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Volume 3, 2025 Journal of North American Bat Research No. 10

Journal of North American Bat Research

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Cover Photograph: Little Brown bats in their roost at Fort Fredrick State Park, MD. Photograph © Alex Freeze.

The ***Journal of North American Bat Research*** (ISSN 2994-1075) is published by the Eagle Hill Institute, PO Box 9, 59 Eagle Hill Road, Steuben, ME 04680-0009. Phone: 207-546-2821 Ext. 4. E-mail: office@eaglehill.us. Webpage: https://www.eaglehill.us/nabr. Published on an article by article basis. **Special issue proposals are welcome**. The ***Journal of North American Bat Research*** is an open access journal. **Authors**: Submission guidelines are available at https://www.eaglehill.us/programs/journals/nabr/nabr.shtml. **Co-published journals:** The *Northeastern Naturalist*, *Southeastern Naturalist*, *Caribbean Naturalist*, and *Eastern Paleontologist*, each with a separate Board of Editors. The Eagle Hill Institute is a tax exempt 501(c)(3) nonprofit corporation of the State of Maine (Federal ID # 010379899).

2025 *Journal of North American Bat Research* 10:1–18

Acoustic Response of Bats to the Brood X Periodical Cicada (*Magicicada* spp.) Emergence

Amber S. Litterer[1], Samuel R. Freeze[1], and W. Mark Ford[2,*]

Abstract - Periodical cicada emergences can positively affect vertebrate reproduction and breeding behavior, yet this response is not well studied for bats. We examined the acoustic response of 6 species/phonic groups of bats in 2021 to the emergence of Brood X periodical cicadas, along the Potomac River corridor, in Maryland and Virginia. Using a before-after-control-impact study design, we deployed ultrasonic acoustic detectors during the summers of 2020–2022 within and just outside the range of the cicada emergence to document bat response. We observed significantly more echolocation passes during the 2021 emergence and the year following within the range of cicadas, relative to changes among years outside of the periodical cicada range. Our study demonstrates that periodical cicadas may serve as a resource that causes an increase in bat activity.

Introduction

In 2021, the largest emergence of 17-year *Magicicada* spp. (periodical cicada) broods occurred in portions of the eastern United States (Liebhold et al. 2013). The 3 species of 17-year periodical cicadas are *Magicicada septendecim* (Linnaeus), *Magicicada cassinii* (Fisher), and *Magicicada septendecula* (Alexander and Moore). They are large, hard-bodied insects that range in length and weight from 24 to 29 mm and 1.11 to 1.21 g, respectively (Alexander and Moore 1962, Karban 2014). Much of their life cycle is spent belowground feeding on tree roots as nymphs. Prior to their final molt, they emerge *en masse* in spring once the soil temperature reaches 17°C; they then climb up trees to complete their life cycle (Kritsky 2021b, Lloyd and Dybas 1966b, White and Lloyd 1975). Approximately 5 days following the molting of individuals into the adult life stage, males start calling in unison at 50–90 dB to attract females (Cooley and Marshall 2004, Maier 1982, Williams and Smith 1991). Adults remain on the landscape for about 4–6 weeks following emergence, during which mating and subsequent ovipositing by females occurs on tree branches (Cooley and Marshall 2004). Eggs hatch weeks later and nymphs drop to the forest floor to burrow below ground and feed on tree roots for the next 17 years (Kritsky 2021b, Marlatt 1907).

Over a million periodical cicadas can emerge per hectare; combined with their lack of predator avoidance, this makes them an abundant prey source for many vertebrate species (Cooley et al. 2009, Kritsky 2021b, Lloyd and Dybas 1966a, Oberdörster and Grant 2007, Williams et al. 1993). Periodical cicada emergences can be considered a ‘resource pulse,’ an event of a large magnitude over an abbreviated period that increases the availability of a resource (Yang et al. 2010). Despite their limited temporal presence on a landscape, an emergence such as that of periodical cicadas can have far-reaching and long-lasting ecological effects on soil nutrient deposition, acorn production, herbivory, and animal population dynamics (Koenig et al. 2022; Koenig and Liebhold 2005; Krohne et al. 1991; Vandegrift and Hudson 2009; Whitaker 2007; Yang 2004, 2008). For small mammals, periodical cicada

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[1]Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061. [2]U.S. Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit, Blacksburg, VA 24061. *Corresponding author: wmford@vt.edu.

Associate Editor: Paul Faure, McMaster University.

emergences can lead to earlier breeding and higher reproductive success (Vandegrift and Hudson 2009). Many species of insectivorous birds also increase recruitment and population size during and following an emergence year, respectively (Koenig and Liebhold 2005). Moreover, these effects can persist for several years (Koenig and Liebhold 2005).

Insectivorous bats are a potential, yet understudied, predator of periodical cicadas. Although bats are nocturnal and periodical cicadas largely are diurnal, there is evidence that bats will take advantage of this irregular, pulsed food resource. Periodical cicadas have been found in guano of *Eptesicus fuscus* (Palisot de Beauvois) (Big Brown Bat) and *Myotis lucifugus* (Le Conte) (Little Brown Bat) during emergence (Isenhour et al. 2024, Storm and Whitaker 2008). Furthermore, bats are known to respond to pulsed resources. For example, *Tadarida brasiliensis* (I. Geoffroy) (Brazilian Free-tailed Bats) will forage at higher altitudes during periods of increased abundance of moths (Krauel et al. 2018). Among bats foraging for emergent aquatic insects, activity was higher where insect mass from malaise traps was greater (Fukui et al. 2006). Given this, a periodical cicada emergence will have potential effects on bat populations or, at minimum, bat activity.

In addition to serving as an abundant food resource during a period of high energy requirement, i.e., pregnancy and lactation, female bats that take advantage of the emergence could have faster body weight recovery and reduced lactation stress, which in turn would lead to faster fetal growth, development, and earlier parturition (Hoying and Kunz 1998, Racey 1982, Racey and Swift 1981). During pregnancy, periods of low prey availability and low ambient temperatures can cause fetal development to slow due to bats entering torpor; additionally, timing of parturition can be based in part on insect availability (Arlettaz et al. 2001, Racey and Swift 1981). High insect abundance during lactation is nutritionally critical, as the physiological process cannot be interrupted once it begins (Racey 1982). It then follows that earlier parturition gives juvenile bats a physiological advantage by allowing them to achieve volancy sooner in the summer prior to the fall swarm and hibernation periods; earlier parturition has a positive effect on first year survival for juvenile bats (Frick et al. 2010). Additionally, survival during hibernation could be increased by improved body condition during mid-summer, leading to increased fat reserves (Kunz et al. 1998). Little Brown Bats with higher fat stores going into hibernation show higher survival rates from white-nose syndrome (Cheng et al. 2019). With wide-ranging population losses from white-nose syndrome, periodical cicada emergences could be a brief, valuable resource that positively affects local bat populations.

Using a before-after-control-impact study design, we tested whether total and individual nightly bat passes for 6 species and phonic groups — grouping of species by echolocation characteristics that can prevent unambiguous automated software identification — increased at sites within the range of the Brood X periodical cicada emergence during 2021 and 1-year post-emergence along the Potomac River corridor in central Maryland and northeastern Virginia. During the emergence, periodical cicadas were present from May to the end of June (Kritsky 2021a). In this area, these dates coincide with primarily lactating and pregnant Big Brown Bats and *Lasiurus borealis* (Müller) (Eastern Red Bat), with the first lactating bats appearing approximately 23 May and 28 May (Fig. 1), respectively (Deeley et al. 2022a). Other than outliers, volant juvenile Big Brown and Eastern Red Bats in this region did not appear until 28 June and 7 July, respectively, indicating that periodical cicadas would be available primarily to adult bats (Fig. 1; Deeley et al. 2022a). As bat acoustic activity at the local scale increases with insect abundance (Charbonnier et al. 2014), we hypothesized that echolocation passes (henceforth, "passes") for all species within the Brood X range would increase during an emergence year, due to an abundance of a novel food source and potential immigration into the local population. We also hypothesized that species-specific bat responses would be most apparent for large-bodied bat species believed more capable of utilizing periodical cicadas as prey. Lastly, we posited that the emergence might manifest itself as higher recruitment rates in the post-emergence year. For the purposes of our analyses, we used higher passes as a surrogate for increased populations.

Field-site Description

We conducted our study at 4 locations: Prince William Forest Park (PRWI) in Virginia, where no periodical cicada emergence occurred in 2021, and McKee-Beshers Wildlife Management Area (MB), Green Ridge State Forest (GR), and Prather's Neck Wildlife Management Area (PN) in Maryland, where the emergence did occur (Fig. 2). The 3 Maryland study areas (MB, PN, and GR) border the Chesapeake and Ohio Canal National Historical Park (CHOH). Prather's Neck and GR are located in the Appalachian Ridge and Valley region, whereas MB and PRWI are located in the Piedmont region to the east of the Appalachian Mountains (Cleland et al. 2007). In general, the Ridge and Valley has a landscape characterized by long linear ridges separated by broad valleys. The Piedmont is characterized by rolling hills of low local relief (McNab et al. 2007).

Owing to old-field succession following acquisition by the National Park Service, forest composition in PRWI is comprised of large *Pinus virginiana* Mill (Virginia Pine), *Liriodendron tulipifera* Linnaeus (Tulip Poplar), *Quercus* spp. (oak), and *Carya* spp. (hickory) although the midstory and understory is mainly comprised of shade-tolerant mesic species such as *Fagus grandifolia* Ehrh (American Beech) (Schmit et al. 2023). Prince William Forest Park has a mean ambient temperature during summer ranging from 17.8 to 25.7°C with

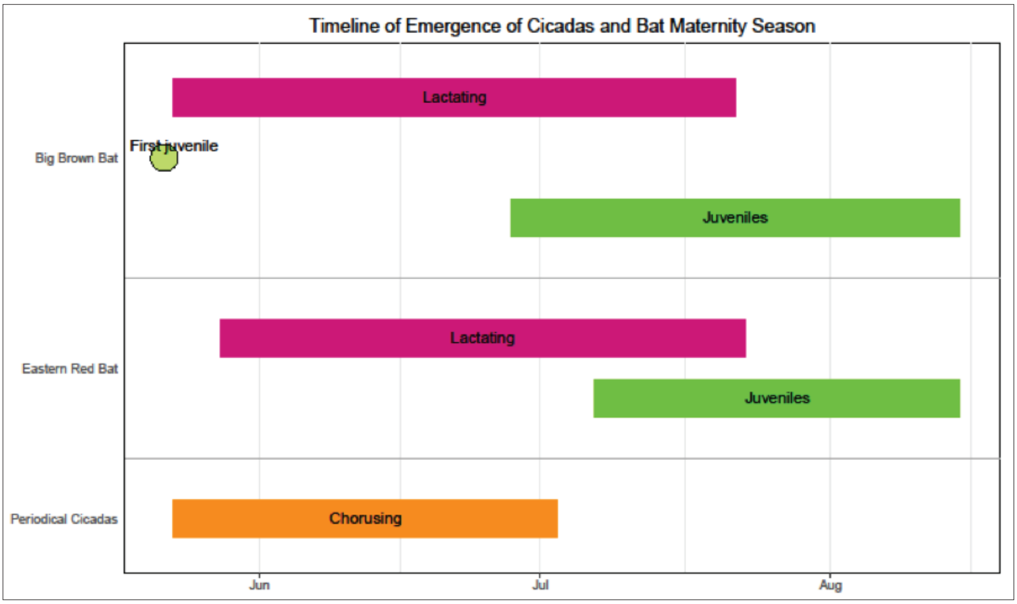

Figure 1. Timeline of reproductive phenology of Big Brown Bat (*Eptesicus fuscus*) and Eastern Red Bat (*Lasiurus borealis*) in the mid-Atlantic region, compared with the earliest and latest recorded chorusing dates of periodical cicadas (*Magicicada* spp.) during the 2021 Brood X Emergence in Maryland. Periods of lactation and appearance of juveniles on the landscape within the mid-Atlantic region are from sampling efforts of Deeley et al. (2022a).

monthly summer rainfall ranging from 8.96 to 11.56 cm (National Centers for Environmental Information 2010). Green Ridge State Forest is comprised of second growth xeric oak-hickory and *Pinus* spp. (pine) stands (Maryland Forest Service 2019). Green Ridge State Forest has low summer rainfall averaging 8.05–10.21 cm and mean summer temperatures of 17.7–24.9°C (National Centers for Environmental Information 2010). Prather's Neck contains a mix of open fields and more mesic oak and Tulip Poplar forests with summer average temperatures ranging between 16.7 and 24.1°C and monthly summer rainfall between 7.98 and 10.24 cm (Maryland Department of Natural Resources 2023a, National Centers for Environmental Information 2010). McKee-Beshers is a lowland floodplain along the Po-

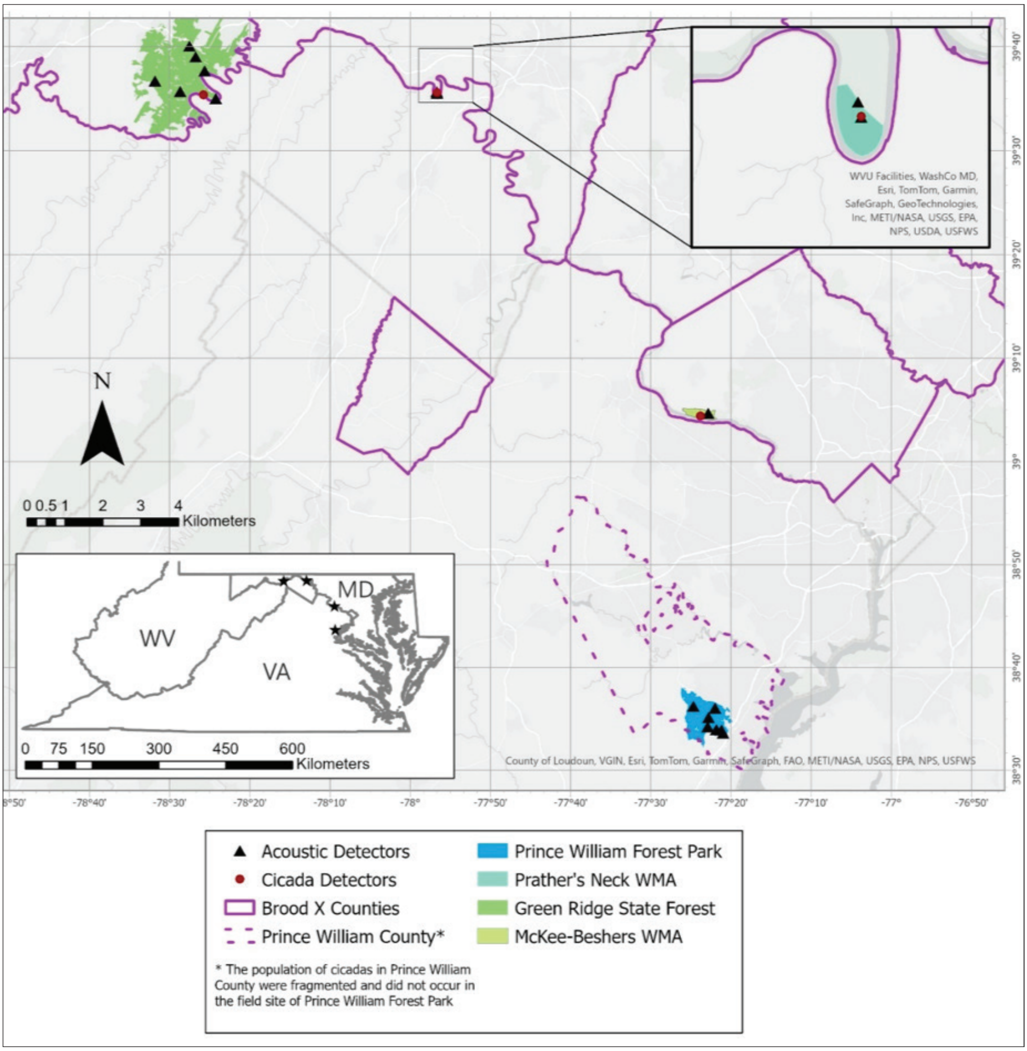

Figure 2. Location of acoustic detectors for bats during the summers of 2020–2022 at Green Ridge State Forest, Prather's Neck Wildlife Management Area, and McKee-Beshers Wildlife Management Area, Maryland, and Prince William Forest Park, Virginia. Counties that have historical records for Brood X Cicadas (Magicicada spp.) are outlined. Although Prince William County has historical records for Brood X cicadas, none emerged within the park itself. Cicada brood county records are from the U.S. Forest Service (2017).

tomac River, containing maintained wildlife food plots and bottomland forests with summer monthly mean temperatures between 16.5 and 23.5°C and summer monthly rainfall ranging between 8.66 and 10.56 cm (Maryland Department of Natural Resources 2023b, National Centers for Environmental Information 2010).

Methods

Data collection

Bat acoustics. During summers (1 May–15 August) 2020–2022, we deployed 16 ultrasonic acoustic detectors (Song Meter SM4Bat ZC and Song Meter Mini Bat, Wildlife Acoustics, Maynard, MA) and microphones (SMM-U1 and SMM-U2, Wildlife Acoustics) at sites in PRWI (n = 7), MB (n = 1), GR (n = 6), and PN (n = 2; Fig. 2), with detector number per site constrained by area size as we attempted to minimize spatial autocorrelation within sites by keeping detectors >300 m apart (De La Cruz et al. 2024). The acoustic detectors were set to record individual passes if the correct minimum frequency trigger was met (>16 kHz) between 60 min before sunset and 60 min after sunrise (Gorman et al. 2021, Loeb et al. 2015). We mounted microphones on extendable poles that were directed into the flyway (Loeb et al. 2015). All sites were in road corridors, canopy gaps, field edges, or over streams to facilitate the acquisition of high-quality echolocation passes (Loeb et al. 2015). We minimized variability by sampling at each detector location in all 3 years of this study. We considered detectors within 100 m of each other in different years to be the same detector site based on the liberal estimate of the effective microphone distance (Wildlife Acoustics 2018).

We used Kaleidoscope Pro 5.4.7 with a Bats of North America 5.4.0 classifier under a '-1' or liberal sensitivity setting (Wildlife Acoustics) to identify species presence and activity levels following U.S. Fish and Wildlife Service protocols (U.S. Fish and Wildlife Service 2019). Ten species were considered: *Aeorestes cinereus* (Palisot de Beauvois) (North American Hoary Bat), Big Brown Bat, *Lasionycteris noctivagans* (Le Conte) (Silver-haired Bat), Eastern Red Bat, *Myotis leibii* (Audubon and Bachman) (Eastern Small-footed Bat), Little Brown Bat, *Myotis septentrionalis* (Trouessart) (Northern Long-eared Bat), *Myotis sodalis* Miller and G.M. Allen (Indiana Bat), *Perimyotis subflavus* (F. Cuvier) (Tricolored Bat), and *Nycticeius humeralis* (Rafinesque) (Evening Bat) (Deeley et al. 2021, Johnson et al. 2008). Our study sites were within the northern extent of the Evening Bat distribution and Evening Bats were recently documented in small numbers at PRWI and CHOH (Deeley et al. 2021, Watkins 1972).

Acoustic passes at each site and of each species identified by the software were grouped into nightly totals. Nights without any acoustic call data during which detector log files indicated operation were coded as 'zero' nights. To calculate bat passes for individual species, we used the U.S. Fish and Wildlife Service's maximum likelihood estimate (MLE) threshold of $P < 0.05$ to ensure high identification certainty of passes. Nightly pass totals that had an MLE $P > 0.05$ for any species were given a value of zero (U.S. Fish and Wildlife Service 2023).

Periodical cicada acoustics. In summer 2021, we deployed 3 additional acoustic detectors with attached microphones (Song Meter SM3 FS and SMM-U2, Wildlife Acoustics) at MB, PN, and GR to record periodical cicadas (Fig. 2). Sites for these detectors were chosen prior to the emergence and were placed alongside roads and streams in forested areas of sufficient age to support periodical cicadas that were present during the last emergence and subsequent egg laying (Kritsky 2021b). These detectors were scheduled to record for

10-min increments every 3 h from sunrise to sunset to capture the peak calling periods of periodical cicadas (Maier 1982, Williams and Smith 1991).

We reviewed all audio files to determine initial and final dates of periodical cicada chorusing and used the minimum (23 May 2021; numerical day 143) and maximum (3 July 2021; numerical day 184) dates as a proxy for the period in which a significant portion of the periodical cicada population was active on the landscape. As most males in an area emerge in a 6-day span and begin calling approximately 5 days after molting, chorusing indicates that a significant portion of the periodical cicada population is present on the landscape (Maier 1982, Williams et al. 1993). We visited each bat detector site once during the emergence to confirm the presence or absence of periodical cicadas. Maryland sites MB, GR, and PN (in), fell within the Brood X emergence whereas PRWI (out) in Virginia fell outside the emergence.

Statistical analyses

We examined the changes in bat echolocation activity during the days periodical cicadas were present on the landscape and during the days periodical cicadas were absent on the landscape the year prior to and after the emergence. We modeled the interaction among years (2020, 2021, and 2022) and periodical cicada range (in or out), numerical day of the year, and the quadratic polynomial numerical day of the year, nightly precipitation, and the random effect of detector site on our response variable of total nightly bat passes using a generalized linear mixed model with a negative binomial distribution using R version 4.2.1 (R Core Team 2022) and the package *glmmTMB* (Brooks et al. 2017). We included the quadratic polynomial numerical day of the year as bat activity often will show a curvilinear pattern rising to a peak in mid-summer and then decline thereafter (Reynolds et al. 2016, Gorman et al. 2021). To calculate nightly precipitation, we gathered hourly precipitation from the nearest airport station to each study area using the Iowa Environmental Mesonet and the package *riem* (Salmon 2022). Hourly precipitation was then converted to total nighttime precipitation. We took a subset of all nightly acoustic passes, including only those from numerical days 143–184, which were the dates of first and last chorusing in 2021. This allowed for a before-after-control-impact assessment.

We fit an all-species model and a model for each of the following 6 species and phonic groups: Big Brown/Silver-haired Bat, *Myotis* spp., North American Hoary Bat, Tricolored Bat, Eastern Red Bat, and Evening Bat. We combined the Big Brown Bat and Silver-haired Bat into 1 group owing to their high rate of inter-specific misclassification (U.S. Fish and Wildlife Service 2019). Additionally, because of white-nose syndrome, Indiana Bats, Eastern Small-footed Bats, Northern Long-eared Bats, and Little Brown Bats often generate nightly echolocation pass numbers insufficient to overcome similar interspecific misclassifications rates; consequently, we created a *Myotis* spp. phonic group (Beilke et al. 2021, Hoyt et al. 2021, Russo et al. 2018). For the all-species model, all nightly bat passes (excluding noise and no ID files) were examined as our response variable, regardless of MLE *P*-value, due to our interest in total bat passes and not just those identifiable to species. For individual species and the 2 phonic groups, we only included high confidence passes from nights with low MLE scores for our response variable. We considered a bat pass to be a single call file. We also fit all nested models and used the small-sample corrected Akaike Information Criterion (*AIC*c) to evaluate the best fit model within 2 *AIC*c units using the package *AICcmodavg* (Mazerolle 2023). If multiple models were within 2 *AIC*c units, the most parsimonious model was selected as the top model. For all models, we checked for overdispersion using the package *performance* (Lüdecke et al. 2021) and used the likelihood ratio test between our top model and the null model to determine if the model was superior to the null model. We visually assessed the residuals of our model to confirm they met assumptions and were random. We predicted nightly bat passes for each species and phonic group model using base R and plotted all models using *ggplot2* (Wickham 2016).

Results

In 2021, Brood X periodical cicadas were confirmed in GR, PN, and MB through both visual assessment and acoustic recordings. Although these cicadas emerged in 2021 in the western and northern portions of Prince William County, Virginia, they were absent from all of PRWI, allowing us to retain that study area as a control (C. Smith, Department of Environmental Science and Policy, George Mason University, Fairfax, VA, USA, pers. comm., 2023). Not all impacted study areas had the same chorusing date ranges; the earliest chorusing dates ranged from 23 to 31 May 2021 and last chorusing dates ranged from 29 June to 3 July 2021. These dates coincided with numerous reports of periodical cicadas emerging in Maryland during the first 2 weeks of May, with chorusing occurring across their range by 18 May 2021 (Kritsky 2021a). Moreover, periodical cicadas from this brood in southern Ohio were last reported chorusing on 2 July 2021 (Kritsky 2021a). The earliest recorded periodical cicada chorusing occurred on 23 May 2021 in PN, and the last recorded chorusing occurred on 3 July 2021 in PN. In contrast, periodical cicadas in GR and MB were recorded from 31 May to 29 June 2021 and 25 May to 30 June 2021, respectively.

From 23 May to 3 July (numerical days 143–184) of 2020–2022, we acoustically recorded 1579 nights of bat activity across 16 sites. We detected all 6 species and phonic groups of bats each year and at all sites within and outside the periodical cicada range.

For all bat activity during the days of the Brood X emergence for the years 2020–2022, there were 3 models within 2 *AIC*c, but the most parsimonious model included the random effect of detector site and the predictor variables of precipitation and the interaction between periodical cicada range and year (Table 1). Although we chose the most parsimonious model within 2 *AIC*c as our top model, we show all models within 4 *AIC*c as they have some empirical support (Table 1). Overall, there was a significantly lower number of bat passes recorded within the range of periodical cicadas compared with

Table 1. *AIC*c (Akaike information criteria, corrected for small sample sizes) table for models of all species nightly bat activity at sites within and outside of the cicada emergence during the summers of 2020–2022. The null model and all generalized linear mixed models with *AIC*c $\leq$ 4 of the top model are included. Twenty-eight models and a null model were evaluated. Parks within the range of the 2021 Brood X Cicada (*Magicicada* spp.) emergence (in) were in Maryland and included Green Ridge State Forest, McKee-Beshers Wildlife Management Area, and Prather's Neck Wildlife Management Area. Prince William Forest Park in Virginia was outside of the range of the 2021 Brood X Cicada emergence (out). *AIC*c score, delta *AIC*c, and model weights are shown. The asterisk denotes an interaction. Predictor variables included the random effect of detector location and the fixed effects of precipitation, numerical day, quadratic numerical day, cicada range, and year.

Model	*AIC*c	Δ*AIC*c	Weight
(1|Detector) + Day + Precipitation + Cicada Range * Year	19809.02	0.00	0.37
(1|Detector) + Precipitation + Cicada Range * Year	19809.28	0.26	0.33
(1|Detector) + Day^2 + Day + Precipitation + Cicada Range * Year	19809.46	0.43	0.30
Null model	20118.02	308.99	0

outside the range ($P < 0.001$). However, bat passes within the range were significantly higher the year during and the year following emergence ($P < 0.001$; Table 2, Fig. 3).

For each of the 6 species and phonic groups, the top models within 2 *AIC*c examining acoustic activity during the numerical days 143–184 of the Brood X emergence for the years 2020–2022 all included the random effect of detector site and the interaction between periodical cicada range and year (Table 3). The top model for the Evening Bat included numeric day as a predictor variable and the top models for the Eastern Red Bat, North American

Table 2. Model output for the top and most parsimonious generalized linear mixed model of all bat activity is shown for years 2020–2022 and days 143–184. The model includes the response of total nightly bat passes to the interaction between cicada range and year plus nightly precipitation for 2020–2022 (Passes ~ (1|Detector) + Cicada Range * Year + Precipitation). Detector sites were at Green Ridge State Forest, McKee-Beshers Wildlife Management Area, Prather's Neck Wildlife Management Area in Maryland and Prince William Forest Park in Virginia. The coefficient values (β), standard errors (*SE*), and probability (*P*) are shown. Range (in) refers to areas that were within the 2021 Brood X periodical cicada emergence. The asterisk denotes an interaction. The numeric day was scaled by dividing the centered values by their standard deviation.

All Bat Passes

Variable	β	*SE*	*P*
Intercept[a]	5.46	0.32	< 0.001
Range (in)	-1.97	0.44	< 0.001
Year (2021)	-0.85	0.10	< 0.001
Year (2022)	-0.27	0.11	0.01
Precipitation	-0.56	0.05	< 0.001
Range (in) * Year (2021)	2.75	0.20	< 0.001
Range (in) * Year (2022)	2.90	0.20	< 0.001

[a] Intercept is for Range (out) and Year (2020).

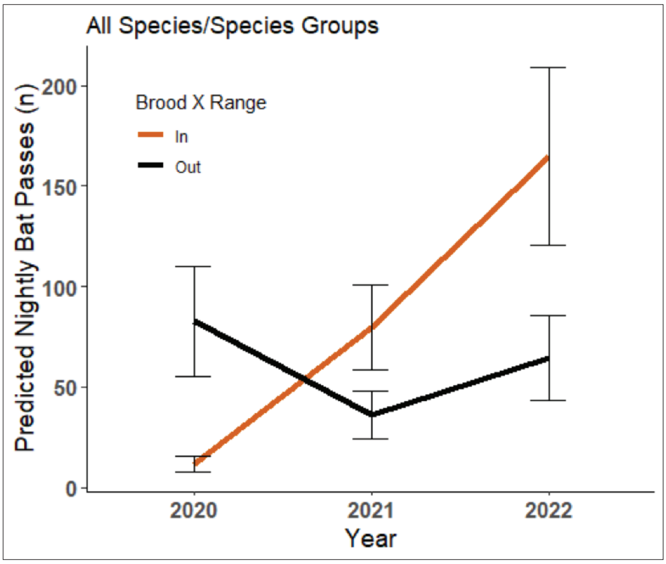

Figure 3. Predicted nightly bat passes with 95% confidence intervals for all species/phonic groups are plotted for years 2020–2022 during the numeric days 143–184. The mean number of predicted total nightly bat passes for each year and range are shown. Sites within (in) the Brood X periodical cicada range (*Magicicada* spp.) include Green Ridge State Forest, McKee-Beshers Wildlife Management Area, and Prather's Neck Wildlife Management Area, Maryland and sites outside (out) include Prince William Forest Park, Virginia.

Table 3. *AIC*c (Akaike information criteria, corrected for small samples sizes) table for models of nightly bat activity for each species/phonic group at sites within and outside of the cicada emergence during the summers of 2020–2022. The null model and all generalized linear mixed models with *AIC*c ≤ 4 of the top model are included. Twenty-eight models and a null model were evaluated. Parks within the range of the 2021 Brood X cicada (*Magicicada* spp.) emergence (in) were in Maryland and included Green Ridge State Forest, McKee-Beshers Wildlife Management Area, and Prather's Neck Wildlife Management Area. Prince William Forest Park in Virginia was outside of the range of the 2021 Brood X cicada emergence (out). *AIC*c score, delta *AIC*c, and model weights are shown. The asterisk denotes an interaction. Predictor variables included the random effect of detector location and the fixed effects of precipitation, numerical day, quadratic numerical day, cicada range, and year.

Species/Phonic Group	Model	AICc	ΔAICc	Weight
Big Brown/Silver-haired Bat (*Eptesicus fuscus - Lasionycteris noctivagans)*	(1|Detector) + Day + Precipitation + Cicada Range * Year	14078.40	0	0.71
	(1|Detector) + Day + Day^2 + Precipitation + Cicada Range * Year	14080.22	1.82	0.29
	Null model	14154.16	75.76	0
Eastern Red Bat (*Lasiurus borealis*)	(1|Detector) + Precipitation + Cicada Range * Year	13008.67	0	0.64
	(1|Detector) + Day + Precipitation + Cicada Range * Year	13010.67	2.0	0.24
	(1|Detector) + Day + Day^2 + Precipitation + Cicada Range * Year	13012.02	3.34	0.12
	Null model	13223.60	214.92	0
North American Hoary Bat (*Aeorestes cinereus*)	(1|Detector) + Precipitation + Cicada Range * Year	7409.16	0	0.41
	(1|Detector) + Day + Precipitation + Cicada Range * Year	7410.76	1.60	0.18
	(1|Detector) + Day + Day^2 + Precipitation + Cicada Range * Year	7411.01	1.85	0.16
	Null model	7421.61	12.45	0
Myotis spp.	(1|Detector) + Precipitation + Cicada Range * Year	12819.11	0	0.56
	(1|Detector) + Day + Precipitation + Cicada Range * Year	12820.52	1.41	0.28
	(1|Detector) + Day + Day^2 + Precipitation + Cicada Range * Year	12821.57	2.46	0.16
	Null model	13019.15	200.04	0
Evening Bat (*Nycticeius humeralis*)	(1|Detector) + Day + Cicada Range * Year	5294.23	0	0.43
	(1|Detector) + Day + Precipitation + Cicada Range * Year	5294.95	0.73	0.30
	(1|Detector) + Day + Day^2 + Cicada Range * Year	5296.22	1.99	0.16
	(1|Detector) + Day + Day^2 + Precipitation + Cicada Range * Year	5296.94	2.71	0.11
	Null model	5326.04	31.82	0
Tricolored Bat *(Perimyotis subflavus*)	(1|Detector) + Day + Precipitation + Cicada Range * Year	6811.31	0	0.52
	(1|Detector) + Day + Day^2 + Precipitation + Cicada Range * Year	6812.57	1.26	0.28
	(1|Detector) + Precipitation + Cicada Range * Year	6813.46	2.15	0.18
	Null model	6866.69	55.38	0

Hoary Bat, and *Myotis* spp. included precipitation as a predictor variable (Table 3). The top models for the Tricolored Bat, and Big Brown Bat/Silver-haired Bat phonic group included numeric day and precipitation as predictor variables (Table 3). For all individual species and phonic groups, bat passes increased the year during and year after emergence within the range of periodical cicadas compared to the year prior to emergence ($P \leq 0.002$; Table 4, Figs. 3–4). Rain had a significant and negative effect on the number of bat passes for all species and phonic groups, not including the Evening Bat top model that did not include precipitation ($P \leq 0.002$; Table 4).

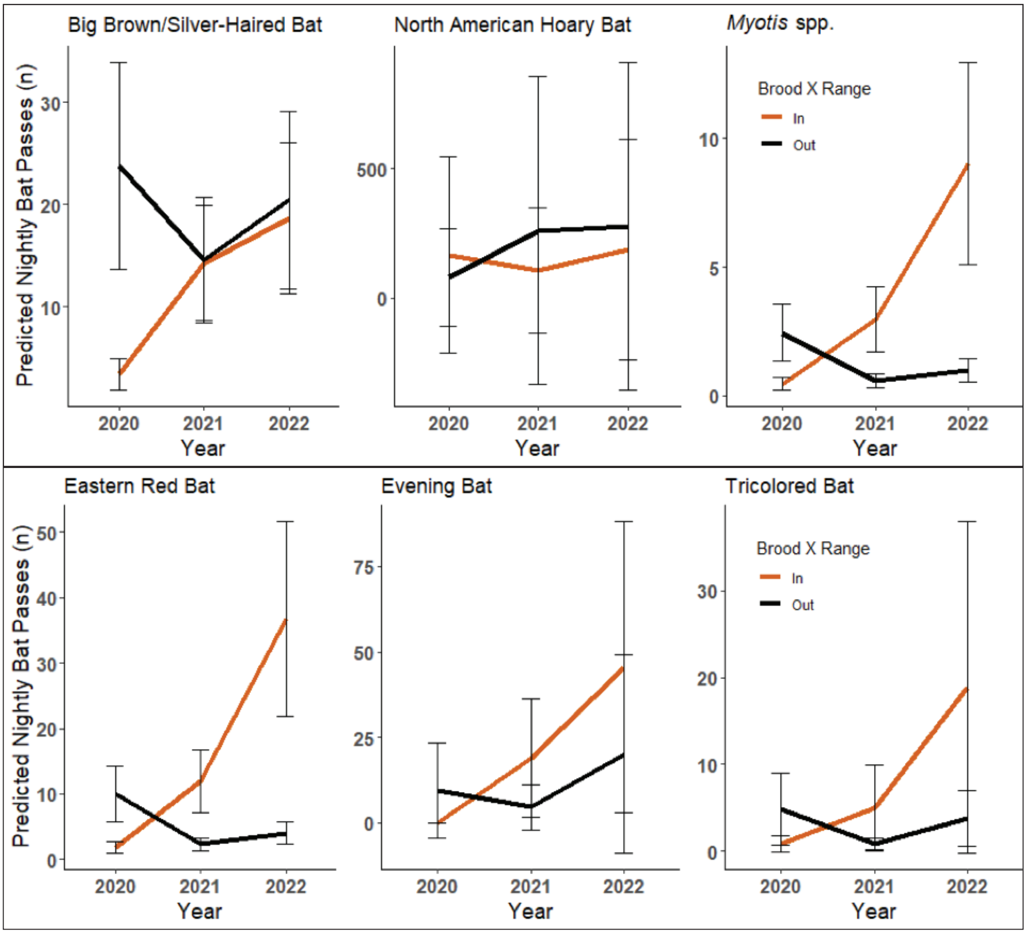

Figure 4. Predicted nightly bat passes with 95% confidence intervals for individual species/phonics groups are plotted for years 2020–2022 during the numeric days 143–184. For all models, the mean number of predicted nightly bat passes for each year and range are shown. Species include Big Brown/Silver-haired Bats (*Eptesicus fuscus - Lasionycteris noctivagans)* North American Hoary Bats (*Aeorestes cinereus*), *Myotis* spp., Eastern Red Bats (*Lasiurus borealis*), Evening Bats (*Nycticeius humeralis*), and Tricolored Bats (*Perimyotis subflavus*). Sites within (in) the Brood X periodical cicada range (*Magicicada* spp.) include Green Ridge State Forest, McKee-Beshers Wildlife Management Area, and Prather's Neck Wildlife Management Area, Maryland and sites outside (out) include Prince William Forest Park, Virginia.

Table 4. Model outputs for the top and most parsimonious generalized linear mixed models for each species or phonic group is shown for years 2020–2022 and days 143–184. All models include the response of low maximum likelihood estimate nightly passes. Detector sites were at Green Ridge State Forest, McKee-Beshers Wildlife Management Area, Prather's Neck Wildlife Management Area in Maryland, and Prince William Forest Park in Virginia. The coefficient values (β), standard errors (*SE*), and probability (*P*) are shown. Range (in) refers to areas that were within the 2021 brood X cicada (*Magicicada* spp.) emergence. The asterisk denotes an interaction. The numerical day was scaled by dividing the centered values by their standard deviation.

Species/Phonic Group	**Variable**	**β**	***SE***	***P***
Passes ~ (1|Detector) + Day + Precipitation + Range * Year				
Big Brown/Silver-haired Bat (*Eptesicus fuscus- Lasionycteris noctivagans*)	Intercept[a]	4.02	0.42	< 0.001
	Day	-0.16	0.04	< 0.001
	Range (in)	-1.96	0.60	0.001
	Year (2021)	-0.49	0.15	< 0.001
	Year (2022)	-0.15	0.16	0.328
	Precipitation	-0.56	0.08	< 0.001
	Range (in) * Year (2021)	1.93	0.29	< 0.001
	Range (in) * Year (2022)	1.86	0.29	< 0.001
Passes ~ (1|Detector) + Precipitation + Range * Year				
Eastern Red Bat (*Lasiurus borealis*)	Intercept[a]	3.57	0.42	< 0.001
	Range (in)	-2.70	0.60	< 0.001
	Year (2021)	-1.19	0.15	< 0.001
	Year (2022)	-0.44	0.16	0.006
	Precipitation	-0.70	0.09	< 0.001
	Range (in) * Year (2021)	3.71	0.31	< 0.001
	Range (in) * Year (2022)	3.93	0.31	< 0.001
Passes ~ (1|Detector) + Precipitation + Range * Year				
North American Hoary Bat (*Aeorestes cinereus*)	Intercept[a]	1.77	0.54	0.001
	Range (in)	-0.64	0.79	0.417
	Year (2021)	-0.47	0.27	0.086
	Year (2022)	-0.29	0.31	0.341
	Precipitation	-0.60	0.16	0.002
	Range (in) * Year (2021)	1.54	0.49	0.002
	Range (in) * Year (2022	1.64	0.50	0.001
Passes ~ (1|Detector) + Precipitation + Range * Year				
***Myotis* spp.**	Intercept[a]	3.52	0.41	< 0.001
	Range (in)	-1.68	0.60	0.005
	Year (2021)	-1.44	0.17	< 0.001
	Year (2022)	-0.90	0.18	< 0.001
	Precipitation	-0.81	0.11	< 0.001
	Range (in) * Year (2021)	3.31	0.33	< 0.001
	Range (in) * Year (2022)	3.89	0.35	< 0.001

Table 4. Continued.

Species/Phonic Group	**Variable**	**β**	***SE***	***P***
Passes ~ (1|Detector) + Day + Range * Year				
Evening Bat (*Nycticeius humeralis*)	Intercept[a]	1.19	1.01	0.239
	Day	0.62	0.16	< 0.001
	Range (in)	-5.17	1.62	0.001
	Year (2021)	-0.69	0.73	0.346
	Year (2022)	0.78	0.53	0.139
	Range (in) * Year (2021)	6.61	1.26	< 0.001
	Range (in) * Year (2022)	6.03	1.14	< 0.001
Passes ~ (1|Detector) + Day + Precipitation + Range * Year				
Tricolored Bat (*Perimyotis subflavus*)	Intercept[a]	1.86	0.94	0.048
	Day	0.20	0.10	0.041
	Range (in)	-1.79	1.38	0.19
	Year (2021)	-1.79	0.39	< 0.001
	Year (2022)	-0.24	0.40	0.540
	Precipitation	-0.89	0.29	0.002
	Range (in) * Year (2021)	3.61	0.75	< 0.001
	Range (in) * Year (2022)	3.39	0.82	< 0.001

[a] Intercept is for Range (out) and Year (2020).

Discussion

We saw a significant increase in bat acoustic activity in both total activity and across all observed bat species and phonic groups within the range of Brood X periodical cicadas the year during and year following emergence compared to the year prior to emergence. In contrast, total echolocation passes outside the emergence area decreased from 2020 to 2021 and did not significantly change from 2021 to 2022. This suggests that bats were responding to the periodical cicada emergence itself. Although acoustic detections of bats have biases that limit inference, i.e., variable detection probabilities (Adams et al. 2012), changes in activity are used broadly as a surrogate for population responses (Evans et al. 2021, Lintott et al. 2013). Therefore, this increase in acoustic activity during and following the emergence suggests an increase in local bat populations.

Bats have shown significant responses to other insect emergences with greater aggregations and intake occurring at sites experiencing outbreaks of *Choristoneura freemani* Razowski (Western Spruce Budworm) (Blažek et al. 2021, Wilson and Barclay 2006). Increases in feeding buzzes of generalist bat species in response to increased pest moth availability also has been observed (Charbonnier et al. 2014). Although fecal samples were not collected during our study to confirm consumption of periodical cicadas, consumption by Big Brown Bats has been documented in other emergence years (Storm and Whitaker 2008) and annual Cicadidae (true cicada) consumption occurs in non-periodic cicada emergence years in our study area (Deeley et al. 2022b). Isenhour et al. (2024) found *Magicicada* spp. DNA from the Brood X emergence in the feces of Little Brown Bats north of our study area, in central Pennsylvania. This indicates that smaller bat species can consume these large prey items. Moreover, examples of prey within the size range of periodical cicadas are common in the literature for several species. Evening Bats consume Lepidopteran agricultural pests with body lengths ranging from 27 to 34 mm (Hughes et al. 2021) and Little Brown Bats are known to feed on species such as *Parcoblatta pensylvanica* (De Greer) (Pennsylvania Wood Cockroach), with a body length of 16.8–24.5 mm for flighted males, and *Chauliodes pectinicornis* (L.) (Summer Fishfly) with a body size of 21–46 mm (Blatchley 1920, O'Rourke et al. 2022, Rasmussen and Pescador 2002). As periodical cicadas are slower flyers than annual cicadas and have limited predator-avoidance strategies, insectivorous bats on the landscape could easily prey on periodical cicadas via hawking or gleaning (Oberdörster and Grant 2007). Because flight activity of periodical cicadas largely is diurnal, this suggests that bats may employ gleaning to prey on these insects at night. The species in our study area, Big Brown Bats, Eastern Red Bats, Little Brown Bats, and Northern Long-eared Bats, have been documented using gleaning behavior (Arh 2009, Jarzonbek 2009, Ratcliffe and Dawson 2003).

The size of the periodical cicada is not the only limiting factor for consumption by bats. The bite force needed to consume different insects is affected by the size and taxon of the insect and the robustness of the bat skull (Freeman 1981, Freeman and Lemen 2007). Hemiptera (true bugs), which includes periodical cicadas, have a wide-ranging hardness index, but one that generally is ranked between Coleoptera (beetles) and Lepidoptera (butterflies and moths) (Freeman 1981, Freeman and Lemen 2007). Big Brown Bats and Evening Bats consume much more Coleoptera (Feldhamer et al. 2009, Long et al. 2013, Whitaker 1995, Whitaker and Clem 1992), whereas Lasiurines consume more Lepidoptera, although their skull and jaw morphology allows them to consume harder prey (Feldhamer et al. 2009, Freeman 1981).

The timing of the emergence in 2021 coincided with the timing of pregnancy and lactation of Big Brown and Eastern Red bats along the CHOH (Deeley et al. 2022a). As increased prey availability during pregnancy possibly led to earlier parturition and subsequent earlier lactation, bat foraging activity, as measured by acoustic detection, could have increased during the periodical cicada emergence in 2021 (Arlettaz et al. 2001, Reynolds and Kunz 2000). This pattern has been observed in Brazilian Free-tailed Bats following the movements and migrations of *Helicoverpa zea* (Boddie) (Corn Earworm Moth) during pregnancy, lactation, and fall migration (McCracken et al. 2012). Overall, many temperate-zone insectivorous bats have flexible diets that allow shifts in response to ephemeral resources (Wilson and Barclay 2006). Additionally, with the potential for earlier volancy leading to higher first-year survival, the increase in acoustic activity the year following emergence could be due to recruitment into the population (Frick et al. 2010). For other vertebrates, movement into an area following a resource pulse is well-documented (Yang et al. 2010). Some individuals and/or their offspring possibly took advantage of this resource pulse and then returned to the landscape the following year, thereby causing the year post-emergence to have continued higher levels of bat activity. Regional changes, such as an emigration from the cicada-absent nearby landscape, could have contributed to the increased activity within the cicada range.

Beyond food availability, periodical cicadas also affect the architecture of the forest through ovipositing of eggs, which subsequently damage branches and cause the wilting of leaves (Smith and Linderman 1974). Ovipositing occurs in various tree species, and injuries to branches can occur the year of or the year after emergence, depending on the species (Smith and Linderman 1974). Positive responses to insect-derived changes in forest structure have been documented in *Barbastella barbastellus* (Schreber) (European Barbastelle) that exclusively formed maternity colonies in spruce trees previously killed by *Ips typographus* L. (European Spruce Bark Beetle) (Kortmann et al. 2018). For species that roost in dead foliage, such as the Lasiurines and the Tricolored Bat, the increase in echolocation passes could result from immigration into an area with more suitable roost availability (Carter and Menzel 2007, Kunz and Lumsden 2003, Newman et al. 2021).

Bats in the mid-Atlantic are experiencing numerous population stressors such as white-nose syndrome, wind-energy development, and forest fragmentation (Hayes 2013, Hoyt et al. 2021). Although periodical cicadas disappear from the landscape before dispersion and migration of bats to hibernacula, increased food availability during the reproductive period may improve bat body condition that, in turn, might contribute to higher survival during hibernation when exposure to white-nose syndrome occurs. For example, to counteract the effects of white-nose syndrome, researchers have artificially increased food resources during critical pre-hibernation foraging periods for bats, which has improved body condition before hibernation, leading to increased survival (Cheng et al. 2019, Frick et al. 2023).

Our research demonstrates a positive response of bats to the periodical cicada emergence, indicative of at least a short-term regional increase in activity. This response is consistent with other vertebrates presented with a periodical cicada emergence (Koenig and Liebhold 2005). Although 1 study found that within-year activity of Big Brown and North American Hoary Bats did not change during an emergence (Proudman et al. 2024), we found activity among years to be significantly different. Overall, resource pulses such as periodical cicada emergences appear to elicit a measurable response by mid-Atlantic bat species beyond the ephemeral presence of the insects on the landscape. As emergences from 15 distinct broods occur across much of the eastern United States, future and long-term studies could contribute to our understanding of whether the effects on activity, movement, and then potentially population and body condition were causal or merely correlative. Increased long-term site monitoring of bats through efforts such as the North American Bat Monitoring Program (Loeb et al. 2015) that will overlap in space and time with the various cicada broods at local and regional scales may be an avenue to validate our conclusions.

Acknowledgments

Michael True, H. Taylor, M. Moran, and R. Green assisted in field efforts. Project funding was provided by the National Park Service Chesapeake Watershed Cooperative Ecosystem Study Unit grant P19AC01216 to Virginia Polytechnic Institute and State University. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. At the time of publication, data were not publicly available from the National Park Service. Amber Litterer (amberlitterer@vt.edu) can be contacted for data availability.

Literature Cited

Adams, A.M., M.K. Jantzen, R.M. Hamilton, and M.B. Fenton. 2012. Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. Methods in Ecology and Evolution 3:992–998.

Alexander, R.D., and T.E. Moore. 1962. The evolutionary relationships of 17-year and 13-year cicadas, and three new species (Homoptera, Cicadidae, *Magicicada*). Miscellaneous Publications, Museum of Zoology, University of Michigan 121:5–59.

Arh, M.R. 2009. Foraging ecology of a bat assemblage. M.S. Thesis. University of Toronto, Toronto, ON, Canada. 80 pp.

Arlettaz, R., P. Christe, A. Lugon, N. Perrin, and P. Vogel. 2001. Food availability dictates the timing of parturition in insectivorous mouse-eared bats. Oikos 95:105–111.

Beilke, E.A., R.V. Blakey, and J.M. O'Keefe. 2021. Bats partition activity in space and time in a large, heterogeneous landscape. Ecology and Evolution 11:6513–6526.

Blatchley, W.S. 1920. Orthoptera of Northeastern America, with Especial Reference to the Faunas of Indiana and Florida. The Nature Publishing Company, Indianapolis, IN. 786 pp.

Blažek, J., A. Konečný, and T. Bartonička. 2021. Bat aggregational response to pest caterpillar emergence. Scientific Reports 11(13634):1–11.

Brooks, M.E., K. Kristensen, K.J. van Benthem, A. Magnusson, C.W. Berg, A. Nielsen, H.J. Skaug, M. Maechler, and B.M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378–400.

Carter, T.C., and J.M. Menzel. 2007. Behavior and day-roosting ecology of North American foliage-roosting bats. Pp. 61–82, *In* M.J. Lacki, J.P. Hayes, and A. Kurta (Eds.). Bats in Forests: Conservation and Management. The Johns Hopkins University Press, Baltimore, MD. 329 pp.

Charbonnier, Y., L. Barbaro, A. Theillout, and H. Jactel. 2014. Numerical and functional responses of forest bats to a major insect pest in pine plantations. PLoS ONE 9:1–8.

Cheng, T.L., A. Gerson, M.S. Moore, J.D. Reichard, J. DeSimone, C.K.R. Willis, W.F. Frick, and A.M. Kilpatrick. 2019. Higher fat stores contribute to persistence of Little Brown Bat populations with white-nose syndrome. Journal of Animal Ecology 88:591–600.

Cleland, D.T., J.A. Freeouf, J.E. Keys, G.J. Nowacki, C.A. Carpenter, and W.H. McNab. 2007. Ecological subregions: Sections and subsections for the conterminous United States. General Technical Report WO-76D. U.S. Department of Agriculture, Forest Service, Washington DC., USA. 1 pp.

Cooley, J.R., and D.C. Marshall. 2004. Thresholds or comparisons: Mate choice criteria and sexual selection in a periodical cicada, *Magicicada septendecim* (Hemiptera: Cicadidae). Behaviour 141:647–673.

Cooley, J.R., G. Kritsky, M. Edwards, J. Zyla, D. Hill, R. Krauss, and C. Simon. 2009. The distribution of periodical cicada Brood X in 2024. American Entomologist 55:106–112.

Deeley, S., W.M. Ford, N. Kalen, S. Freeze, M. St. Germain, M. Muthersbaugh, E. Barr, A. Kniowski, A. Silvis, and J. De La Cruz. 2022a. Mid-Atlantic Big Brown and Eastern Red Bats: Relationships between acoustic activity and reproductive phenology. Diversity 14:1–10.

Deeley, S., S. Freeze, and L. Rohrbaugh. 2021. Post-white-nose syndrome bat communities in the National Capital Region: Part 1-final report. Natural Resource Report NPS/NCRO/NRR—2021/2319. U.S. Department of the Interior, National Park Service, Natural Resource Stewardship and Science, Fort Collins, CO. 104 pp.

Deeley, S., L. Kang, P. Michalak, E. Hallerman, and W.M. Ford. 2022b. DNA metabarcoding-based evaluation of the diet of Big Brown Bats (*Eptesicus fuscus*) in the mid-Atlantic Region. Northeastern Naturalist 29:454–473.

De La Cruz, J.L., N.J. Kalen, E.L. Barr, E.D. Thorne, R.J. Reynolds, and W.M. Ford. 2024. Seasonal drivers of activity in the endangered Northern Long-eared Bat in eastern North Carolina and Virginia. Journal of the Southeastern Association of Fish and Wildlife Agencies 11:185–195.

Evans, K.O., A.D. Smith, and D. Richardson. 2021. Statistical power of mobile acoustic monitoring to detect population change in southeastern U.S. bat species, a case study. Ecological Indicators 125:1–10.

Feldhamer, G.A., T.C. Carter, and J.O. Whitaker, Jr. 2009. Prey consumed by eight species of insectivorous bats from southern Illinois. American Midland Naturalist 162:43–51.

Freeman, P.W. 1981. Correspondence of food habits and morphology in insectivorous bats. Journal of Mammalogy 62:166–173.

Freeman, P.W., and C.A. Lemen. 2007. Using scissors to quantify hardness of insects: Do bats select for size or hardness? Journal of Zoology 271:469–476.

Frick, W.F., Y.A. Dzal, K.A. Jonasson, M.D. Whitby, A.M. Adams, M.C. Long, J.E. Depue, C.M. Newman, C.K.R. Willis, and T.L. Cheng. 2023. Bats increased foraging activity at experimental prey patches near hibernacula. Ecological Solutions and Evidence 4:1–11.

Frick, W.F., D.S. Reynolds, and T.H. Kunz. 2010. Influence of climate and reproductive timing on demography of Little Brown Myotis *Myotis lucifugus*. Journal of Animal Ecology 79:128–136.

Fukui, D., M. Murakami, S. Nakano, and T. Aoi. 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. Journal of Animal Ecology 75:1252–1258.

Gorman, K.M., E.L. Barr, L. Ries, T. Nocera, and W.M. Ford. 2021. Bat activity patterns relative to temporal and weather effects in a temperate coastal environment. Global Ecology and Conservation 30:1–13.

Hayes, M.A. 2013. Bats killed in large numbers at United States wind energy facilities. BioScience 63:975–979

Hoying, K.M., and T.H. Kunz. 1998. Variation in size at birth and post-natal growth in the insectivorous bat *Pipistrellus subflavus* (Chiroptera: Vespertilionidae). Journal of Zoology 245:15–27.

Hoyt, J.R., A.M. Kilpatrick, and K.E. Langwig. 2021. Ecology and impacts of white-nose syndrome on bats. Nature Reviews Microbiology 19:33–36.

Hughes, M.J., E.C. Braun de Torrez, and H.K. Ober. 2021. Big bats binge bad bugs: Variation in crop pest consumption by common bat species. Agriculture, Ecosystems and Environment 314(107414).

Isenhour, Z.W., G.L. Harris, R.L. Stewart, E.D. Hampton, M.R. Scafini, G.G. Turner, and S.E. Bergsten. 2024. Dietary flexibility of insectivorous bats, *Eptesicus fuscus* and *Myotis lucifugus*, during *Magicicada* spp. Brood X emergence. Canadian Journal of Zoology e-first.

Jarzonbek, L.Z. 2009. Aerial-hawking bats can glean prey items from surfaces similar to wind turbine towers: Implications for reducing bat fatalities at wind facilities. M.S. Thesis. Texas Agricultural and Mechanical University at Galveston, Galveston, TX. 55 pp.

Johnson, J.B., J.E. Gates, and W.M. Ford. 2008. Distribution and activity of bats at local and landscape scales within a rural-urban gradient. Urban Ecosystems 11:227–242.

Karban, R. 2014. Transient habitats limit development time for periodical cicadas. Ecology 95:3–8.

Koenig, W.D., and A.M. Liebhold. 2005. Effects of periodical cicada emergences on abundance and synchrony of avian populations. Ecology 86:1873–1882.

Koenig, W.D., A.M. Liebhold, J.M. LaMontagne, and I.S. Pearse. 2022. Periodical cicada emergences affect masting behavior of oaks. The American Naturalist 201:755–762.

Kortmann, M., J. Hurst, R. Brinkmann, M. Heurich, R. Silveyra González, J. Müller, and S. Thorn. 2018. Beauty and the beast: How a bat utilizes forests shaped by outbreaks of an insect pest. Animal Conservation 21:21–30.

Krauel, J.J., J.M. Ratcliffe, J.K. Westbrook, and G.F. McCracken. 2018. Brazilian Free-tailed Bats (*Tadarida brasiliensis*) adjust foraging behaviour in response to migratory moths. Canadian Journal of Zoology 96:513–520.

Kritsky, G. 2021a. One for the books: The 2021 emergence of the periodical cicada Brood X. American Entomologist 67:40–46.

Kritsky, G. 2021b. Periodical Cicadas: The Brood X Edition. Ohio Biological Survey, Columbus, OH. 157 pp.

Krohne, D.T., T.J. Couillard, and J.C. Riddle. 1991. Population responses of *Peromyscus leucopus* and *Blarina brevicauda* to emergence of periodical cicadas. The American Midland Naturalist 126:317–321.

Kunz, T.H., and L.F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Pp. 3–69, *In* T.H. Kunz and M.B. Fenton (Eds.). Bat Ecology. The University of Chicago Press, Chicago, IL. 834 pp.

Kunz, T.H., J.A. Wrazen, and C.D. Burnett. 1998. Changes in body mass and fat reserves in prehibernating Little Brown Bats (*Myotis lucifugus*). Écoscience 5:8–17.

Liebhold, A.M., M.J. Bohne, and R.L. Lilja. 2013. Active periodical cicada broods of the United States. Available online at https://www.fs.usda.gov/foresthealth/docs/CicadaBroodStaticMap.pdf. Accessed 7 December 2023.

Lintott, P.R., E. Fuentes-Montemayor, D. Goulson, and K.J. Park. 2013. Testing the effectiveness of surveying techniques in determining bat community composition within woodland. Wildlife Research 40:675–684.

Lloyd, M., and H.S. Dybas. 1966a. The periodical cicada problem. I. Population ecology. International Journal of Organic Evolution 20:133–149.

Lloyd, M., and H.S. Dybas. 1966b. The periodical cicada problem. II. Evolution. Evolution 20:466–505.

Loeb, S.C., T.J. Rodhouse, L.E. Ellison, C.I. Lausen, J.D. Reichard, K.M. Irvine, T.E. Ingersoll, J.T.H. Coleman, W.E. Thogmartin, J.R. Sauer, C.M. Francis, M.L. Bayless, T.R. Stanley, and D.H. Johnson. 2015. A plan for the North American Bat Monitoring Program (NABat). General Technical Report SRS-280. U.S. Forest Service, Southern Research Station, Asheville, NC. 100 pp.

Long, B.L., A. Kurta, and D.L. Clemans. 2013. Analysis of DNA from feces to identify prey of Big Brown Bats (*Eptesicus fuscus*) caught in apple orchards. American Midland Naturalist 170:287–297

Lüdecke, D., M.S. Ben-Shachar, I. Patil, P. Waggoner, and D. Makowski. 2021. Performance: An R package for assessment, comparison and testing of statistical models. Journal of Open Source Software 6(60):3139.

Maier, C.T. 1982. Observations on the seventeen-year periodical cicada, *Magicicada septendecim* (Hemiptera: Homoptera: Cicadidae). Annals of the Entomological Society of America 75:14–23.

Marlatt, C.L. 1907. The Periodical Cicada. No. 71. U.S. Department of Agriculture, Bureau of Entomology, Washington, DC. 181 pp.

Maryland Department of Natural Resources. 2023a. McKee-Beshers Wildlife Management Area. Available online at https://dnr.maryland.gov/wildlife/pages/publiclands/central/mckeebeshers.aspx. Accessed 1 November 2023.

Maryland Department of Natural Resources. 2023b. Prather's Neck Wildlife Management Area. Available online at https://dnr.maryland.gov/wildlife/pages/publiclands/western/prathersneck.aspx. Accessed 1 November 2023.

Maryland Forest Service. 2019. Sustainable forest management plan for Green Ridge State Forest. Maryland Division of Natural Resources, Annapolis, MD. 284 pp.

Mazerolle, M.J. 2023. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c) R package version 2.3.2. Available online at https://www.maths.bris.ac.uk/R/web/packages/AICcmodavg/AICcmodavg.pdf. Accessed 15 January 2024.

McCracken, G.F., J.K. Westbrook, V.A. Brown, M. Eldridge, P. Federico, and T.H. Kunz. 2012. Bats track and exploit changes in insect pest populations. PLoS ONE 7(8):e43839.

McNab, W.H., D.T. Cleland, J.A. Freeouf, J.E. Keys Jr., G.J. Nowacki, and C.A. Carpenter. 2007. Description of "ecological subregions: sections of the conterminous United States". General Technical Report WO-76B, USDA Forest Service, Washington D.C. 80 pp.

National Centers for Environmental Information. 2010. U.S. Annual Climatological Summaries. National Oceanographic and Atmospheric Administration. Available online at https://www.ncei.noaa.gov/access/metadata/landing-page/bin/iso?id=gov.noaa.ncdc:C00040. Accessed 1 January 2024.

Newman, B.A., S.C. Loeb, and D.S. Jachowski. 2021. Winter roosting ecology of Tricolored Bats (*Perimyotis subflavus*) in trees and bridges. Journal of Mammalogy 102:1331–1341.

O'Rourke, D., N.P. Rouillard, K.L. Parise, and J.T. Foster. 2022. Spatial and temporal variation in New Hampshire bat diets. Scientific Reports 12,14334.

Oberdörster, U., and P.R. Grant. 2007. Predator foolhardiness and morphological evolution in 17-year cicadas (*Magicicada* spp.). Biological Journal of the Linnean Society 90:1–13.

Proudman, A.S., L.R. Jones, M.O. Watkins, E.A. Flaherty. 2024. Activity responses of a mammal community to a 17-year cicada emergence event. *Journal of Mammalogy* 105:1190–1199.

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Available online at https://www.r-project.org/. Accessed 10 September 2023.

Racey, P.A., and S.M. Swift. 1981. Variations in gestation length in a colony of Pipistrelle Bats (*Pipistrellus pipistrellus*) from year to year. Journal of Reproduction and Fertility 61:123–129.

Racey, P.A. 1982. Ecology of bat reproduction. Pp. 57–93, *In* T.H. Kunz (Ed.). Ecology of Bats 1st ed. Plenum Publishing Corporation, New York, NY. 425 pp.

Rasmussen, A.K., and M.L. Pescador. 2002. A guide to the Megaloptera and Aquatic Neuroptera of Florida. Florida Department of Environmental Protection, Tallahassee, FL. 78 pp.

Ratcliffe, J.M., and J.W. Dawson. 2003. Behavioural flexibility: The Little Brown Bat, *Myotis lucifugus*, and the Northern Long-eared Bat, *M. septentrionalis*, both glean and hawk prey. Animal Behaviour 66:847–856.

Reynolds, S., and T.H. Kunz. 2000. Changes in body composition during reproduction and postnatal growth in the Little Brown Bat, *Myotis lucifugus* (Chiroptera: Vespertilionidae). Ecoscience 7:10–17.

Reynolds, R.J., K.E. Powers, W. Orndorff, W.M. Ford, and C.S. Hobson. 2016. Changes in rates of capture and demographics of *Myotis septentrionalis* (Northern Long-eared Bat) in western Virginia before and after onset of white-nose syndrome. Northeastern Naturalist 23:195–204.

Russo, D., L. Ancillotto, and G. Jones. 2018. Bats are still not birds in the digital era: echolocation call variation and why it matters for bat species identification. Canadian Journal of Zoology. 96(2):63–78.

Salmon, M. 2022. riem: Accesses weather data from the Iowa environment mesonet. R package version 0.3.0. Available online at https://github.com/ropensci/riem. Accessed 18 February 2024.

Schmit, J.P., E. Matthews, and A. Brolis. 2023. Trends in woody forest vegetation in Prince William Forest Park, 2006–2017. National Park Service, Natural Resource Report NPS/NCRN/NRR–2023/2495. Fort Collins, CO. 99 pp.

Smith, F.F., and R.G. Linderman. 1974. Damage to ornamental trees and shrubs resulting from oviposition by periodical cicada. Environmental Entomology 3:725–732.

Storm, J.J., and J.O. Whitaker, Jr. 2008. Prey selection of Big Brown Bats (*Eptesicus fuscus*) during an emergence of 17-year cicadas (*Magicicada* spp.). American Midland Naturalist 160:350–357.

U.S. Fish and Wildlife Service. 2023. Range-wide Indiana Bat and Northern Long-eared Bat survey guidelines. U.S. Fish and Wildlife Service, Region 3, Bloomington, MN. 95 pp.

U.S. Fish and Wildlife Service. 2019. Automated acoustic bat ID software programs. Available online at https://www.fws.gov/media/automated-acoustic-bat-id-software-programs. Accessed 25 November 2023.

Vandegrift, K.J., and P.J. Hudson. 2009. Response to enrichment, type and timing: Small mammals vary in their response to a springtime cicada but not a carbohydrate pulse. Journal of Animal Ecology 78:202–209.

Watkins, L.C. 1972. *Nycticeius humeralis*. Mammalian Species 23:1–4.

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. 2007. Food habits of mammals during an emergence of 17-year cicadas (Hemiptera: Cicadidae: *Magicicada* spp.). Proceedings of the Indiana Academy of Science 116:196–199.

Whitaker, J.O., Jr., and P. Clem. 1992. Food of the Evening Bat *Nycticeius humeralis* from Indiana. American Midland Naturalist 127:211–214.

White, J.A., and M. Lloyd. 1975. Growth rates of 17 and 13-year periodical cicadas. The American Midland Naturalist 94:127–143.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York, NY. 260 pp.

Wildlife Acoustics. 2018. How far can my microphone "hear"? Available online at https://www.wildlifeacoustics.com/resources/blog/how-far-can-my-microphone-hear. Accessed 8 July 2023.

Williams, K.S., and K.G. Smith. 1991. Dynamics of periodical cicada centers. Journal of Insect Behavior 4:275–291.

Williams, K.S., K.G. Smith, and F.M. Stephen. 1993. Emergence of 13-Yr periodical cicadas (Cicadidae: *Magicicada*): Phenology, mortality, and predator satiation. Ecology 74:1143–1152.

Wilson, J.M., and R.M.R. Barclay. 2006. Consumption of caterpillars by bats during an outbreak of Western Spruce Budworm. American Midland Naturalist 155:244–249.

Yang, L.H. 2004. Periodical cicadas as resource pulses in North American forests. Science 306:1565–1567.

Yang, L.H. 2008. Pulses of dead periodical cicadas increase herbivory of American Bellflowers. Ecology 89:1497–1502.

Yang, L.H., K. Edwards, J. Byrnes, J. Bastow, A. Wright, and K. Spence. 2010. A meta-analysis of resource pulse–consumer interactions. Ecological Monographs 80:125–151.