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Volume 2, 2024 Journal of North American Bat Research No. 2

Journal of North American Bat Research

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Cover Photograph: Rocky outcrop hibernacula used by bats in Ohio. Clockwise from top left are examples of shallow rock shelters, crevices, ledges, and pockets used as hibernacula. The rock ledge at bottom right shows a hibernating *Eptesicus fuscus*. Photograph © Levi Johnson.

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Widespread Use of Rocky Outcrops by Hibernating Bats in Ohio and Pennsylvania

Levi E. Johnson[1], Gregory G. Turner[1], Michael R. Scafini[1], Eman Anis[2], and Joseph S. Johnson[3,*]

Abstract - Bats commonly use subterranean environments for hibernation; however, few studies have investigated bat use of rocky outcrops for overwintering. We searched rocky outcrops from 15 December to 15 March, 2018–2021, and found 333 bats in 179 winter roosts. *Eptesicus fuscus* (Big Brown Bat) was found most often, but *Lasionycteris noctivagans* (Silver-haired Bat), *Perimyotis subflavus* (Tricolored bat), *Myotis lucifugus* (Little Brown Myotis), and *Myotis leibii* (Eastern Small-footed Myotis) were also observed. Average winter temperatures of 8 roosts were similar to temperatures in randomly sampled rock features. *Pseudogymnoascus destructans* was not detected on any bats. Winter roosts of *Eptesicus fuscus* were higher above the ground, in areas with greater forest cover, and at lower elevations than random features. Bat use of rocky outcrops as hibernacula appears widespread, and we recommend further research into use of these habitats.

Introduction

The environment in which bats hibernate influences overwinter survival. Roosting conditions can increase the chances of winter mortality through exposure to predators, floods, and freezing temperatures (Estók et al. 2010; O'Shea et al. 2016; Richter et al. 1993). Conditions in hibernacula also influence energy and water balance (McGuire et al. 2021), as well as opportunities for euthermic processes (Boyles et al. 2020). Additionally, the environment can affect disease outcomes. The most notable disease of hibernating bats in North America is white-nose syndrome (WNS), caused by the fungus *Pseudogymnoascus destructans* (Gargas, Trest, Christensen, Volk, and Blehert). Environmental transmission of *P. destructans* is an important factor in the spread of WNS (Sewall et al. 2023), and the pathogen can persist in the absence of bats (Hoyt et al. 2015, Lorch et al. 2013, Urbina et al. 2021). Furthermore, temperature (Verant et al. 2012) and humidity (Marroquin et al. 2017) affect the growth rate of *P. destructans,* and unsurprisingly, temperature and humidity correlate with population estimates from hibernacula affected by WNS (Hopkins et al. 2021, Langwig et al. 2012, Turner et al. 2022). Therefore, understanding environmental conditions in hibernacula is important for prioritizing conservation efforts (Sewall et al. 2016) and furthering our knowledge of bat natural history.

Bats use a variety of habitats as hibernacula, including caves and anthropogenic structures, such as mines, tunnels, and culverts (Dunn et al. 1989, Meierhofer et al. 2019, Slider and Kurta 2011). Biologists in the mid-twentieth century speculated that bats hibernated in geological features other than caves and mines (Griffin 1945), and these speculations have proven correct. Various North American species overwinter in crevices of rock outcrops, cliffs, scree slopes, and the milieu souterrain superficiel (MSS), which is a network of

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Associate Editor: Rob Schorr, Colorado Natural Heritage Program

underground, air-filled voids (Blejwas et al. 2021, Johnson et al. 2017, Lausen and Barclay 2006, Lewis et al. 2022, Moosman et al. 2017, Neubaum 2018, Neubaum et al. 2006, White et al. 2020). These habitats apparently are important to *Eptesicus fuscus* (Palisot de Beauvois) (Big Brown Bat), *Lasionycteris noctivagans* (Le Conte) (Silver-haired Bat), and several *Myotis* species. Our knowledge about bats hibernating in caves, mines, and similar anthropogenic habitats is much greater than that of bats using alternative habitats. This disparity potentially overshadows the diversity of winter strategies within and among species, and failure to appreciate the full suite of habitats used by bats may undermine efforts to understand disease spread (Maher et al. 2012), quantify population trends (Cheng et al. 2021), or identify important areas for conservation (Blomberg et al. 2021, Lemen et al. 2016).

Research into the use of rocky outcrops as hibernacula has been limited due to the difficulties of observing bats hidden in deep crevices (Schorr et al. 2022). Documentation of use of rock structures by bats is often accomplished through acoustic detection or capturing emerging bats (Blomberg et al. 2021, White et al. 2020). However, several radio-telemetry studies have described hibernacula in rock outcrops, including roost dimensions, microclimates, and characteristics of the surrounding environment (Lausen and Barclay 2006, Perry et al. 2010). One such study found that Big Brown Bats exhibited a preference and fidelity to deep crevices that could offer more stable microclimates (Klüg-Baerwald et al. 2017). Thus, crevices in rocky outcrops can offer thermal properties similar to cave and mine hibernacula (Boyles and McKechnie 2010).

If rocky outcrops provide suitable microclimates for hibernating bats, they may also provide suitable habitat for *P. destructans*. However, the growth and spread of *P. destructans* in these habitats may differ from that observed in caves and mines, and rock crevices may offer bats some refuge from the disease. For example, the cold, dry conditions of rock crevices in southern Canada (Klüg-Baerwald et al. 2017) may slow fungal growth compared to the warmer, more humid microclimates of caves in the eastern United States. Furthermore, small rock crevices (Klüg-Baerwald et al. 2017) and passages within the MSS (Blejwas et al. 2021) may support smaller groups of hibernating bats than caves and mines, which may, in turn, decrease physical contact among bats and slow the spread of *P. destructans*. Small roosting groups may not prevent mass mortality from WNS, as small groups of *Myotis septentrionalis* (Trouessart) (Northern Myotis) hibernate in the MSS (Lewis et al. 2022), yet have still suffered severe declines from WNS (Cheng et al. 2021). Nevertheless, there has been no research on the capacity for *P. destructans* to grow or exist in rock crevices during winter, and this is an important gap in our knowledge of WNS.

The goal of our study was to enhance understanding of bat use of rocky outcrops as hibernacula by describing the conditions and features of these environments, documenting the species that use them, and surveying for *P. destructans*. We also contrasted rocky outcrops used as hibernacula by Big Brown Bats with randomly sampled rock features to identify roost characteristics that support the winter roosting needs of Big Brown Bats.

Field-site Description

We surveyed for bats along rock outcrops in Ohio and Pennsylvania, USA (Fig. 1). In this region, bats hibernate in caves, mines, and railroad tunnels (Johnson and Johnson *in press*, Turner et al. 2022), although caves are typically limited to areas with carbonate bedrock (Dunn et al. 1989, Weary and Doctor 2014). Deep recesses in sandstone cliffs are often informally referred to as “caves” in eastern Ohio, but these features typically lack dark zones and cave fauna. Nevertheless, such features may provide winter habitat for bats

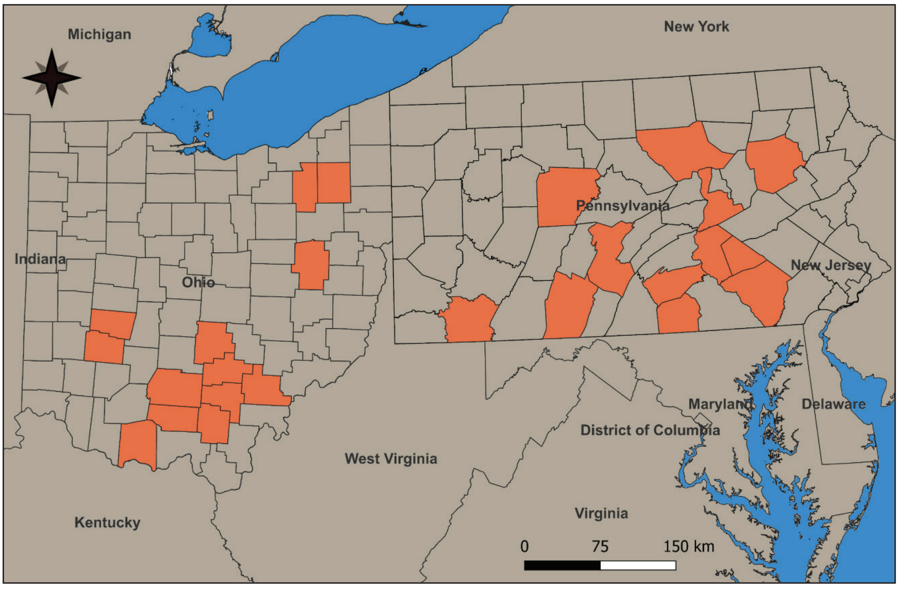

Figure 1. A partial map of eastern North America showing the distribution of sampling effort across Ohio and Pennsylvania, 2018–2021. Counties shaded orange indicate areas where we searched rocky outcrops for hibernating bats.

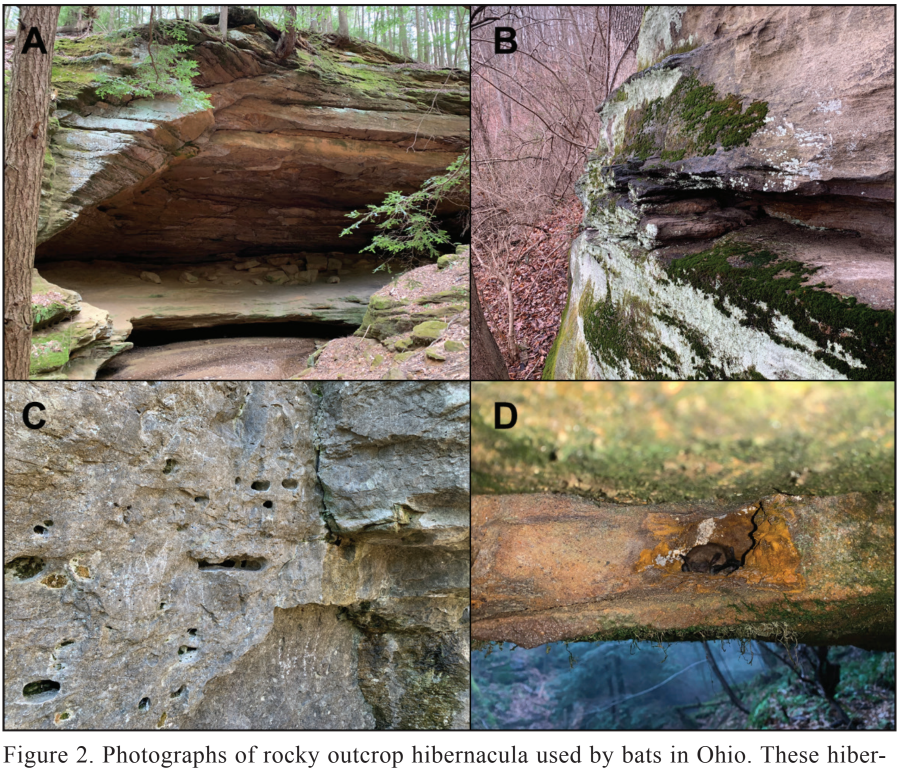

Figure 2. Photographs of rocky outcrop hibernacula used by bats in Ohio. These hibernacula included shallow rock shelters (A), crevices located in exposed rock walls (B), pockets (C), and rock ledges, which were typically found within rock shelters (D).

(Fig. 2). In particular, the Black Hand Sandstone of the Cuyahoga Formation weathers in a manner that forms cliffs and gorges, with many crevices and pockets that may support bat roosting (Steeg 1947). Similar features, along with boulder and scree slopes, and large stretches of uplifted bedrock, also occur throughout Pennsylvania. To determine if these rocky outcrops are important to bats, we selected 32 properties in Ohio and 21 properties in Pennsylvania as study sites. Selected properties were public lands and nature preserves owned by non-governmental organizations. We selected study sites based on our knowledge of these areas and recommendations from colleagues.

Methods

We searched rocky outcrops for hibernating bats between 15 December and 15 March, 2018–2021. Rocky outcrops ranged from <1–50 m in height and from <1 m to >1 km in length. Two or more biologists with expertise in bat identification used flashlights to inspect outcrops from 0 to 2.5 m above ground level. Surveys of rocky outcrops often required >1 day to complete. We surveyed 42 locations once and 11 additional locations more than once during the winter. We recorded where surveys occurred with a mobile application (Avenza Maps, Avenza Systems, Inc., Toronto, Canada). Total length of cliffs surveyed was >147 km.

We noted the number of each bat species present and recorded their location using a handheld global position device (GPSMap 64s, Garmin International, Inc., Olathe, KS). We then classified each roost as a crevice, ledge, pocket, or shelter (Fig. 2). We defined a crevice as a void in a wall or within a shelter that narrowed in height as it extended into the rock. A ledge was a platform of rock that projected from an outcrop or from a wall within a rock shelter. A pocket was a void in rock that became wider or taller as it extended into the rock. Finally, a rock shelter was a recessed area within an outcrop where bats could hang from the wall or ceiling. All rock shelters were <10-m deep and lacked dark zones, which distinguished them from caves.

We measured the height (m) above the ground of any bat roost and the azimuth (degrees) of the roost opening. We also measured the maximum length (cm) and maximum width (cm) of roosts when applicable and when they could be measured without disturbing bats. We decided that the risk of disturbing bats was unacceptable when bats could be inadvertently touched. Length and width could not be measured for pockets with entrances that were too narrow to access with measuring tools, and these measurements were deemed not applicable when bats were roosting in ledges or in rock shelters.

We used digital elevation models in QGIS (QGIS Development Team 2023) to determine the elevation and the terrain ruggedness index (TRI), a measure of topographic heterogeneity, of each roost (Riley et al. 1999). We used the 2019 National Landcover Dataset (Dewitz and U.S. Geological Survey 2021) to quantify the amount of forest cover within a 1-km radius of the roost. Finally, we calculated the distance to the nearest known hibernaculum in a cave, mine, or railroad tunnel, using data provided by the Ohio Department of Natural Resources and Pennsylvania Game Commission.

To understand the habitat characteristics of rocky outcrops used as hibernacula, we compared them to rock features selected at random within the boundaries of each property we surveyed. Random features were chosen by generating random points in QGIS prior to surveys. We located areas of rocky outcrops nearest to random points and used a random number generator to determine a height above the ground (0–2.5 m) for sampling. Any rock crevice, ledge, shelter, or pocket on the cliff or outcrop was considered available to bats. We examined each random feature with flashlights to determine if bats were present before taking measurements.

We used logistic regression models to compare random features to roosts used by Big Brown Bats, which was the most common species detected. We created a series of logistic regression models in R (R Core Team 2022), with roost type (roost vs. random feature) as the response variable, and we included 1 or more predictor variables. We then used model selection based on Akaike's Information Criterion for small sample sizes (AIC_c) to determine which candidate models best fit our data. Because crevice length and width could not be measured for some roosts and were not applicable for others, these variables were not included in the analysis but are presented (means ± SD) for comparison to other studies of bat roosting. Before analysis, we ensured that variables were not correlated, using Pearson's correlation coefficient, and that variables in models did not exhibit multicollinearity, using variance inflation factors (Fox and Weisberg 2019). We considered models with ΔAIC_c values ≤ 2 to be competitive as the best model explaining the variability in our data (Burnham and Anderson 2002), and we calculated the odds ratios for each variable in the top model. Finally, we used the area under the receiver operating characteristic curve (AUC) to assess the fit of the top model (Robin et al. 2011).

To understand the conditions within roosts, we measured temperatures during surveys and monitored temperatures at a subset of locations for the entire winter. During surveys, we measured each bat's skin temperature (T_{sk}) and the temperature of the rock on which the bat roosted (T_{rock}), using an infrared laser thermometer (Model 568, Fluke Corporation, Everett, WA). Temperature measurements were taken with the thermometer positioned <10–30 cm from the target. The thermometer had a distance-to-spot ratio of 50:1, which means that, at 30 cm, the typical temperature reading point was <0.75-cm wide. We recorded T_{sk} by sighting the thermometer on the center of the bat and measured T_{rock} by sighting the thermometer approximately 1–3 cm away within the roost. We also deployed microclimate data loggers (Models MX2301A and MX2202, Onset Computer Corporation, Bourne, MA) in 12 roosts and 7 random features in Ohio to record air temperatures (T_{roost} and T_{random}, respectively). We placed dataloggers in crevice, pocket, and ledge roosts without touching hibernating bats. Roosts with narrow entrances could not be sampled with dataloggers. We programmed dataloggers to record every 15 minutes from November through March, and we calculated an overall average and range of winter temperatures for each sampling location. We compared T_{sk} to T_{rock} using a linear model (R Core Team 2022) and compared T_{roost} to T_{random} using a Mann-Whitney U Test (R Core Team 2022). We compared T_{random} to T_{roost} for only Big Brown Bats because of low sample sizes for other species.

To determine if *P. destructans* was present in cliff and rock outcrop hibernacula, we swabbed 72 bats. For most bats, we gently rubbed a sterile swab against the face and forearms without removing bats from their roost. The amount of *P. destructans* present on swabs was determined through quantitative polymerase chain reaction (qPCR) (Muller et al. 2013). All samples were run alongside positive controls. A sample with a cycle threshold (C_t) greater that the assay cutoff ($C_t > 35$) was considered negative for *P. destructans*.
We also temporarily removed 15 Big Brown Bats from their roosts during late winter (mid-March), when infection rates of *P. destructans* should be highest (Janicki et al. 2015), and photographed (EOS Rebel T5, Canon USA, Melville, NY) their wings under ultraviolet light (UV) (Turner et al. 2014). We created a dark room in the field, using black curtains suspended from nearby rocks and vegetation, and photographed the dorsal surface of both wings while each was stretched over a lightbox containing 2 UV light bulbs (368 nm; Way Too Cool, LLC, Glendale, AZ). We inspected photographs for the presence of orange-yellow fluorescence indicative of *P. destructans* infection (Turner et al. 2014).

Results

We found 179 rocky outcrop hibernacula, consisting of 97 crevices, 39 pockets, 31 ledges, and 12 shallow rock shelters. Of these hibernacula, Big Brown Bats used 155 features; Silver-haired Bats, 10; *Perimyotis subflavus* (Cuvier) (Tricolored Bat), 11; *Myotis lucifugus* (Le Conte) (Little Brown Myotis), 2; and *Myotis leibii* (Audubon and Bachman) (Eastern Small-footed Myotis), 1 (Table 1). All 5 species were found in Ohio, but only Big Brown Bats and Tricolored Bats were discovered in Pennsylvania. Roosts were occupied by 1–18 bats ($\bar{x}$ = 1.9 ± 2.2), with a total of 333 bats observed. The largest group contained 18 Big Brown Bats in a crevice.

All bats were torpid when discovered, with T_{sk} significantly correlated with T_{rock} ($F_{1, 301}$ = 16,340, $P < 0.01$, $r^2 = 0.98$). T_{sk} varied from -1.4 to 13.3 °C ($\bar{x}$ = 3.8 ± 2.4 °C) for Big Brown Bats (n = 276); from 0.3 to 5.9 °C ($\bar{x}$ = 2.7 ± 1.9 °C) for Silver-haired Bats (n = 11); from 1.9 to 9.2 °C ($\bar{x}$ = 6.3 ± 1.9 °C) for Tricolored Bats (n = 14); and from 1.3 to 6.9 °C for Little Brown Myotis (n = 2). We did not measure the temperature of 30 bats because of equipment failures. Average roost temperatures for all species ranged from 2.4 to 4.4 °C (Table 2). For Big Brown Bats, we found no evidence that T_{roost} average (W = 21, P = 0.46) or T_{roost} range (W = 31, P = 0.78) differed from T_{random} average or T_{random} range, respectively.

A model with forest cover, height above ground, and elevation best explained the variability in rocky outcrops used as hibernacula by Big Brown Bats (Table 3). No other model had a $\Delta AIC_c < 2$. Odds ratios of the variables in the top model showed that for each square kilometer increase in amount of forest surrounding a rock feature, the probability of use by Big Brown Bats increased by 216% (odds ratio = 3.16, 95% CI = 2.00–5.20). Forest cover surrounding Big Brown Bat roosts ranged from 0.6 to 3.1 km^2 (Table 1, Fig. 3). Height above ground also had a positive effect, with each meter increase in height above the ground increasing the probability of use by 62% (odds ratio = 1.62, 95% CI = 1.18–2.98). Roost heights ranged from 0.38 to 2.5 m (Table 1, Fig. 4A). Finally, elevation had a negative effect, with each meter rise above sea level resulting in a 1% decrease in probability of use (odds ratio = 0.99, 95% CI = 0.988–0.995). Roosts were found at elevations of 91–420 m (Fig. 4B). The model had a good fit, with an AUC of 0.72.

Table 1. Characteristics of 178 rocky outcrops used as hibernacula by bats in Ohio and Pennsylvania, 2018–2021. Values are mean ± SD.

	Big Brown Bat (n = 155)	Silver-haired Bat (n = 10)	Tricolored Bat (n = 11)	Little Brown Myotis (n = 2)
Height above ground (m)	1.7 ± 0.71	2.3 ± 1.3	2.0 ± 1.4	2.0†
Azimuth (°)	158 ± 84.3	96 ± 84.2	132 ± 78.2	94.5†
Crevice width (cm)	58.5 ± 143	23 ± 24.0	9.0†	—
Crevice height (cm)	17.9 ± 37.0	5.75 ± 3.89	14.0†	—
Elevation (m)	256 ± 38.1	263 ± 35.3	264 ± 20.7	253†
Forest cover (km^2)	2.7 ± 0.48	2.9 ± 0.17	2.9 ± 1.1	2.9†
Topographic ruggedness (unitless)	1.5 ± 1.6	1.1 ± 0.64	1.8 ± 1.8	1.3†
Distance to hibernaculum (km)	18.2 ± 24.9	13.3 ± 17.2	10.3 ± 4.3	2.6†

† Standard deviation not included due to sample size.

Table 2. Winter temperatures (°C) in roosts used by 3 bat species and in randomly sampled locations, in Ohio, 2018–2021. Temperatures were recorded using dataloggers installed within roosts (see Methods). Data presented are means ± SD.

	Average Temperature	Minimum Temperature	Maximum Temperature	Temperature Range
Big Brown Bat (n = 8)	3.07 ± 1.58	-5.15 ± 5.96	11.67 ± 2.22	15.02 ± 5.66
Silver-haired Bat (n = 4)	4.02 ± 1.50	-5.26 ± 8.18	12.47 ± 1.99	14.58 ± 6.20
Little Brown Myotis (n = 1)	3.54†	-1.29†	14.41†	15.7†
Tricolored Bat (n = 1)	4.44†	-1.12†	9.01†	10.13†
Random Features (n = 7)	2.44 ± 1.28	-1.52 ± 1.73	12.80 ± 2.11	15.23 ± 3.54

† Standard deviation not included due to sample size.

Table 3. Models of rocky outcrop hibernacula used by Big Brown Bats in Ohio and Pennsylvania, 2018–2021. K = number of parameters; AIC_c = Akaike's Information Criterion for small sample size; ΔAIC_c = difference in AIC_c between this model and the top model; Weight = AIC_c model weight; TRI = terrain ruggedness index.

Model Description	K	AIC_c	ΔAIC_c	Weight
Forest cover + Elevation + Height above ground	4	392.26	0	0.81
Forest cover + Elevation + TRI	4	395.92	3.67	0.13
Forest cover + TRI + Height above ground	4	399.21	6.96	0.03
Forest cover + Elevation	3	399.54	7.29	0.02
Forest cover + Distance to hibernacula + Elevation	4	400.71	8.45	0.01
Forest cover + Distance to hibernacula + Height above ground	4	411.52	19.26	0
TRI + Distance to hibernacula + Height above ground	4	413.46	21.2	0
Forest cover + Height above ground	3	414.24	21.99	0
TRI + Height above ground	3	415.88	23.63	0
Distance to hibernacula + TRI + Forest cover	4	415.97	23.72	0
Forest cover + TRI	3	416.36	24.11	0
Elevation + Distance to hibernacula + Height above ground	4	416.8	24.55	0
TRI + Elevation	3	416.87	24.62	0
Elevation + Height above ground	3	417.6	25.34	0
Elevation	2	423.1	30.84	0
Distance to hibernacula + Elevation	3	423.28	31.03	0
Forest cover + Distance to hibernacula	3	423.32	31.07	0
Forest cover	2	424.61	32.36	0
Distance to hibernacula + Height above ground	3	247.21	34.96	0
Distance to hibernacula + TRI	3	429.56	37.31	0
TRI	2	430.63	38.37	0
Height above ground	2	430.77	38.52	0
Distance to hibernacula	2	436.49	44.23	0
Null	1	438.62	46.36	0

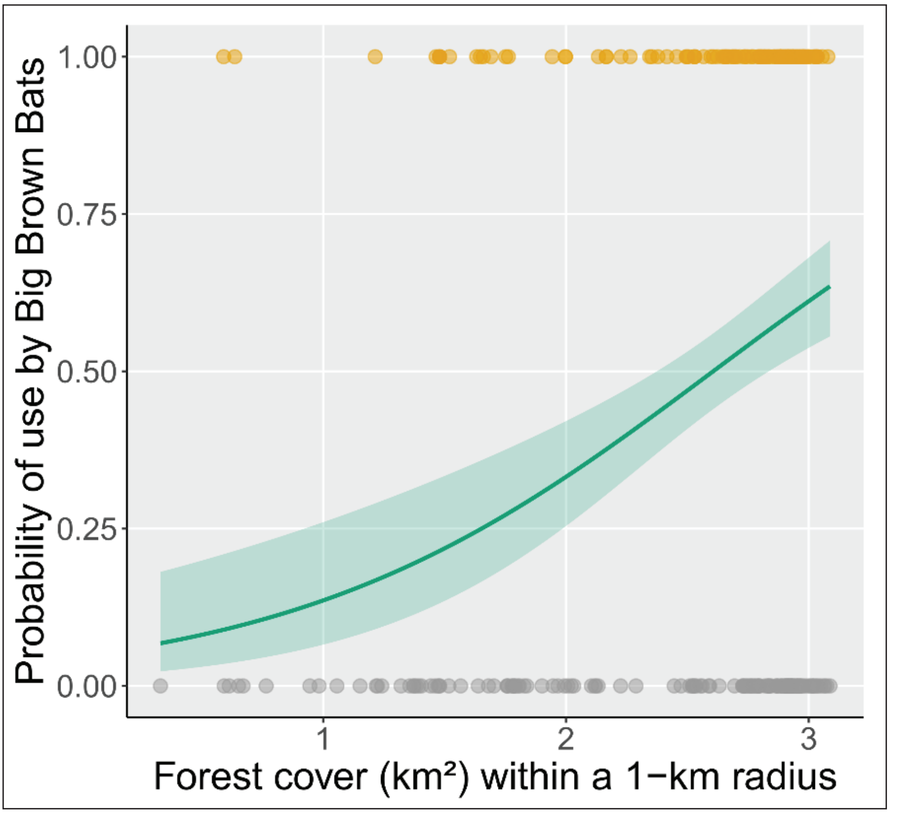

Figure 3. The probability that rocky outcrops were used as hibernacula by Big Brown Bats in Ohio and Pennsylvania increased with the area covered by forest within a 1-km radius centered on the roost. Circles denote hibernacula (probability = 1) and randomly sampled locations (probability = 0).

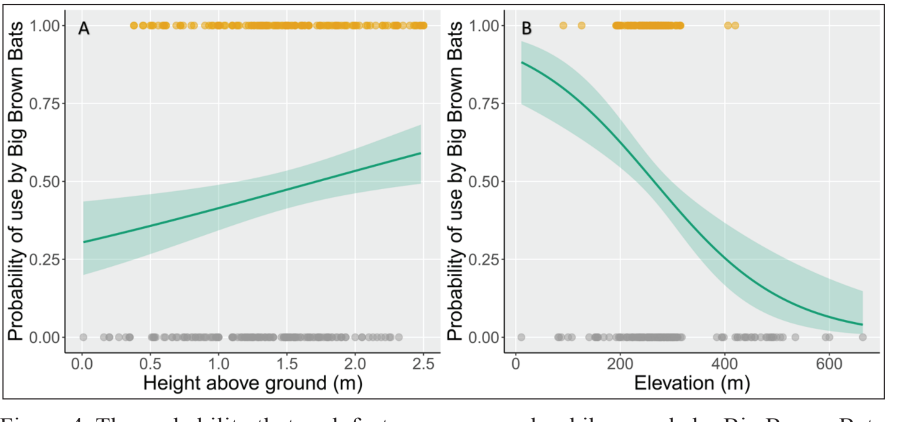

Figure 4. The probability that rock features were used as hibernacula by Big Brown Bats in Ohio and Pennsylvania increased with height above ground (A) and decreased with elevation (B). Circles denote hibernacula (probability = 1) and randomly sampled locations (probability = 0).

Roosts of Silver-haired Bats, Tricolored Bats, Little Brown Myotis, and Eastern Small-footed Myotis were not compared to random features because of low sample sizes. Silver-haired Bats roosted >15-cm deep in shelves ($n = 2$), pockets ($n = 3$), and crevices ($n = 3$) and were often difficult to see. Tricolored Bats typically hibernated in crevices ($n = 3$) or hanging on the walls ($n = 7$) of shallow rock shelters in sandstone cliffs, although 1 roost was in a crevice within a rock outcrop. Little Brown Myotis roosted in shelters and rock outcrops, and the sole Eastern Small-footed Myotis was exposed on the side of a rock shelter. We swabbed 72 bats, including 60 Big Brown Bats, 7 Silver-haired Bats, 3 Tricolored Bats, and 1 Eastern Small-footed Myotis, but none tested positive for *P. destructans*. Furthermore, no fluorescence was observed on any of the 15 Big Brown Bats photographed with UV light.

Discussion

We documented 5 species hibernating in crevices, pockets, and ledges in rocky outcrops. Big Brown Bats were the most commonly observed species, with *Myotis* spp., Tricolored Bats, and Silver-haired Bats seldom located, likely because these species are simultaneously less common and more difficult to detect. Temperatures in the winter roosts were cold (mean = 3 °C) and variable (average range of 16 °C). We found bats in these roosts on even the coldest of winter days, with freezing or near-freezing skin temperatures recorded for Big Brown and Silver-haired Bats. While it is well documented that Big Brown Bats are not cave-obligate hibernators (Whitaker et al. 1992), the extent to which the species uses rocky outcrops in our region is underappreciated and may lead to incorrect conclusions about population trends when examining counts from caves and mines alone (Cheng et al. 2021). Additionally, these data provide important insights into the winter ecology of the Silver-haired Bat, as we are aware of only 1 published record of this species hibernating in rock crevices (Perry et al. 2010). Finally, our data show that Tricolored Bats and Little Brown Myotis hibernate outside caves in our region, a behavior typically associated with the southern and western portion of their ranges (Blejwas et al. 2021, Meierhofer et al. 2019, Newman et al. 2021).

Several factors influenced the probability that a cliff or rock outcrop would be used by Big Brown Bats. Although height above ground was a significant predictor of use, the odds ratios likely underestimated the statistical effect, because we only surveyed the lower 2.5 m of rocky outcrops. Height above ground may be important because higher crevices are less likely to be reached by a predator (Lausen and Barclay 2002) and may facilitate flight by giving bats enough height to drop and generate lift when leaving the roost (Neubaum et al. 2006). Although we agree with the rationale for these hypotheses, we found solitary Big Brown Bats in crevices as low as 0.38 m above the ground and clusters of up to 4 bats as low as 0.5 m above the ground.Rocky hibernacula at similar heights above ground were reported by Moosman et al. (2017), and we believe low-roosting bats were still protected from predators due to the depth of roost crevices.

We did not measure crevice depth, because crevices were typically tight, irregular spaces. However, these crevices were often sufficiently deep and narrow that bats could roost >10 cm from the external surface of the rock, protecting themselves from predators even at low heights. However, crevices in our study were rarely as deep as those used by Big Brown Bats for hibernacula in Alberta ($\bar{x}$ = 150 cm) or Colorado ($\bar{x}$ = 40 cm) (Klüg-Baerwald et al. 2017, Neubaum et al. 2006). Deep crevices may be more important for Big Brown Bats in colder climates where greater buffering from extreme cold is required. Conversely, use of deep crevices may be underrepresented in our study, because tight fissures in the rock formations may provide spaces where bats can escape detection (Schorr et al. 2022).

Big Brown Bats were more likely to hibernate in cliffs and outcrops surrounded by greater amounts of forest cover, which probably benefits hibernating bats in several ways. First, some Big Brown Bats may be sedentary, hibernating in the same areas where they raise their young in summer (McGuire and Boyle 2013). Sedentary populations would likely benefit from the presence of both ample summer and winter habitat. Although summer habitat for Big Brown Bats includes buildings (Agosta 2002), forests provide both natural roosts and important foraging habitats (Duchamp et al. 2004, Titchenell et al. 2011). Thus, Big Brown Bats may be more likely to use rocky habitat surrounded by greater forest cover because these areas can sustain larger populations during summer.

Forest cover surrounding rocky outcrops may also benefit bats by reducing variability in temperatures. Cold hibernacula with variable temperatures, such as those documented in our rocky hibernacula, may require bats to increase torpid metabolic rate if they cannot compensate through behavior (Boyles and McKechnie 2010). If forest cover reduces this variability, by providing shade or protection from wind, bats may select for higher forest cover to reduce torpid metabolic rates. Our findings suggest that conservation of forests and their associated rocky habitats is important for the protection of Big Brown Bats and likely other species.

Finally, Big Brown Bats were more likely to roost in cliffs and rock outcrops at elevations lower than the elevations of randomly sampled features. At elevations >2000 m in Colorado, Neubaum and colleagues (2006) detected a negative effect of elevation on selection of rock-crevice hibernacula by Big Brown Bats. Thus, in Colorado, where ambient temperatures typically decrease with elevation, bats may migrate upslope to environments colder than their summer range, but may not overwinter at the highest elevations because temperatures are too low (Neubaum et al. 2006). By comparison, the properties we surveyed were always <700 m in elevation and rarely experienced temperatures as cold as those reported by Neubaum and colleagues (2006). Furthermore, while temperature had a negative relationship with elevation in Colorado, the reverse is sometimes true in the narrow valleys where we often found bats. Cold air becomes trapped in these areas, with warmer temperatures located on the tops of the surrounding hillsides (Monarchino et al. 2020). During winter, the bottom and top of these valleys have similar daily minimum temperatures, but the tops have greater high temperatures (Monarchino et al. 2020). We speculate that the narrower range of ambient temperatures at lower elevations within the sandstone gorges and other narrow ravines of Ohio and Pennsylvania are advantageous because bats can reduce torpid metabolic rates in these cold hibernacula (Boyles and McKechnie 2010). We encourage further research comparing crevice temperatures across elevational gradients, along with comparisons of winter activity patterns.

We found no differences in microclimate between roosts of Big Brown Bats and randomly sampled features. In contrast, Big Brown Bats in Alberta selected crevices with average temperatures that were higher and less variable than random sites (Klüg-Baerwald et al. 2017). In Colorado, temperatures in crevices used by hibernating Big Brown Bats were also less variable than temperatures in transient roosts where bats did not hibernate (Neubaum et al. 2006). Our finding that roost microclimate was less important for roost selection by Big Brown Bats may result from differences in climate. For example, the average temperature recorded in our random features (3.8 °C) was higher than in random crevices in Alberta (-4.9 °C) or transient roosts in Colorado (0.4 °C) (Klüg-Baerwald et al. 2017, Neubaum et al. 2006). Nevertheless, both roosts of Big Brown Bats and random features experience temperatures < 0 °C in our study. Because these conditions require bats to burn vital fat reserves to avoid freezing (Boyles et al. 2020), we speculate that bats either switch roosts or move within roosts to help thermoregulate during winter.

Although we did not locate enough hibernacula used by other species to compare them to random features, documentation of these roosts is notable. Populations of Tricolored Bats and Little Brown Myotis are under extreme threat from WNS (Cheng et al. 2021) and documenting the use of cliffs and rock outcrops is a critical first step for effective conservation. Tricolored Bats often hibernated within alcoves of rock shelters, where they hung from the ceiling or walls, similar to their behavior in a cave or mine. These small, recessed areas within rock shelters possibly have microclimates that differ from the rest of the rock shelter, providing warmer or more stable temperatures. Nevertheless, temperatures in these rock shelters were more variable than in caves historically used by Tricolored Bats in our region (Johnson et al. 2016; Johnson and Johnson, *in press*). Although the importance of these roosts to the regional population of Tricolored Bats cannot be determined from our study, we recommend further research into the winter habits of this species and conservation of rocky outcrops.

The 3 hibernacula used by Little Brown Myotis or Eastern Small-footed Myotis add to a growing body of literature showing that these species are not cave obligates. Although Little Brown Myotis were recently found hibernating within the MSS in Alaska (Blejwas et al. 2021) and are suspected to hibernate in talus slopes in Colorado (Neubaum 2018) and Wyoming (Johnson et al. 2017), our study is the first to document winter roosting in rock outcrops in eastern North America. Eastern Small-footed Myotis are known to hibernate outside of caves (Moosman et al. 2017), but this is the first observation of this species roosting in rocky outcrops during winter in Ohio. Silver-haired Bats were found in crevices within rock shelters and along cliffs, and these bats were occasionally found <1 m from hibernating Big Brown Bats, although in different crevices. Silver-haired Bats were previously believed only to migrate through Ohio and have not been documented in the state during winter (Ohio Department of Natural Resources, unpublished data). The seasonal distribution and winter habits of the Silver-haired Bat are largely unresolved (Cryan 2003), but winter records throughout the Midwest United States are not rare, although they are mostly from buildings in areas dominated by glacial till (Kurta et al. 2018). We encourage additional surveys of the winter habitats of Silver-haired Bats to improve knowledge of the species' natural history and roost selection in areas that differ in surface geology.

Pseudogymnoascus destructans was not detected on any bat from rocky outcrops nor was infection detected on any bat. However, our sample of swabbed and photographed bats consisted primarily of Big Brown Bats, a species resistant to the effects of WNS (Frank et al. 2014, Moore et al. 2018). Despite resistance of Big Brown Bats to the effects of WNS, other studies have shown that members of this species can be infected with *P. destructans* and test positive for fungal DNA (Janicki et al. 2015, Turner et al. 2014). Thus, prevalence of *P. destructans* may be lower for Big Brown Bats hibernating in rocky outcrops than for bats in caves and mines. Factors that may have limited the prevalence of *P. destructans* at hibernacula in this study include low and variable roost temperatures, few bats roosting at each location, and low amounts of organic matter that may provide nutrients for the fungus (Forney et al. 2022).

Hibernation in rocky outcrops has been under-studied, and this lack of effort has likely biased population estimates and our understanding of the natural history of multiple species of bats. Rocky outcrops are important winter habitat for bats and should receive conservation attention, similar to caves and mines. Limiting activities such as highwall mining (extracting coal from exposed seams in an open pit mine) during the hibernation period should also be considered, and the effects of various forms of human disturbance on these habitats should be studied (Wilson 2019). While further research on hibernacula in rocky outcrops is necessary to develop management strategies, our research suggests that protecting forested areas surrounding cliff lines and rock outcrops could be an important first step for protecting these habitats.

Acknowledgments

We thank the Ohio Department of Natural Resources, for funding, and Crane Hollow Nature Preserve, for land access, assistance with field research, and helping to develop this study over several years. We also thank J. Moosebrugger, A. Waag, H. Bencin, M. Perdicas, J. Whittle, A. Nolder, and numerous technicians from the Pennsylvania Game Commission, for assistance in the field, and M. Lewis and L. Williams, for field and intellectual contributions to this work.

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