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Cover Photograph: An Audiomoth acoustic bat detector deployed outside an abandoned mine opening in southern Ohio, USA.

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External Characteristics of Abandoned Mines as Predictors of Bat Activity during the Fall Swarm

Lucille M. Williams¹ and Joseph S. Johnson^{2,*}

Abstract - Abandoned coal mines are habitat for bats, but are often sealed for safety. We used acoustic detectors to evaluate bat activity outside 61 abandoned mines in Ohio during the fall swarm period. Only 10% of mines had activity rates comparable to a known hibernaculum and swarming site. *Perimyotis subflavus* (Tricolored Bat) and *Myotis* spp. activity peaked in late August and early September. *Myotis* spp. activity was positively affected by presence of bat gates, but decreased with the ratio of entrance height to width. Tricolored Bat activity increased with mine entrance size and decreased with the number of proximate swarming sites. Activity of *Eptesicus fuscus* (Big Brown Bat) declined as autumn progressed and was positively affected by the presence of bat gates. We demonstrate how external characteristics of mines can be used to identify swarming habitat for conservation and monitoring efforts.

Introduction

Populations of many bat species are declining across North America because of fatalities due to wind turbines (Frick et al. 2017), white-nose syndrome (WNS) (Cheng et al. 2021), and habitat loss (Farrow and Broders 2011). Elucidating the factors influencing bat presence and activity can inform conservation efforts, such as enhancing habitat quality or mitigating potential threats (Frick et al. 2023, Good et al. 2022). Abandoned coal mines can be important habitat for bats. These underground workings offer potential refuge and roosting sites for threatened species (Johnson et al. 2006, Lacki and Bookhout 1983, Williams 2019), but are human safety hazards (USGAO 2020) and sources of pollution (Cherry et al. 2001). Concerns over environmental health and safety have led to the closure of abandoned mines (USGAO 2020, Watkins 2002), possibly destroying suitable bat habitat. The ability to identify abandoned mines that are important to bats is critical for safeguarding important habitats during reclamation projects.

Evaluating the use of underground habitats by bats is challenging because many underground systems contain spaces large enough for bats, but too small for humans to access, (Lewis et al. 2022, Mammola et al. 2016), or are too dangerous for people to enter (USGAO 2020). This is often true of coal mines in the Appalachian region of North America, where billions of tons of coal have been extracted since the 1700s (Dixon and Bilbrey 2015). As mines were abandoned, thousands of potential bat roosts were created. However, roof-supporting structures deteriorate in abandoned mines, creating a risk of collapse, and consequently, such failing mines are often backfilled to prevent human access (Watkins 2002).

When mines cannot be entered and thoroughly evaluated, bat activity at mine openings can be studied by using ultrasonic bat detectors, positioning infrared cameras, or by capturing bats as they emerge from or return to the roost (Thomas and Davison 2022). One period when bats are often studied outside mines is the fall swarm, during which activity increases around the entrance from late summer through autumn (Hall and Brenner 1968, Parsons et

¹Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071. ²School of Information Technology, University of Cincinnati, Cincinnati, OH 45221. *Corresponding author - joseph.johnson@uc.edu.

al. 2003). Bats of many species copulate during this time, with individuals from different summer ranges converging on the same swarming sites (Dekeukeleire et al. 2016), and thus, these locations are important for gene flow (Rivers et al. 2005). Also, these sites are likely important winter habitats, because bats often hibernate where these animals swarm (Van Schaik et al. 2015). Seasonal use of swarming sites typically results in increased acoustic activity outside underground openings during late summer and early autumn, followed by a decline leading into winter (Bergmann et al. 2022, Muthersbaugh et al. 2019, Thomas and Davison 2022). Because acoustic detectors can be deployed for long periods at low cost, these tools can help biologists identify important swarming habitats and hibernacula in landscapes with many mines that cannot be surveyed internally.

Despite the promise of acoustic detectors for identifying swarming sites, some landscapes have more abandoned mine openings than can be realistically surveyed. In these regions, external features of mines may indicate use by bats (Johnson et al. 2006, Moran et al. 2023). External characteristics may be important to swarming bats for a variety of reasons. For example, the size and number of entrances to mines and caves affects the flow of air through the habitat and can influence use by hibernating bats (Hayes et al. 2011, Perry 2013, Raesly and Gates 1987). Furthermore, the shape of entrances and characteristics of the surrounding landscape can also influence the number of animals using a site (Johnson et al. 2006, Moran et al. 2023). By understanding the relationship between external variables and bat use, managers can make informed decisions about which management actions are warranted for abandoned mines when internal surveys are not possible.

Our goal was to determine if external features of abandoned coal mines can be used to predict levels of bat activity during fall swarming. We sought to determine how characteristics of mine entrances (e.g., size and shape) and the surrounding aboveground environment (e.g., forest cover and density of potential hibernacula) influenced acoustic activity. We used a model selection approach to determine which variables best predicted activity of *Myotis* species, *Perimyotis subflavus* (F. Cuvier) (Tricolored Bat), and *Eptesicus fuscus* (Palisot de Beauvois) (Big Brown Bat) at abandoned mines, and we compared those results to data obtained at a known hibernaculum.

Field-site Description

We collected data on the external features of entrances to abandoned coal mines and bat activity at these mines in eastern Ohio, USA (Fig. 1). Species known to hibernate and potentially swarm in Ohio include *Myotis lucifugus* (Le Conte) (Little Brown Myotis), *Myotis septentrionalis* (Trouessart) (Northern Myotis), *Myotis sodalis* Miller and G.M. Allen (Indiana Myotis), Tricolored Bat, and Big Brown Bat (Johnson and Johnson 2024, Johnson et al. 2024). There are >1800 known abandoned underground coal mines throughout eastern Ohio, and an unknown number of sealed or collapsed mines (Ohio Department of Natural Resources 2023). Potential study locations were limited to coal mines on public lands, for which we could obtain necessary permits. We deployed acoustic detectors outside 61 randomly selected mines and also outside the second-largest known hibernaculum of Little Brown Myotis (120–130 bats) and Tricolored Bats (10–20 bats) in Ohio. Because there are no published accounts of seasonal trends in acoustic activity at Ohio swarming sites, we included the hibernaculum, an abandoned railroad tunnel in Belmont County, to allow comparison of bat activity between a known overwintering site and our randomly selected mines.

Methods

Data Collection

We deployed acoustic detectors (AudioMoth v1.50, Open Acoustics, Southampton, United Kingdom) from late July to late October 2021. This period encompassed the swarming season in our study area (Muthersbaugh et al. 2019, Lewis et al. 2022). Individual mine openings were surveyed on a rotating basis beginning in late July. Acoustic detectors were deployed at 10 sites and remained in the field for ~1 week. After this time, detectors were moved to different sites. Once all sites were surveyed, a second rotation of sampling began with the sampling order identical to the first. Detectors failed on 2 instances, but were later redeployed. The average time between the end of the first sampling period and the start of the second was 31 (± 9 SD) days. Overall, each site was surveyed

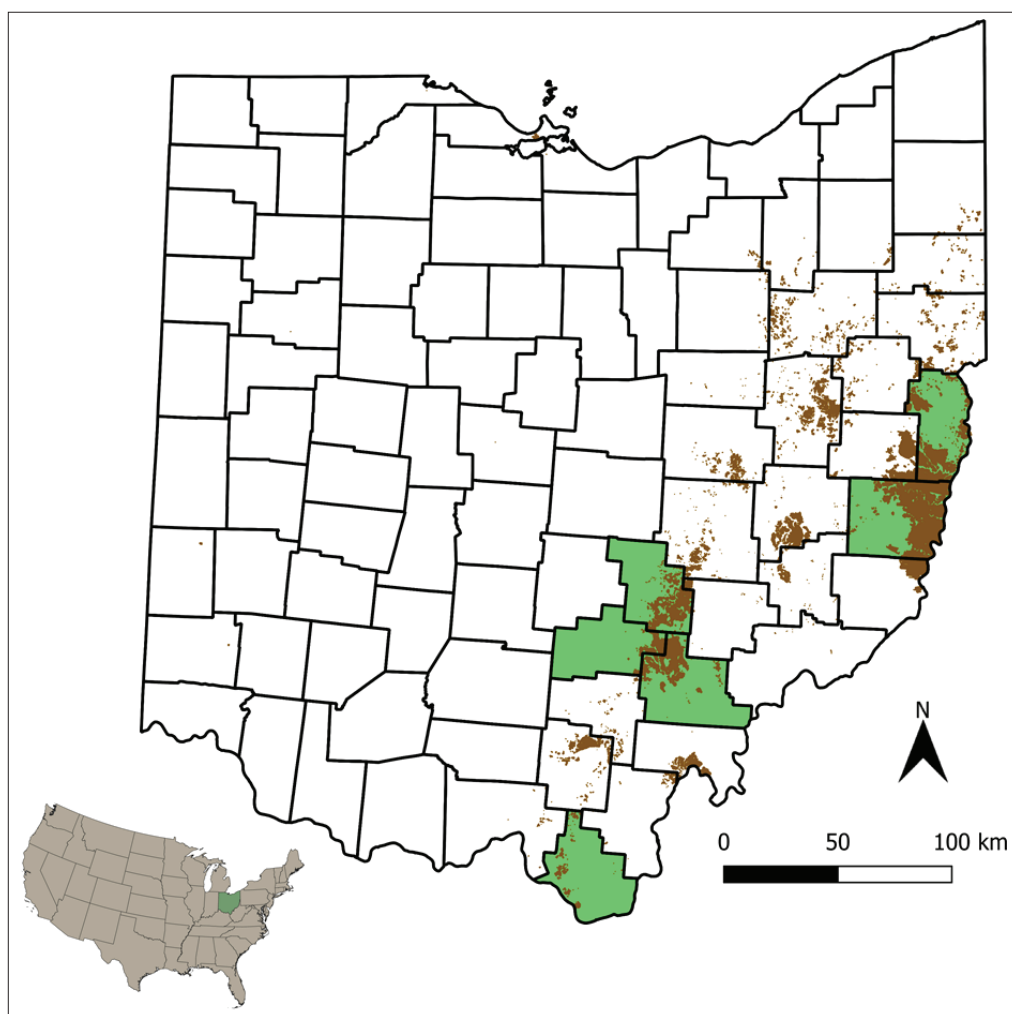


Figure 1. A map of Ohio, USA, showing the distribution of acoustic sampling effort during fall swarming, July–October 2021. Acoustic monitoring was conducted outside mines in counties shaded green. Areas shaded brown represent the extent of abandoned underground mines in the state. Inset shows location of Ohio (green) within USA.

for an average of $11.3 (\pm 2.7)$, range = 6–21) nights, for a total of 691 nights of sampling. This sampling protocol balanced the need to survey many sites with uncertainty regarding when bat activity would be greatest. The reference hibernaculum was continuously monitored from 30 July through 30 October.

Recording commenced 30 min before sunset and continued until 30 min after sunrise. The sampling rate was set to 250 kHz, gain was set to medium, and the sleep and recording durations were set to 5 and 10 sec, respectively. We enabled the high filter on the AudioMoths to record frequencies >16 kHz and used an amplitude threshold of 512 to generate .wav files. Each Audiomoth was placed in a waterproof enclosure, with a waterproof membrane over the microphone opening, and positioned on a tree ~2 m above the ground (Fig. 2). To record bat activity immediately in front of and within the opening, we stationed Audiomoths <5 m from the entrance, with the microphone directed at the mine opening. The enclosure prevented the detection of sound from behind the detector, and hence, we assumed that bats recorded at the mine opening were visiting that location.

We collected data on each mine opening to determine if external features influenced bat activity during the swarming period. Using information provided by the Ohio Department of Natural Resources (2023), we confirmed the type of entrance (hereafter, *EntType*) as either horizontal (adit), vertical (shaft), or sloped (incline). We used a measuring tape to determine the area of the entrance (*EntArea*, m²). This measure represents available space for passage of air or flight by a bat and can influence bat use of underground habitats (Johnson et al. 2006, Raesly and Gates 1987). We calculated the shape of the entrance (*Shape*) by dividing height by width (Johnson et al. 2006) and confirmed the presence or absence of bat gates (*BatGate*).

We used QGIS (QGIS Development Team 2023) to examine landscape features surrounding each entrance. Specifically, we quantified the amount of forest within a 1-km radius of each site (*For1k*, km²) based on the 2019 National Landcover Database (Dewitz 2019). We also determined the number of alternative swarming sites within a 1-km radius (*Sites1k*), by tallying the number of known mine entrances, caves, and abandoned railroad tunnels (Johnson and Johnson 2024, Ohio Department of Natural Resources 2023). Finally, we obtained average daily temperature (i.e., the average of the daily maximum and minimum temperature; *AvgTemp*, °C) for each sampling day at each sampling location (PRISM Climate Group 2023).

Data Analyses

We identified each echolocation call sequence (an individual file containing ≥ 1 bat sounds) to species using SonoBat 4.2.1 and the regional classifier for the northeastern United States (Szewczak 2017). We manually vetted all sequences from the 61 mines; however, at the reference hibernaculum, we only vetted calls identified as *Myotis* species, Big Brown Bat, and Tricolored Bat, because of a high volume of recorded files. Vetting consisted of visually examining sequences to confirm the identification provided by SonoBat, and we overturned SonoBat's identification when a sequence contained features diagnostic of other species. We grouped species of *Myotis* due to uncertainty in identification of their calls to species level. Calls not identified to species or genus were classified as "high-frequency calls" if the lowest apparent frequency was ≥ 40 kHz, or "low-frequency calls", if it was <40 kHz. In our area, high-frequency calls typically are from *Myotis*, Tricolored Bats, and *Lasiurus borealis* (Müller) (Eastern Red Bats), while low-frequency calls usually are from Big Brown Bats, *Lasionycteris noctivagans* (Le Conte) (Silver-haired Bats), and *Lasiurus cinereus* (Palisot de Beauvois) (Hoary Bats).

To determine mine characteristics associated with swarming activity, we constructed generalized linear mixed models (GLMMs) with negative binomial distributions in the R



Figure 2. Photograph of typical placement of bat detector, immediately outside a mine opening, in eastern Ohio, USA. Detectors with directional microphones were stationed <5 m from openings and pointed towards the entrance.

package *glmmTMB* (Brooks et al. 2023). A unique set of models was constructed for *Myotis*, Tricolored Bats, and Big Brown Bats (Tables S1–S3; see Supplemental File 1, available online at <https://eaglehill.us/nabronline/suppl-files/nabr-017-Johnson-s1.pdf>). We used the zero-inflated formula for *Myotis* and Tricolored Bats, but not for Big Brown Bats, which were detected more regularly. We modeled bat activity, using the number of call sequences recorded per species or genus per night as the response variable, site as a random effect (to avoid pseudo-replication), and ≥ 1 environmental variables as fixed effects (Table 1). For Tricolored Bats and *Myotis*, preliminary analyses revealed a curvilinear relationship between the number of sequences recorded/detector/night and day of the year. We, therefore, used Julian day (*Day*) and the square of Julian day (*Day*²) to account for this curvilinear trend. However, for Big Brown Bats, preliminary analysis showed a linear trend, and consequently, *Day*² was not included in candidate models. Before analysis, we checked for correlation between variables, using Pearson's correlation coefficient, and tested for multicollinearity among variables by calculating variance inflation factors (Sheather 2009). *Day* was correlated with *AvgTemp* ($F_{1, 689} = 337.9$, $r^2 = 0.33$, $P < 0.01$), so both variables were never used in the same model.

We used Akaike's Information Criterion for small samples (AIC_c) to determine which model best explained activity of each species, using the R package *AICcmodavg* (Mazerolle 2017). Any models with $\Delta AIC_c < 2$ were considered possible top models. The amount of variation explained by top models was calculated as the conditional R^2 in the R package *pscl* (Jackman et al. 2015). We also tested for temporal autocorrelation on simulated residuals of the top models, using the R package *DHARMA* (Hartig et al. 2017). Finally, we created generalized additive models (GAMs) of trends in activity of *Myotis*, Big Brown Bats, and Tricolored Bats at the reference hibernaculum, using the R package *mgcv* (Wood 2015). Each GAM used a smoothing function for *Day* and produced a plot of predicted activity over time based on the recorded data.

Table 1. Description of fixed-effect variables used in analyses of acoustic activity of *Myotis*, Tricolored Bats, and Big Brown Bats, outside abandoned coal mines in eastern Ohio, USA, July–October 2021.

Fixed Effect	Definition	Means \pm SD (range)
<i>Day</i>	Ordinal day: a numeric representation of the day of the year, with possible values ranging from 1–366 (1 January–31 December)	242 \pm 23 (203–288)
<i>AvgTemp</i>	Average daily temperature outside each mine	21.2 \pm 3.8 °C (11.8–27.9 °C)
<i>BatGate</i>	Presence or absence of a bat gate at the entrance	Absent ($n = 51$) or present ($n = 10$)
<i>Sites1k</i>	Number of mines (possible hibernacula) within 1-km radius	63.0 \pm 20.8 (6–122)
<i>EntType</i>	Type of entrance	Horizontal ($n = 36$), vertical ($n = 4$), or slope ($n = 21$)
<i>EntArea</i>	Area of entrance (height * width)	4.74 \pm 6.7 m ² (0.04–37.2 m ²)
<i>Shape</i>	Shape of entrance, a unitless ratio (height/width)	0.60 \pm 0.91 (0.07–4.70)
<i>Forest1k</i>	Amount of forest cover within 1-km radius	2.90 \pm 0.16 km ² (2.1–3.1 km ²)

Results

We recorded 12,413 call sequences at the 61 mines and 33,038 sequences at the reference hibernaculum (Table 2). Of these, SonoBat identified 2362 (19%) sequences to species. Big Brown Bats were the most frequently identified group outside mines, followed by *Myotis*, Eastern Red Bats, and Tricolored Bats. Although Eastern Red Bats were frequently identified, 63% ($n = 242$) of these sequences were recorded outside 3 mines (5% of sites). Silver-haired Bats and Hoary Bats each represented $<0.1\%$ ($n = 52$ and 28 , respectively) of activity. High-frequency sequences made up 50% of all recordings outside mines ($n = 6195$), and included unidentifiable sequences presumably produced by *Myotis*, Tricolored Bats, and Eastern Red Bats. Low-frequency sequences made up 31% of all recordings outside mines ($n = 3864$) and included unidentifiable sequences presumably produced by Big Brown Bats, Hoary Bats, and Silver-haired Bats.

Myotis were detected outside 56 (90%) mines on at least 1 night. However, *Myotis* were only detected on 30% of nights ($n = 205$), and this resulted in a low rate of activity (0.93 ± 0.96 sequences/night). Activity at the mines was only 3% of that recorded at the reference hibernaculum (29 ± 2.5 sequences/night), where zero data were obtained

Table 2. Descriptive statistics of bat activity recorded outside abandoned mines during fall swarming, July–October 2021, in eastern Ohio, USA. See Methods for descriptions of “high-frequency” and “low-frequency” groups.

Species or Group	Number of sites present (%)	Number of call sequences recorded	Rate (mean \pm SD) of sequences/site/night
Mines ($n = 61$)			
Big Brown Bat	52 (84)	1,105	1.5 ± 2.0
<i>Myotis</i> species	56 (90)	667	$0.93 \pm 0.1.0$
Tricolored Bat	31 (50)	123	0.18 ± 0.32
Eastern Red Bat	28 (45)	387	0.62 ± 1.6
Silver-haired Bat	15 (24)	52	0.07 ± 0.31
Hoary Bat	7 (11)	28	0.04 ± 0.14
High-frequency	57 (92)	6,195	9.1 ± 23
Low-frequency	57 (92)	3,864	6.2 ± 18
Reference hibernaculum			
Big Brown Bat		598	6.7 ± 14.7
<i>Myotis</i> species		2,605	29.3 ± 23.5
Tricolored Bat		402	4.5 ± 7.9
Eastern Red Bat		130	1.5 ± 2.9
Hoary Bat		24	0.3 ± 0.8
High-frequency		28,021	314.8 ± 302.3
Low-frequency		1,258	14.1 ± 21.1

on only 2% of nights ($n = 2$; Table 2). However, *Myotis* activity was comparable to that of the reference hibernaculum at 2 mines (3% of sites), with activity as high as 48 sequences/night.

A model with *Day*, *Day*², *Shape*, and *BatGate* best explained the variability in activity of *Myotis* at mine openings (*Shape* = -0.56 ± 0.18 , $P < 0.01$; *BatGate* = 1.19 ± 0.37 , $P < 0.001$ [reference condition was no gate present]; *Day* = 0.71 ± 0.12 , $P < 0.01$; *Day*² = -0.0015 ± 0.0002 , $P < 0.01$; conditional model pseudo $R^2 = 0.50$) (Fig. 3, Table S1). Specifically, *Myotis* activity increased until late August and early September, after which activity gradually declined. Activity was greatest at sites where a bat gate was present and at mines with entrances that were wider than their peak height. No other model had $\Delta AIC_c < 2$. The GAM for *Myotis* activity at the reference hibernaculum revealed that the smoothed term for *Day* was significant ($P < 0.01$; Fig. 4A). The deviance explained by the overall model was 58.2%. The trend in *Myotis* activity was similar to that modeled at mines. The entrance to the reference hibernaculum was 0.74-m tall by 2.2-m wide (*Shape* = 0.34). Confirmed sequences from *Myotis* were recorded throughout the study period at this tunnel.

Tricolored Bats were detected at 31 (50%) mines on at least 1 night, but were only detected on 10% of nights ($n = 68$). This resulted in a low average rate of Tricolored Bat activity (0.2 ± 0.32 sequences/night), which was 4% of the nightly activity at the reference hibernaculum (4.5 ± 0.8 sequences/night) (Table 2), where zero data were obtained on 49% of nights ($n = 44$). Tricolored Bat activity was comparable to the refer-

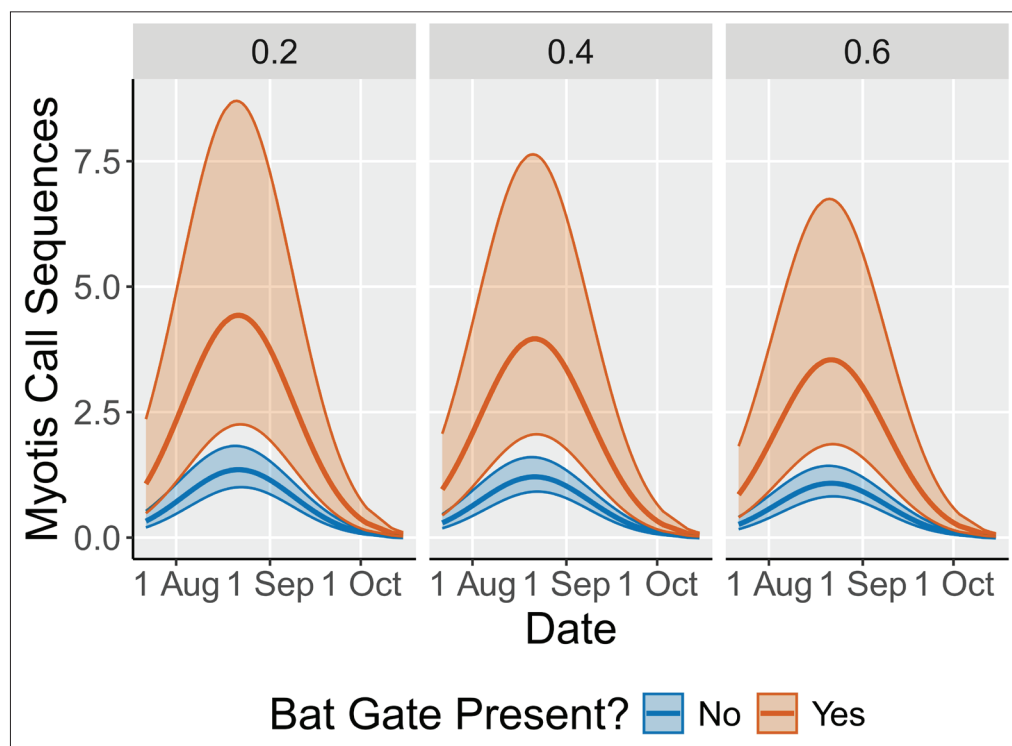


Figure 3. Acoustic activity of *Myotis* outside coal mines in Ohio, USA. Lines represent predicted values derived from a generalized linear mixed model, surrounded by 95% confidence intervals. Numbers at the top of each graph represent the ratio of entrance height to width.

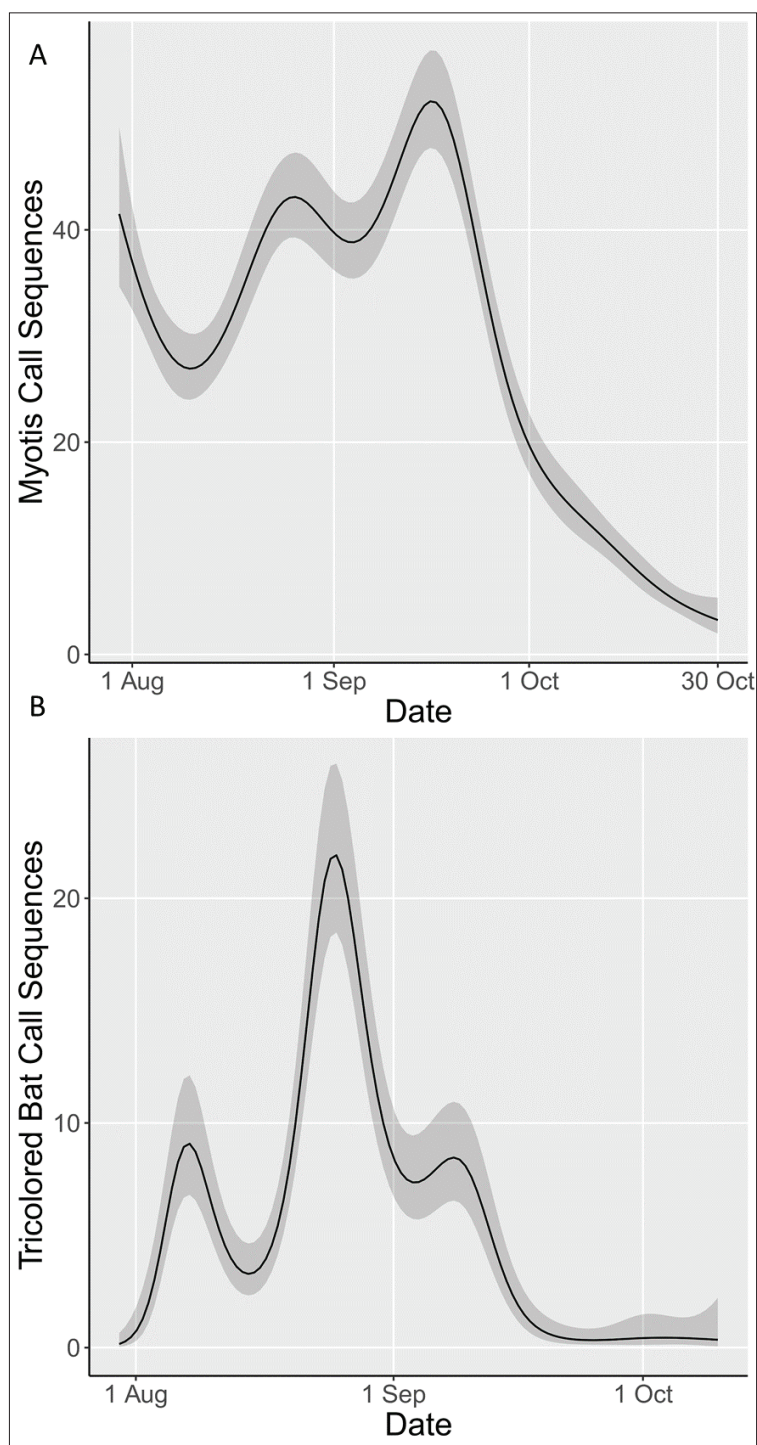


Figure 4. Seasonal trend in acoustic activity of *Myotis* (A) and Tricolored Bats (B) at a known hibernaculum (a railroad tunnel) in Ohio, USA, during fall 2021. Data shown are predicted values, with a 95% confidence interval, generated by a generalized linear mixed model.

ence hibernaculum at 6 mines (10% of sites), with activity as high as 6 sequences/night.

A model with *Day*, *Day*², *Sites1k*, and *EntArea* best predicted Tricolored Bat activity (*EntArea* = 0.06 ± 0.03 , $P = 0.04$; *Sites1k* = -0.02 ± 0.01 , $P = 0.04$; *Day* = 1.14 ± 0.21 , $P < 0.01$; *Day*² = -0.0024 ± 0.0004 , $P < 0.01$; conditional model pseudo $R^2 = 0.55$) (Fig. 5, Table S2). As with *Myotis*, recordings of Tricolored Bats increased throughout early autumn, peaked from late August through early September, and then declined. Tricolored Bat activity increased with entrance size and decreased with increasing number of potential swarming sites within 1 km. One other model had a ΔAIC_c value <2 (Table S2). This model was simpler than the top model in that it did not include *EntArea* (*Sites1k* = -0.03 ± 0.01 , $P = 0.03$; *Day* = 1.14 ± 0.21 , $P < 0.01$; *Day*² = -0.0024 ± 0.0004 , $P < 0.01$; conditional model pseudo $R^2 = 0.56$). The GAM for Tricolored Bat activity at the reference hibernaculum revealed that the smoothed term for *Day* was significant ($P < 0.01$; Fig. 4B). The deviance explained by the overall model was 54.0%. The trend in activity was similar to that modeled at mines. The last confirmed call sequence of Tricolored Bats at the reference hibernaculum was recorded on 6 October.

Big Brown Bats were detected at 52 (84%) mines and the reference hibernaculum. Activity of Big Brown Bats at mines (1.5 ± 2.0 sequences/night) was 22% of that at the reference hibernaculum (6.7 ± 1.6 sequences/night) (Table 2). Activity comparable to the reference hibernaculum (>6 sequences/night) was recorded at 28 mines (46%).

A model with *Day*, *Shape*, and *BatGate* (*Shape* = -0.52 ± 0.25 , $P = 0.03$; *BatGate*

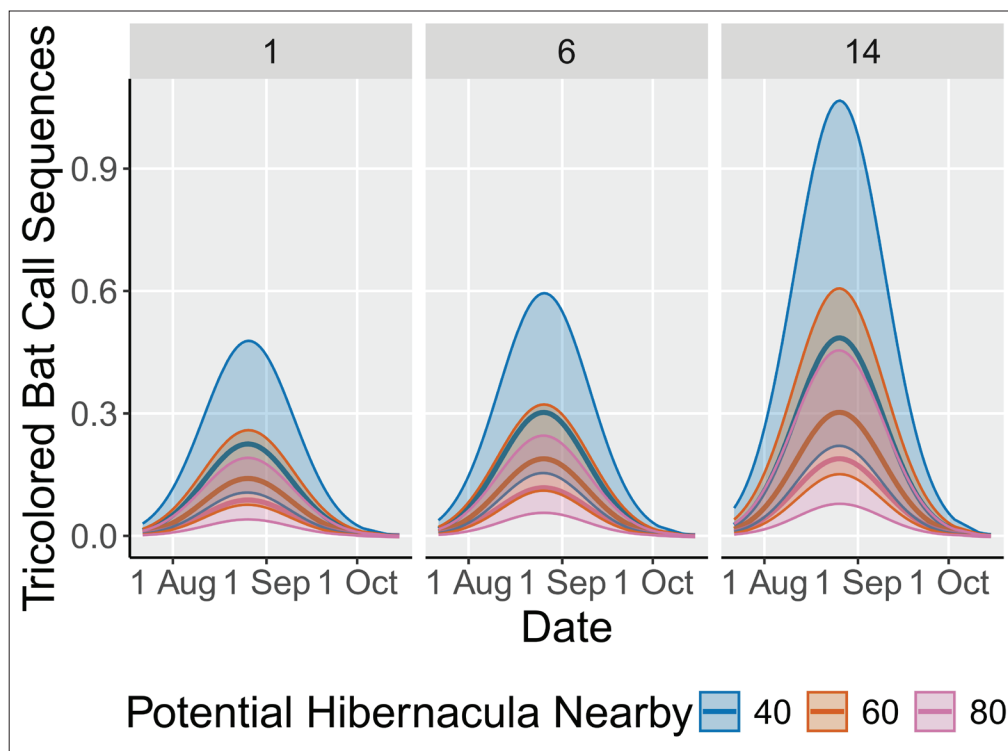


Figure 5. Acoustic activity of Tricolored Bats outside mines in Ohio, USA, during fall 2021. Lines represent predicted values, derived from a generalized linear mixed model, surrounded by 95% confidence intervals. Numbers at the top of each graph represent the area of the mine entrance (m²).

$= 1.33 \pm 0.56$, $P = 0.02$; $Day = -0.052 \pm 0.006$, $P < 0.01$; conditional model pseudo $R^2 = 0.66$) best predicted activity of Big Brown Bats. No other model had $\Delta AIC_c < 2$. Big Brown Bat activity decreased with Day , was greater at sites with bat gates, and decreased with $Shape$ (Fig. 6A, Table S3). The GAM for Big Brown Bat activity at the reference hibernaculum revealed that the smoothed term for Day was significant ($P < 0.01$; Fig. 6B). The deviance explained by the model was 52.7%. Confirmed Big Brown Bat sequences were recorded through 28 October. The trend in Big Brown Bat activity at the reference hibernaculum was similar to activity at mines.

Discussion

Abandoned coal mines are abundant across parts of North America, and while they pose hazards to humans and the environment, some are valuable bat habitat (Johnson et al. 2006, Moran et al. 2023). We found that most abandoned coal mines in this study were visited by Tricolored Bats and *Myotis* during the fall swarm (Table 2). Although overall activity rates were low, activity of both groups was significantly higher during peak swarming (mid-August–early September; Figs. 3 and 5). Indeed, 10% of mines had Tricolored Bat activity comparable to the railroad tunnel hibernaculum, and 2% of mines had *Myotis* activity similar to the tunnel. Given the >1800 abandoned coal mines in Ohio (Ohio Department of Natural Resources 2023), our data suggest that important hibernacula for *Myotis* and Tricolored Bats are currently unrecognized, leading to missed opportunities for monitoring and management efforts. Furthermore, failure to recognize important mines may harm bat populations if suitable swarming, and potentially winter, habitats are sealed.

Myotis activity displayed a temporal trend expected of swarming, with the number of sequences increasing from August through September, then declining throughout October (Kurta et al. 1997, Muthersbaugh et al. 2019, Thomas and Davison 2022) (Fig. 3). At the reference hibernaculum, multiple peaks of activity occurred throughout the fall that were not seen at the mines (Fig. 4). Multiple peaks in swarming activity have been documented previously, but remain unexplained (Lewis et al. 2022, Whitaker and Rissler 1992), although some authors believe that these peaks may represent activity of different sexes and potentially different phenomena (Ignaczak et al. 2019).

Our models of activity suggest *Myotis* may select swarming sites based on the shape of a mine entrance. *Myotis* activity increased at mines as the ratio of entrance height to width decreased (Fig. 3). Our reference hibernaculum was a good example of such an entrance, with a height of 0.74 m, but width of 2.2 m ($Shape = 0.34$). These results contrast with findings from West Virginia, where the ratio of height to width was positively correlated with the number of Little Brown and Northern *Myotis* that were captured during swarming (Johnson et al. 2006). It is unclear why entrance shape was a significant predictor of activity in our study. Given that our top model of *Myotis* activity left a substantial amount of variation unexplained, other mine characteristics are needed to understand the role of entrance shape during swarming.

Presence of bat gates had a positive effect on *Myotis* activity (Fig. 3). Although gates were associated with greater activity, it is unclear if gates impart an overall positive, neutral, or negative effect on the bats. For example, a gate may protect a winter colony from human disturbance, resulting in increased use by bats and, therefore, increased activity during the swarm (Tobin et al. 2018). Alternatively, increased acoustic activity could result from increased flight activity in front of the mine opening, as bats investigate or are unsure of the gate, and not from a positive conservation outcome (Spanjer and Fenton 2005, Tobin

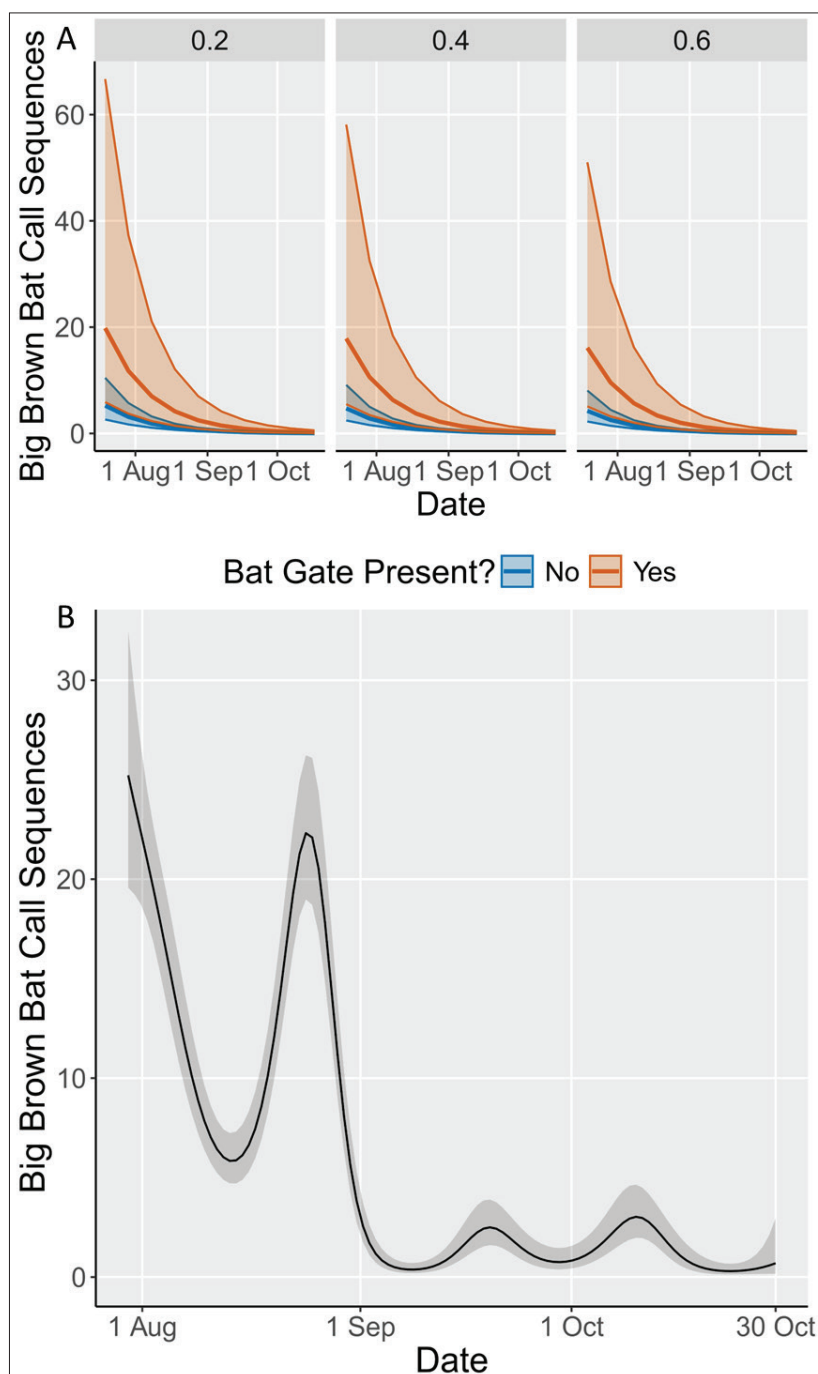


Figure 6. Activity of Big Brown Bats outside mines in Ohio, USA, decreased from late July through late October 2021 (A). Lines represent predicted values derived from a generalized linear mixed model, surrounded by 95% confidence intervals. Numbers at the top of each graph represent the ratio of entrance height to width. Panel B shows activity of Big Brown Bats at a known hibernaculum (a railroad tunnel) during the same period.

and Chambers 2017). Unfortunately, few studies have quantified the effect of gating (Meierhofer et al. 2023). Complicating our evaluation of the importance of bat gates is that the gated mines do not have access doors, preventing human entry and any attempt to correlate acoustic activity with winter use by bats.

Acoustic activity of Tricolored Bats decreased with increasing availability of alternative swarming sites, similar to findings from West Virginia (Johnson et al. 2006) (Fig. 5). Isolated mines may receive more bat activity due to a lack of alternative swarming sites (Johnson et al. 2006), and, therefore, isolation may not represent an important habitat characteristic but, rather, a limiting resource on the landscape. Understanding that Tricolored Bats use isolated mines can help biologists identify the scarce resources this uncommon bat requires and guide monitoring programs and management efforts. Given the imperiled status of this species due to WNS (Cheng et al. 2021), such knowledge can help identify where and when to minimize disturbance, conduct studies of autumn foraging behavior, or prioritize other management programs. Although our reference hibernaculum had a small entrance (1.6 m²), it was more isolated than most mines, with only 6 potential swarming sites within 1 km, compared to the mean of 63 nearby alternatives (Table 1). Previous researchers have shown that swarming activity of Tricolored Bats increases with entrance area size (Johnson et al. 2006) and that the species uses hibernacula with entrance areas comparable to those in our study (Raesly and Gates 1987).

Big Brown Bat activity was not influenced by external features at coal mines. We found weak or little evidence that entrance shape and presence of gates influenced acoustic activity of Big Brown Bats during autumn. Unlike *Myotis* and Tricolored Bats, activity of Big Brown Bats declined consistently throughout autumn (Fig. 6). Although autumn is a period when bats engage in important activities associated with a transition from summer maternity colonies to winter hibernation (Fenton 1969, Fraser and McGuire 2023), the extent to which Big Brown Bats swarm is unclear. Acoustic activity of this species outside hibernacula is often recorded during autumn (Muttersbaugh et al. 2019). However, direct observation of swarming behavior is not, and number of Big Brown Bats captured during this time is typically low (Hall and Brenner 1968, Johnson et al. 2006, Whitaker and Rissler 1992). Because this species usually hibernates outside caves and mines in Ohio (Johnson et al. 2024), the observed activity patterns likely are not associated with swarming. We hypothesize that the decreasing Big Brown Bat activity at mines during autumn is associated with decreased foraging activity, resulting from declining temperatures and insect availability (Gorman et al. 2021).

In the United States, there are >140,000 open mines on government lands (USGAO 2020). Closure of mines is often necessary, because they can pose public health hazards and be sources of pollution. Such closures may actually benefit bats where subsidence or flooding may occur, but some closures inevitably result in loss of suitable and scarce roosting resources. Because the species relying on these underground sites are becoming increasingly imperiled (Cheng et al. 2021), it is imperative to base conservation efforts on evidence (Mammola et al. 2022). We show that, when visual surveys for hibernating bats are not possible, external characteristics of mines can predict acoustic activity of *Myotis* and Tricolored Bats, and this apparent swarming activity (Thomas and Davidson 2022) suggests winter use (Van Schaik et al. 2015). Systematically deploying passive acoustic detectors and evaluating the dimensions of mine openings can identify important roosts and help prioritize conservation, management, and research efforts, especially when the number of potential sites is large. Such efforts should help facilitate rigorous evaluation of mines as potential habitat for wildlife and aid resource managers in deciding whether these sites should be sealed to protect human and environmental safety.

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Literature Cited

- Bergmann, A., L.S. Burchardt, B. Wimmer, K. Kugelschafter, F. Gloza-Rausch, and M. Knörnschild. 2022. The soundscape of swarming: Proof of concept for a noninvasive acoustic species identification of swarming *Myotis* bats. *Ecology and Evolution* 12:e9439.
- Brooks, M., B. Bolker, K. Kristensen, M. Maechler, A. Magnusson, M. McGillicuddy, H. Skaug, A. Nielsen, C. Berg, K. van Benthem, N. Sadat, D. Lüdtke, R. Lenth, J. O’Brien, C.J. Geyer, M. Jagan, B. Wiernik, D.B. Stouffer, and M. Agronah. 2023. glmmTMB: Generalized linear mixed models using Template Model Builder. Available online at: <https://cran.r-project.org/web/packages/glmmTMB/index.html>. Accessed 2 March 2025.
- Cheng, T.L., J.D. Reichard, J.T.H. Coleman, T.J. Weller, W.E. Thogmartin, B. Reichert, A. Bennett, H.G. Broders, J. Campbell, K. Etchison, D.J. Feller, R. Geboy, T. Hemberger, C. Herzog, A.C. Hicks, S. Houghton, J. Humber, J.A. Kath, R.A. King, S.C. Loeb, A. Masse, K.M. Morris, H. Niederriter, G. Nordquist, R.W. Perry, R. Reynolds, D.B. Sasse, M.R. Scafani, R.C. Stark, C.W. Stihler, S.C. Thomas, G.G. Turner, S. Webb, B. Westrich, and W.F. Frick. 2021. The scope and severity of white-nose syndrome on hibernating bats in North America. *Conservation Biology* 35:1586–1597.
- Cherry, D.S., R.J. Currie, D. J. Soucek, H.A. Latimer, and G.C. Trent. 2001. An integrative assessment of a watershed impacted by abandoned mined land discharges. *Environmental Pollution* 111:377–388.
- Deukeleire, D., R. Janssen, A.J. Haarsma, T. Bosch, and J. Van Schaik. 2016. Swarming behaviour, catchment area and seasonal movement patterns of the Bechstein’s Bats: implications for conservation. *Acta Chiropterologica* 18:349–358.
- Dewitz, J. 2019. National Land Cover Database (NLCD) 2019 Products (ver. 3.0, February 2024). Available online at <https://www.usgs.gov/data/national-land-cover-database-nlcd-2019-products-ver-30-february-2024>. Accessed 2 March 2025.
- Dixon, E.L., and K. Bilbrey. 2015. Abandoned Mine Land Program: A policy analysis for Central Appalachia and the nation. AML Policy Priorities Group. Whitesburg, KY. 172 pp.
- Farrow, L.J., and H.G. Broders. 2011. Loss of forest cover impacts the distribution of the forest-dwelling Tri-colored Bat (*Perimyotis subflavus*). *Mammalian Biology* 76:172–179.
- Fenton, M.B. 1969. Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. *Canadian Journal of Zoology* 47:597–602.
- Fraser, E.E., and L.P. McGuire. 2023. Prehibernation swarming in temperate bats: A critical transition between summer activity and hibernation. *Canadian Journal of Zoology* 101:408–422.
- Frick, W.F., E.F. Baerwald, J.F. Pollock, R.M.R. Barclay, J.A. Szymanski, T.J. Weller, A.L. Russell, S.C. Loeb, R.A. Medellin, and L.P. McGuire. 2017. Fatalities at wind turbines may threaten population viability of a migratory bat. *Biological Conservation* 209:172–177.
- Frick, W.F., Y.A. Dzal, K.A. Jonasson, M.D. Whitby, A.M. Adams, C. Long, J.E. Depue, C.M. Newman, C.K.R. Willis, and T.L. Cheng. 2023. Bats increased foraging activity at experimental prey patches near hibernacula. *Ecological Solutions and Evidence* 4:e12217.
- Good, R.E., G. Iskali, J. Lombardi, T. McDonald, K. Dubridge, M. Azeka, and A. Tredennick. 2022. Curtailment and acoustic deterrents reduce bat mortality at wind farms. *Journal of Wildlife Management* 86:e22244.

- Gorman, K.M., E.L. Barr, L. Ries, T. Nocera, and W.M. Ford. 2021. Bat activity patterns relative to temporal and weather effects in a temperate coastal environment. *Global Ecology and Conservation* 30:e01769.
- Hall, J.S., and F.J. Brenner. 1968. Summer netting of bats at a cave in Pennsylvania. *Journal of Mammalogy* 49:779–781.
- Hartig, F., L. Lohse, and M. de Souza Leite. 2017. DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. Available online at <https://cran.r-project.org/web/packages/DHARMa/index.html>. Accessed 2 March 2025.
- Hayes, M.A., R.A. Schorr, and K.W. Navo. 2011. Hibernacula selection by Townsend's Big-eared Bat in southwestern Colorado. *Journal of Wildlife Management* 75:137–143.
- Ignaczak, M., T. Postawa, G. Lesiński, and I. Gottfried. 2019. The role of autumnal swarming behaviour and ambient air temperature in the variation of body mass in temperate bat species. *Hystrix* 30:65–73.
- Jackman, S., A. Tahk, A. Zeileis, C. Maimone, J. Fearon, and Z. Meers. 2015. Package 'pscl': Political Science Computational Laboratory. Available online at <https://cran.r-project.org/web/packages/pscl/index.html>. Accessed 2 March 2025.
- Johnson, J.B., P.B. Wood, and J.W. Edwards. 2006. Are external mine entrance characteristics related to bat use? *Wildlife Society Bulletin* 34:1368–1375.
- Johnson, L.E., G.G. Turner, M.R. Scafani, E. Anis, and J.S. Johnson. 2024. Widespread use of rocky outcrops by hibernating bats in Ohio and Pennsylvania. *Journal of North American Bat Research* 2:1–15.
- Johnson, L.E., and J.S. Johnson. 2024. Preference for hibernacula microclimates varies among 3 bat species susceptible to white-nose syndrome. *Journal of Mammalogy* 105:1022–1031.
- Kurta, A., J. Caryl, and T. Lipps. 1997. Bats and Tippy Dam: Species composition, seasonal use, and environmental parameters. *Michigan Academician* 29:473–490.
- Lacki, M.J., and T.A. Bookhout. 1983. A survey of bats in Wayne National Forest, Ohio. *Ohio Journal of Science* 83:45–50.
- Lewis, M.A., G.G. Turner, M.R. Scafani, and J.S. Johnson. 2022. Seasonal roost selection and activity of a remnant population of Northern Myotis in Pennsylvania. *PLoS ONE* 17:e0270478.
- Mammola, S., P.M. Giachino, E. Piano, A. Jones, M. Barberis, G. Badino, and M. Isaia. 2016. Ecology and sampling techniques of an understudied subterranean habitat: The Milieu Souterrain Superficiel (MSS). *The Science of Nature* 103:1–24.
- Mammola, S., M.B. Meierhofer, P.A.V. Borges, R. Colado, D.C. Culver, L. Deharveng, T. DeliĆ, T. Di Lorenzo, T. Dražina, R.L. Ferreira, B. Fiasca, C. Fišer, D.M.P. Galassi, L. Garzoli, V. Gero-vasileiou, C. Griebler, S. Halse, F.G. Howarth, M. Isaia, J.S. Johnson, A. Komerički, A. Martínez, F. Milano, O.T. Moldovan, V. Nanni, G. Nicolosi, M.L. Niemiller, S. Pallarés, M. Pavlek, E. Piano, T. Pipan, D. Sanchez-Fernandez, A. Santangeli, S.I. Schmidt, J.J. Wynne, M. Zagmajster, V. Zakšek, and P. Cardoso. 2022. Towards evidence-based conservation of subterranean ecosystems. *Biological Reviews* 97:1476–1510.
- Mazerolle, M.J. 2017. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). Available online at <https://cran.r-project.org/web/packages/AICcmodavg/index.html>. Accessed 2 March 2025.
- Meierhofer, M.B., J.S. Johnson, J. Perez-Jimenez, F. Ito, P.W. Webela, S. Wiantoro, E. Bernard, K.C. Tanalgo, A. Hughes, P. Cardoso, T. Lilley, and S. Mammola. 2023. Effective conservation of subterranean-roosting bats. *Conservation Biology* 38:e14157.
- Moran, M.L., J.C. Steven, J.A. Williams, and R.E. Sherwin. 2023. Bat use of abandoned mines throughout Nevada. *Wildlife Society Bulletin* 47:e1468.
- Muthersbaugh, M.S., W.M. Ford, A. Silvis, and K.E. Powers. 2019. Activity patterns of cave-dwelling bat species during pre-hibernation swarming and post-hibernation emergence in the central Appalachians. *Diversity* 11:1–24.
- Ohio Department of Natural Resources. 2023. Mines of Ohio. Available online at <https://gis.ohiodnr.gov/MapView/?config=OhioMines#>. Accessed 2 March 2025.

- Parsons, K.N., G. Jones, and F. Greenaway. 2003. Swarming activity of temperate zone microchiropteran bats: Effects of season, time of night and weather conditions. *Journal of Zoology* 261:257–264.
- Perry, R.W. 2013. A review of factors affecting cave climates for hibernating bats in temperate North America. *Environmental Reviews* 21:28–39.
- PRISM Climate Group. 2023. PRISM climate data. Available online at <https://prism.oregonstate.edu/>. Accessed 2 March 2025.
- QGIS Development Team. 2023. QGIS overview. Available online at <http://qgis.osgeo.org/project/overview>. Accessed 2 March 2025.
- Raesly, R.L., and J.E. Gates. 1987. Winter habitat selection by north temperate cave bats. *American Midland Naturalist* 118:15–31.
- Rivers, N.M., R.K. Butlin, and J.D. Altringham. 2005. Autumn swarming behaviour of Natterer’s bats in the UK: Population size, catchment area and dispersal. *Biological Conservation* 127:215–226.
- Sheather, S. 2009. *A Modern Approach to Regression with R*. Springer Science & Business Media, New York, NY. 392 pp.
- Spanjer, G.R., and M.B. Fenton. 2005. Behavioral responses of bats to gates at caves and mines. *Wildlife Society Bulletin* 33:1101–1112.
- Szewczak, J.M. 2017. SonoBat v. 4.2.1. Available online at <https://sonobat.com/>. Accessed 2 March 2025.
- Thomas, R.J., and S.P. Davison. 2022. Seasonal swarming behavior of *Myotis* bats revealed by integrated monitoring, involving passive acoustic monitoring with automated analysis, trapping, and video monitoring. *Ecology and Evolution* 12:e9344.
- Tobin, A., and C.L. Chambers. 2017. Mixed effects of gating subterranean habitat on bats: A review. *Journal of Wildlife Management* 81:1149–1160.
- Tobin, A., R.J.M. Corbett, F.M. Walker, and C.L. Chambers. 2018. Acceptance of bats to gates at abandoned mines. *Journal of Wildlife Management* 82:1345–1358.
- United States Government Accountability Office (USGAO). 2020. Abandoned hardrock mines: Information on number of mines, expenditures, and factors that limit efforts to address hazards. GAO-20-238, 2020. Available online at www.gao.gov/assets/710/706589.pdf. Accessed 2 March 2025.
- Van Schaik, J., R. Janssen, T. Bosch, A.J. Haarsma, J.J.A. Dekker, and B. Kranstauber. 2015. Bats swarm where they hibernate: Compositional similarity between autumn swarming and winter hibernation assemblages at five underground sites. *PLoS ONE* 10:e0130850.
- Watkins, F. 2002. North American bats and mines project: A cooperative interagency approach to bat conservation through mine land reclamation. Pp. 429–437, *In* R. Barnhisel and M. Collins (Eds.). *Proceedings of the National Meeting of the American Society of Mining and Reclamation*. American Society of Mining and Reclamation, Lexington, KY. 1206 pp.
- Whitaker, J.O., Jr., and L.J. Rissler. 1992. Seasonal activity of bats at Copperhead Cave. *Proceedings of the Indiana Academy of Science* 101:127–134.
- Williams, E.R. 2019. Seasonal occupancy of abandoned mines by cave-dwelling bats in the western Blue Mountains, New South Wales. *Australian Journal of Zoology* 67:301–304.
- Wood, S. 2015. mgcv: Mixed GAM Computation Vehicle with automatic smoothness estimation. Available online at <https://cran.r-project.org/web/packages/mgcv/index.html>. Accessed 2 March 2025.