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RESEARCH ARTICLE

Bats increased foraging activity at experimental prey patches near hibernacula

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Abstract

1. Emerging infectious diseases in wildlife can threaten vulnerable host populations. Actions targeting habitat improvements to aid population resilience and recovery may be beneficial long-term strategies, yet testing the efficacy of such strategies before major conservation investments are made can be challenging.
2. The disease white-nose syndrome (WNS) has caused severe declines in several species of North American hibernating bats. We tested a novel conservation approach targeted at improving foraging conditions near bat hibernacula by experimentally manipulating insect density in the pre-hibernation fattening period and spring emergence recovery period. We measured foraging (feeding buzzes) and echolocation activity of little brown bats *Myotis lucifugus* at ultraviolet (UV) light lures to determine behavioural response to augmented foraging conditions and characterized insect availability at UV light lures.
3. In the fall, bat foraging activity was three times greater (95% CI: 1.5–5.8; $p = 0.002$) when UV lights were on, but there was no statistical support for differences in echolocation activity response when our experimental design alternated between nights with lights on and off. In the spring, we allowed UV light lures to run consistently each night and compared with a control location in similar habitat. Bat foraging activity was 8.5 times greater (95% CI: 4.5–16.0; $p < 0.0001$) and echolocation activity was 4.4 times higher (95% CI: 3.0–6.5; $p < 0.0001$) at UV light lures in the spring experiment. In both the fall and spring, UV light lures resulted in concentrated insect availability, attracting primarily moths (Order: Lepidoptera). In both seasons, nightly temperature had a strong influence on bat foraging, echolocation and insect activity.

4. We show that a bat species threatened by WNS used enhanced foraging habitats near hibernacula during the critical pre- and post-hibernation phases of their annual cycle. While light lures are unlikely to be a long-term management strategy, our experiment provides initial evidence that bats behaviourally respond with increased foraging activity in areas with augmented insect prey availability. Our experimental results support developing management strategies focused on habitat protection, including restoration and enhancement of foraging habitats, in the immediate vicinity of bat hibernacula.

KEYWORDS
bats, conservation evidence, foraging behaviour, habitat protection, habitat restoration, insect prey, white-nose syndrome, wildlife disease management

1 | INTRODUCTION

Emerging infectious diseases in wildlife have been steadily increasing since the mid-1900s, posing a threat to global biodiversity (Cunningham et al., 2017; Daszak et al., 2000; Fisher et al., 2012; Jones et al., 2008). These epizootic events often cause rapid and widespread mortality in host populations that may directly threaten species with extinction (Frick et al., 2010; LaPointe et al., 2012; Scheele et al., 2019) or leave populations vulnerable to compounding effects of other stressors (Dirzo et al., 2014) that can impede population recovery and hasten species extinction (Castro & Bolker, 2005). While conservation strategies targeted at reducing host mortality from disease may prevent immediate loss, these approaches may be too little too late (Grider et al., 2022; Voyles et al., 2015), be logistically challenging to implement long-term and at broad scales (Bernard et al., 2020; Fletcher et al., 2020; Woodroffe, 1999), or fail to address cumulative or synergistic impacts from other stressors (Deem et al., 2001). Solutions toward improving host survival following epizootics are needed to aid population recovery and prevent extinctions, particularly in the face of increasing human pressures on ecosystem integrity.

White-nose syndrome (WNS) is a disease of hibernating bats caused by the fungal pathogen *Pseudogymnoascus destructans* (Pd). WNS has caused rapid and severe population declines of several bat species in North America and raised conservation alarm for over a decade (Blehert et al., 2009; Cheng et al., 2021; Frick et al., 2010; Hoyt et al., 2021). Since WNS first emerged in North America, sustained research efforts have advanced the understanding of the ecology of the disease (Frick et al., 2017; Hoyt et al., 2018, 2021; Langwig et al., 2012) and population impacts to vulnerable bat species (Cheng et al., 2021; Frick et al., 2010; Langwig et al., 2012; Turner et al., 2011). Substantial investments have also been made to develop and test treatments that target pathogen control in bats or the environmental reservoir (Cornelison et al., 2014; Raudabaugh & Miller, 2013; Sewall et al., 2023) or enhance host immune response in bats (Hoyt et al., 2019; Rocke et al., 2019). Other approaches have focused on changing habitat conditions to improve survival (Boyles & Willis, 2010; Turner et al., 2022; Wilcox & Willis, 2016).

Body condition and maintenance of a positive energy balance play a critical role in the pathology of WNS (Verant et al., 2014; Warnecke et al., 2013), as well as host recovery (Fuller et al., 2020), reproduction (Jonasson & Willis, 2011) and survival (Cheng et al., 2019). WNS disrupts bat hibernation physiology, repeatedly rousing infected bats from torpor during winter, which often results in premature depletion of fat stores, starvation, dehydration and ultimately mortality during hibernation (Langwig et al., 2014; Reeder et al., 2012; Verant et al., 2014; Warnecke et al., 2013). Bats that survive the winter with WNS experience an energetic bottleneck when they emerge from hibernation in the spring to travel to summer habitats. These energetic limitations are especially dire for females that must replenish energy stores and prepare for reproduction when ambient temperatures are cold, and insect prey are scarce (Bernard et al., 2021; Czenze & Willis, 2015; Jonasson & Willis, 2011; Norquay & Willis, 2014). Bats recovering from WNS often experience an energetically costly inflammatory response to heal the severe wing damage caused by the cutaneous fungal infection (Davy et al., 2017; Fuller et al., 2020; Meteyer et al., 2009, 2012). These pathophysiological consequences of WNS carry over to the summer maternity season and can further reduce the fitness of WNS survivors (Francl et al., 2012; Johnson et al., 2021).

Given that a positive energy balance is important for the survival and recovery of bats with WNS, foraging success and energy intake could be key contributors to the survival and persistence of individuals with WNS (Bernard et al., 2021; Cheng et al., 2019). Habitats that provide high-quality insect prey near hibernacula, which reduces foraging and commuting costs, could help bats accumulate more fat in the fall and recover from WNS more quickly in the spring (Bernard et al., 2021; Bernard & McCracken, 2017). This could ultimately improve survival and reproduction and aid population resilience and recovery. Determining whether enhancing foraging habitats near hibernacula will succeed as a beneficial conservation strategy first depends on whether bats would find and exploit such areas during pre- and post-hibernation.

We experimentally manipulated foraging habitat quality in the vicinity of little brown bat *Myotis lucifugus* hibernacula to test the potential of foraging habitat restoration and enhancement as a potential management action for hibernating bats vulnerable to WNS. We created insect prey patches using ultraviolet (UV) light lures during the fall pre-hibernation fattening and spring recovery periods. We investigated behavioural foraging response of bats during fall and spring by measuring whether *M. lucifugus* increase foraging (i.e. feeding buzzes) and echolocation activity at UV light lures near hibernacula and characterized insect activity at UV light lures. We hypothesized that *M. lucifugus* would behaviourally respond by increasing foraging and echolocation activity at light lures and that UV lights would attract insects commonly consumed by bats (Bernard et al., 2021). Our experimental approach is an initial step toward creating evidence-based conservation strategies to benefit bat species threatened by WNS.

2 | MATERIALS AND METHODS

All experimental methods were approved by the University of Winnipeg Animal Care Committee (Protocol 14040) and Michigan scientific permit (# SC1675).

2.1 | Study area and design

We selected hibernacula sites with persisting colonies of at least ~100 *M. lucifugus* hibernating in abandoned copper mines in the Keweenaw region of the Upper Peninsula of Michigan (Kurta & Smith, 2014). Prior to WNS, 90% of hibernating bats in the region were *M. lucifugus* and roughly 10% were northern long-eared bats *Myotis septentrionalis* (Kurta & Smith, 2014). Northern hardwoods and conifers comprise the dominant forest type and the region is characterized by long, cold winters with bats typically entering hibernation in late September and leaving in late April (Kurta & Smith, 2014). We used five hibernacula sites in the fall of 2019 and repeated sampling at three of those five sites, with an additional site added in the spring of 2021. Data collection was disrupted in 2020 due to travel restrictions during the covid-19 pandemic.

We conducted our experiment during fall swarm (1 September to 4 October 2019) and spring emergence (19 April to 25 May 25 2021). In the fall, each site had a single UV light, and we alternated between control (UV light lure off) and treatment (UV light lure on) nights to assign any differences in bat response to the treatment (UV light lure on). In spring 2021, we changed the experimental design to paired sites with treatment (UV light lure present) and a control (UV light lure absent). The change to a paired site design allowed for UV light lures to be on every night for bats to learn and respond to consistent prey availability at UV light lures. In both years, the UV lights were distanced at least 250 m from the hibernaculum entrance to avoid illuminating the entrance. In spring 2021, we established a control location at least 250 m from the same hibernaculum entrance and the UV light lure, selecting an area with similar forest and vegetation clutter to minimize site-related variation.

We deployed a 320–400 nm UV light (model 2851L; BioQuip) 3 m above the ground under the forest canopy (Figure S1). Lights of this wavelength are known to attract nocturnal flying insects and *Myotis* species (Cravens et al., 2018; Cravens & Boyles, 2019; Minnaar et al., 2015; Svensson & Rydell, 1998). The UV lights were powered by deep-cycle batteries and solar panels and equipped with a timer (model FC-Q00050A1; Favolcano) to operate the lights from sunset to sunrise.

2.2 | Data collection and processing

2.2.1 | Bat echolocation and foraging activity

We used bat acoustic detectors (Song Meter SM4BAT or Song Meter Mini Bat ultrasonic recorders; Wildlife Acoustics) to record bat echolocation activity at each sample site each night from 1 September to 4 October 2019 and 19 April to 25 May 2021 (Table S1). Echolocation activity was recorded from sunset to sunrise using a 256 kHz sample rate and default trigger settings of minimum trigger frequency of 16 kHz, trigger level of 12 db and a 3 s trigger window. We processed echolocation recordings using SonoBat Software v.4.4.5 (SonoBat) set to the Great Lakes Midwest bat species classifier for automated signal classification using Sonobatch with acceptable call quality set to 0.80 and default settings of sequence decision threshold set to 0.9 and max number of calls per file set to 16. We then filtered the auto-ID output from Sonobat to count files with echolocation frequencies between 34 and 47 kHz, which is the characteristic frequency range of *Myotis lucifugus* (Wund, 2006). Classifying species from echolocation has uncertainty due to similarities in echolocation signals (Wright et al., 2020). We assume >90% of these echolocation files are *M. lucifugus*, given the historic and current species composition at these hibernacula (Kurta & Smith, 2014). We calculated echolocation activity as the total number of echolocation sequence recordings per night.

We reviewed all recordings for presence of feeding buzzes. Feeding buzzes have a characteristic increase in pulse rate and drop in terminal frequency compared to search-phase calls and indicate prey capture (or attempted capture) events (Schnitzler & Kalko, 2001). To distinguish feeding buzzes from search-phase calls, we visualized each echolocation sequence file using the real-time viewer in SonoBat Software v. 4.4.5 (SonoBat). For each recording, we used the Sonobat ruler and placed it across the approximate characteristic frequency range of the search-phase calls and manually scanned each file for occasions when the characteristic frequency dropped below 34 kHz (Figure S2). We calculated foraging activity as the total number of feeding buzz events per night. In the few instances where there were multiple feeding buzzes within a single echolocation recording, we counted each feeding buzz.

2.2.2 | Insect activity

In the fall, we sampled insects every night from sunset to sunrise from 1 to 15 September 2019 (Table S1) and then disassembled the insect collection funnel and bucket to reduce interference with bat foraging behaviour. In the spring, we sampled insects from sunset to sunrise one night a week from 19 April to 25 May 2021 (Table S1). By switching to sampling one night per week in the spring, we aimed to characterize nocturnal insect activity at the UV light over the course of the spring emergence period, but with minimal disruption to insect prey availability for bat foraging.

To collect insects attracted to the UV light lure, we used the funnel and bucket provided with Universal Black-Light Traps (model 2851L; BioQuip) with liquid solution to kill trapped insects (Figure S1). In the fall, we initially hung a malaise flight-interception trap (model 2869; BioQuip) for passive sampling below the UV light lure during light on and off nights. We discontinued use of the malaise trap because it potentially impeded flight paths near the light and caught negligible amounts of nocturnal volant insects (<5% of all insects). The aim of insect collection was to characterize insect prey availability at the UV light lures. For the purposes of a control, we placed the same funnel and bucket but without the UV light lure.

We collected insects from traps in the morning and transferred them into air-tight containers for immediate processing. We sorted and identified insects to order (Eaton & Kaufman, 2007). We then dried insects at 60°C for 48 h and weighed them to quantify dry biomass (Johnston & Cunjak, 1999) as an indicator of insect availability.

2.2.3 | Ambient temperature

We recorded temperatures at each detector location using the internal temperature logger of the bat detector, which records temperature every minute. We used nocturnal temperature data as an index of nightly ambient air temperature averaged from sunset to sunrise for each night at each site as a covariate to account for potential variation in insect and bat activity response due to nocturnal temperature.

2.3 | Statistical analysis

We used generalized linear mixed effects models to examine the treatment effect of UV light lures on foraging activity (measured as total nightly feeding buzzes), echolocation activity (measured as total nightly echolocation sequence files) and insect prey biomass (measured as total nightly dry insect mass; package GLMMTMB; Brooks et al., 2017). We compared models in an information-theoretic approach using Akaike Information Criteria (Burnham & Anderson, 2002) for each season (fall 2019, spring 2021) and each response separately (Table 1). In all model comparison sets, we included treatment as a categorical fixed effect and mean nightly temperature as an additive or interactive linear fixed effect. We accounted for site variation by including site as a random intercept.

We used model diagnostics (package DHARMA; Hartig, 2022) to evaluate model fit and determine the best error distribution for each response. For bat foraging and echolocation activity, we fit a negative-binomial distribution to account for overdispersion. We tested for zero inflation (package DHARMA; Hartig, 2022) and for models requiring a zero-inflation term we compared models with and without mean nightly ambient temperature in the zero-inflation term. For insect prey biomass, data were zero-inflated and right-skewed; thus, we fit the data with a gamma-log link hurdle model. We excluded models if they failed to converge and selected the best-supported model if it was greater than two AIC scores from the closest model. If models were within two AIC scores of each other, we chose the most parsimonious model that included the treatment effect. We calculated the treatment effect size of UV light lures with 95% confidence intervals using beta estimates from each of the best-supported models. We used software R version 4.0.5 for all statistical analyses.

3 | RESULTS

3.1 | Fall results

Foraging activity (number of feeding buzzes) was three times greater when UV lights were on compared to nights when lights were off (95% CI: 1.5–5.8; $p = 0.002$; Figure 1a; Table S2). There was no statistical support for meaningful differences in bat echolocation activity on nights when UV lights were on during fall. Models with and without treatment terms had equivalent support by AIC ($\Delta\text{AIC} < 2$; Table 1), and the estimated effect size was small (Figure 1b; Table S3). Dried insect biomass was 16.7 times greater when UV light lures were on in the fall (95% CI: 6.4–43.2; $p < 0.001$; Figure 1c; Table S4). Nightly temperature had a strong influence on all three responses (Figure 1; Table 1).

3.2 | Spring results

Bat foraging activity was 8.5 times greater (95% CI: 4.5–16.0; $p < 0.001$; Table S5) and echolocation activity was 4.4 times greater (95% CI: 3.0–6.5; $p < 0.001$; Table S6) at UV light lures compared to control locations in similar habitats in the spring (Figure 2). Dried insect biomass was 26.1 times greater at UV light lure sites (95% CI: 9.2–72.9; $p < 0.001$; Table S7; Figure 2c). Similar to the fall results, nightly temperatures in the spring had a strong influence on all three responses (Figure 2; Table 1). Moths (Lepidoptera) comprised the majority of insects collected in both fall and spring (Table S8, Figure S3).

4 | DISCUSSION

Bats increased foraging activity at insect prey patches created by UV light lures near hibernacula during fall swarm and spring emergence,

TABLE 1 Model structure and comparison using Akaike information criteria (AIC) to determine best fit models in each season (fall and spring) for each response type (foraging activity, echolocation activity and insect activity). A priori model comparisons used fixed effects of treatment (UV light vs. control: treat) and nightly temperature (temp) with site included as random intercept (1|site). We tested residuals for zero-inflation and temporal autocorrelation using package DHARMa in Program R and use zero-inflation terms (zi) and first-order autoregressive term (ar1), where appropriate.

Response	Distribution	Model	*df*	dAIC
Fall dataset				
Foraging activity (buzzes/night)	Negative binomial	treat + temp + (1|site)	5	0
		treat * temp + (1|site)	6	1.99
		temp + (1|site)	4	7.12
		treat + (1|site)	4	23.29
		1 + (1|site)	3	28.32
Echolocation activity (sequences/night)	Negative binomial	temp + (1|site)	4	0
		treat + temp + (1|site)	5	1.75
		treat * temp + (1|site)	6	1.95
		1 + (1|site)	3	13.59
		treat + (1|site)	4	15.42
Insect activity (total dry biomass/night)	Zero-inflated gamma hurdle (log-link)	treat + (1|site), zi = temp	6	0
		treat + temp + (1|site), zi = temp	7	0.31
		treat + (1|site), zi = 1	5	1.53
		treat + temp + (1|site), zi = 1	6	4.02
		1 + (1|site), zi = temp	5	13.87
		temp + (1|site), zi = temp	6	14.33
		temp + (1|site), zi = 1	5	18.04
		1 + (1|site), zi = 1	4	26.48
Spring dataset				
Foraging activity (buzzes/night)	Zero-inflated negative binomial	treat + temp + ar1(day_of_year|site), zi = temp	8	0
		treat + temp + ar1(day_of_year|site)	6	5.38
		treat + ar1(day_of_year|site)	5	30.51
		1 + ar1(day_of_year|site)	4	45.39
		treat + temp + (1|site)	5	53.31
		treat * temp + (1|site)	6	53.75
		treat + (1|site)	4	88.46
		1 + (1|site)	3	96.51
		treat + (1|site), zi = temp	6	1140.9
Echolocation activity (sequences/night)	Zero-inflated negative binomial	treat + temp + ar1(day_of_year|site), zi = temp	8	0
		treat + temp + ar1(day_of_year|site)	6	15.16
		treat + ar1(day_of_year|site)	5	26.61
		1 + ar1(day_of_year|site)	4	46.65
		treat * temp + (1|site)	6	88.95
		treat + temp + (1|site)	5	90.55
		treat + (1|site), zi = temp	6	107.53
		treat + (1|site)	4	118.98
		1 + (1|site), zi = ~temp	5	119.03
		treat + (1|site), zi = 1	5	120.98
		1 + (1|site)	3	128.8

(Continues)

TABLE 1 (Continued)

Response	Distribution	Model	*df*	dAIC
Insect activity (total dry biomass/night)	Zero-inflated gamma hurdle (log-link)	treat + temp + (1|site), zi = temp	7	0
		treat + temp + (1|site), zi = 1	6	0.29
		treat + (1|site), zi = temp	6	7.21
		treat + (1|site), zi = 1	5	7.51
		temp + (1|site), zi = temp	6	10.07
		temp + (1|site), zi = 1	5	10.36
		1 + (1|site), zi = temp	5	12.19
		1 + (1|site), zi = 1	4	12.49

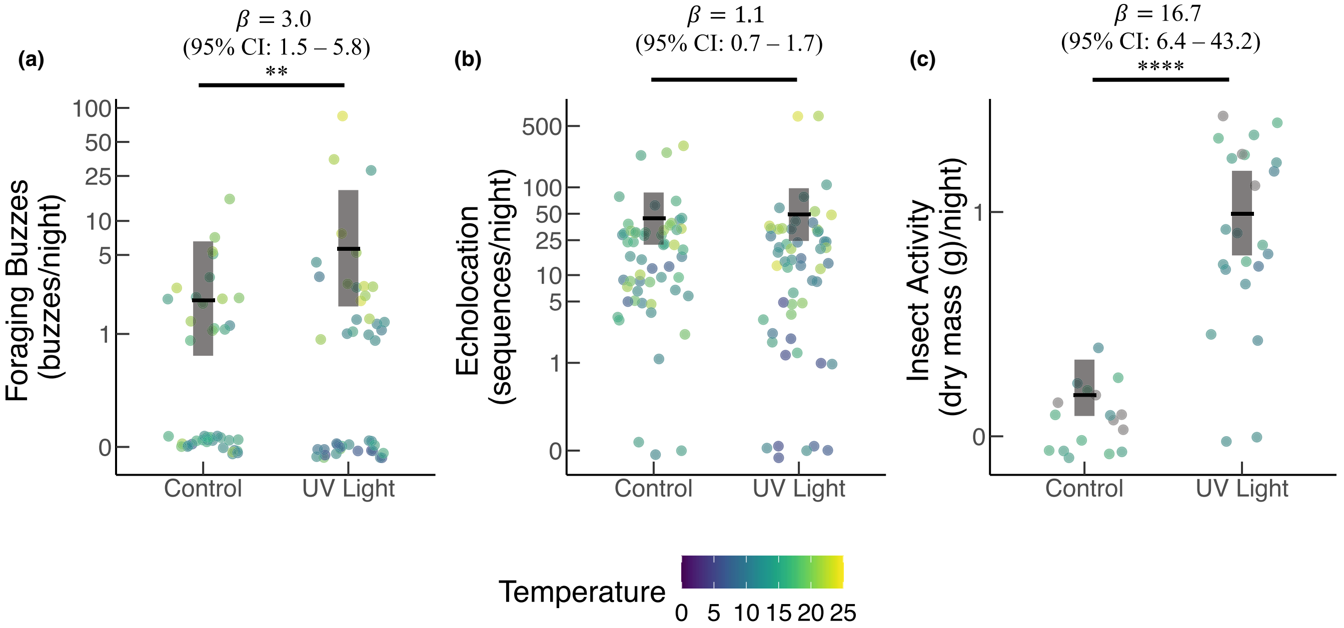

FIGURE 1 Foraging activity (a), echolocation activity (b) and insect activity (c) at experimental ultraviolet (UV) light lures near *Myotis lucifugus* hibernacula in Michigan during fall. Raw points are plotted and coloured by mean nightly temperature and shown with predicted means (black horizontal bar) with 95% prediction intervals (shaded bars) from best-supported models (Table 1). Means are predicted at the upper quartile temperatures (19°C for bat foraging and echolocation activity and 15°C for insect activity). Mean treatment effect (*β*, back-transformed) is shown with 95% confidence intervals in parentheses and level of significance (**$p < 0.01$; ****$p < 0.0001$).

which are critical periods when bats must achieve positive energy balance to build fat reserves for hibernation or recover from WNS in spring. Our experiment provides initial evidence that *M. lucifugus* hibernating in a region characterized by long, cold winters will make use of high-quality foraging habitat in the immediate vicinity of hibernacula. Our results contribute to a growing body of evidence of the importance of bat foraging near hibernacula (Bernard et al., 2021). By showing that bats behaviourally respond to enhanced foraging conditions, we contribute supporting evidence that managing foraging resources near hibernacula could be developed as a strategy to aid resilience and recovery of bat populations impacted by WNS.

Bat species impacted by WNS, including *M. lucifugus*, are typically insect consumer generalists (Bernard et al., 2021). Foraging on energy-rich moths at lights may allow bats to forage more efficiently, if insect prey patches are available in close proximity to hibernacula. For example, Rydell (1992) found that *Eptesicus nilssonii* were able to gain twice as much energy by feeding on moths at lights compared to smaller dipterans in woodlands. Our results showing that *M. lucifugus* increased foraging activity at experimental prey patches suggests that efforts to improve habitat near hibernacula may improve foraging efficiency by lowering commuting costs, if suitable and high-quality prey are available nearby.

Artificial lights can have both positive and negative influences on the nocturnal behaviour of bats (Rowse et al., 2015; Stone et al., 2009, 2015; Voigt et al., 2021). We were unsure whether *M. lucifugus* might be deterred from lights, but found that *M. lucifugus* responded with increased feeding activity at UV lights in this study. These results are consistent with studies that some bat species preferentially feed on moths attracted to artificial lights, especially those emitting in the UV spectrum (Eisenbeis & Eick, 2006; van Langevelde et al., 2011). Generally, light type strongly influences the response of bats, with considerable variation occurring among bat

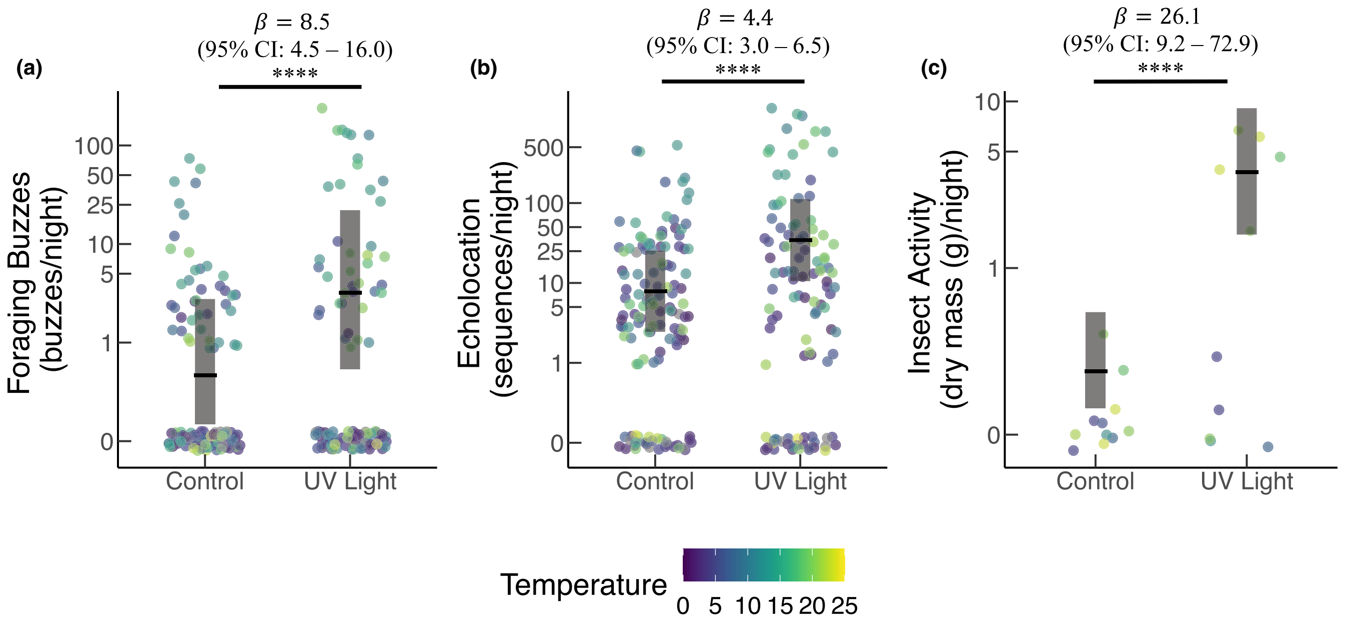

FIGURE 2 Foraging activity (a), echolocation activity (b) and insect activity (c) at experimental ultraviolet (UV) light lures near *Myotis lucifugus* hibernacula in Michigan during spring. Raw points are plotted and coloured by mean nightly temperature and shown with predicted means (black horizontal bar) with 95% prediction intervals (shaded bars) from best-supported models (Table 1). Means are predicted at the upper quartile temperatures (19°C for bat foraging and echolocation activity and 15°C for insect activity). Mean treatment effect (β, backtransformed) is shown with 95% confidence intervals in parentheses and level of significance (****$p < 0.0001$).

species (Rowse et al., 2015; Stone et al., 2015; Voigt et al., 2021). Lights emitting short blue wavelengths may deter bats and should be avoided (Falchi et al., 2011) while light-emitting diode (LED) lights attract fewer insects (Eisenbeis & Eick, 2006) and may not be as effective in creating insect prey patches.

Although UV light lures may not be practical as a long-term management strategy, they could serve in the near-term as a targeted management action at certain hibernacula to benefit some remnant bat populations. However, potential non-target effects should be evaluated before management recommendations are implemented at broader scales (Bernard et al., 2020; Bernard & Grant, 2019). Concerns about artificially concentrating insects at UV light lures for prey patches for bats include the possibility of negatively impacting local insect populations (Bruce-White & Shardlow, 2011). The wavelength and intensity of the UV light we used are thought to attract insects from a distance of about 15 m (Kirkeby et al., 2013). Thus, any effects on insect populations would be highly localized. For our experiment, UV lights were active for about 6–8 weeks in the fall and spring when insect activity is naturally low. Compared to the broader impact of light pollution from human-dominated landscapes (Wilson et al., 2021), the use of a single or few UV lights at targeted locations for short periods seems unlikely to negatively impact insect population dynamics. Another potential non-target effect is increased predation risk to bats foraging at UV light lures. In an on-going related study, we are using camera traps to record any potential activity of owls or other predators and have not recorded any predation events to date.

In this initial study, we observed a stronger response by *M. lucifugus* to UV light lures in the spring than in the fall, which could relate to changes in our experimental design as well as seasonal differences in foraging response and behaviours. We changed experimental designs between the fall and spring because we realized that turning the lights on and off each night might result in an unpredictable prey patch, which could influence response given that bats often use spatial memory for foraging (Egert-Berg et al., 2018; Prat & Yovel, 2020). In the spring, UV light lures operated consistently each night to maximize the reliability of the prey patch. This design change could have increased the foraging response at lights if bats learned and re-visited prey patches. Differences in seasonal behaviours could also contribute to observed response. In the fall, bats must put on sufficient fat reserves but are also engaged in fall swarm mating behaviours (Fraser & McGuire, 2023). In the spring, bats emerge from hibernation and females must recover their body condition and migrate to maternity roosts before giving birth (Norquay & Willis, 2014). Prior to this study, little was known about the foraging habits of *M. lucifugus* during the fall swarm or spring emergence period, including whether bats would forage near hibernacula in regions with long, cold winters. Our data suggest bats respond to localized concentrations of insect prey and that reliability of the prey patch may be important.

This study represents a first step in developing long-term strategies to facilitate bat population recovery. As a next step, we are using UV light lures to test foraging habitat enhancement across the established range of WNS to quantify variation in response of multiple bat species that have declined from WNS. The ideal metric of success would be to demonstrate increased overwinter survival of bats at rates that would meaningfully benefit population growth (Fletcher et al., 2020; Grider et al., 2022). The time and money required to obtain adequate sample sizes to measure effectiveness as a change in survival or reproduction may prove prohibitive relative to time scales needed to aid conservation decision-making. Measuring changes in body condition of bats is an appealing alternative, yet repeat capture and handling to measure changes in body condition is not only logistically challenging, but could also disrupt behavioural response and body condition. Measuring energy intake by bats captured at prey patches, perhaps by using plasma metabolite analysis (e.g. McGuire et al., 2016) and using energetic models to estimate fat accumulation and overwinter survival with WNS (Cheng et al., 2021) could provide valuable additional lines-of-evidence that enhanced foraging habitats can improve body condition overwinter survival and WNS recovery to benefit population growth (Bernard et al., 2020).

WNS has caused severe declines in several hibernating bat species, threatening the persistence of populations in areas where the disease has established (Cheng et al., 2021). Bats may be persisting via mechanisms of resistance, tolerance, or changes in behaviour (Cheng et al., 2019; Frick et al., 2017; Langwig et al., 2016; Lilley et al., 2016). In these regions, conservation efforts may benefit from focusing on bolstering population stability and supporting population growth (Langwig et al., 2015). Providing high-quality foraging habitats by investing in habitat restoration and enhancement efforts is a strategy focused on improving the resilience of bat colonies that could be combined with efforts directed at reducing disease severity, such as vaccines (Rocke et al., 2019) or modifying roosting habitats (Turner et al., 2022).

We used an experimental approach to measure behavioural response of free-ranging bats in their natural habitats to inform conservation strategies for species endangered by disease. Our results show that bats will behaviourally respond by increasing foraging at highly localized insect prey patches immediately outside their hibernacula during periods of seasonal transition. Investment in habitat protection, restoration and enhancement to increase insect abundance and density in the areas outside hibernacula may serve as a beneficial strategy for supporting bat population resilience and recovery in areas where WNS is now endemic. We recommend future research into measuring response to enhancing foraging conditions by bat species impacted by WNS across the WNS established range to inform mitigation planning and potential investments in foraging habitat restoration or enhancements.

AUTHOR CONTRIBUTIONS

Winifred F. Frick and Craig K. R. Willis conceived the idea; Winifred F. Frick and Christian M. Newman secured the funding; Winifred F. Frick, Craig K. R. Willis, Yvonne A. Dzal, Tina L. Cheng, Kristin A. Jonasson, Amanda M. Adams and Christian M. Newman designed the methodology; Yvonne A. Dzal, Kristin A. Jonasson, Amanda M. Adams and John E. Depue collected the data; Christen Long processed the acoustic data; Tina L. Cheng, Michael D. Whitby, Kristin A. Jonasson and Winifred F. Frick analysed the data; Winifred F. Frick, Tina L. Cheng and Yvonne A. Dzal led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare they have no conflict of interest. WFF, MDW, AMA, CL and TLC are employed by Bat Conservation International, a non-profit organization. CMN is employed by the Electric Power Research Institute, a non-profit organization. JED is employed by the Michigan Department of Natural Resources, a state agency. YAD and CKRW are employed at academic institutions.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.7291/D1HM40 (Frick et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Number of nights at each site where sampling occurred to measure *Myotis lucifugus* foraging activity, *Myotis lucifugus* echolocation activity, and insect activity in the fall and spring. Data were analysed separately for each season for each response type. In the fall, treatment vs. control comparisons were between nights with light on vs. light off at each same site. In the spring, treatment vs. control comparison was between a UV light site and a paired site located in similar forest habitat and vegetation clutter placed within 250 m from the same hibernaculum entrance.

Table S2. Coefficient estimates from the best-supported model for foraging activity (nightly feeding buzzes) in fall 2019 using a negative binomial error distribution. Coefficient estimates are on link scale and control (UV light off) is the reference group.

Table S3. Coefficient estimates from the best-supported model for echolocation activity (nightly echolocation sequence recordings) in fall 2019 using a negative binomial error distribution. Coefficient estimates are on link scale and control (UV light off) is the reference group.

Table S4. Coefficient estimates from the best-supported model for insect activity (total dry biomass/night) in fall 2019 using a zero-inflated gamma hurdle (log link) model. Coefficient estimates are on link scale and control (UV light off) is the reference group.

Table S5. Coefficient estimates from the best-supported model for foraging activity (nightly feeding buzzes) in spring 2021 using a zero-inflated negative binomial model. Coefficient estimates are on link scale and control (UV light off) is the reference group.

Table S6. Coefficient estimates from the best-supported model for echolocation activity (nightly echolocation sequence recordings) in spring 2021 using a zero-inflated negative binomial model. Coefficient estimates are on link scale and control (UV light off) is the reference group.

Table S7. Coefficient estimates from the best-supported model for foraging activity (total dry biomass/night) in spring 2021 using a zero-inflated gamma hurdle (log link) model. Coefficient estimates are on link scale and control (UV light off) is the reference group.

Table S8. Proportion of each insect order by treatment sampled during fall swarm and spring emergence. Total dried mass (g) of each insect order is reported by order per treatment and sampling period (fall swarm or spring emergence). Proportion of insect order is calculated by dividing the total mass of the weighed insect order by the grand total mass of all insects sampled for each treatment and sampling period.

Figure S1. Photographs showing the experimental UV light lure. (A) UV light lure and Song Meter Mini Bat detector deployed in site in Upper Peninsula, MI in spring 2021. (B) UV light lure shown with insect collection funnel and bucket installed on nights used to sample insects attracted to the light. (C) Photograph of the UV light at night suspended from a tree in fall 2021.

Figure S2. Spectrograph shown in Sonobat Viewer of a *Myotis lucifugus* echolocation sequence with increase in pulse rate and the drop in frequency characteristic of a feeding buzz event.

Figure S3. Proportion of each insect order in total nightly dried insect biomass collected during fall swarm in 2019 (A) and spring emergence in 2021 (B).

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