Received: 7 September 2023 | Revised: 18 April 2024 | Accepted: 21 April 2024

DOI: 10.1111/ele.14437

LETTER

ECOLOGY LETTERS WILEY

Heterogenous effects of bat declines from white-nose syndrome on arthropods

Amy K. Wray[1] | **Marcus Z. Peery**[1] | **Jade M. Kochanski**[2,3] | **Emma Pelton**[2,4] | **Daniel L. Lindner**[5] | **Claudio Gratton**[2]

[1]Department of Forest & Wildlife Ecology, University of Wisconsin-Madison, Madison, Wisconsin, USA

[2]Department of Entomology, University of Wisconsin-Madison, Madison, Wisconsin, USA

[3]Department of Integrative Biology, University of Wisconsin-Madison, Madison, Wisconsin, USA

[4]Xerces Society for Invertebrate Conservation, Portland, Oregon, USA

[5]Center for Forest Mycology Research, Northern Research Station, USDA Forest Service, Madison, Wisconsin, USA

Correspondence
Amy K. Wray, Department of Forest & Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA.
Email: amykwray7@gmail.com

Funding information
USDA, Grant/Award Number: Hatch Formula Fund WIS01841

Editor: Laura Figueroa

Abstract

In North America, white-nose syndrome (WNS) has caused precipitous declines in hibernating bat populations, raising the question of whether the rapid loss of arthropodivorous bats may affect the abundance of their prey. During the summers of 2015–2018 (1 year after the arrival of WNS in Wisconsin, USA), we performed intensive arthropod black-light trapping, ultrasonic acoustic monitoring, and emergence counts at 10 little brown (*Myotis lucifugus*) and big brown (*Eptesicus fuscus*) bat maternity roosts with paired control sites. For little brown bats, which are severely affected by WNS, roost counts declined by 95% over the four-year period, compared to a 38% decline in big brown bat roost counts. Total arthropod abundance decreased by 49%, although decreases among common little brown bat prey were less severe. Our natural predator exclusion experiment supports existing evidence that bats can have measurable trophic impacts on arthropod communities, primarily via top-down effects on common prey.

KEYWORDS

Eptesicus fuscus, food webs, *Myotis lucifugus*, predator–prey, top-down control

INTRODUCTION

Disease-related losses in biodiversity have conservation, public health, and economic consequences (Dirzo et al., 2014; Estes et al., 2011; Keesing et al., 2010). Rapid disease-related declines can also provide novel opportunities for understanding the trophic effects of predators and their prey (Monk et al., 2022; Trewby et al., 2007). When the disease in question is specific to a single host or a similar group of hosts, the effects of the decline of one species can be detected without necessarily being confounded by environmental variables or by unintentional exclusion of other species. Indeed, several recent wildlife disease outbreaks, including infectious cancer in Tasmanian devils, white-nose syndrome (WNS) in North American bats, and wasting disease in sea stars meet these criteria (Bates et al., 2009; Cunningham et al., 2020; Frick et al., 2010; Hollings et al., 2016). Natural experiments using disease-related declines can be affected by other factors such as changes in foraging behaviours or nutritional demands (Fenton & Rands, 2006; Venesky et al., 2009). Nonetheless, given the limitations of exclosure studies (Evans et al., 2018; Perillo et al., 2015), treating disease-related population declines as a natural exclusion experiment offers unique circumstances for studying the influences of declining species in their respective food webs.

The emergence and spread of WNS currently threatens hibernating bats on a continent-wide scale (Cheng et al., 2021; Frick et al., 2010; Hoyt et al., 2021). WNS results from infection with the fungus *Pseudogymnoascus destructans* (Pd), which causes torpid bats to increase their arousal, metabolism, and rates of evaporative water loss, thereby depleting energy and fluid reserves (McGuire et al., 2017; Reeder et al., 2012; Willis, 2015). Since the initial detection of Pd in 2006, millions of bat deaths have been reported (Dzal et al., 2011). Like other vertebrate arthropodivores, bats can influence

arthropod abundance (Kalka et al., 2008; McCracken et al., 2012; Mooney et al., 2010), with natural pest suppression provided by bats valued nationally at $3.7–53 billion per year (Boyles et al., 2011). However, the potential loss of ecosystem services and other top-down effects of arthropodivorous bat population declines due to WNS have not been thoroughly assessed.

WNS was initially detected in Wisconsin in 2014 and consequent declines in bat populations in the region were predicted to occur within 3–4 years (Wilder et al., 2011). Little brown bats (*Myotis lucifugus*) experience severe mortality from white-nose syndrome, often in excess of 90%, whereas big brown bats (*Eptesicus fuscus*) typically display much lower mortality rates (Cheng et al., 2021; Frank et al., 2014; Frick et al., 2010). Leveraging expected WNS-induced declines in little brown bat populations in Wisconsin, we hypothesized that bats as generalist predators exert top-down effects on populations of their prey and thus influence local-scale arthropod abundance. We designed a quasi before-after-control-impact study (sensu Green, 1979) to test our hypothesis by comparing arthropod abundance with little brown and big brown bat activity throughout the summers of 2015–2018 (Figure 1). Specifically, we quantified the effects of expected bat declines on annual arthropod abundance by conducting intensive arthropod sampling at paired subsites near (hereafter referred to as "treatment subsites") and far (hereafter referred to as "control subsites") from large bat maternity roosts, with high and comparatively lower bat activity, respectively (Figure 1a; Figure S1). We predicted that as little brown bat populations declined substantially from WNS, the abundance of their most common prey items would increase at treatment subsites relative to paired control subsites with lower bat activity (Figure 1b,c).

MATERIALS AND METHODS

Study species

Little brown and big brown bats are among the most common bat species in North America (Fenton, 1980; Kurta & Baker, 1990). Little brown bats are high-frequency echolocators that tend to be generalist in their foraging habits, often consuming insects that swarm at the aquatic-terrestrial ecotone (such as chironomid midges), as well as other prey-like smaller moths, true bugs, beetles, and spiders (Buchler, 1976; Clare, Symondson, Broders, et al., 2014; Whitaker Jr & Lawhead, 1992). In contrast, big brown bats are lower-frequency echolocators and are frequently referred to as "beetle specialists" but are well known to consume various other arthropods such as flies, caddisflies, true bugs, and moths (Agosta, 2002; Clare, Symondson, & Fenton, 2014; Whitaker Jr, 1995). We selected little brown bats as a focal study species because, prior to WNS-related declines, they were the most common bat species in the study region as measured by capture efforts, with big brown bats as the second most common (Huebschman, 2019). We selected big brown bats as a second focal study species because they were expected to decline less from WNS (based on previous population trends observed in the Eastern region of North America, e.g., Frick et al., 2015). Little brown and big brown bats are the only species in our study area that frequently form large maternity colonies, usually in human-built structures that further facilitate the ease of detection and monitoring between years.

Study sites

Study sites for arthropod trapping were selected at 10 bat maternity roosts in southern Wisconsin (Figure 2a). Each site included a subsite located 50–100 m away from a known bat maternity roost (hereafter referred to as a "treatment"), and an additional subsite located 3–10 km from each respective bat roost (hereafter referred to as a "control"). For each site, paired control subsites were selected such that immediate landscape composition was similar to treatment subsites but with comparatively lower levels of bat activity due to the distance outside of the expected core foraging areas of each maternity roost (Henry et al., 2002; Wilkinson & Barclay, 1997), which was then validated via acoustic activity indexing. For each subsite, landscape composition within a 3 km buffer (representing relevant bat foraging distances) was extracted from the USDA CropScape Cropland Data Layer (https://nassgeodata.gmu.edu/CropScape/) using ArcGIS version 10.5.1 (Esri, Redlands, CA, USA; Figure S2; Table S1).

Arthropod sample collection and enumeration

Black-light traps were used to collect night-flying moths and other arthropods that are presumed to form the majority of prey in little brown and big brown bat diets. Black-light trapping protocols followed Wray et al. (2021), with traps turned on automatically from 20:00 to 5:00 for a consecutive 3-night period (Thursday–Saturday) from late May to late August in 2015 and mid-May to early September in 2016–2018. Insect and arthropod samples were identified and counted (or estimated via subsampling and extrapolation) by microscope, also following Wray et al., 2021. Briefly, arthropods were identified to order, and within orders, all specimens were identified to the 43 most commonly detected groups (representing 95% of all captured arthropods), with remaining rare families identified as "other Order", e.g., "other Coleoptera." Damaged or degraded samples were identified to the lowest taxonomic level possible. Arthropods were subsequently aggregated into categories based on general functional groups, as well as into groups that

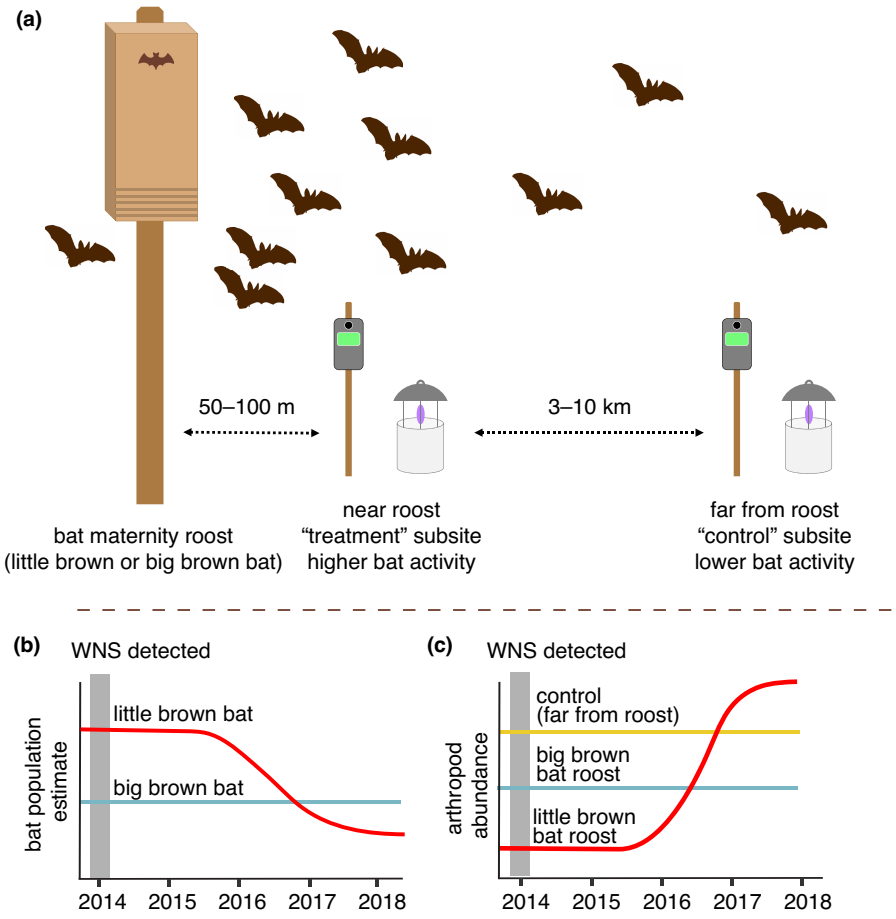

FIGURE 1 Conceptual diagram. (a) Study site design, with passive acoustic monitors and black-light traps located near and far from bat roosts to quantify bat acoustic activity and arthropod abundance, respectively. (b) Predictions for bat population declines following detection of white-nose syndrome (WNS) in Wisconsin in 2014. (c) Predictions for arthropod abundance at treatment and control subsites following the expected declines in bat populations. Blue corresponds to big brown bat (*Eptesicus fuscus*), red corresponds to little brown bat (*Myotis lucifugus*). Diagram not to scale.

represent little brown bat common prey (Chironomidae and micromoths) and big brown bat common prey (all beetles, except Heteroceridae), which are further detailed in Table S4.

Bat activity indexing

Roost emergence counts were conducted annually using visual surveys during ordinal weeks 24–25 and 29–30, roughly corresponding to pre- and post-volancy periods for bat pups. These surveys were conducted as part of a state-wide community science-based monitoring initiative, and counts were averaged between each survey.

Bat activity was indexed by deploying Songmeter SM3ZC passive acoustic recording devices (Wildlife Acoustics, Maynard, MA) at all treatment and control subsites ($n=20$ subsites). Recordings occurred nightly from sunset to sundown during the summer period (late May–early September). Signal parameters were set between 8–120 kHz and 2–500 ms, with a maximum inter-syllable gap of 500 ms and a minimum of 2 pulses. Raw acoustic data were processed in batches using Kaleidoscope PRO version 4.1.0 (Wildlife Acoustics, Maynard, MA) using the Bats of North America classifier, with the region set to Wisconsin. To avoid noise contamination and potential bat attraction effects, we removed all nights when black-light traps were on (Thursday, Friday, and Saturday). Next, we grouped the number of pulses matching a particular bat species into high and low-frequency categories to account for the inherent shortcomings of autoclassification software (Lemen et al., 2015). We selected this approach because (1) little brown and big brown bats are well-documented as the most common bat species in the region according to numerous capture studies (e.g., Huebschman, 2019), (2) these are the only bat species that frequently form large colonies in the study area, and (3) we were able to further validate acoustic activity trends using emergence counts at known roosts that have been continuously monitored for several years as part of state-wide bat survey efforts. Finally, high-frequency and low-frequency pulses were aggregated by subsite, year, and ordinal week, with the arithmetic mean taken to account for uneven sampling.

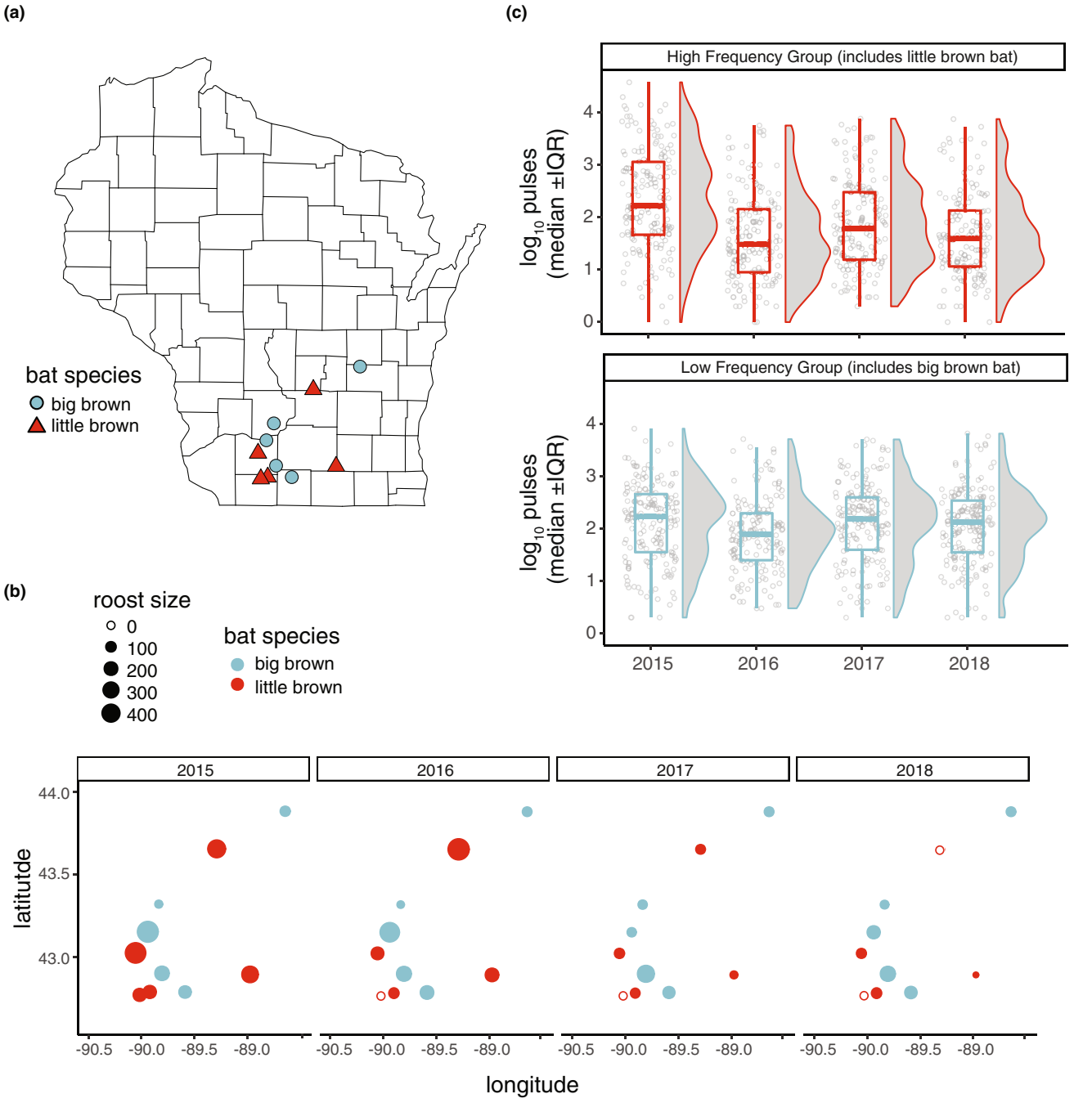

FIGURE 2 Bat population size and acoustic activity estimations. (a) Map of maternity roost locations in Wisconsin, USA, with lines indicating county boundaries. (b) Spatially-arranged changes in roost size by year, determined as the mean value of pre- and post-volancy roost emergence counts. (c) Total nightly identified pulses at all study sites, 2015–2018. High-frequency group (HFG) includes little brown bats, low-frequency group (LFG) includes big brown bats. Bars indicate median values, while boxplots indicate the interquartile range and whiskers indicate the full range of values. Half-violin plots indicate the distribution of observed values. Points are jittered for visibility. Blue corresponds to big brown bat (*Eptesicus fuscus*), red corresponds to little brown bat (*Myotis lucifugus*).

Statistical analyses: study design validation

To evaluate the a priori assumption that subsites close to roosts (i.e., "treatment") had higher bat activity than subsites far from roosts ("controls"), we compared acoustic activity at paired subsites for the frequency category corresponding to the type of bat roost present (i.e., high-frequency activity for little brown bat sites and low-frequency activity for big brown bat sites). We tested for differences in the mean number of pulses in each category at paired treatment and control subsites using Wilcoxon signed-rank tests. This analysis indicated that 9 of 10 sites had significantly higher total bat activity for the expected frequency group at the treatment subsite in comparison to the control subsite (Figure S1). One site (site D) had higher low-frequency bat activity

at the control subsite in comparison to the treatment subsite and was therefore excluded from all subsequent paired analyses. To determine how bat activity changed over time, yearly differences high-frequency and low-frequency acoustic activity were also assessed using unpaired Wilcoxon rank sum tests.

Statistical analyses: trends in arthropod abundance

Analysis 1: Comparing arthropod abundance at control and treatment subsites

In before-after-control-impact study designs, averaging among taxonomic groups and aggregating into higher order taxonomic groups has been shown to reduce the influences of temporal and spatial heterogeneity (Rassweiler et al., 2021). As such, our initial analyses compared total arthropod abundance and three functional groups: herbivorous, aquatic, and predator/parasitoid arthropods, based on aggregations of family-level taxa. We separately assessed micromoths and Chironomidae (common prey of little brown bats in the study area), Carabidae (common prey of big brown bats in the study area), and Noctuidae (less common prey for both bats, but which includes many agricultural pest taxa of interest). Since data were highly variable between sampling weeks, we averaged arthropod abundances within each year for each subsite to reduce the effects of sampling error and temporal autocorrelation. Next, we used linear mixed effects models to assess whether arthropod abundance differed at treatment versus control sites over time. Count data were transformed using a log base 10 $(x+1)$ transformation to preserve information present among zero values. As arthropod count data for most groups had high variance, this approach was chosen for its robustness under a wide range of conditions (Ives, 2015).

To improve the interpretability of results given the three-way interaction between time period, bat species, and treatment vs. control subsites, separate models were created for each arthropod group of interest. Fixed effects included year, bat species at each site, treatment (i.e., the identity of a subsite as near versus far from a known bat maternity roost), and the interactions between year, bat species, and treatment. To account for the paired study design and repeated sampling, we used site as a random intercept. Since yearly trends were not necessarily linear, we treated year as a factor variable. Model assumptions (linearity, homogeneity of variance, normal distribution of residuals) were also tested and confirmed. We then used post hoc Tukey tests to determine pairwise contrasts between different levels of fixed predictor variables. Contrast estimates were considered meaningful if 95% confidence intervals did not overlap zero. To obtain ratios, estimates were back-transformed from the $\log_{10}$ scale. For statistical analyses, we used the R packages "lmerTest", "lme4", "lsmeans", and "emmeans" (Bates et al., 2014; Kuznetsova et al., 2017; Lenth et al., 2018; Lenth & Lenth, 2018).

Analysis 2: Paired comparisons of the abundance of common prey for each bat species

We leveraged the paired study design to assess changes in the respective common prey of each bat species at control and treatment subsites. For this analysis, we only included samples for which paired samples from the same site pair, week, and year were successfully collected. For each year, we computed effect sizes, expressed as Hedges' *g*, using data estimation with 10 000 bootstrap replicates implemented through the R package "dabestr" (Ho et al., 2019).

Analysis 3: Comparing the abundance of common bat prey as a proportion of total arthropod abundance

To estimate how the abundance of the common prey of each bat species changed over time, we assessed the weekly abundance of little brown bat common prey items (Chironomidae and micromoths) and big brown bat common prey items (all Coleoptera except Heteroceridae, which were never detected in big brown bat diets in this study area) as a proportion of total arthropod abundance at all study sites. Yearly common prey abundance for each bat species was averaged across all sites, then compared using a 2-sample z-test for equality of proportions with continuity correction to compare the first study year (2015) with each subsequent year (2016–2018). We also compared the number of weeks where the average proportion of common prey was higher than the global average across all 4 years.

Additional tools used for data processing and data visualization included the R packages "maps", "tidyverse", and "wesanderson" (Becker et al., 2013; Ram & Wickham, 2018; Wickham et al., 2019) as well as SankeyMATIC (Bogart, 2018).

RESULTS

Bat roost counts and acoustic activity

Roost counts for little brown bats declined by 95.0% from an average of 232.8 bats per roost in 2015 (ranging from 118 to 409 bats) to an average of 11.6 bats per roost in 2018 (ranging from 0 to 50 bats), with two roosts abandoned (Figure 2b; Table S1). Roost counts for big brown bats declined by 37.8% from an average of 152.8

bats per roost in 2015 (ranging from 22 to 428 bats) to an average of 95 bats per roost in 2018 (ranging from 30 to 180 bats; Figure 2b; Table S1). Passive acoustic surveys, which included a total of 6245 recording nights across all sites, were generally consistent with the results of visual observations at roosts. These surveys yielded a total of 1,460,540 identified low-frequency pulses and 2,109,930 identified high-frequency pulses. High-frequency acoustic activity (which includes little brown bats) declined by 79.1% between the first and last year of the study ($p<0.001$), whereas low-frequency acoustic activity (which includes big brown bats) did not change significantly (Figure 2c; Table S2a). Although treatment subsites generally maintained higher average acoustic activity in comparison to paired control subsites throughout the study period at little brown bat sites, the magnitude of difference in high-frequency acoustic activity between treatment and control subsites tended to decline over time (Figure 3a; Table S2b).

Changes in yearly arthropod abundance

In total, we captured, identified, and enumerated 2,003,493 arthropods (Figure 3b). Over the course of the study (2015–2018), the mean total arthropod abundance decreased by 48.9%. This trend held true for all major orders, with decreases between 2015 and 2018 ranging from −15.7% for total Diptera to −92.7% for total Hymenoptera (Figure 3c; Table S3). To assess connections between bat declines and arthropod abundance, we selected three complementary analyses: (1) comparing the weekly abundance of arthropod functional groups (based on the most common habits of arthropod groups during their adult stage, see Table S4) and key bat prey taxa at control and treatment subsites within each year, (2) comparing the abundance of the most common prey for each bat species at paired sites with bootstrap replication, and (3) comparing the abundance of common prey as a proportion of total arthropod abundance for each bat species. We provide the raw abundance data for the main arthropod groups used in our analyses (Table S5). Two little brown bat roosts were abandoned during the study (e.g., roosts that had a bat colony in 2015, but where no bats were observed during emergence counts or site visits in subsequent years), and one of the sites had a 99% decline in roost size from 2015 to 2018. For these sites, we visualized raw data for total arthropod abundance, and for grouped Chironomidae and micromoths, then we calculated group differences using a Wilcoxon rank-sum test with a Bonferroni correction for multiple comparisons (Figure S3). Generally, we found that in years following roost abandonment or severe declines in bat counts, site-level data reflected a relative increase in abundance of total arthropods and Chironomidae at treatment subsites, although trends in micromoth abundance did not follow our predictions.

Analysis 1: Comparing arthropod abundance at control and treatment subsites

After accounting for site-level variance using linear mixed effects models, post hoc tests using pairwise contrasts indicated that total arthropod abundance at little brown bat control and treatment subsites differed in the first year of the study (Figure 4a; Table S6). Specifically, little brown bat treatment subsites had 0.56 times as many total arthropods (95% CI =0.33–0.92 times as many total arthropods) in comparison to subsites in 2015, which translates to an average of 1514 fewer total arthropods per sample (95% CI=851–2692 fewer total arthropods) at treatment subsites versus control subsites (Figure 4a; Table S6). Conversely, in 2016 (the first year after WNS-related declines were detected among little brown bats), little brown bat treatment subsites had no statistically meaningful difference between treatment and control groups (Figure 4a; Table S6). In subsequent post-WNS years, trends were similar, with no meaningful difference in total arthropod abundance at treatment versus control subsites. Arthropod abundance at big brown bat treatment subsites did not differ in comparison to control subsites in any years during the duration of the study (Figure 4a; Table S6).

At little brown bat paired sites, the trends in total arthropod abundance at control versus treatment subsites differed within arthropod groups, but the most notable effects were among Chironomidae and herbivores (Figure 4a; Figure S4a; Table S6). There was no meaningful difference in Chironomidae abundance at control and treatment subsites in 2015. However, in 2016, little brown bat treatment subsites had 2.5 times as many Chironomidae (95% CI=1.21–5.07 times as many Chironomidae) in comparison to control subsites, which translates to an average of 82 more total Chironomidae (95% CI=27–252 more total Chironomidae) per sample (Figure 4a; Table S6). In 2015, little brown bat treatment subsites had 0.47 times as many herbivorous arthropods in comparison to control subsites (Figure S4a; Table S6), whereas subsequent years displayed no statistically meaningful difference. We did not observe any statistically meaningful differences between treatment and control subsites nor any changes in trends between years for other arthropod groups (Figure 4a; Figure S4a; Table S6).

Analysis 2: Paired comparisons of the abundance of common prey for each bat species

Paired sample analyses (samples matched by site, week, and year) indicated that the abundance of little brown bat common prey at treatment and control subsites did not differ in 2015. However, treatment subsites at little brown bat sites had 2.4 times more common prey relative to control subsites in 2016 (95% CI=1.5–4.1 times as

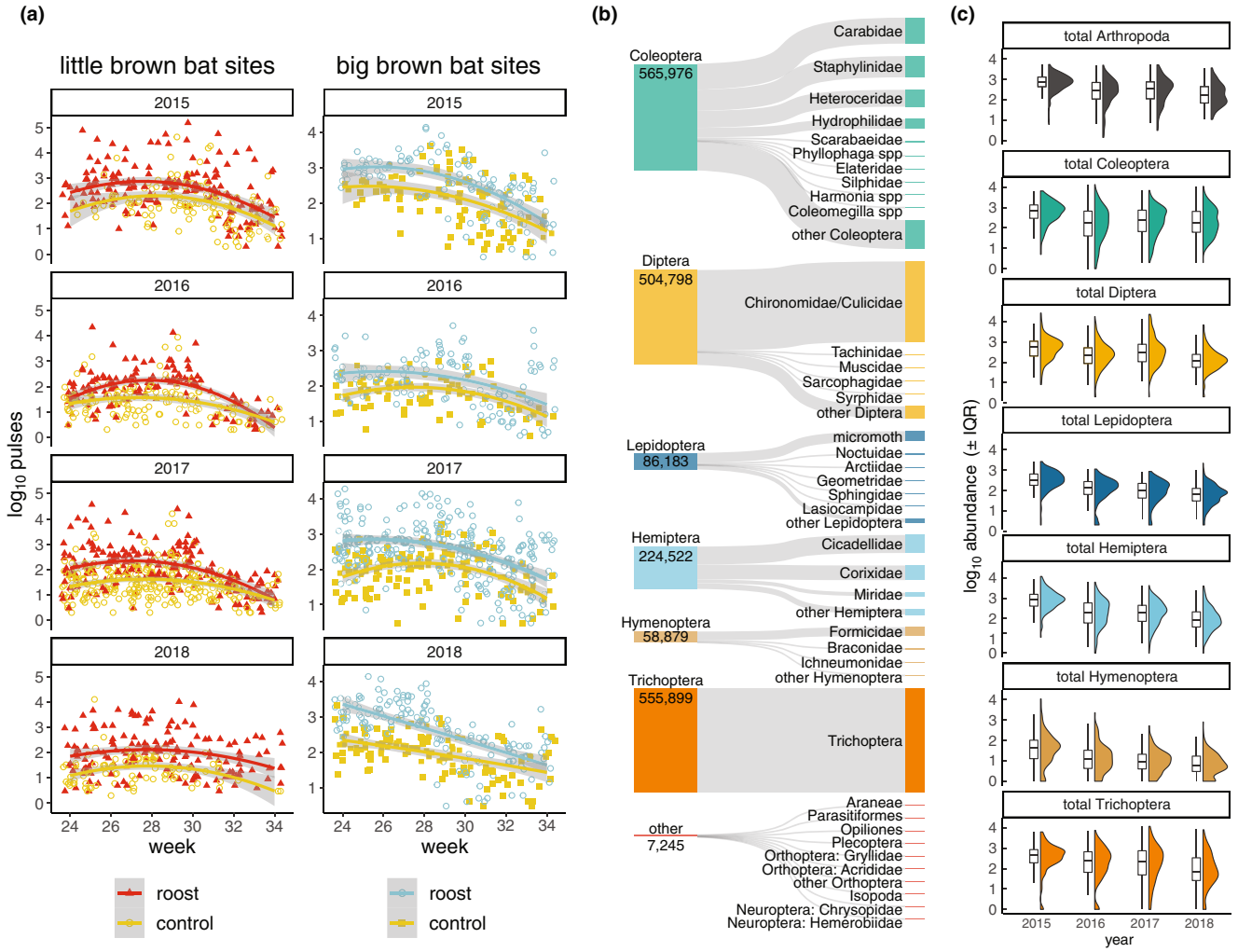

FIGURE 3 Summary of bat acoustic activity and arthropod abundance from black-light trap samples. (a) Comparison between bat activity across all bat roost (treatment) and control subsites. For little brown bat sites, average nightly high-frequency acoustic activity is shown, while for big brown bat sites, average nightly low-frequency acoustic activity is shown. The quadratic curves (with grey areas representing standard error) are used to visualize general patterns in activity, which tended to peak in the middle of the summer sampling period. Site pair D was excluded from this visualization because it did not meet the a priori assumptions of having higher bat activity at the bat roost (treatment) subsite. (b) Sankey diagram of the total abundance of arthropods identified by microscope. (c) Yearly abundance of total arthropods and major arthropod orders, 2015–2018. Bars indicate the median values, while boxplots indicate the interquartile range and whiskers indicating the full range of values. Half-violin plots indicate the distribution of observed values.

many common prey; Figure 4b; Table 1), and 2.1 times more common prey in 2017 (95% CI = 1.1–4.7 times as many common prey; Figure 4b; Table 1), although no differences were observed in 2018 (95% CI = 0.36–1.6 times as many common prey; Figure 4b; Table 1). These results further support the linear mixed effects model analyses, which yielded similar ratios and confidence intervals for Chironomidae in 2016. For these pairwise comparisons, Hedges' *g*, a measure of statistical effect size, indicated medium effects of 0.64 (95% CI = 0.28–0.97) and 0.42 (95% CI = 0.002–0.83) in 2016 and 2017, respectively (Figure 4b; Figure S4b; Table 1). At big brown bat sites, the paired analysis also indicated that the abundance of common big brown bat prey did not differ between control and treatment subsites or between years (Figure 4b; Figure S4b; Table 1).

Analysis 3: Comparing the abundance of common bat prey as a proportion of total arthropod abundance

To assess regional changes in arthropod communities following WNS-related little brown bat declines, we compared the abundance of common little brown and big brown bat prey as a proportion of total arthropod abundance averaged across all study sites. In 2015, weekly abundance of little brown bat common prey as a proportion of total arthropod abundance remained below the global average, whereas from 2016 onward there were more sampling weeks where the proportional abundance of little brown bat common prey exceeded the global average (Figure 4c). Average yearly abundance of little brown bat prey as a proportion of

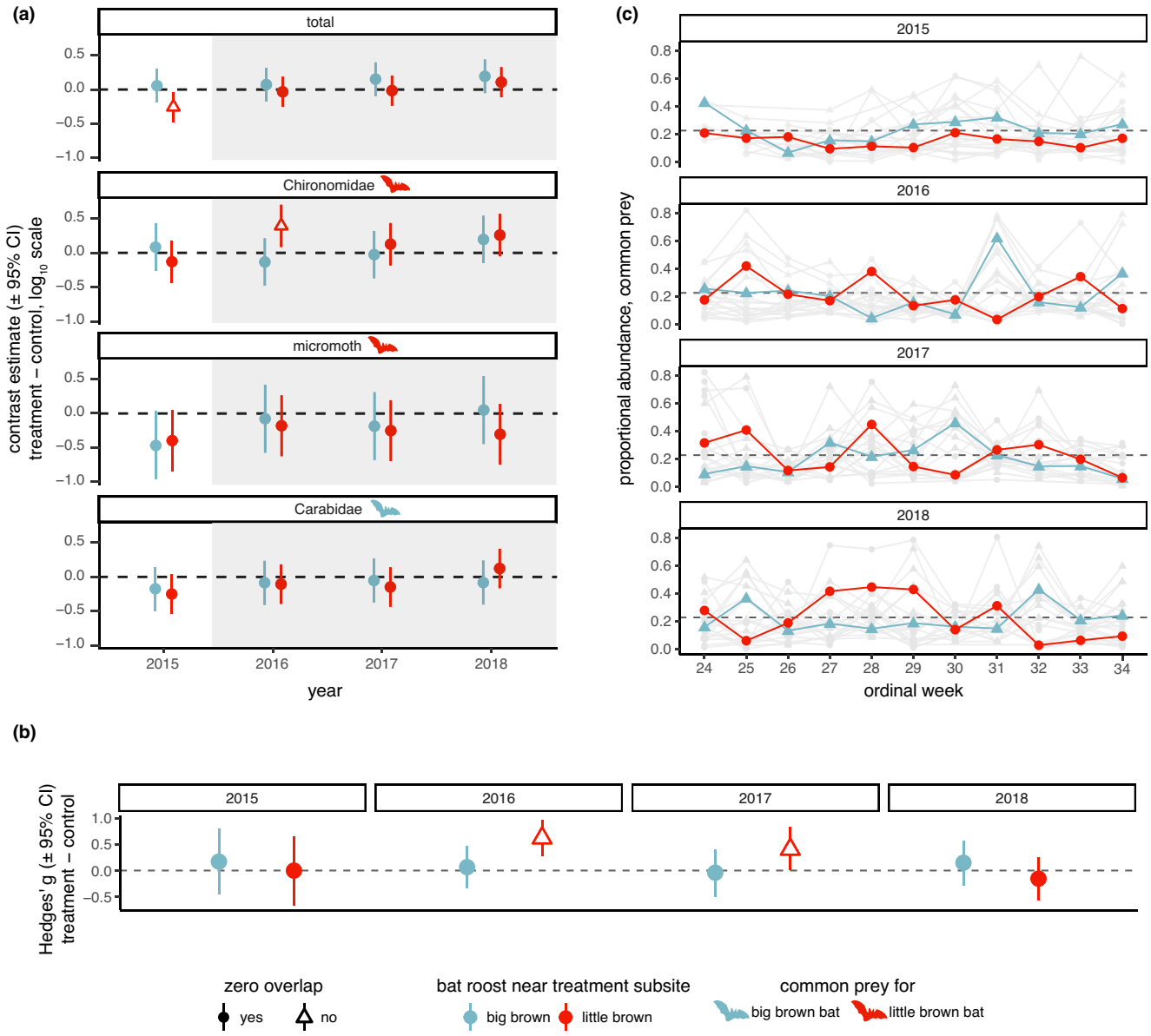

FIGURE 4 Changes in arthropod abundance over time with comparisons between treatment and control subsites and between common bat prey items as a proportion of total arthropod abundance. (a) Results from linear mixed effects models (Analysis 1), demonstrating the estimate and 95% confidence intervals of pairwise contrasts (between treatments and controls) from post hoc testing. Estimates are shown on the $\log_{10}$ scale. Shaded grey areas indicate years after WNS-related little brown bat declines were detected. Bat silhouette colours indicate common prey for each bat species. (b) Effect sizes from bootstrapped estimations of pairwise comparisons of common prey abundance at control and treatment subsites paired by sampling week and year (Analysis 2). For panels a and b, closed circles indicate overlap with zero, while open triangles indicate nonoverlap with zero which suggests a statistically meaningful effect. For panels a and b, dashed lines indicates zero. (c) Common bat prey items as a proportion of total arthropod abundance, averaged across sites for each respective bat species (Analysis 3). Here, the dashed line indicates the average proportional abundance of common prey across all weeks and all years. Grey lines and points indicate average proportional abundance for each site. Blue corresponds to big brown bat (*Eptesicus fuscus*), red corresponds to little brown bat (*Myotis lucifugus*).

total abundance increased from 0.16 in 2015 to 0.22 in 2016, with values of 0.28 and 0.25 in 2017 and 2018, respectively. Two-sided tests of equal proportions indicated that the abundance of common little brown bat prey as a proportion of total arthropod abundance in years 2016–2018 were meaningfully greater than 2015 ($\chi^2_{2016–2015} = 36.7$, df = 1, $p < 0.001$; $\chi^2_{2017–2015} = 120.3$, df = 1, $p < 0.001$; $\chi^2_{2018–2015} = 57.6$, df = 1, $p < 0.001$). When aggregated across all sampling sites, big brown bat common prey represented a higher abundance as a proportion of total arthropod abundance at several time points (Figure 4c). The average yearly abundance of common big brown bat prey as a proportion of total abundance was 0.26 in 2015 and 0.28 in 2016, which was not meaningfully different ($\chi^2_{2016–2015} = 2.67$, df = 1, $p = 0.10$). In 2017, the proportion of common big brown bat prey decreased meaningfully to 0.18 ($\chi^2_{2017–2015} = 59.7$, df = 1, $p < 0.001$), then returned to 0.23

TABLE 1 Ratios of abundance and effect sizes for common little brown bat prey (micromoths + Chironomidae) and big brown bat prey (Coleoptera, except Heteroceridae) for paired samples from treatment and control subsites.

Species	Year	*n* (paired samples)	Ratio of prey abundance, treatment/control		Effect size	
			Paired mean difference [95% CI]		Hedges' *g* [95% CI]	
Little brown bat (*Myotis lucifugus*)	2015	18	0.999	[0.495, 2.312]	−0.001	[−0.676, 0.649]
	2016	59	2.421	[1.500, 4.055]	0.640	[0.276, 0.966]
	2017	42	2.143	[1.053, 4.732]	0.423	[0.002, 0.829]
	2018	47	0.743	[0.356, 1.607]	−0.156	[−0.570, 0.256]
Big brown bat (*Eptesicus fuscus*)	2015	20	1.192	[0.662, 2.193]	0.171	[−0.447, 0.803]
	2016	47	1.120	[0.569, 2.234]	0.065	[−0.341, 0.462]
	2017	39	0.947	[0.537, 1.675]	−0.041	[−0.495, 0.404]
	2018	43	1.245	[0.665, 2.301]	0.149	[−0.292, 0.572]

in 2018, which also represented a meaningful decrease in comparison to 2015 ($\chi^2_{2018-2015} = 4.3$, df = 1, $p = 0.04$).

DISCUSSION

Changes in bat roost size and acoustic activity between 2015 and 2018 followed our predictions. Rates of high-frequency activity declines were consistent with a previous study in New York state, which found a 78% decline in little brown bat acoustic activity (Dzal et al., 2011). Since its initial detection in Wisconsin, WNS was considered to have spread through much of the southern portion of the state by the winter of 2015–2016, and by the winter of 2016–2017 was specifically confirmed or suspected in the counties where 9 of 10 study sites were located (Lorch et al., 2016; USGS, 2020). Roost size and acoustic activity declines in this study can therefore be largely attributed to effects from WNS, which particularly afflicts little brown bats as well as other small-bodied, high-frequency echolocating bats in the study area, such as tri-coloured and northern long-eared bats (Frick et al., 2015).

Our experimental design provides a framework where the primary difference between treatment and control subsites is related to the presence of large bat maternity roosts and corresponding higher bat activity. Thus, despite an unexpected decreasing trend in arthropod abundance, relative changes at treatment and control subsites can still be compared to assess whether WNS-related bat declines lead to a measurable release in predation pressure on arthropod communities. Arthropod populations can vary in response to many biotic and abiotic factors, and the 4-year length of our study period does not adequately capture the full cycle of shifts in arthropod abundance (Montgomery et al., 2020; Shortall et al., 2009; Thomas et al., 2019). Uncertainties related to multiple factors that can influence arthropod abundance highlight the utility of using paired sampling with similar landscape composition, weather, and land treatment practices at control and treatment subsites.

Our results indicate some changes in the relative total arthropod abundance at little brown bat treatment subsites relative to control subsites following declines in population size and acoustic activity, which may suggest a release in predation pressure on certain arthropod groups due to WNS. This interpretation is further supported by less variable trends in the relative total arthropod abundance at big brown bat treatment and control subsites, which also correspond with the less affected big brown bat populations. The observed proportional increases in common little brown bat prey in post-WNS years provide additional evidence that severe declines in little brown bat populations may influence the abundance of some arthropods. However, we note that we had only 1 year of baseline data prior to declines (in 2015), which had fewer samples collected due to a shorter collection season, although we restricted our yearly comparisons only to the weeks that had samples collected across all years. Considering the many factors that govern arthropod abundance, it remains possible that other factors could explain the trends observed in this study.

Together, our three analyses suggest that the main prey of little brown bats increased in local relative abundance, as shown by comparisons between treatment and control subsites. Similarities between abundance at control and treatment subsites in 2018 for selected arthropod groups may indicate that these trends do not necessarily persist in the longer term. For total arthropod abundance and for the abundance of most arthropod groups, the magnitude of the differences between control and treatment subsites did not change substantially at big brown bat sites. These results are in accordance with our hypothesis, as relative changes in arthropod abundance between treatment and control subsites were stronger for little brown bats in comparison to big brown bats. Overall, these findings provide evidence that WNS-related declines among little brown bats appear to have

top-down influences leading to a short-term increase in the relative abundance of their common prey.

Despite the difficulties associated with detecting measurable changes in complex communities, this study represents one of the most comprehensive attempts to characterize the influences of bats on arthropod abundance without the use of exclosures. As volant organisms, bats can travel long distances to reach foraging habitats, potentially as a way to exploit temporal changes in arthropod abundance (Brigham, 1991). As such, linking the effects of disease-related bat declines with local-scale differences in arthropod abundance at sites near and far from bat roosts remains challenging. Like all arthropod survey methods, black-light trap sampling methods carry biases in terms of which arthropods are most attracted, and therefore do not perfectly reflect the abundance of all arthropod taxa (Kirkeby et al., 2013; Kremen et al., 1993). Although traps can influence the estimated abundance of different arthropod groups, our paired study design accounts for these effects and assumes that trap-related biases remained consistent between treatment and control subsites. Although we chose paired subsite distances to represent areas that bats from each known roost were unlikely to travel to for foraging, arthropod communities may also shift on a smaller scale and therefore our paired sites—despite our best efforts to match on as many factors as possible—may retain latent differences that could also influence arthropod abundance.

Though arthropodivorous bats are small-bodied, the total biomass of arthropods consumed by bats each season is substantial (Morrison & Lindell, 2012), and the loss of millions of bats from white-nose syndrome thus represents a biomass displacement that could have regional effects on the nocturnal arthropod food web. For example, Boyles et al. (2011) estimated that one million little brown bats consume between 660 and 1320 metric tons of insects each year. However, particularly for herbivorous insects, bottom-up effects (i.e., the availability of resources) influence population dynamics (Vidal & Murphy, 2018), and for highly fecund arthropod taxa, bat predation may not be sufficient to register measurable influences on prey communities. The potential influences of bottom-up forces and intrinsically high variability in arthropod populations may partially explain why we did not detect differences between control and treatment subsites in some arthropod groups. Nonetheless, following little brown bat declines we observed trends that may represent different types of top-down effects: (1) the loss of a previous difference in arthropod abundance at subsites near bat roosts relative to paired control subsites and (2) a relative increase in the abundance of common little brown bat prey groups at subsites near bat roosts relative to paired control subsites. The impact of bats on local suppression of arthropods (i.e., driving lower abundance) vs. local regulation of arthropods (i.e., preventing excessive abundance) could be further investigated by future efforts. Although our study attempts to quantify the effects of arthropodivorous predator declines, other factors such as climate change, pesticide use, habitat loss, non-consumptive effects of predators on prey behaviour, or compensation by other predator taxa remain important to consider.

In summary, we found that abrupt and substantial WNS-related bat population declines may influence the abundance of some arthropod groups. Given substantial little brown bat population declines, relative increases in arthropods such as Chironomidae—the most common prey of little brown bats in the study region—suggest that the observed differences between treatment and control subsites in the later years of the study could be related to some level of temporary predation pressure release. The trends among other arthropod groups and from big brown bat paired sites also provide evidence that top-down effects of bat predation on arthropods are heterogenous and could potentially involve changes in foraging patterns among bat species that are less severely afflicted by WNS or other arthropodivores. Though little brown and big brown bats share some overlap in dietary composition in our study region (e.g., Wray et al., 2021; Wray & Peery, 2022), comparisons between pre- and post-WNS bat diet composition in this region indicated that brown bats did not substantially shift their diet composition nor did they readily adopt the common prey items of little brown bats species following declines (Wray et al., 2022). Moreover, the disproportionate population declines among smaller-bodied bat species due to WNS may be particularly concerning, as persisting populations of larger-bodied bat species are not physiologically adapted for fulfilling the same functional role as predators. Although body condition influences WNS survival (Cheng et al., 2019; Jonasson & Willis, 2011), few studies have examined how arthropod prey availability influences the ability of bats to acquire adequate nutrition prior to hibernation. Considering the observed decreasing arthropod abundance in this study and in other broader-scale studies, further investigation of potential interactions between prey abundance, body condition, and WNS severity may be warranted. We also suggest that future studies on the top-down influences of arthropod predators examine broader spatial and temporal scales or incorporate movement and capture data to further clarify functional roles.

AUTHOR CONTRIBUTIONS

MZP, CG, and DLL designed the study. AKW, JMK, & EP coordinated and conducted fieldwork and arthropod identifications. AKW analysed the data and created figures. AKW, ZP, and CG wrote the manuscript. All authors reviewed & edited the manuscript.

ACKNOWLEDGEMENTS

The authors thank Brenna Decker, Erin Green, Michael Stocking, Tim Lorenz, and Mat Bohne for designing and building the solar powered black-light traps. For

assistance with fieldwork and arthropod identifications, we thank Marcelo Ferreira, Will Sandvold, and Jing Jamie Wang. We thank Mike & Jane Balch, Rhonda & Danny Enge, Jeanne Foster, Leigh Hale, Marci & Jim Hess, Elaine Horn, Gary Jansen, Phillip & Ronald Kerl, Doug Kiel, Jeremy Lynch, Pat Tesar, Elaine Swanson, Jimmy Voegeli, and Jean Warrior for allowing sampling at their properties. We thank John Arthur, Bruce Folley, Kathleen Gruentzel, Heather Kaarakka, Darren Marsh, Thomas Meyer, and J. Paul White for assistance coordinating sampling at state and county parks. We thank Heather Kaarakka, J. Paul White, and participants of the Great Wisconsin Bat Count for providing emergence count data. We also thank Jon Pauli, Ben Zuckerberg, Jake Goheen, and three anonymous reviewers for valuable comments and/or discussions leading to the improvement of this manuscript.

FUNDING INFORMATION

USDA, Grant/Award Number: Hatch Formula Fund WIS01841.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14437.

DATA AVAILABILITY STATEMENT

https://doi.org/10.6084/m9.figshare.24954366.v1.

ORCID

Amy K. Wray https://orcid.org/0000-0001-9685-8308

REFERENCES

Agosta, S.J. (2002) Habitat use, diet and roost selection by the big brown bat (Eptesicus fuscus) in North America: a case for conserving an abundant species. *Mammal Review*, 32, 179–198.

Bates, A.E., Hilton, B.J. & Harley, C.D. (2009) Effects of temperature, season and locality on wasting disease in the keystone predatory sea star Pisaster ochraceus. *Diseases of Aquatic Organisms*, 86, 245–251.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) *lme4: linear mixed-effects models using eigen and S4*. R package version 1.1.7, http://CRAN.R-project.org/package=lme4

Becker, R.A., Wilks, A.R., Brownrigg, R., Minka, T.P. & Deckmyn, A. (2013) *maps: Draw geographical maps*. R package version 2.3.2, https://CRAN.R-project.org/package=maps

Bogart, S. (2018) SankeyMATIC: A Sankey diagram builder for everyone. https://github.com/nowthis/sankeymatic. Last accessed 18 November 2020

Boyles, J.G., Cryan, P.M., McCracken, G.F. & Kunz, T.H. (2011) Economic importance of bats in agriculture. *Science*, 332, 41–42.

Brigham, R.M. (1991) Flexibility in foraging and roosting behaviour by the big brown bat (Eptesicus fuscus). *Canadian Journal of Zoology*, 69, 117–121.

Buchler, E.R. (1976) Prey selection by Myotis lucifugus (chiroptera: vespertilionidae). *The American Naturalist*, 110, 619–628.

Cheng, T.L., Gerson, A., Moore, M.S., Reichard, J.D., DeSimone, J., Willis, C.K. et al. (2019) Higher fat stores contribute to persistence of little brown bat populations with white-nose syndrome. *The Journal of Animal Ecology*, 88, 591–600.

Cheng, T.L., Reichard, J.D., Coleman, J.T., Weller, T.J., Thogmartin, W.E., Reichert, B.E. et al. (2021) The scope and severity of white-nose syndrome on hibernating bats in North America. *Conservation Biology*, 35, 1586–1597.

Clare, E.L., Symondson, W.O., Broders, H., Fabianek, F., Fraser, E.E., MacKenzie, A. et al. (2014) The diet of Myotis lucifugus across Canada: assessing foraging quality and diet variability. *Molecular Ecology*, 23, 3618–3632.

Clare, E.L., Symondson, W.O. & Fenton, M.B. (2014) An inordinate fondness for beetles? Variation in seasonal dietary preferences of night-roosting big brown bats (Eptesicus fuscus). *Molecular Ecology*, 23, 3633–3647.

Cunningham, C.X., Johnson, C.N. & Jones, M.E. (2020) A native apex predator limits an invasive mesopredator and protects native prey: Tasmanian devils protecting bandicoots from cats. *Ecology Letters*, 23, 711–721.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J. & Collen, B. (2014) Defaunation in the Anthropocene. *Science*, 345, 401–406.

Dzal, Y., McGuire, L.P., Veselka, N. & Fenton, M.B. (2011) Going, going, gone: the impact of white-nose syndrome on the summer activity of the little brown bat (Myotis lucifugus). *Biology Letters*, 7, 392–394.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. et al. (2011) Trophic downgrading of planet earth. *Science*, 333, 301–306.

Evans, P., Davis, E.L., Gedalof, Z.E. & Brown, C.D. (2018) Small herbivore exclosure cages alter microclimate conditions. *Forest Ecology and Management*, 415, 118–128.

Fenton, A. & Rands, S. (2006) The impact of parasite manipulation and predator foraging behavior on predator–prey communities. *Ecology*, 87, 2832–2841.

Fenton, M.B. (1980) Myotis Lucifugus. *Mammalian Species*, 142, 1–8.

Frank, C.L., Michalski, A., McDonough, A.A., Rahimian, M., Rudd, R.J. & Herzog, C. (2014) The resistance of a north American bat species (Eptesicus fuscus) to white-nose syndrome (WNS). *PLoS One*, 9, e113958.

Frick, W.F., Pollock, J.F., Hicks, A.C., Langwig, K.E., Reynolds, D.S., Turner, G.G. et al. (2010) An emerging disease causes regional population collapse of a common north American bat species. *Science*, 329, 679–682.

Frick, W.F., Puechmaille, S.J., Hoyt, J.R., Nickel, B.A., Langwig, K.E., Foster, J.T. et al. (2015) Disease alters macroecological patterns of north American bats. *Global Ecology and Biogeography*, 24(7), 741–749.

Green, R.H. (1979) *Sampling design and statistical methods for environmental biologists*. Hoboken, NJ, USA: John Wiley & Sons.

Henry, M., Thomas, D.W., Vaudry, R. & Carrier, M. (2002) Foraging distances and home range of pregnant and lactating little brown bats (Myotis lucifugus). *Journal of Mammalogy*, 83, 767–774.

Ho, J., Tumkaya, T., Aryal, S., Choi, H. & Claridge-Chang, A. (2019) Moving beyond P values: data analysis with estimation graphics. *Nature Methods*, 16, 565–566.

Hollings, T., Jones, M., Mooney, N. & McCallum, H. (2016) Disease-induced decline of an apex predator drives invasive dominated states and threatens biodiversity. *Ecology*, 97, 394–405.

Hoyt, J.R., Kilpatrick, A.M. & Langwig, K.E. (2021) Ecology and impacts of white-nose syndrome on bats. *Nature Reviews Microbiology*, 19, 1–15.

Huebschman, J.J. (2019) Bats in southwest Wisconsin during the era of white-nose syndrome. *Northeastern Naturalist*, 26, 168–182.

Ives, A.R. (2015) For testing the significance of regression coefficients, go ahead and log-transform count data. *Methods in Ecology and Evolution*, 6, 828–835.

Jonasson, K.A. & Willis, C.K. (2011) Changes in body condition of hibernating bats support the thrifty female hypothesis and predict consequences for populations with white-nose syndrome. *PLoS One*, 6, e21061.
Kalka, M.B., Smith, A.R. & Kalko, E.K. (2008) Bats limit arthropods and herbivory in a tropical forest. *Science*, 320, 71.
Keesing, F., Belden, L.K., Daszak, P., Dobson, A., Harvell, C.D., Holt, R.D. et al. (2010) Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature*, 468, 647–652.
Kirkeby, C., Græsbøll, K., Stockmarr, A., Christiansen, L.E. & Bødker, R. (2013) The range of attraction for light traps catching Culicoides biting midges (Diptera: Ceratopogonidae). *Parasites & Vectors*, 6, 67.
Kremen, C., Colwell, R., Erwin, T., Murphy, D., Noss, R.A. & Sanjayan, M. (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology*, 7, 796–808.
Kurta, A. & Baker, R.H. (1990) Eptesicus fuscus. *Mammalian Species*, 356, 1–10.
Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H. (2017) lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software*, 82, 1–26 https://CRAN.R-project.org/package=lmerTest
Lemen, C., Freeman, P.W., White, J.A. & Andersen, B.R. (2015) The problem of low agreement among automated identification programs for acoustical surveys of bats. *Western North American Naturalist*, 75, 218–225.
Lenth, R. & Lenth, M.R. (2018) Package 'lsmeans'. *The American Statistician*, 34, 216–221 https://CRAN.R-project.org/package=lsmeans
Lenth, R., Singmann, H., Love, J., Buerkner, P. & Herve, M. (2018) *Emmeans: estimated marginal means, aka least-squares means*. R Package version 1.3.0. https://CRAN.R-project.org/package=emmeans
Lorch, J.M., Palmer, J.M., Lindner, D.L., Ballmann, A.E., George, K.G., Griffin, K. et al. (2016) First detection of bat white-nose syndrome in western North America. *MSphere*, 1, e00148-16.
McCracken, G.F., Westbrook, J.K., Brown, V.A., Eldridge, M., Federico, P. & Kunz, T.H. (2012) Bats track and exploit changes in insect pest populations. *PLoS One*, 7, e43839.
McGuire, L.P., Mayberry, H.W. & Willis, C.K. (2017) White-nose syndrome increases torpid metabolic rate and evaporative water loss in hibernating bats. *American Journal of Physiology. Regulatory, Integrative and Comparative Physiology*, 313, R680–R686.
Monk, J.D., Smith, J.A., Donadío, E., Perrig, P.L., Crego, R.D., Fileni, M. et al. (2022) Cascading effects of a disease outbreak in a remote protected area. *Ecology Letters*, 25, 1152–1163.
Montgomery, G.A., Dunn, R.R., Fox, R., Jongejans, E., Leather, S.R., Saunders, M.E. et al. (2020) Is the insect apocalypse upon us? How to Find out. *Biological Conservation*, 241, 108327.
Mooney, K.A., Gruner, D.S., Barber, N.A., Van Bael, S.A., Philpott, S.M. & Greenberg, R. (2010) Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. *Proceedings of the National Academy of Sciences*, 107, 7335–7340.
Morrison, E.B. & Lindell, C.A. (2012) Birds and bats reduce insect biomass and leaf damage in tropical forest restoration sites. *Ecological Applications*, 22, 1526–1534.
Perillo, A.C., Kucharik, C.J., Meehan, T.D., Serbin, S.P., Singh, A., Townsend, P.A. et al. (2015) Use of insect exclusion cages in soybean creates an altered microclimate and differential crop response. *Agricultural and Forest Meteorology*, 208, 50–61.
Ram, K. & Wickham, H. (2018) Wesanderson: a Wes Anderson palette generator. R package version 0.3.6 https://CRAN.R-project.org/package=wesanderson
Rassweiler, A., Okamoto, D.K., Reed, D.C., Kushner, D.J., Schroeder, D.M. & Lafferty, K.D. (2021) Improving the ability of a BACI design to detect impacts within a kelp-forest community. *Ecological Applications*, 31, e02304.
Reeder, D.M., Frank, C.L., Turner, G.G., Meteyer, C.U., Kurta, A., Britzke, E.R. et al. (2012) Frequent arousal from hibernation linked to severity of infection and mortality in bats with white-nose syndrome. *PLoS One*, 7, e38920.
Shortall, C.R., Moore, A., Smith, E., Hall, M.J., Woiwod, I.P. & Harrington, R. (2009) Long-term changes in the abundance of flying insects. *Insect Conservation and Diversity*, 2, 251–260.
Thomas, C., Jones, T.H. & Hartley, S.E. (2019) "Insectageddon": a call for more robust data and rigorous analyses. *Global Change Biology*, 25, 1891–1892.
Trewby, I.D., Wilson, G.J., Delahay, R.J., Walker, N., Young, R., Davison, J. et al. (2007) Experimental evidence of competitive release in sympatric carnivores. *Biology Letters*, 4, 170–172.
USGS. (2020) White-nose Syndrome occurrence map—by year. Available at: https://www.whitenosesyndrome.org/resources/map. Last Accessed 18 November 2020
Venesky, M.D., Parris, M.J. & Storfer, A. (2009) Impacts of Batrachochytrium dendrobatidis infection on tadpole foraging performance. *EcoHealth*, 6, 565–575.
Vidal, M.C. & Murphy, S.M. (2018) Bottom-up vs. top-down effects on terrestrial insect herbivores: a meta-analysis. *Ecology Letters*, 21, 138–150.
Whitaker, J.O., Jr. (1995) Food of the big brown bat Eptesicus fuscus from maternity colonies in Indiana and Illinois. *American Midland Naturalist*, 134, 346–360.
Whitaker, J.O., Jr. & Lawhead, B. (1992) Foods of Myotis lucifugus in a maternity colony in central Alaska. *Journal of Mammalogy*, 73, 646–648.
Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D.A., François, R. et al. (2019) Welcome to the Tidyverse. *Journal of Open Source Software*, 4, 1686 https://CRAN.R-project.org/package=tidyverse
Wilder, A.P., Frick, W.F., Langwig, K.E. & Kunz, T.H. (2011) Risk factors associated with mortality from white-nose syndrome among hibernating bat colonies. *Biology Letters*, 7, 950–953.
Wilkinson, L.C. & Barclay, R.M. (1997) Differences in the foraging behaviour of male and female big brown bats (Eptesicus fuscus) during the reproductive period. *Ecoscience*, 4, 279–285.
Willis, C.K. (2015) Conservation physiology and conservation pathogens: white-nose syndrome and integrative biology for host–pathogen systems. *Integrative and Comparative Biology*, 55, 631–641.
Wray, A.K., Gratton, C., Jusino, M.A., Wang, J.J., Kochanski, J.M., Palmer, J.M. et al. (2022) Disease-related population declines in bats demonstrate non-exchangeability in generalist predators. *Ecology and Evolution*, 12, e8978.
Wray, A.K. & Peery, M.Z. (2022) Comparing little brown and big brown bat isotopic niches over the past century in an agriculturally dominated landscape. *Journal of Mammalogy*, 103, 1045–1057.
Wray, A.K., Peery, M.Z., Jusino, M.A., Kochanski, J.M., Banik, M.T., Palmer, J.M. et al. (2021) Predator preferences shape the diets of arthropodivorous bats more than quantitative local prey abundance. *Molecular Ecology*, 30, 855–873.

SUPPORTING INFORMATION

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

How to cite this article: Wray, A.K., Peery, M.Z., Kochanski, J.M., Pelton, E., Lindner, D.L. & Gratton, C. (2024) Heterogenous effects of bat declines from white-nose syndrome on arthropods. *Ecology Letters*, 27, e14437. Available from: https://doi.org/10.1111/ele.14437