationInternational 2021), thus all *C. rafinesquii* calls were reclassified manually.

Manual identification of the recordings was done conservatively, and most ambiguous calls were classified as either “high frequency unknown” or “low frequency unknown”. The presence of a terminal buzz would occasionally result in an ambiguous or erroneous classification due to the sudden change in frequency, duration, and interval. Therefore, all automatically-classified calls containing terminal buzzes were manually corrected. For recordings that were below the quality threshold of automatic classification (0.90), but were still clearly visible on the sonogram, we manually identified the bat species conservatively according to known patterns for the species (Table 1). After exporting to a spreadsheet, the classifications for *Myotis lucifugus* and *M. sodalis* were combined into one label, “Luso”, because of their highly overlapping call characteristics. We treated Luso as a separate species for all subsequent analyses.

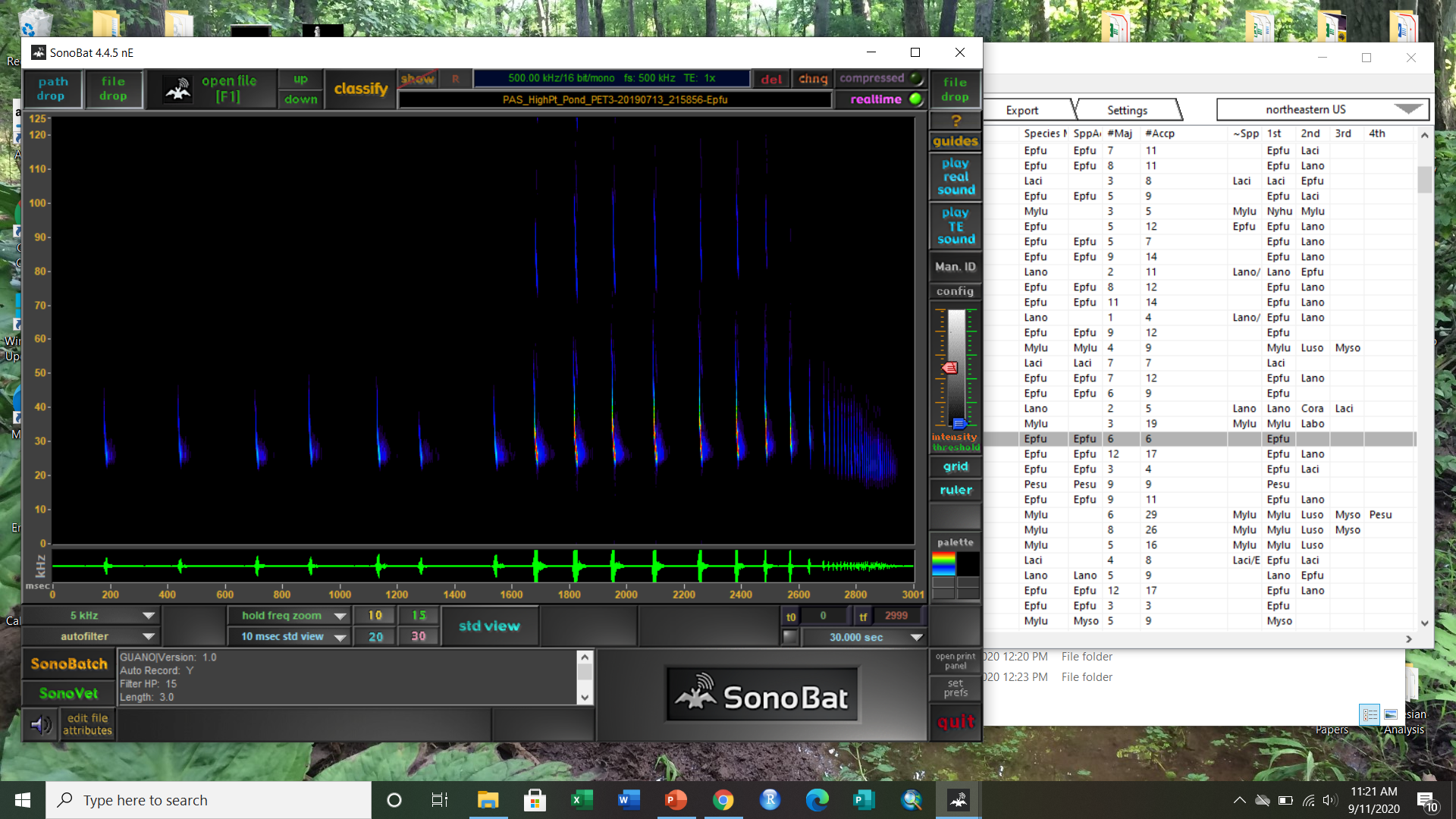


Figure 1. A sonogram of an echolocating bat displayed on SonoBat. The blue lines represent echolocation pulses, and the red box contains a terminal buzz.

Every recording was visually examined for indicators of feeding activity. Evidence of hunting behavior is characterized by a slight drop in the characteristic frequency, a reduced interval between calls, and a lateral compression of each call in the “terminal buzz”, making the calls appear as vertical lines (Figure1). The buzzes are readily visible on the SonoBat viewing window, and they can be heard as a distinct drumroll when the audio file is played at 10x reduced speed.

Table 1. Species classification decisions based on echolocation characteristics of bats in Northeastern United States.

|  |  |  |  |
| --- | --- | --- | --- |
| Characteristic frequency (Fc) | | | |
| Fc ≥ 40 KHz | 40KHz > Fc ≥ 35 KHz | 35 KHz > Fc ≥ 25 KHz | Fc < 25 KHz |
| *Myotis spp.* if calls are above 40 KHz, have tails, and a steep FM\* | *Lasiurus borealis* if Fc shifts irregularly from one call to the next | *Eptesicus fuscus* if calls show a strongly curved shape on the sonogram (gradual FM) | *Lasiurus cinereus* if calls have little FM |
| “High frequency unknown” if otherwise | *Nycticeius humeralis* if Fc shifts regularly between two frequencies | *Lasionycteris noctivagans* if calls show a bilinear shape on the sonogram (abrupt FM) | “Low frequency unknown” if otherwise |
|  | *Perimyotis subflavus* if calls maintain consistent Fc and show little FM | “Low frequency unknown” if otherwise |  |
|  | “High frequency unknown” if otherwise |  |  |
| \*FM = frequency modulation. The total change in frequency during the span of one call. | | | |
| Decisions based on trends described by Janet Tyburec of Bat Survey Solutions at an acoustic data workshop (<https://batsurveysolutions.com>) | | | |

*2.4. Geographic Information Systems – Data Sources, Manipulation, and Analyses*

Spatial data were manipulated in ArcMap version 10.8.1 (ESRI 2020). Golf course polygon shapefiles were downloaded from NJ Department of Environmental Protection, Division of Science, Research and Technology (NJDEP 2001). A 2km buffer was created around the perimeter of each golf course to represent the approximate roost-to-forage distance of the local bat species (Brigham 1991, Crampton and Barclay 1998, Elmore et al. 2005, Sparks et al. 2005, Walters et al. 2007). Thus, all bats roosting in our 2km buffer could reasonably be expected to consider the golf course as a potential foraging habitat, and vice versa. Buffers were created using the “outside only” method so as to not include the course itself in the buffer.

We downloaded 2015 land use polygon shapefile from NJDEP (NJDEP 2019). After clipping the shapefiles to each 2km buffer, we converted the polygons to rasters with a cell size of 10m using the “LU15” attribute. We reclassified the different land use types into more specific categories thought to be more relevant to bats using the “Label15” attribute (Appendix 2).

A line shapefile containing information on streams was downloaded from NJ National Hydrography Dataset (NHD) Waterbody and Stream Network (NJDEP 2010). This dataset is a subset of the larger NHD dataset that is specific to New Jersey. The most recent 2011 NHDFlowline feature class was used for determining the length (km) of streams surrounding the local golf course. We further refined this dataset by considering only streams that are within 100m of a forested landscape in order to eliminate the ocean and bay region of the shapefile, which have been incorrectly identified as a densely-packed cluster of streams.

Certain landscape characteristics were quantified using Fragstats (McGarigal 2012). We first projected our land use rasters into NAD83 (2011) NJ state plane in meters, because Fragstats assumes cell size units are meters. We used Fragstats to determine the percent of the surrounding 2km buffer that consisted of each of the land use types (e.g. %Urban, %Agriculture, etc.). Because forests represent especially important resources for bats (Lacki et al. 2007), we also used Fragstats to determine the density of forest edge in the surrounding landscape (meters per hectare), and the largest patch index (LPI) of forest. LPI is used as a measure of dominance over a landscape, and represents the size of the largest continuous patch of forest within a 2km radius of the golf course.

*2.5. Statistics and Modeling*

Though we deployed our microphones for a total of 8 detector nights per course per year, occasional malfunction and battery life restrictions would result in the loss of a detector night. We excluded sites from our data set if they had fewer than 4 detector nights per site per year, the minimum standard for acoustic monitoring (Loeb et al. 2015). We recorded the number of confirmed bat calls per night for all courses in our study, and we used these observations as a measurement of total bat activity per night. When possible, we also counted the total number of calls per species per night as a measure of species-specific activity. Lastly, we recorded the number of terminal buzzes per night as a measure of feeding activity. Total bat activity, species-specific activity, and feeding activity per detector night were used as response variables for generalized linear mixed effect models (GLMMs).

We used the R package “lme4” to construct our GLMMs (Douglas Bates et al. 2020). We started each model set with a global GLMM using three different error distributions: normal, Poisson, and negative binomial. We compared the three error structures using AIC, and we selected the best model for further testing. Our global models contained a candidate list of 6 fixed effects (Table 2) in our global model. We checked for correlation among our variables using Pearson’s r, and included variables with correlation coefficients below 0.70. We scaled our fixed effects by dividing by the standard deviation of each effect. We included the golf course identifier and year as random effects to account for similarities among repeated measurements from the same time and/or place. We assessed the fixed effects using the package “lmerTest” (Alexandra Kuznetsova et al. 2020), which assigns a p-value to each covariate in the model. We then selected the best fixed effect structure using top-down model selection, and by eliminating the insignificant covariate with the smallest effect size in each iteration until AIC ceased to improve. After each iteration, we compared the reduced model to the previous model using the package “lmtest” (Torsten Hothorn et al. 2020) to perform a likelihood ratio test to assure that minimal information was lost upon the removal of the lowest performing fixed effect. We repeated this process for all response variables of interest until a winning model remained for each response variable. Model performance and residuals were assessed using “DHARMa” (Florian Hartig and Lohse 2021).

Table 2. A list of fixed effects used in our GLMMs to predict bat activity.

|  |  |
| --- | --- |
| **Covariate** | **Description** |
| *Urban* | The percentage of the 2km buffer with an urban land use. Calculated in FragStats using a reclassified version of the 2015 land use polygon shapefile from the NJDEP. |
| *Suburban* | The percentage of the 2km buffer with a suburban land use. Calculated in FragStats using a reclassified version of the 2015 land use polygon shapefile from the NJDEP. |
| *Agriculture* | The percentage of the 2km buffer with an agricultural land use. Calculated in FragStats using a reclassified version of the 2015 land use polygon shapefile from the NJDEP. |
| *Field* | The percentage of the 2km buffer with a field land use. Calculated in FragStats using a reclassified version of the 2015 land use polygon shapefile from the NJDEP. |
| *Forested streams* | Stream shapefile from NJ National Hydrography Dataset (NHD) Waterbody and Stream Network. This dataset has been filtered to include only reaches of streams that are within 100m of a forest patch. This was done to avoid overinflation of this number by the dense network of streams near the coast that bats are unlikely to utilize as corridors. |
| *Forest LPI* | The largest continuous patch of forest within the 2km buffer around the golf course. Calculated in FragStats using a reclassified version of the 2015 land use polygon shapefile from the NJDEP. |

Depending on the biology of the species, certain landscape features were considered to be foraging habitat or roosting habitat for each bat in our study (Table 3).

Table 3. Species-specific habitat associations based on previous studies. Landscape features included in our study were placed in each cell if they represent documented roosting or foraging habitat for the bat species.

|  |  |  |  |
| --- | --- | --- | --- |
| **Species** | **Potential Roosting Habitat** | **Potential Foraging Habitat** | **Justification** |
| *Eptesicus fuscus* | Suburban, Urban | Agriculture, Forest LPI, Forested streams | (Geggie and Fenton 1985, Williams and Brittingham 1997, Duchamp et al. 2004, Lausen and Barclay 2006, Neubaum et al. 2007) |
| *Lasiurus borealis* | Forest LPI | Field, Forest LPI, Forested streams | (Hutchinson and Lacki 2000, Leput 2004, Elmore et al. 2005, Walters et al. 2007, Hann et al. 2017) |
| *Lasiurus cinereus* | Forest LPI | Agriculture, Field | (Barclay 1985, Willis and Brigham 2005, Perry and Thill 2007) |
| *Lasionycteris noctivagans* | Forest LPI | Agriculture, Field | (Campbell et al. 1996, Patriquin and Barclay 2003) |
| *Myotis lucifugus/sodalis* | Forest LPI, Suburban, Urban | Forest LPI, Forested streams | (Crampton and Barclay 1998, Jung et al. 2004, Sparks et al. 2005, Olson 2011, Bergeson et al. 2015, Fabianek et al. 2015, Nelson and Gillam 2017) |
| *Nycticeius humeralis* | Forest LPI, Suburban | Agriculture, Forest LPI, Forested streams | (Watkins and Shump Jr 1981, Menzel et al. 2001, Carter et al. 2004, Duchamp et al. 2004) |
| *Perimyotis subflavus* | Forest LPI | Agriculture, Forested streams, Forest LPI | (Leput 2004, Quinn and Broders 2007, Helms 2011) |

**3. Results**

We recorded a total of 33,272 bat echolocation signatures on our microphones (Table 4). Approximately 73% of our recordings were from our 2020 surveys. The most recordings at a site for a single season occurred at Atlantis in 2020 with 5,548 calls. The fewest recordings occurred at Rutgers golf course in 2020 with only 375 bat calls. *Eptesicus fuscus* was the most common bat species observed in our study, representing ~77% of all identifiable recordings (Figure 2). Our two rarest bat species were *Myotis leibii* and *M. septentrionalis*, with only 2 recordings each. Due to the low number of observations for these two species, they were not included in our subsequent models.

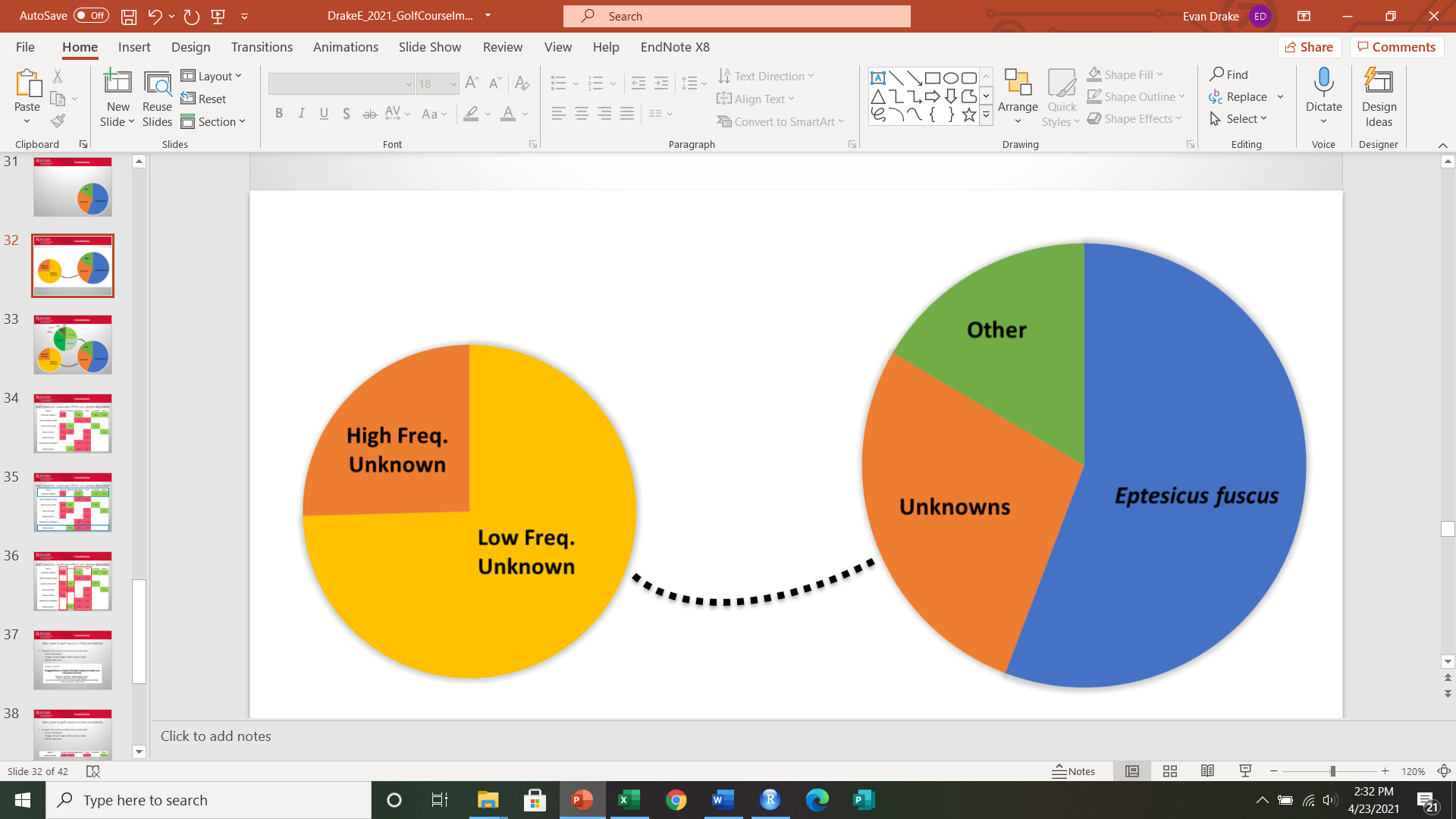


Figure 2. The majority of recorded echolocations can be attributed to *Eptesicus fuscus*. Because they are considered a low-frequency echolocator, the majority of low frequency unknowns are likely to be *E. fuscus* recordings as well.

Table 4. The yearly site totals for bat observations. Unclassified recordings were labeled as either high or low frequency unknowns. When possible, recordings were identified to a species-level classification. Number of terminal buzzes per site is a measure of foraging activity.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Year | Site | Terminal Buzzes | Total Activity | Low Freq. Unknown | High Freq. Unknown | *Eptesicus fuscus* | *Lasiurus borealis* | *Lasiurus cinereus* | *Lasionycteris noctivagans* | *Myotis lucifugus/sodalis* | *Myotis leibii* | *Myotis septentrionalis* | *Nycticeius humeralis* | *Perimyotis subflavus* |
| 2019 | Avalon | 58 | 637 | 138 | 62 | 341 | 92 | 0 | 4 | 0 | 0 | 0 | 0 | 0 |
| Cream Ridge | 10 | 415 | 88 | 50 | 182 | 38 | 19 | 38 | 0 | 0 | 0 | 0 | 0 |
| Eastlyn | 57 | 1099 | 129 | 159 | 514 | 228 | 5 | 31 | 1 | 0 | 2 | 12 | 18 |
| Harbor Pines | 86 | 1953 | 503 | 68 | 1057 | 71 | 114 | 123 | 15 | 0 | 0 | 2 | 0 |
| High Point | 64 | 579 | 54 | 23 | 304 | 10 | 65 | 71 | 48 | 0 | 0 | 0 | 4 |
| Neshanic Valley | 12 | 434 | 110 | 8 | 248 | 8 | 22 | 38 | 0 | 0 | 0 | 0 | 0 |
| Overpeck | 99 | 1169 | 65 | 27 | 494 | 54 | 446 | 36 | 0 | 0 | 0 | 0 | 47 |
| Rutgers | 68 | 1259 | 278 | 8 | 893 | 14 | 1 | 65 | 0 | 0 | 0 | 0 | 0 |
| Sea Oaks | 49 | 915 | 200 | 70 | 333 | 96 | 73 | 134 | 6 | 0 | 0 | 3 | 0 |
| Stanton Ridge | 27 | 369 | 75 | 28 | 214 | 30 | 8 | 14 | 0 | 0 | 0 | 0 | 0 |
| 2020 | Atlantis | 136 | 5548 | 989 | 670 | 2757 | 380 | 103 | 483 | 6 | 1 | 0 | 158 | 1 |
| Avalon | 30 | 649 | 74 | 129 | 208 | 54 | 63 | 69 | 0 | 0 | 0 | 52 | 0 |
| Eastlyn | 176 | 4019 | 522 | 281 | 2669 | 103 | 188 | 144 | 4 | 0 | 0 | 108 | 0 |
| Harbor Pines | 263 | 4843 | 1085 | 165 | 2855 | 30 | 199 | 435 | 10 | 0 | 0 | 64 | 0 |
| High Point | 8 | 666 | 336 | 91 | 205 | 3 | 5 | 13 | 6 | 0 | 0 | 1 | 6 |
| Neshanic Valley | 51 | 2478 | 611 | 14 | 1733 | 6 | 23 | 90 | 0 | 0 | 0 | 1 | 0 |
| Overpeck | 181 | 3730 | 664 | 284 | 2289 | 61 | 147 | 178 | 3 | 1 | 0 | 99 | 4 |
| Rutgers | 14 | 375 | 125 | 59 | 185 | 1 | 2 | 3 | 0 | 0 | 0 | 0 | 0 |
| Stanton Ridge | 71 | 2135 | 821 | 145 | 1082 | 28 | 14 | 24 | 1 | 0 | 0 | 20 | 0 |
|  | Grand Total | 1460 | 33272 | 6867 | 2341 | 18563 | 1307 | 1497 | 1993 | 100 | 2 | 2 | 520 | 80 |

For all response variables, the best error structure for our GLMMs was a negative binomial distribution. The GLMMs revealed that the surrounding landscape significantly predicted total bat activity, species-specific activity, and feeding behavior on golf courses (Table 5). Total bat activity on golf courses was negatively influenced by agricultural landscapes, but it was positively influenced by suburban areas in the surrounding landscape. As the most dominant species in our study, *Eptesicus fuscus* had a similar response to suburban landscape. Compared to our total activity model for all species combined, suburban areas in the surrounding landscape had a greater effect on *E. fuscus* (Figure 3).

Table 4. Models for total activity, species-specific activity, and combined foraging activity with the effect sizes (standard error) for relevant covariates.

Significance codes for p-values: ‘\*’ < 0.05, ‘\*\*’ < 0.01, ‘\*\*\*’ < 0.001

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Model | intercept | Forested Streams | Suburban Land | Agricultural Land | Open Field | Forest LPI | Urban Land |
| Total Activity | 5.29\*\*\* |  | 0.78\* | -0.40\* | -0.54\* |  |  |
| (0.56) |  | (0.31) | (0.19) | (0.27) |  |  |
| *Eptesicus fuscus* | 3.75\*\*\* |  | 1.00\* |  |  |  |  |
| (0.57) |  | (0.40) |  |  |  |  |
| *Lasionycteris noctivagans* | 3.45\*\*\* |  |  | -0.67\* | -1.26\*\* |  | 0.54 |
| (0.61) |  |  | (0.30) | (0.49) |  | (0.36) |
| *Lasiurus borealis* | 5.86\*\*\* | -2.23\*\*\* | -1.49\* |  | -1.97\*\*\* |  | 1.32\* |
| (0.82) | (0.53) | (0.72) |  | (0.50) |  | (0.53) |
| *Lasiurus cinereus* | 4.69\*\*\* | -2.26\* |  |  | -1.00 |  |  |
| (1.13) | (0.89) |  |  | (0.57) |  |  |
| *Myotis lucifugus/sodalis* | -3.22\*\* |  |  |  |  | 1.90\* |  |
| (0.98) |  |  |  |  | (0.80) |  |
| *Nycticeius humeralis* | 6.03\*\*\* | -8.12\*\*\* | 6.37\*\*\* | -2.85\*\*\* | -0.96\*\* |  | -4.59\*\*\* |
| (1.41) | (1.26) | (1.40) | (0.57) | (0.36) |  | (1.09) |
| *Perimyotis subflavus* | -6.67\* | -7.68\*\* |  | 4.02\*\* |  | 6.30\*\* | 5.18\*\*\* |
| (2.85) | (2.79) |  | (1.29) |  | (1.95) | (1.44) |
| Foraging | 3.20\*\*\* | -0.99\*\* | 0.87\*\* | -0.57\*\* | -0.63\* |  |  |
| (0.55) | (0.34) | (0.33) | (0.20) | (0.28) |  |  |

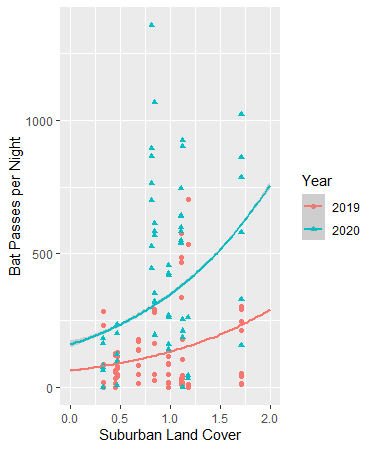
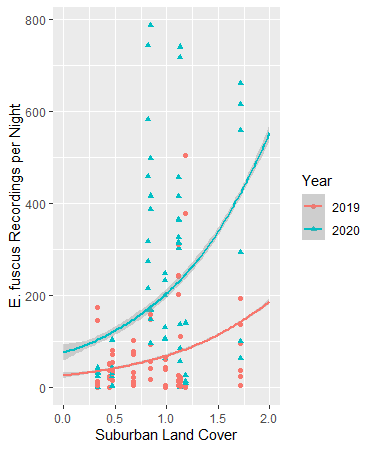


Figure 3. Effects of suburban landscape on bat activity at golf courses. On the left, total bat activity increases when the golf course has more suburban area around it. On the right, *Eptesicus fuscus* has a similar response to suburban landscapes.

*Lasiurus borealis* activity notably differed from the *E. fuscus* by having a negative relationship with the percent of suburban area in the surrounding landscapes. They also had a negative relationship with open field in the landscape and the length of forested streams (Figure 4), but they were positively influenced by urban areas in the surrounding landscape. *L. cinereus* was similarly negatively influenced by open field and forested streams in the surrounding landscape.

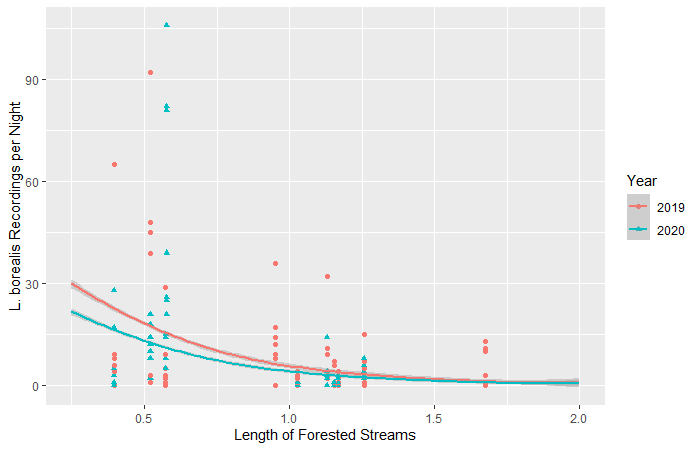


Figure 4. Effects of forested streams on *Lasiurus borealis* activity at golf courses.

*Lasionycteris noctivagans* activity on golf courses was negatively influenced by agricultural areas and open fields in the surrounding landscape. The multi-species complex “Luso” (*Myotis lucifugus* + *M. sodalis*) was rarely observed on most golf courses, and it had only 100 total recordings for both years. Their activity on golf courses was positively influenced by the size of the largest patch of continuous forest in the surrounding landscape (or “Forest LPI”).

Feeding activity was observed 1460 times over the two seasons and ranged from 8 – 263 terminal buzzes per course per season. The amount of terminal buzzes recorded on a golf course per detector night was positively influenced by the amount of suburban area in the surrounding landscape (Figure 5), but it was negatively influenced by the length of forested streams in the surrounding landscape (Figure 6), agricultural areas, and open fields.

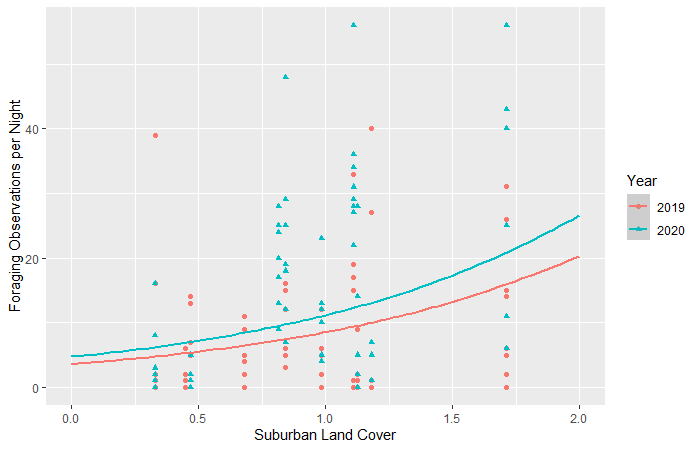


Figure 5. Effects of suburban areas on feeding activity at golf courses.

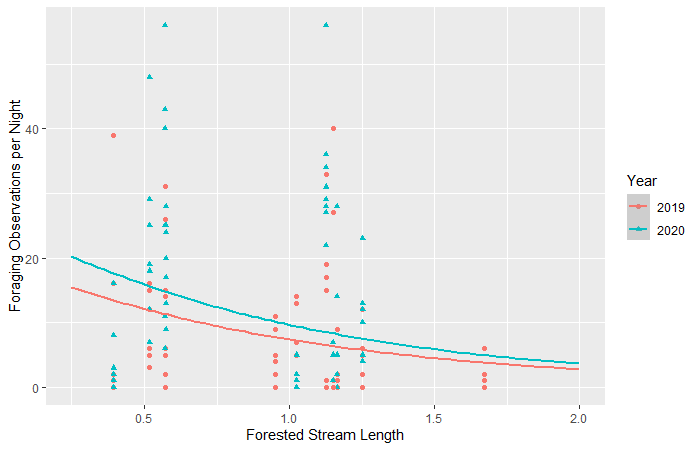


Figure 6. Effects of forested streams on feeding activity at golf courses.

**4. Discussion**

Given that golf courses are abundant in the United States, their potential to serve as patches of habitat is worth considering for conservation purposes. Taxa that are facing significant threats are of particular interest for their ability/inability to cope with man-made green spaces. North American bats are struggling against multiple major threats to their population, and some species in our study (*Myotis lucifugus* and *Perimyotis subflavus*) are listed on the IUCN list as endangered and vulnerable, respectively (IUCN 2021). Bats were found on all golf courses surveyed in this study, though their activity and species-composition differed by site. Determining factors that increase or decrease their use of golf courses is becoming increasingly relevant as the sport grows in popularity.

*4.1. Total Bat Activity Models*

Bats are likely using golf courses depending on what resources are available in the surrounding landscape. According to our models, total bat activity (all recordings combined) decreased on golf courses when the surrounding landscape contained more open fields and agricultural land. Both of these land types represent open spaces. Because golf courses are also a type of open space, bats may be treating them as a substitute field when they have fewer alternatives in the surrounding landscape. Total bat activity increased when there were more suburban areas in the surrounding landscape. There is a growing body of literature suggesting that bats, while sensitive to urban areas, make extensive use of suburban areas (Threlfall et al. 2012). Suburban areas may be suitable areas for roosting in many bat species (Evelyn et al. 2004). Indeed, certain common species have become well-acclimated to anthropogenically modified areas. Residential properties often provide attics, loose siding, and full-crowned shade trees for roosting sites. It is also common for the streets in suburban areas to be lined with trees, thus creating a type of forested corridor that bats prefer to travel along (Hein et al. 2009). These factors may make it easier for a bat to travel to a golf course when there are fewer alternative open spaces in the surrounding landscape.

*4.2. Species-Specific Activity Models*

Bats need roosting sites, foraging habitat, and a source of water. The species observed in our study vary in their preferred foraging habitat and roosting sites, and therefore vary in their use of the surrounding landscape. Our most common bat, *Eptesicus fuscus*, is a notorious occupant of man-made structures such as attics (Williams and Brittingham 1997, Lausen and Barclay 2006, Neubaum et al. 2007). Our models show that *E. fuscus* activity on golf courses was positively influenced by the amount of suburban area in the surrounding landscape. This suggests that an ample supply of roosting sites in the surrounding area is an important determinant of *E. fuscus* activity on a given site.

However, roosting sites were not the most important factor for all species in our study. *Lasiurus borealis* and *L. cinereus* are both species that roost in clumps of foliage (Elmore et al. 2004, Leput 2004, Perry and Thill 2007, Veilleux et al. 2009), but forest LPI was not a significant factor for predicting their activity on golf courses. Both species showed decreased activity on golf courses when the surrounding landscape contained more streams. Streams serve as important resources for bats because they provide drinking water, natural corridors for travel, and insect-rich foraging habitat (Seidman and Zabel 2001, Fukui et al. 2006, Nelson and Gillam 2020). If the surrounding environment is deficient in streams, then *L. borealis* and *L. cinereus* may use golf courses more frequently. Additionally, *L. borealis* showed increased golf course use when the surrounding landscape contained more urban areas, but fewer open fields and suburban areas. Our findings support the existing body of literature on *L. borealis* habitat preferences (Elmore et al. 2005, Walters et al. 2007). Namely, that it avoids urban areas and forages over water and near fields.

The multispecies complex “Luso” (*Myotis lucifugus* and *M. sodalis*) is composed of endangered species (COSEWIC 2013). They were more active on golf courses when the surrounding landscape contained larger patches of continuous forested habitat (high forest LPI). However, this is somewhat challenging to explain due to key differences in the roosting habits of the two species. Much like *Eptesicus fuscus*, *M. lucifugus* is commonly found roosting in man-made structures (Riskin and Pybus 1998). However, the similar species, *M. sodalis*, is less flexible in its roost site selection, opting for dead trees with crevices and exfoliating bark (Carter and Feldhamer 2005, Bergeson et al. 2015). Both species prefer to forage in forested and/or riparian habitat, and they tend to avoid landscapes with more open space (Sparks et al. 2005, Bergeson et al. 2013, Nelson and Gillam 2017). Because golf courses themselves are a series of connected fields, we may not expect to find high Luso activity on golf courses regardless of the landscape matrix. This, combined with their scarcity following the introduction of *Pseudogymnoascus destructans* (Pettit and O'Keefe 2017), may explain their rarity in our dataset. When they are present on golf courses, it could be due to chance observations as they commute to and from their foraging ground in the forest. This conclusion would also explain why they only appear briefly on each night they are observed. They are not staying on the golf course for very long, but they are instead traveling through it.

Our models showed that *Lasionycteris noctivagans* was less active on golf courses when there were more fields and agricultural lands in the surrounding landscape matrix. *L. noctivagans* is known to forage in open spaces due to their larger, less maneuverable build (Patriquin and Barclay 2003). This supports our models, which suggest that *L. noctivagans* is more active on golf courses when their preferred foraging habitat is scarce in the surrounding environment. They are also known to roost in cavities and crevices of dead trees, but this was not evident in our winning model. This suggests that foraging habitat may be more important than roosting habitat for determining *L. noctivagans* site use.

In 2019, *Nycticeius humeralis* was mostly absent from our study, but they were much more common in 2020. Their echolocation signature overlaps highly with *Lasiurus borealis*, so the two are often mistaken for each other by automatic species classification software. Because *L. borealis* is more common, it is unclear how many of our *N. humeralis* recordings are cases of mistaken identity. Our models show that many of our landscape characteristics significantly influenced *N. humeralis* activity on golf courses, but the two landscape characteristics with the largest effect sizes were the amount of suburban area and the length of streams in the surrounding landscape. *N. humeralis* was less active on golf courses when there were more suburban areas, but fewer forested streams. This may be explained by an avoidance of suburban areas when selecting a roost site (Duchamp et al. 2004). *N. humeralis* is considered to be a flexible forager, and it is capable of using many landscapes to feed (Kwon et al. 2019). Their indifference to foraging habitat may explain their inconsistent use of golf courses from year to year.

The tri-colored bat was rarely recorded on our microphones. It was heavily impacted by fungal pathogens (Pettit and O'Keefe 2017), and is now endangered in Canada (COSEWIC 2013). Our models showed that *Perimyotis subflavus* is more active on golf courses when the surrounding area has larger patches of continuous forest. This is likely because it is a tree-roosting bat that uses clumps of foliage as day-roosts (Poissant 2009, Heritage 2015, Schaefer 2016). *P. subflavus* was also influenced by the potential foraging habitat in the surrounding landscape. When there were fewer forested streams nearby, it was more likely to be seen on golf courses. Additionally, *P. subflavus* strongly avoided anthropogenically modified landscapes. It was more active on golf courses when the surrounding landscape contained more urban and agricultural areas. Our model strongly supports previous studies on *P. subflavus* habitat that show a similar pattern; favoring natural areas while avoiding farms and developments (Farrow and Broders 2011).

*4.3. Foraging Models*

Because the presence of a terminal buzz in the recording makes it more difficult to identify the species of bat producing it, we are unable to confidently report species-specific feeding behavior. However, it is likely that *Eptesicus fuscus* is responsible for the majority of the terminal buzzes reported in our study based on the proportion of all calls that were identified as *E. fuscus*. Observations of terminal buzzes occurred more frequently on golf courses with more suburban area in the surrounding landscape, and golf courses with fewer nearby forested streams, open fields, and agricultural areas. Increased foraging on suburban golf courses is best explained by the prevalence of *E. fuscus* in our dataset because suburban area around the golf course was the best predictor of general *E. fuscus* activity. It is likely that *E. fuscus* is more likely to feed at a golf course when there are ample roosting sites nearby. A lack of alternative foraging habitat may also increase feeding behavior on golf courses, and that is reflected in our models by the negative relationship with forested streams. The effects of fields and agricultural lands in the surrounding landscape were comparatively smaller, but still indicate that bats are more likely to feed on golf courses when these land types are scarce. Many of our species-specific models shared this relationship with open space, as they are common foraging sites. The only three species that did not show increased activity in more open landscapes were the generalist *Eptesicus fuscus*, and the forest specialists *Perimyotis subflavus* and Luso.

**5. Conclusion**

Golf courses can generally be described as a network of fields with scattered ponds and forest patches. These features are connected by corridors (golf cart paths), and they are often bordered by trees. We find that these qualities provide suitable habitat for the bats of eastern temperate forests, but habitat use varies by species and adjacent landscape characteristics. Larger, less maneuverable bats that prefer to forage in open spaces (*Lasionycteris noctivagans*, *Lasiurus cinereus*, and *Nycticeius humeralis*) were less active on golf courses when the surrounding landscape provided more of their preferred foraging habitat. Bats that prefer to roost in manmade structures (*Eptesicus fuscus*) were more active on golf courses when there were more suburban areas nearby, and bats that prefer to roost in trees (*Perimyotis subflavus* and *Myotis lucifugus/sodalis*) were more active on golf courses when there were larger patches of forest nearby. Many bats use riparian areas and streams to forage, and when these features were more common in the surrounding landscape, most bat species were less active on the golf courses.

Known habitat preferences mesh well with our conclusions. Golf courses may be providing bats with a refuge from the surrounding environment. When that environment is less favorable, bats may use the golf courses more. Additionally, bats may be less frequently observed on golf courses when the surrounding landscape adequately meets their needs. Depending on the biology of the bat species, we find that golf courses are more important for bats when there are 1) more suitable roost sites in the surrounding landscape and 2) fewer high-quality foraging habitats.

**6. Appendices**

*Appendix 1: System settings*

* 1 – User Profiles
  + Samp freq: 500
  + Pretrig: off
  + Rec length: 3 seconds
  + HP Filter: yes
  + Auto rec: yes
  + T-sense: med
* 2 – Record Settings
  + Input gain: 70
  + Trig level: 120
  + Interval: 0
* 3 – Timers
  + Start time: 15 minutes before sunset
  + Stop time: 15 minutes after sunrise
* 4 – Time Settings
  + 24 hour, military time
  + DST: off
  + Time zone: -5

*Appendix 2: Land Use Reclassification Decisions*

Land use codes are based on the classification system modified from Anderson et al., “New Label” indicates the land use type after reclassification, “Old Label” is the former land use type. Change is indicated by an asterisk (\*).

|  |  |  |  |
| --- | --- | --- | --- |
| Land Use Code | New Label | Old Label | Change\* |
| 1110 | Urban | Urban |  |
| 1150 | Urban | Urban |  |
| 1200 | Urban | Urban |  |
| 1211 | Urban | Urban |  |
| 1214 | Urban | Urban |  |
| 1300 | Urban | Urban |  |
| 1400 | Urban | Urban |  |
| 1410 | Urban | Urban |  |
| 1411 | Urban | Urban |  |
| 1419 | Urban | Urban |  |
| 1420 | Urban | Urban |  |
| 1440 | Urban | Urban |  |
| 1462 | Urban | Urban |  |
| 1500 | Urban | Urban |  |
| 1600 | Urban | Urban |  |
| 1700 | Urban | Urban |  |
| 1810 | Urban | Urban |  |
| 1120 | Suburban | Urban | \* |
| 1130 | Suburban | Urban | \* |
| 1140 | Suburban | Urban | \* |
| 2100 | Agriculture | Agriculture |  |
| 2140 | Agriculture | Agriculture |  |
| 2150 | Agriculture | Agriculture |  |
| 2200 | Agriculture | Agriculture |  |
| 2300 | Agriculture | Agriculture |  |
| 2400 | Agriculture | Agriculture |  |
| 4120 | Forest | Forest |  |
| 4220 | Forest | Forest |  |
| 4230 | Forest | Forest |  |
| 4312 | Forest | Forest |  |
| 4322 | Forest | Forest |  |
| 6210 | Forest | Wetlands | \* |
| 6220 | Forest | Wetlands | \* |
| 6221 | Forest | Wetlands | \* |
| 6251 | Forest | Wetlands | \* |
| 6252 | Forest | Wetlands | \* |
| 4110 | Forest | Forest |  |
| 4210 | Forest | Forest |  |
| 4311 | Forest | Forest |  |
| 4321 | Forest | Forest |  |
| 4500 | Forest | Forest |  |
| 1461 | Field | Urban | \* |
| 1463 | Field | Urban | \* |
| 1710 | Field | Urban | \* |
| 1711 | Field | Urban | \* |
| 1800 | Field | Urban | \* |
| 1804 | Field | Urban | \* |
| 1850 | Field | Urban | \* |
| 4410 | Field | Forest | \* |
| 4411 | Field | Forest | \* |
| 4420 | Shrub | Forest | \* |
| 4430 | Shrub | Forest | \* |
| 4440 | Shrub | Forest | \* |
| 6130 | Shrub | Wetlands | \* |
| 1499 | Water | Urban | \* |
| 5100 | Water | Water |  |
| 5190 | Water | Water |  |
| 5200 | Water | Water |  |
| 5300 | Water | Water |  |
| 5410 | Water | Water |  |
| 5411 | Water | Water |  |
| 5412 | Water | Water |  |
| 5420 | Water | Water |  |
| 5430 | Water | Water |  |
| 1741 | Wetland | Urban | \* |
| 1750 | Wetland | Urban | \* |
| 6111 | Wetland | Wetlands |  |
| 6112 | Wetland | Wetlands |  |
| 6120 | Wetland | Wetlands |  |
| 6141 | Wetland | Wetlands |  |
| 6231 | Wetland | Wetlands |  |
| 6232 | Wetland | Wetlands |  |
| 6233 | Wetland | Wetlands |  |
| 6234 | Wetland | Wetlands |  |
| 6240 | Wetland | Wetlands |  |
| 6241 | Wetland | Wetlands |  |
| 6290 | Wetland | Wetlands |  |
| 6500 | Wetland | Wetlands |  |
| 7100 | Barren | Barren |  |
| 7200 | Barren | Barren |  |
| 7300 | Barren | Barren |  |
| 7400 | Barren | Barren |  |
| 7430 | Barren | Barren |  |
| 7440 | Barren | Barren |  |
| 7500 | Barren | Barren |  |
| 7600 | Barren | Barren |  |

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