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Cover Photograph: A composite of multiple photos inside room 8 of the spillway at Tippy Dam, near Wellston, Michigan. © A. Kurta.

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Environmental Parameters, Arousal Patterns, and Wing Damage in a Population of Little Brown Bats (*Myotis lucifugus*) Unaffected by White-nose Syndrome

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Abstract - The population of *Myotis lucifugus* (Little Brown Bats) hibernating in the spillway at Tippy Dam in Michigan did not decline after detection of *Pseudogymnoascus destructans* (*Pd*), the causative agent of white-nose syndrome. In winter 2019–2020, 5 years after the fungus arrived, we evaluated aspects of the environment, pathogen virulence, and host susceptibility. High internal temperatures in autumn (10–15°C) and spring (7–11°C) should have favored rapid growth of the fungus, but this did not occur. Median percent of wing area that fluoresced under ultraviolet light (a measure of disease severity) was only 0.01–0.04%. Although infection with *Pd* typically leads to frequent arousals from torpor, mean torpor bout length in the dam (16.8 days), which was determined with temperature-sensitive radio-transmitters, was similar to published values for uninfected animals. Our observations, combined with previous reports, suggest that some aspect of the environment intrinsic to the dam is inhibiting the fungus, and we propose testable hypotheses concerning summer temperatures and low-frequency sound/vibrations.

Introduction

Most small mammals rely on some type of shelter to care for their young, avoid predators, and aid thermoregulation (e.g., Deeming 2023, Kinlaw 1999). Although typically beneficial to the occupant, burrows, nests, and similar structures can lead to a decrease in fitness by concentrating and promoting the transmission of parasites and pathogens, especially when many hosts gather at communal sites (Ward and Webster 2016, Webber and Willis 2016). For example, white-nose syndrome (WNS), a cutaneous fungal disease, has devastated species of bats in North America that typically shelter in large numbers inside mines or caves during hibernation (Cheng et al. 2021, Kurta and Smith 2020). The fungus is transmitted by contact with conidia (spores) carried by roostmates or found on the roosting substrate (Hicks et al. 2023). Differences in disease severity among populations of the same species are strongly related to the extent of the environmental reservoir of conidia that is present on the walls of a hibernaculum when bats return in autumn (Fischer et al. 2021, Hoyt et al. 2020).

White-nose syndrome is caused by a psychrophilic fungus, *Pseudogymnoascus destructans* (Blehert and Gargas) Minnis and D.L. Lindner (*Pd*). Infection by *Pd* begins with invasion of the epidermis and dermis by fungal hyphae, which leads to a cascade of physiological

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effects, increased evaporative water loss, and ultimately a greater frequency of arousal from torpor (Cryan et al. 2010, Meteyer et al. 2009, Reeder et al. 2012, Verant et al. 2014, Warnecke et al. 2012). The increased rate of arousal often results in depletion of energy stores, starvation, and death by midwinter (Reeder et al. 2012). After infected individuals appear, overwintering populations of many species decline by 75–90% within 2–5 years (Frick et al. 2010, Kurta and Smith 2020).

However, an unusual hibernaculum, the spillway at Tippy Dam, in northern Lower Michigan, is an exception to this devastating trend. Despite detection of the fungus in winter 2014–2015, the population at the dam has not decreased, and even individuals that are 18–26-years old have survived several years of presumed contact with the fungus (Kurta et al. 2020); mean population size, during 9 counts in February between 2012 and 2024, is 24,522 ± 2662 (*SD*) bats (Gmutza et al. 2024; A. Kurta, unpubl. data). Most individuals (>99%) continue to be *Myotis lucifugus* (LeConte) (Little Brown Bat), with a few (≤15) *Perimyotis subflavus* (F. Cuvier) (Tricolored Bat) present every year, along with an occasional *M. sodalis* Miller and Allen (Indiana Bat). Although *M. septentrionalis* (Trouessart) (Northern Long-eared Bat) historically comprised up to 3% of the hibernating individuals (Kurta et al. 1997), that species has not been detected during 8 wintertime visits between 2019 and 2024.

Together, a suitable environment for a pathogen, the virulence of the pathogen, and a susceptible host (i.e., the components of the disease triangle) lead to disease in a population (McNew 1960, Scholthof 2007). Ameliorating any of these drivers results in decline of a pathogen, or even its absence, and our study has 3 objectives that, together, examine the disease triangle at Tippy Dam. The first objective is to monitor temperature and humidity within the spillway, to help determine whether ambient conditions in winter are suitable for growth of *Pd* on the bats and walls (Marroquin et al. 2017, Verant et al. 2012). Our second objective is to compare disease severity between early and late hibernation by evaluating the effects of a particular virulence factor, the fungal metabolite riboflavin, which erodes the skin (Flieger et al. 2016). Riboflavin fluoresces under ultraviolet light (UV), and disease severity (damage to the wings) can be quantified by measuring the area of fluorescence (McGuire et al. 2016, Moore et al. 2017). The third objective is to record patterns of thermoregulatory behavior of overwintering bats with temperature-sensitive radio-transmitters. Although thermoregulatory behavior is not a direct reflection of susceptibility, data on arousal frequency may demonstrate whether host response at the dam differs from patterns observed in affected populations (Reeder et al. 2012). Understanding why bats persist at Tippy Dam, despite continued presence of the fungus (McDevitt-Galles et al. 2025), could lead to management strategies to reduce the impacts of the disease at other sites or on other species.

Field-site Description

Tippy Dam is a hydroelectric facility located on the Manistee River, near Wellston, Michigan (44°13′01″ N, 85°57′28″ W). The dam (Fig. 1), built in 1918, consists of an earthen embankment, a powerhouse, and a hollow concrete spillway. The bats hibernate inside the spillway, which is only 45-m long and divided into 10 consecutive rooms. Humans access the spillway through a trapdoor in the ceiling of a small entrance chamber, room 1. A catwalk, 1.5-m wide and suspended 8 m above the floor, is the only connection between rooms 2–9, which form the bulk of the spillway (Fig. 2). These rooms are semi-triangular (i.e., narrow at the top and wide at the bottom) and are 12.5-m high, 3.5-m long (north to south, along the walkway), and 21-m wide (upstream to downstream) at the base (Fig. 2). A short staircase in room 9 leads to a narrow compartment, room 10, at the southern end. The concrete walls that separate each internal chamber from the impounded water upstream and the external air downstream are ~0.6-m thick. The owners of the dam restrict human activity to the catwalk for safety, and prohibit employees from entering the spillway between 1 September and 1 June, to prevent disturbance to hibernating bats (Kurta 1995b).

Internal air temperature (T_a) closely tracks and is controlled by changes in the temperature of water stored behind the dam, and consequently, T_a typically varies <1°C among the different rooms during any 24-h period (Kurta 1995a, 1998, 2002; Kurta et al. 1997). However, as the impounded water warms or cools with the changing seasons, internal T_a also changes so that, in October or May, internal T_a can be 10–14°C greater than in February. High humidity occurs throughout the structure, with water flowing down some walls, and shallow pools covering the bottom of many chambers. Dim light, as well as the bats, enter the spillway through narrow ventilation holes in the downstream wall of rooms 2–9 (5 holes, with minimum diameter of 15 or 30 cm, in each room) and a single opening in the ceiling of room 10 (Gmutza et al. 2024, Kurta 1995a, Kurta et al. 1997).

As is typical at northern hibernacula (Fenton 1970, Hitchcock 1950), males dominate (~70%) the overwintering population (Kurta and Teramino 1994; Kurta et al. 1997, 2020). Most bats gather in large, irregular clusters on the walls separating the chambers (Gmutza et al. 2024; Fig. 2). Almost all bats (>99%) roost at heights >5 m from the bottom, where roosting surfaces can never be flushed or submerged, and due to the small size of the

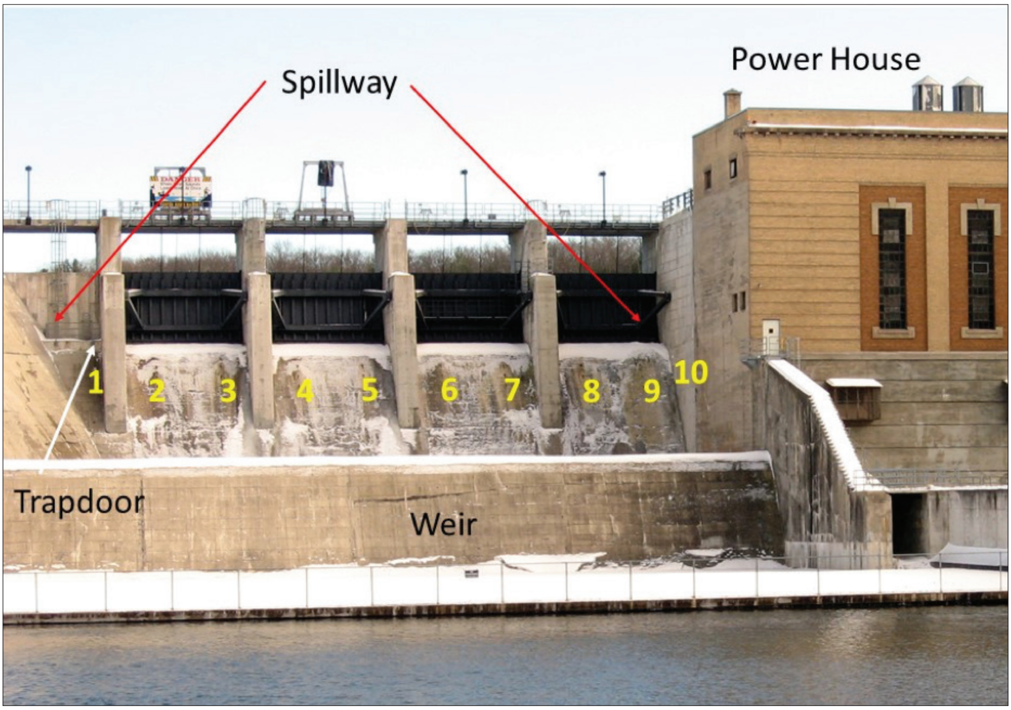

Figure 1. Downstream view of Tippy Dam, showing concrete spillway, topped by 4 metal spill gates, adjacent to the brick powerhouse. The entire spillway is only 45-m long, and its internal rooms are arranged in a linear fashion, from north (left) to south (right). Numbers in the photo indicate the position of each of the 10 rooms, directly behind the 60-cm-thick concrete walls. Humans enter through a trapdoor, into room 1, and pass sequentially into the other chambers. The dam is located on the Manistee River, near Wellston, Manistee County, Michigan.

structure, most bats are found within ~12 m of a ventilation opening. The population begins building in early September and peaks during mid-October (Kurta et al. 1997). Bats start departing in mid-April, but a third of the population, mostly males, is still present during the first half of May.

Methods

Environment

We determined relative humidity (RH) and T_a with 2 psychrometers that we stationed ~7 m apart, in small openings ("windows") near the ceiling, between rooms 6 and 7 and rooms 8 and 9 (Fig. 2). Each psychrometer consisted of a data logger (MX2303, Onset Computer Corporation, Bourne, MA) with 2 external temperature sensors (see Fig. S9 in Grimaudo et al. 2024). One sensor was encased in a cotton sleeve that acted as a wick, and the other end of the sleeve was placed in a reservoir of distilled water. T_a was determined by the dry sensor, and the difference in temperature between the dry and the wet sensors was used to calculate RH (Brice and Hall 2013). RH, however, cannot be used to compare the dryness of the air or the potential for evaporative water loss when temperature varies (Kurta 2014); therefore, we converted RH to water vapor pressure deficit (WVPD). Loggers began recording on 22 October 2019 and were removed on 11 August 2020; measurements from noon every day were used to characterize the internal environment.

Figure 2. A composite of multiple flash photos of the top of the south wall in room 8, on 14 February 2019. Rooms 2–9, which form the bulk of the spillway, are identical to that shown in the photo. Note the large clusters of bats and the elevated walkway, which is 8 m above the floor and connects the rooms. Portions of room 9 are visible beyond the doorway, and the stairs in room 9 lead to the terminal compartment, room 10. The "window" between rooms 8 and 9, where environmental sensors were placed, is above the doorway at the top of the photo. The downstream wall, which separates each chamber from the external air, is on the right in the photo; impounded water is behind the concrete wall on the left. Distance from the walkway to the ceiling is 4.5 m. Distance between the upstream and downstream wall at the level of the walkway (i.e., the base of the photo) is ~12 m.

We then compared our data to published values that indicated suitable levels of moisture and temperature for growth of *Pd* in the laboratory (e.g., Frick et al. 2022, Verant et al. 2012) and in the field (e.g., Hopkins et al. 2021).

Paired readings of the dry sensors and paired readings of the wet sensors from both locations typically differed by <0.25°C, which was the accuracy of individual MX2303 sensors (Onset Computer Corporation 2017). In addition, recorded temperatures and calculated RH and WVPD from the 2 locations were highly correlated (all Pearson's $r > 0.99$). The similarity in humidity and temperature in different parts of this small structure mirrors the results of previous studies (e.g., Kurta et al. 1997), and for simplicity, we only present data recorded between rooms 6 and 7.

Study animals

We compared disease severity and arousal frequency between early and late hibernation, using Little Brown Bats that were captured in December and February. To prevent potential stress to females, we used only adult males. We identified males as adults based on ossified finger joints, an expanded epididymis, and body mass. We arbitrarily selected animals from various sites within reach of the walkway and used only those that weighed >8 g in December and >7 g in February, to reflect the greater mass of adults at the start of hibernation and the expected loss in mass over the intervening 68 days of hibernation (0.013g/day; Fenton 1970). Although this procedure may have biased the results toward healthy individuals, it ensured that the weight of our animals matched those at other northern hibernacula (Fenton 1970) and that we did not unduly burden an unusually small bat with a large transmitter.

Bats were carried in clean cloth bags to the powerhouse, where UV photography and transmitter placement occurred. Fresh disposable gloves were used for handling each bat at each stage, and standard decontamination protocols were followed (US Fish and Wildlife Service 2020). All procedures with animals were approved by the US Fish and Wildlife Service and the Institutional Animal Care and Use Committee of Eastern Michigan University (2017-08 and 2017-084) and covered under federal (TE809630-4) and state (SC620) permits issued to AK.

Arousals

To detect arousals during hibernation, we monitored skin temperature (T_{sk}) with temperature-sensitive radio transmitters (BD-2, Holohil Systems, Carp, ON, Canada). Transmitters were placed on 29 animals on 6 December 2019 (Group 1) and on a different set of 28 bats on 14 February 2020 (Group 2). After trimming fur between the scapulae, we attached a transmitter to the skin with latex adhesive (Osto-Bond, Montreal Ostomy Center, Vaudreuil-Dorion, QC, Canada). Transmitters weighed ~0.75 g (~8% of body mass). Although this percentage exceeded the standard "5% rule", that guideline was suggested specifically for active animals that maneuver for hours each night while foraging (Aldridge and Brigham 1988). Hibernating bats, though, expend little energy while roosting, due to a tendon-locking mechanism (Simmons and Quinn 1994), and at northern latitudes, they usually spend only a few minutes in flight each month. Tags weighing up to 1.1 g have been successfully deployed on hibernating Little Brown Bats (Jonasson and Willis 2012, Reeder et al. 2012) without apparent ill effects.

Bats were released inside the spillway, typically 1–2 h after initial capture. Radio signals were subsequently collected by 3-element yagi antennas (Wildlife Materials, Murphysboro, IL), with 1 antenna in each of rooms 2–10. All antennas were connected to a single scanning logger-receiver (SRX800-MD4, Lotek Wireless, Newmarket, ON, Canada) that was programmed to calculate and record the time between pulses, for each transmitter frequency, every 6 min. The receiver was continuously powered through an extension cord, connected to an electrical outlet near the powerhouse, and snaked through a ventilation opening into the spillway. We eventually used inter-pulse interval to calculate T_{sk} from calibration data provided by the manufacturer.

We determined patterns of thermoregulation following Reeder et al. (2012). A bat was considered torpid if T_{sk} was ≥10°C below the maximum T_{sk} recorded for that animal during an individual arousal. If T_{sk} was within 10°C of maximum T_{sk} over 2 separate readings, which spanned an interval of 12 min, we considered the event an arousal; an arousal ended when T_{sk} again was ≥10°C below the maximum. We defined torpor-bout length (TBL) as the mean number of days between arousals. TBL was averaged for each bat. Temperatures from the first 24 h after tagging were excluded from analyses, as were readings that became unstable as the transmitter battery was depleted (Jonasson and Willis 2012). Ultimately, we compared our data on arousal frequency with those from previously published studies of uninfected and infected Little Brown Bats that also were monitored during hibernation with temperature-sensitive transmitters (Czenze at al. 2017, Reeder et al. 2012, Warnecke et al. 2012).

Wing fluorescence

We photographed both wings of each bat in a windowless room in the powerhouse before placing a transmitter. We used a digital camera (EOS Rebel T2i, Canon USA, Melville, NY), mounted on a tripod, with a zoom lens (24–105 mm) and fixed shutter speed (1.6 sec), ISO (200), and f-stop (4). During photography, wings were transilluminated with UV light (368 nm) from a 9-W lamp (BRC 100, Way Too Cool, Glendale, AZ).

Later, we manually traced visible areas of the wings and fluorescent spots, using a drawing tablet (Intuos, Wacom, Saitama, Japan) and the software ImageJ (Schneider at al. 2012). Total area of the wing and of each spot was calculated with the RGB channel in CellProfiler (Broad Institute 2021, Moore et al. 2017). The summed area of all fluorescent spots divided by total wing area yielded the proportion of infected tissue for each wing, which we then averaged to obtain a single value per bat. We later used these values to examine changes in disease severity during hibernation and to make comparisons with other populations of infected Little Brown Bats (Gagnon et al. 2025, Grimaudo et al. 2022, McGuire et al. 2016).

Statistics

All statistical tests were 2-tailed, with alpha set at 0.05, and all means were stated as ± 1 *SD*. We calculated *t*-tests to compare TBL between groups 1 and 2. However, data for percent fluorescence were not normally distributed, so we performed a Mann-Whitney *U* test. All analyses were conducted with Program R, v. 3.6.2 (R Core Team 2019).

Results

Environment

As we expected from previous work (Kurta et al. 1997), internal T_a fluctuated seasonally (Fig. 3). T_a was highest (12.6°C) on 22 October, near the beginning of hibernation, and reached its low point (1.7–1.8°C) during 5 days, from 26 February to 1 March. T_a increased gradually beginning in March and reached 7.0°C by 7 April and 11.0°C by 15 May. From 7 December to 8 April, when data from transmitters were recorded, average T_a was 3.3 ± 1.1°C. However, average T_a in early hibernation (22 October–6 December) was 8.0 ± 2.3°C, and the mean in late hibernation (1 April–15 May) was 7.2 ± 1.5°C. In summer, when no bats were present, T_a was typically 20–23°C and peaked at 24.0°C on 9 July.

Ambient moisture was more consistent than temperature (Fig. 4). From October until April, RH remained above 95%, before becoming variable (77–98%) during spring warm-up, which was consistent with previous years (Kurta 2002, Kurta et al 1997). During 7 December–8 April, mean RH was 96.9 ± 2.2%, and average WVPD was 0.25 ± 0.21 hPa. A black crust accumulated on the sleeve of both wet sensors late in the study and may have interfered with migration of water from the reservoir to the sensor, making data for humidity unreliable in summer. To be conservative, we discarded humidity data obtained after 1 May.

Arousals

We obtained useful data from 65% of the transmitters—19 from December and 18 from February. We discarded the data, if any, from the other transmitters because of the usual problems associated with intermittent transmission, short recordings without 2 arousals that prevented calculation of TBL, and non-detection, possibly due to location of the bat, drift in frequency, or battery failure. Bats from Group 1 and from Group 2 yielded data between 7 December and 3 February and between 15 February and 8 April, respectively. Average TBL was not significantly different ($t_{35} = 0.31$; $P = 0.76$) between Group 1 (16.4 ± 7.1 days) and Group 2 (17.1 ± 5.7 days). The combined mean was 16.8 ± 6.4 days.

Wing fluorescence

Every bat photographed at the dam had a small amount of fluorescence on the wings, suggesting an active infection. Fluorescence was only slightly higher for wings from February (median = 0.04%; $n = 28$) versus December (median = 0.01%; $n = 29$), even though

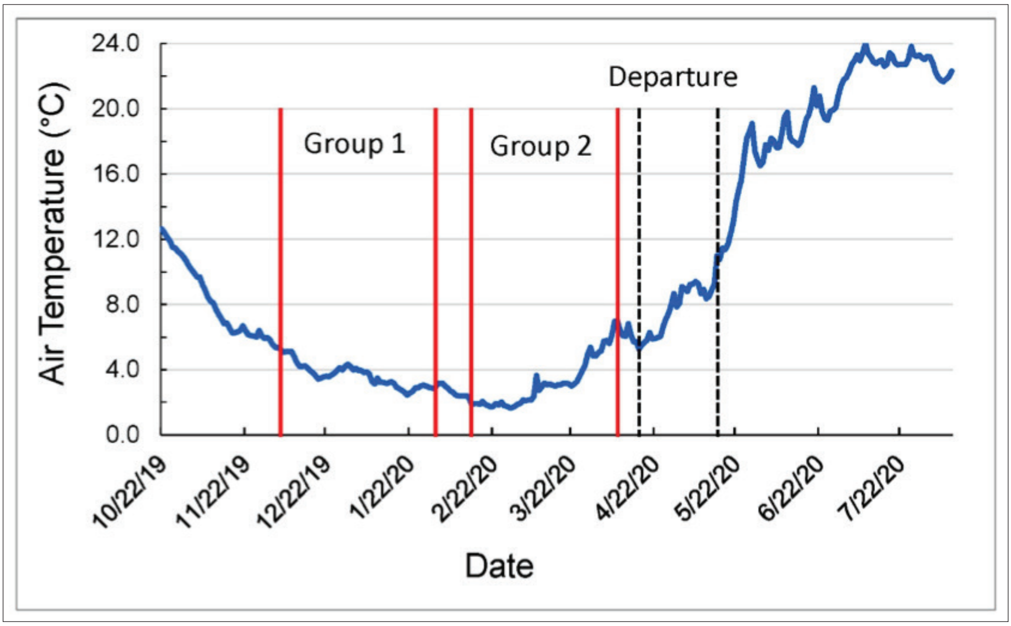

Figure 3. Ambient temperature in the spillway at Tippy Dam, at noon, from 22 October 2019 until 11 August 2020. The population of torpid bats peaks in mid-October, and most bats leave the spillway from about 15 April to 15 May (dashed lines) (Kurta et al. 1997). Red lines indicate the span over which data were accumulated for bats with transmitters placed on 6 December (Group 1) and 14 February (Group 2).

bats photographed on 4 February had been hibernating in the presence of *Pd* for over 100 days, and 68 days longer than bats from 6 December. Nevertheless, this slight difference was statistically significant (*U* = 596.5; *P* = 0.002). Maximum values, though, were small in both months (December range: 0.001–0.09%; February range: 0.001–0.7%).

Discussion

Environment

Temperature near the start of hibernation (12.6°C), on 22 October, approximated the optimum T_a (12.5–15.8°C) for growth of *Pd* in the laboratory (Verant et al. 2012). These high autumnal temperatures were commonly measured in previous years as well. For example, during 5 years between 1995 and 2014, T_a on 1 October, when one third of the population typically would be present, was 15.2 ± 5.8°C. On 22 October, after all bats likely had begun hibernating, T_a was 12.4 ± 0.6°C. Based on an analysis of multiple sites in Michigan and Wisconsin after arrival of *Pd*, Hopkins et al. (2021) suggested that survivorship of bats was lowest in hibernacula that were warm in fall, when bats began hibernating, because such conditions allowed rapid establishment of an infection and growth of the pathogen. Clearly, the lack of severe infection and mortality at Tippy Dam conflicts with this hypothesis, suggesting that Tippy Dam differs from a typical hibernaculum.

Air temperature in the dam during midwinter was low (3.3 ± 1.1°C), compared to the mean temperature of 81 mines used as hibernacula in the Upper Peninsula of Michigan (5.7 ± 2.9°C; Kurta and Smith 2014). Low T_a throughout hibernation could decrease the rate of mortality from *Pd* (Langwig et al. 2012; Turner et al. 2022). However, fungal growth does

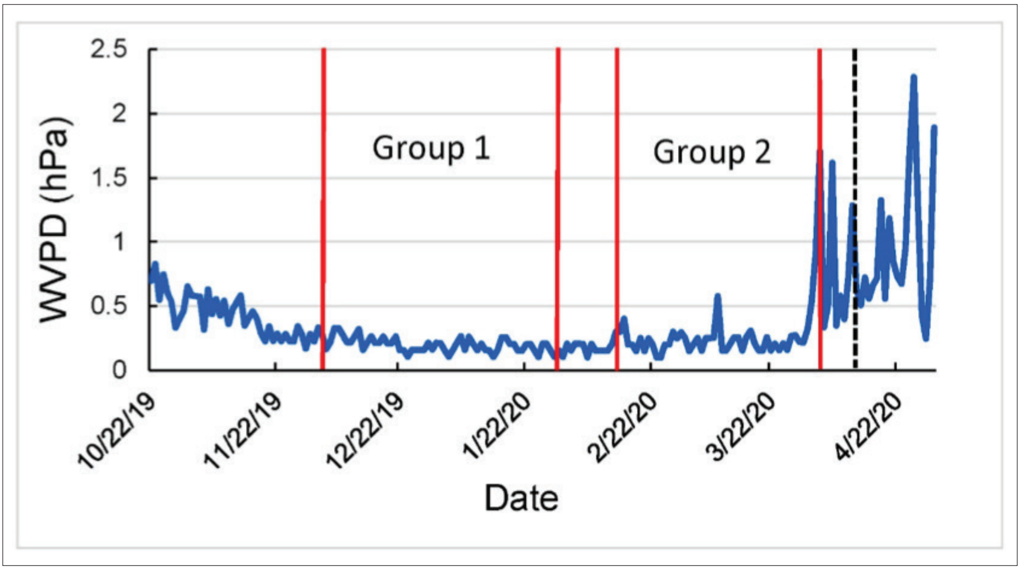

Figure 4. Water vapor pressure deficit (WVPD) in the spillway at Tippy Dam, at noon, from 22 October 2019 until 1 May 2020. The population of torpid bats peaks in mid-October, and bats start leaving the spillway on about 15 April (dashed line) (Kurta et al. 1997). Red lines indicate the span over which data were accumulated for bats with transmitters placed on 6 December (Group 1) and 14 February (Group 2).

not cease at such temperatures, and animals in cold sites are not immune to WNS (Grieneisen et al. 2015, Grimaudo et al. 2022, Verant et al. 2012). For example, Barnes et al. (2026) analyzed populational changes and T_a at 48 mines in northern Michigan after arrival of *Pd*. Seven (15%) of the mines had a winter T_a of 2.4–3.9°C and originally sheltered from <30 to >15,000 Little Brown Bats, but even in those cold environments, the population at each mine decreased by 39–100%. Similar declines also occurred at cold sites (≤4°C) in other northern regions (e.g., Vanderwolf and MacAlpine 2020). We are unaware of any substantial population of Little Brown Bats, in a hibernaculum as cold or colder than Tippy Dam in midwinter, with no apparent decline after the epidemic began. Furthermore, fungal development should have increased substantially as the spillway warmed over the last 3 months (March–May) of hibernation (Fig. 3). Tippy Dam, unlike other sites, is a cold hibernaculum for only 3 months of hibernation, but an average to very warm site for the other 4–5 months (Fig. 3). Nonetheless, there was no apparent decrease in the population of Little Brown Bats after 10 winters of exposure to *Pd* (2014–2015 through 2023–2024; Gmutza et al. 2024; A. Kurta unpubl. data).

In the dam, WVPD was low (<0.3 hPa) throughout most of hibernation, indicating a moist environment (Fig 4). In the laboratory, *Pd* grew well at higher (drier) WVPDs of 0.5–1.5 hPa, and mycelial growth and conidiation did not become greatly reduced until WVPD approached 4.5 hPa (Frick et al. 2022, Marroquin et al. 2017). Furthermore, WVPD at Tippy Dam also was lower than the average WVPD in mines of the Upper Peninsula (0.7 hPa), where hibernating *Myotis* were decimated by *Pd* (Kurta and Smith 2014, 2020). Hence, ambient moisture in the spillway appeared sufficient to support fungal development during hibernation.

Arousals

Frequent arousals are indicative of an infected host response. For example, Warnecke et al. (2012) recorded a mean TBL of 16.0 days for uninfected Little Brown Bats in the laboratory, whereas animals inoculated with *Pd* aroused every 9.0 days. Similarly, average TBL was 16.3 days for free-living Little Brown Bats in caves and mines before arrival of *Pd*, but only 7.9 days for individuals that succumbed at similar sites after the epidemic began (Reeder et al. 2012). Despite hibernating for several months in the presence of *Pd*, the bats monitored at Tippy Dam showed no evidence of these short bouts of torpor, and aroused infrequently, every 16.8 days.

Wing fluorescence

Disease severity (UV fluorescence) in the dam was low and changed little during hibernation, unlike a typical site where *Pd* had been present for multiple years (Frick et al. 2017, Hoyt et al. 2020). Similarly, the median and maximum values reported from the dam in February were 6–30 times less than the percent fluorescence detected elsewhere on the same species, although the timing of the measurements and the environmental conditions differed slightly among studies (Daly 2024, Gagnon et al. 2025, Grimaudo et al. 2022, McGuire et al. 2016). One explanation for low disease severity is a low fungal load, which was confirmed by McDevitt-Galles et al. (2025), using polymerase chain reaction. Despite the high autumn temperatures, average fungal load ($\log_{10}$) on 15 December 2022 was significantly lower for bats in the dam (1.16 ± 0.82 fg; $n = 30$) than the load on animals obtained 1 day later from a mine chamber in northern Michigan that was cool (5–6°C) throughout hibernation (3.03 ± 0.64 fg; $n = 30$).

We only monitored adult male Little Brown Bats, and juveniles or adult females may be more susceptible to *Pd* (Gagnon et al. 2025, Grieneisen et al. 2015, Kailing et al. 2023).

Nevertheless, if these groups were experiencing much greater damage to their skin than adult males, arousing much more often than adult males, and dying as a result, then the total population of 20,000 animals should have decreased markedly. Instead, we detected no reduction in the population over 10 winters, suggesting that disease severity in juveniles or adult females at our study site did not differ greatly from that of adult males.

Persistence of Bats at Tippy Dam: A Summary and Hypotheses

Multiple lines of evidence indicate that Little Brown Bats from the dam are not being severely impacted by WNS. For example, we show that disease severity (fluorescence) in February is only marginally higher than in December, and torpor patterns are similar in early and late hibernation and comparable to those of an unaffected population (Czenze at al. 2017, Reeder et al. 2012). Fungal loads on bats in December, despite the optimum-to-near-optimum temperatures inside the spillway during autumn (Fig. 3), are actually much lower than on animals hibernating in a typical subterranean site that is cool throughout winter (McDevitt-Galles et al. 2025). The bats continue to form large clusters (Fig. 2), unlike at other hibernacula, where the animals become increasingly solitary after arrival of *Pd*, presumably to reduce exposure to the pathogen (Kurta and Smith 2020, Langwig et al. 2012, Vanderwolf and MacAlpine 2020). Although clustering likely saves energy during arousals from torpor (Gmutza et al. 2024), such social thermoregulation cannot explain the low disease severity and low fungal loads or torpor bouts that match those of uninfected animals. Nevertheless, bats in the spillway are susceptible to the disease, despite the apparent lack of severe infections. When Little Brown Bats are removed from the dam in December and challenged with a set dose of *Pd* in the laboratory, they have mortality rates (~40%) and wing damage equivalent to those of animals taken from a cold mine (McDevitt-Galles et al. 2025).

We agree with Cheng et al. (2024:809) that Tippy Dam should not be considered a “remnant population” in which “WNS emerged, mortality occurred, and bats are now recovering due to changes in the host, pathogen, or environment”. We suggest that an inherent characteristic of the dam itself, i.e., a site-specific trait that was present before arrival of WNS, restricts the size of the environmental reservoir, leading to limited fungal growth and disease progression every year (Hoyt et al. 2020, McDevitt-Galles et al. 2025). Although many factors may affect persistence of fungal spores outside a laboratory (e.g., Raudabaugh and Miller 2013), we propose 2 possible mechanisms, based on the unusual environment of the spillway, that might result in a small reservoir—the first involving summer temperatures and the other concerning constant sounds and vibrations. These hypothesized mechanisms are not mutually exclusive, and many aspects could be tested in the laboratory.

High temperature in summer. In the laboratory, *Pd* exhibits malformed hyphae and conidia beginning at T_a as low as 12°C, and all hyphae and conidia assume atypical shapes at T_a >18°C (Verant et al. 2012). Growth rate decreases rapidly at T_a >18°C, and all growth ceases between 19.0 and 19.8°C, indicating a stress response to the warm temperatures. When properly formed conidia (e.g., those produced at 7°C) are incubated at T_a ≥24°C, ability to germinate becomes greatly reduced, depending on the specific temperature and the composition of the artificial medium that is used. Campbell et al. (2020), for example, evaluated survival of conidia at 24, 30, and 37°C, using 3 different types of media. Survival declined to 0 on all 3 media at 30°C and 37°C, after 60 and 30 days, respectively. After 60 days at 24°C, survival was 0 on 2 of the media and was reduced by ~76% on the third substance. To our knowledge, though, no study has examined germination of conidia after long-term (>35 days) exposure to T_a of 18–24°C, on either artificial media enhanced with nutrients or natural roosting substrates similar to the walls of a mine, cave, tunnel, or dam (e.g., Fischer et al. 2021).

As shown in our study, elevated temperatures (18–24°C) are pervasive in the spillway of Tippy Dam between mid-June and mid-August (Fig. 3), and earlier monitoring from multiple years indicates that these warm temperatures frequently continue into mid-September (Kurta 2002, Kurta et al. 1997; A. Kurta unpubl. data). We suggest that consistent exposure to T_a >18°C for 60–90 days during summer could result in a small environmental reservoir of viable conidia when bats return in autumn. If this hypothesis is true, then *Pd* also may have little impact on bats hibernating in culverts or other exposed locations in the southern United States, because many such sites also experience a T_a >18°C throughout summer (e.g., Lutsch et al. 2022) and presumably would have a low environmental reservoir in fall.

Sound and vibration. Another unusual aspect of the dam environment, though, is that, unlike most caves and mines, the spillway is not silent. Generators and flowing water inside the powerhouse of any hydroelectric dam create continuous sounds, including sounds that are near or below the human limit of hearing, as well as constant physical vibrations of the structure (e.g., Pilz et al. 2021). Low-frequency vibration or sound can inhibit growth and reproduction of certain ascomycete fungi. For instance, mycelial growth and spore germination by *Botrytis cinerea* Pers. (Gray Mold) is reduced when it is subjected to continuous sound of 5 kHz for only 3 days (Jeong et al. 2013), and growth of *Aspergillus niger* Tiegh (Black Mold) is slowed after exposure to 250 Hz for 10 days (Razavizadeh et al. 2024).

In 2024, we performed a preliminary analysis of sound and vibration in the spillway of Tippy Dam over 10 days, using a low-frequency microphone and an accelerometer (Fig. S1; see Supplemental File 1, available online at http://www.eaglehill.us/NABRonline/suppl-files/nabr-036-Kurta-s1.pdf). Although various frequencies were detected, 1 of the most intense sounds that was consistently detected was at 120.12 Hz, with a sound pressure up to 0.0084 Pa (52 dB; Fig. S2). Similarly, the strongest and most consistent vibration of the structure was at an identical frequency of 120.12 Hz, with an intensity up to 0.0066 m/sec^2 (Fig. S3). Such constant sounds and vibrations could contribute to a small load of viable spores in the spillway, perhaps by disrupting cellular membranes (Bochu et al. 2001) or altering gene expression (Kim et al. 2015). Unlike high temperatures in summer, though, these sounds and vibrations would occur year-round, which could explain the low environmental reservoir in autumn, as well as the small changes in fungal load and fluorescence over winter.

Concluding Remarks

To our knowledge, the spillway at Tippy Dam shelters the only significant hibernating population (i.e., >10,000 individuals) of Little Brown Bats that has remained stable in the face of long-term exposure to WNS (Cheng et al. 2021). Although multiple factors likely contribute to the unusual survival of these bats, we propose that simple explanations involving the environmental side of the disease triangle are likely involved. The potential negative effects on *Pd* by low-frequency sound and vibration or by summer temperatures of 18–24°C are testable hypotheses that focus on documented, but unusual, aspects of the environment at this novel hibernaculum. Unraveling the reasons for the continued survival of this population may offer insight into designing artificial hibernacula or controlling the disease at other locations.

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