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Bat activity patterns relative to temporal and weather effects in a temperate coastal environment☆

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ABSTRACT

The northeastern and mid-Atlantic coasts of the United States are important summer maternity habitat and seasonal migratory corridors for many species of bats. Additionally, the effects of weather on bat activity are relatively unknown beyond coarse nightly scales. Using acoustic detectors, we assessed nightly and hourly activity patterns for eight species of bats over 21 consecutive months at Fire Island National Seashore, New York. The site is an important bat conservation area because it hosts one of the few confirmed northern long-eared bat (*Myotis septentrionalis*) maternity colonies in the region despite their widespread extirpation due to white-nose syndrome (WNS). There have been no reported captures of little brown bats (*M. lucifugus*), Indiana bats (*M. sodalis*), or tri-colored bats (*Perimyotis subflavus*) at the site post-WNS. Overall, we found mean hourly temperature, time since sunset, day of year, and year to be the most important predictors of bat activity levels for all examined species. Most non-hibernating, migratory species in our study demonstrated a positive relationship to mean temperature at the hourly timescale, whereas cave-hibernating bats tended to show a negative relationship to mean temperature during the time of year when they are expected to be active. Although most bat activity occurred in the late spring through early autumn, peaking in summer, some activity occurred periodically in the winter months, mostly attributable to the big brown bat (*Eptesicus fuscus*) and silver-haired bat (*Lasionycteris noctivigans*) phonic group. Unexpectedly, relationships of bat activity to wind and precipitation were largely equivocal. Initial presence (as early as March 30) and departure (between November 1–4) for northern long-eared bats at our study area occurred earlier in the spring and later in the fall than occurs for inland populations, suggesting that the species overwinters on Long Island rather than at inland karst caves or mines. A peak in spring activity characteristic of migratory behavior in the central Appalachians and Atlantic Coast was not observed at Fire Island, although Eastern red bats (*Lasiurus borealis*) and hoary bats (L.

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cinereus) – both migratory species – did show a notable rise in activity in the late summer and early fall, suggesting these populations may migrate to and from Fire Island. Understanding the temporal and weather relationships to bat activity in this coastal environment may have important implications for tailoring more effective conservation and management strategies by identifying optimal timing for surveys, tracking bats during peak migratory windows, and providing insights that minimizes impacts to extant bats from activities such as wind-energy development or land management, i.e., forestry.

1. Introduction

In temperate environments, many bat species make seasonal migrations between winter and summer habitats and often are exposed to anthropogenic-induced mortality (i.e., collisions with wind turbines) during these movements (Kunz et al., 2007; Arnett et al., 2008; Arnett and Baerwald, 2013). For example, Smallwood and Bell (2020) recently estimated bat fatalities from wind turbine strikes in the United States exceed 1.7 million bats annually, a number that may grow as this energy production sector expands. Additionally, populations of cave-hibernating bats are being reduced by white-nose syndrome (WNS), which has resulted in population declines of over 90% and local extirpations of many affected species such as the little brown bat (*Myotis lucifugus*), the northern long-eared bat (*M. septentrionalis*), and the tri-colored bat (*Perimyotis subflavus*; Frick et al., 2010; Turner et al., 2011; Cheng et al., 2021). Mortality-causing events such as these may result in changes to species-protection status. For example, the northern long-eared bat was listed as a federally-threatened species under the Endangered Species Act in 2015 (ESA; Silvis et al., 2016; USFWS, 2016) due to landscape-scale population declines related to WNS, and the little brown bat and tri-colored bat are currently petitioned for listing (USFWS, 2020).

In addition to possible changes in regulatory status of impacted species, negative impacts to ecosystem integrity as a result of declining bat populations are a concern. Although WNS is not a human-health threat, bat population declines and/or extinction can have cascading ecological effects that can impact other biodiversity components, forestry and agriculture (Frick et al., 2010; Kunz et al., 2011; Jachowski et al., 2014; Maine and Boyles, 2015).

Maternal colonies of northern long-eared bats have persisted in coastal areas of the Northeast and mid-Atlantic (Grider et al., 2016; Dowling et al., 2017; Dowling and O'Dell, 2018; De La Cruz et al., 2020), likely because these bats inhabit hibernacula free of WNS or spend less time in WNS-infected caves by arriving later in fall and departing earlier in spring, or by remaining partially active throughout winter months. If coastal areas serve as refugia for surviving residual cave bat communities in the post-WNS environment or as important non-hibernating migratory bat flyways, understanding temporal patterns of presence and activity is paramount for guiding management efforts in these important bat conservation areas.

To date, little research has examined bat responses to climatic conditions long-term at the hourly scale or across a full suite of seasons, particularly in the northeastern United States (Johnson et al., 2011; Grider et al., 2016; Nocera et al., 2019b). Documenting hourly patterns of bat activity broadly are needed to inform wind-energy best management practices that help reduce bat mortality (i.e., minimum wind cut in speeds and variation in nightly and seasonal bat activity). However, examining bat activity at the hourly timescale also can help elucidate fine-scale or site-specific external triggers that influence bat activity directly relatable to mitigating wind-energy impact. Jachowski et al. (2014) showed that WNS-impacts to community composition that resulted in changes in niche-partitioning was most apparent when fine-scaled temporal bat activity was examined. Similarly, because nightly temporal patterns may vary by season and weather, there is a need for these patterns to be assessed over an annual timeframe.

Bat activity has a positive relationship with temperature (Whitaker and Rissler, 1992; Cryan and Brown, 2007; Ruczyński and Bartoń, 2020). Additionally, bat activity typically declines with increasing precipitation and wind speed as well as changes in barometric pressure (Patriquin et al., 2016; Smith and McWilliams, 2016; Dechmann et al., 2017; Muthersbaugh et al., 2019a). Weather affects not only bat activity and prey availability, but also plays a role in the timing and pattern of longer-distance migratory movements, i.e., to hibernacula or overwintering grounds in the case of non-hibernating bats (Muthersbaugh et al., 2019a, 2019b).

Relationships between weather conditions and activity among bat species have the potential to be more pronounced in coastal areas, which tend to be windier, with less extreme temperature ranges compared with inland areas along the Atlantic Coast (Grider et al., 2016). For this study, we investigated the influence of weather conditions (i.e., temperature, wind speed, and precipitation) on hourly bat activity of bats in a northeastern coastal environment throughout the year at the William Floyd Estate (WIFL) portion of Fire Island National Seashore, NY, USA. This land remains as a relatively intact forest block along the eastern periphery of the New York City metro area, and because of its location along the Atlantic Coastal Plain, WIFL is believed to provide critical foraging and roosting habitats for migratory and cave-hibernating bats species in the region. Accordingly, our objectives were to use acoustic sampling methods to determine hourly activity patterns for eight species of bats at WIFL and compare the levels of activity to local weather data over the course of the active season. Additionally, we investigated whether or not ecologically similar bats, such as *Myotis* species and tri-colored bats (cave-hibernating species), local year-round resident big brown bats (*Eptesicus fuscus*), and non-hibernating migratory tree bats such as silver-haired bats (*Lasionycteris noctivigans*), eastern red bats (*Lasiurus borealis*), and hoary bats (L. *cinereus*) would exhibit similar responses to weather variables (Ford et al., 2011; Nocera et al., 2019b). In addition to informing wind-energy development, understanding these patterns may give managers insights into the timing of potential land management stewardship actions, therefore minimizing any negative impacts to bats when they are most vulnerable (early hibernation emergence and during the maternity season before young are volant). Moreover, determining these patterns in warmer, more moderate coastal areas may provide

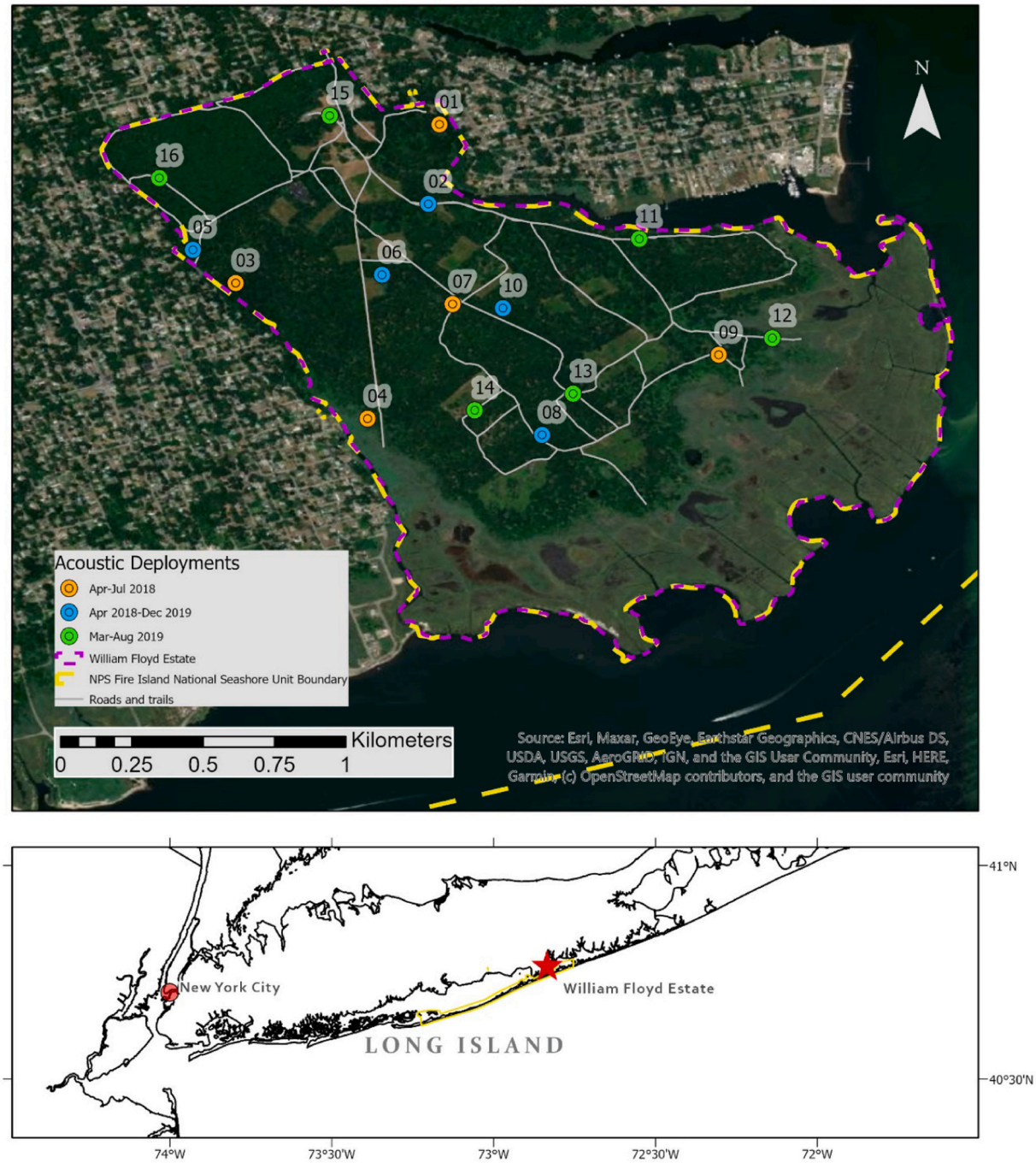

Fig. 1. Location of acoustic detectors at William Floyd Estate (WIFL; purple dashed line), Fire Island National Seashore (yellow dashed line), New York, USA, Apr 2018–Dec 2019.Gray lines indicate roads and trails throughout WIFL.

insights into the responses of bats and/or their plasticity in response to future climate changes and these inferences would perhaps be applicable to bats in inland areas (Gorman et al., 2021).

2. Study area

We conducted our study at the 248-ha WIFL unit of Fire Island National Seashore (40.77°N, 72.82°W) in Suffolk County, New York, USA (Fig. 1). Located on the Atlantic Coastal Plain, the regional climate was classified as humid temperate with a maritime influence, and averaged 180–200 frost-free days per year. Precipitation was evenly distributed throughout the year, with a mean of 119.71 cm (U.

Table 1
Deployment window, total recording nights, and total recording hours for each detector at the William Floyd Estate, Fire Island National Seashore, New York, April 2018 – December 2019 (see Fig. 1 for detector locations).

Detector ID	Deployment window	Total recording nights	Total recording hours
01	25 Apr 2018–24 Jul 2018	93	1,127
02	26 Apr 2018–30 Nov 2019	582	8,385
03	25 Apr 2018–24 Jul 2018	93	1,129
04	25 Apr 2018–26 Jul 2018	95	1,149
05	25 Apr 2018–4 Dec 2019	576	8,339
06	25 Apr 2018–8 Dec 2019	595	8,609
07	25 Apr 2018–20 Jun 2018	59	717
08	25 Apr 2018–8 Dec 2019	595	8,604
09	25 Apr 2018–24 Jul 2018	595	8,599
10	20 Jun 2018 –2 Dec 2018	515	7,506
11	16 Mar 2019–1 Aug 2019	141	1,786
12	16 Mar 2019–1 Aug 2019	141	1,786
13	16 Mar 2019–22 Jul 2019	30	326
14	16 Mar 2019–1 Aug 2019	140	1,774
15	16 Mar 2019–1 Aug 2019	140	1,774
16	16 Mar 2019–1 Aug 2019	140	1,774
Total		**4530**	**63,384**

S. Climate Data, 2020), though the coast often could be subject to heavy precipitation events from tropical depressions and winter nor'easter storms (NOAA's National Centers for Environmental Information, 1996). The vegetation cover consisted of mature coastal oak (*Quercus* spp.)-ericaceous heath forest (65%), tidal marshes and wetlands (25%), and open fields (5%). The remainder of the estate was developed land (Klopfer et al., 2002). The entire property sat at an elevation $\leq$ 2 m above sea level. Common tree species at WIFL were pitch pine (*Pinus pungens*), red maple (*Acer rubrum*), black locust (*Robinia pseudoacacia*), white oak (*Q. alba*), scarlet oak (*Q. coccinea*), and sassafras (*Sassafras albidum*). The understory was dominated by dense greenbrier (*Smilax* spp.) and poison ivy (*Toxicodendron radicans*; Klopfer et al., 2002).

3. Methods

3.1. Acoustic monitoring

In April of 2018, we deployed nine stationary SM4BAT zero-crossing/frequency division acoustic detectors with SMM-UI omnidirectional microphones (Wildlife Acoustics, Maynard, MA, USA; hereafter, Songmeter[1]) within WIFL along single-track roads, trails, and fields in forest and marsh-edge habitats. Of these, we removed four at the end of July in 2018 for other research deployments and maintained the five recorders through the following year. In April of 2019, we deployed an additional six detectors ($n = 11$) on previously unmonitored trails near northern long-eared bat maternity roosts that we identified in 2018 during mist-net surveys (Fig. 1, Table 1). Microphones were mounted two meters off the ground on telescoping poles along road/trail corridors or open fields to maximize echolocation call quality acquisition (Nocera et al., 2019b, De La Cruz et al., 2020). We set detectors to record from 30 min prior to sunset until 30 min following sunrise.

We used Kaleidoscope Pro (Wildlife Acoustics, Maynard, MA, USA; Version 5.1.0; Classifier Version 5.1.0; 0 Sensitivity Setting[2]) to process echolocation calls following U.S. Fish and Wildlife Service acoustic monitoring protocols (USFWS Midwest Region Endangered Species, 2019). We set a minimum threshold of three pulses per call file to minimize bat species misclassification (Muthersbaugh et al., 2019a). Following species lists of known or suspected bats for the Long Island area (Seatuck Environmental Association, 2017), we included the following species as potentially occurring at WIFL: big brown bats, silver-haired bats, Eastern red bats, hoary bats, little brown bats, Indiana bats, northern long-eared bats, and tri-colored bats. We further visually examined a random sample of calls classified with high confidence per species per detector per night according to protocols set forth by the North American Bat Monitoring Program ($n = 36{,}232$; U.S. Geological Survey, 2018) to determine accuracy of species identification and presence, but did not change calls from software classifications to avoid introducing additional bias (Nocera et al., 2019a). Because of previously documented misclassification between little brown and Indiana bats and big brown and silver-haired bats (U.S. Geological Survey, 2019), we combined these species into two phonic groups for analysis, respectively (Menzel et al., 2002; Johnson et al., 2008; Austin et al., 2018). We concluded that the classifications provided by the software were acceptable to continue with our analysis (Nocera et al., 2019a), recognizing that some inherent error remained.

To assess the effects of weather on bat activity, we obtained hourly weather variables from Aviation Routine Weather Reports (Iowa Environmental Mesonet, 2020) that were measured by Automated Surface Observing Systems (ASOS) at the nearby

[1] Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

[2] Overall correct classification accuracy for each species in this assembly state is as follows: big brown bat (77%), Eastern red bat (71%), hoary bat (13%), silver-haired bat (41%), little brown bat (69%), northern long-eared bat (81%), Indiana bat (64%), tri-colored bat (64%; U.S. Geological Survey, 2019).

Table 2
Active window beginning and end dates for each species used in the analyses. Dates were chosen as first and last acoustic detections, respectively, for each species across both years. Peak activity window calculated using confidence intervals on generalized additive model trend lines for each species. Numbers outside parentheses are Day of year numbers as used in analyses.

Species/Species group	First day of detection	Peak activity	Last day of detection
Big brown bat/silver-haired bat phonic group	1 (1 Jan)	48–267 (17 Feb–24 Sep)	363 (29 Dec)
Eastern red bat	74 (15 Mar)	70–268 (11 Mar–25 Sep)	349 (15 Dec)
Hoary bat	1 (1 Jan)	84–255 (25 Mar–12 Sep)	362 (28 Dec)
Little brown bat/Indiana bat phonic group	74 (15 Mar)	60–270 (1 Mar–27 Sep)	356 (22 Dec)
Northern long-eared bat	89 (30 Mar)	50–201 (19 Feb–20 Jul)	308 (4 Nov)

Shirley/Brookhaven Airport seven kilometers north of WIFL. These variables included the mean hourly wind speed (KPH), mean hourly temperature (°C), and total hourly precipitation (mm) for each night of our study.

3.2. Statistical analyses

We used R version 3.6.1 to perform all statistical tests and analyses for assessing bat activity with weather and temporal periods (R Core Team 2019). We tested for multicollinearity among our predictor variables using the corrplot package (Wei and Simko, 2017) and we found no correlation $\geq |0.6|$ between predictors, and therefore none were removed from further analyses. We combined echolocation call totals into hourly blocks per night for each acoustic detector and assigned values of zero to detectors when no calls were recorded for a given hour. We calculated time since sunset of any given hour using the suncalc package (Thieurmel and Elmarhraoui, 2020). To visualize seasonal trends of bat activity at WIFL, we modeled nightly bat activity by species using generalized additive models (GAMs) using ggplot2 (Wickham, 2016). To remove biases of non-detections during the winter, we selected an "active" window by using just the first Day of year of acoustic detection to last Day of year of acoustic detection for each bat species or phonic group (Table 2). Because knowing the timing of bat arrival and departure as well as summer peaks (i.e., parturition and juvenile volancy) are important to inform site-level conservation measures to protect bats, we then fit GAM trend lines post hoc for every bat species/phonic group using the ggplot2 package for better visualization of these activity patterns (Fig. 2; Wickham, 2016). We calculated a peak activity window start date when the lower confidence level of the GAM > 0 in the spring and ≥ 0 in the fall (Table 2, Fig. 2). Prior to analysis, we transformed Day of year to radians using the package aspace (Bui et al., 2012) to make it a circular variable (i.e., the last day of the year [365] is followed by the first day of the year [1]).

For estimating hourly bat activity by species, we created a set of 36 candidate models relative to wind, temperature, precipitation, time since sunset, Day of year, and year (2018 or 2019). We included interaction terms between all of the variables using generalized linear mixed models (GLMMs) with a zero-inflated negative binomial distribution function to account for the non-normality of our echolocation count data and excess zeros (attributed to minimal activity). We set our detector ('site') covariate as a random variable using the glmmTMB package (Brooks et al., 2020). Hour was the smallest unit of time, enabling us to avoid the misleading effect of partial night rain on bat activity. We scaled all weather variables to 0–1 prior to analyses using the R package BBmisc (Bischl et al., 2017) so that the effect size for beta (β) coefficients could be easily compared across variables. Following GLMM model selection, we then ranked models using Akaike's information criteria (AIC; Burnham and Anderson, 2002). For each analysis, we only considered the top-ranking model to be the best-supported model if no other competing model was within two ΔAIC units for any bat species (Burnham and Anderson, 2002). Model R^2 values were calculated using the performance package (Lüdecke et al., 2021).

4. Results

From April 2018 to December 2019, we recorded acoustic data for 63,384 h and 4,530-detector nights over 595 calendar days at WIFL (Table 1). We detected all target species for our study with the big brown/silver-haired phonic group, Eastern red bats, and hoary bats being most frequently detected (proportion of recording nights with a positive species/species group detection for each detector; Table 3). Recording was not continuous at all detectors throughout this period due to periodic malfunctions, i.e., battery depletion, and because some detectors were only present during the maternity season. Peak activity windows as calculated using GAM trend lines ranged from mid-February/late March to September for all species except northern long-eared bats that had a peak ending in late July (Table 2). Eastern red bats, northern long-eared bats, and hoary bats had two distinct waves of activity throughout the summer (Fig. 2).

There were no competing GLMM models (within two ΔAIC units) within species and species groups, therefore, we selected the top model for each according to AIC rank (Appendix Table 1). Model fit was low for all models ($R^2 \leq 0.14$), suggesting a large portion of variability in activity was not captured by our selected weather variables. Though predictor interactions and presence in the models varied somewhat by species for the top models, mean hourly temperature, Day of year, and year were significant predictors of hourly activity for all species, except for year, which was not significant for Eastern red bats (Table 4, Appendix Table 2). Mean hourly wind speed and total hourly precipitation were not significant predictors in the top model for any species examined. We excluded tri-colored bat from GLMM analysis because of low detection rates.

For each species and species group, mean hourly temperature was a significant predictor of hourly bat activity, whereas mean hourly wind speed and total hourly precipitation were not included (Table 4). Hourly activity had a positive relationship with mean temperature for the big brown bat/silver-haired bat phonic group, Eastern red bats, and hoary bats and a negative relationship for the

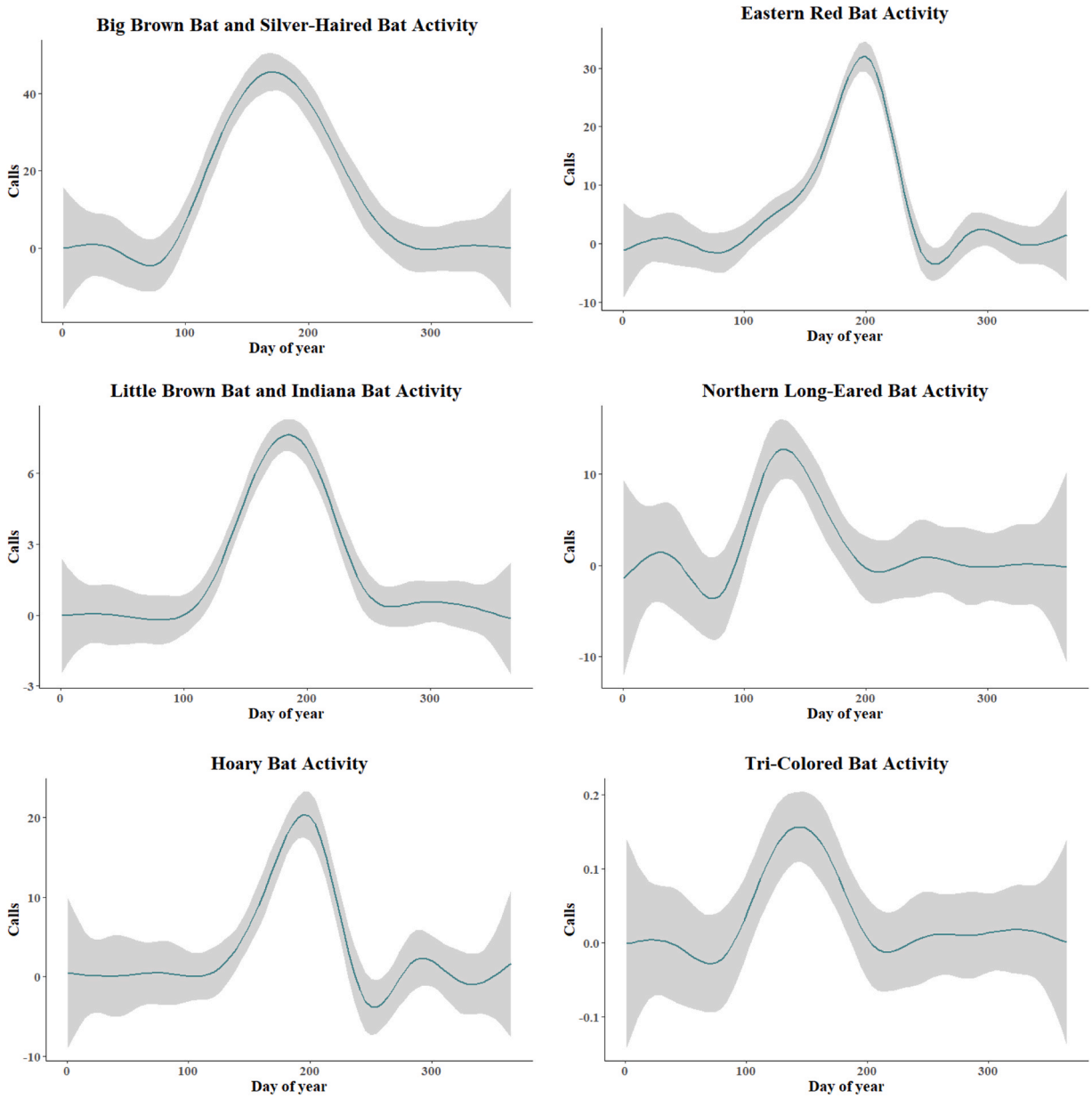

Fig. 2. Nightly activity patterns for each species/group at the William Floyd Estate, Fire Island National Seashore, New York, April 2018–December 2019. Raw call file data were smoothed using generalized additive models in order to show seasonal trends; note that y-axes are varied across species/groups. Grey shading is the 95% confidence intervals. Big brown bats (*Eptesicus fuscus*) and silver-haired bats (*Lasionycteris noctivigans*) constitute one phonic group; likewise, little brown bats (*Myotis lucifugus*) and Indiana bats (*M. sodalis*) are combined into one phonic group. Due to the low nightly variation for tri-colored bats (*Perimyotis subflavus*), activity was smoothed according to date and hourly call totals.

little brown bat/Indiana bat phonic group and northern long-eared bats (Table 4).

The big brown bat/silver-haired bat phonic group activity had a negative relationship to time since sunset, meaning their activity predominated at the beginning of the night. Eastern red bat activity had a positive, albeit weak, relationship to time since sunset, as their activity was more evenly spaced throughout the night. Northern long-eared bat activity had a stronger positive relationship to time since sunset (meaning, as time since sunset increased, so did acoustic activity levels), indicating later foraging bouts in the evening and/or closer to sunrise.

Hoary bats showed a very strong positive relationship to year and Day of year. However, this relationship was reversed when examined in the context of the year*Day of year interaction (the relationships became negative). When examined in the context of the interaction between all three variables (year, Day of year, and temperature) this relationship was positive. The little brown bat/Indiana bat phonic group demonstrated a negative relationship to individual temporal predictors.

Table 3
Proportion of nights in which a species or species group was acoustically present at each detector. Detectors marked with * were deployed for the duration of the study, including winter months (see Table 1 for exact deployment dates). Big brown bats (*Eptesicus fuscus*) and silver-haired (*Lasionycteris noctivigans*) bats were combined into one phonic group for this analysis, as were little brown bats (*Myotis lucifugus*) and Indiana bats (*M. sodalis*).

Detector ID	Big brown/silver-haired bat	Eastern red bat	Hoary bat	Little brown/Indiana bat	Northern long-eared bat	Tri-colored bat
01	0.75	0.46	0.60	0.20	0.06	0.00
02 *	0.39	0.26	0.30	0.23	0.08	0.04
03	0.70	0.57	0.55	0.69	0.69	0.19
04	0.34	0.14	0.20	0.12	0.39	0.00
05 *	0.60	0.39	0.38	0.45	0.28	0.16
06 *	0.47	0.40	0.31	0.29	0.11	0.08
07	0.63	0.07	0.27	0.20	0.14	0.00
08 *	0.49	0.28	0.20	0.32	0.11	0.04
09	0.10	0.11	0.08	0.05	0.01	0.01
10 *	0.50	0.35	0.24	0.45	0.38	0.08
11	0.31	0.07	0.21	0.10	0.06	0.01
12	0.34	0.21	0.36	0.20	0.05	0.01
13	0.20	0.00	0.00	0.03	0.00	0.00
14	0.67	0.53	0.44	0.17	0.01	0.01
15	0.63	0.54	0.46	0.16	0.18	0.00
16	0.50	0.31	0.32	0.41	0.23	0.13

5. Discussion

Most bat activity at WIFL is predicted to occur between 10 and 30 °C regardless of the strength or direction of the modeled relationship. The midpoint at which activity decreases slightly appears to be around 20 °C, particularly for Eastern red bats (Fig. 3). Nonetheless, *Myotis* species were more active at lower temperatures at the hourly timescale. We attributed this to either being a result of an early spring arrival and initial summer residency in or near WIFL, rather than migratory species that would pass through later in the summer when temperatures are higher and/or after these cave bats have already dispersed.

As the only meteorological variable included in our top models, temperature likely plays a role in triggering either movement along migratory routes (Muthersbaugh et al., 2019a) or establishment of summer residency of cave-hibernating bats (Humphrey, 1975; Tuttle and Stevenson, 1982; Faure-Lacroix et al., 2020); this could be a result of higher prey availability in warm weather (Turbill, 2008). The seasonal trends in activity among all species show an initial rise in activity approximately between 29 May and 19 July (days 150–200), which was likely due to an increase in foraging by pregnant and lactating females (Deeley, 2019). This was followed by a decline and subsequent, smaller rise in activity at the end of the summer season (Fig. 2). Depending on species, this fluctuation could be a migration pulse or an indication of newly volant pups appearing on the landscape (Ford et al., 2011; Nocera et al., 2019b).

Lacki (1984) and Cryan et al. (2014) suggested that females and males of the same bat species may react to different environmental cues, although the positive association with temperature still holds regardless of sex (Baerwald and Barclay, 2011). It is likely that many of our call files that were attributed to *Myotis* species early in the year are foraging females from resident maternity colonies, as opposed to the migratory bats which could be either sex. This assumption is further bolstered by our mist-net captures at WIFL in 2018 and 2019, whereby only two out of 22 captured northern long-eared bats were adult males.

In the context of the mean hourly temperature*year interactive term, the little brown bat/Indiana bat phonic group was more likely to be active in warmer temperatures despite declines in overall acoustic activity from the first year to the second (the decline presumably due to continued WNS impacts or simply normal annual variability). The decline in activity at higher temperatures may have been a sampling artifact of our "active" season window used in the analysis (1 January–29 December). The relationship between activity and temperature looks negative when plotted against one another, however there are more hours with > 0 calls at higher temperatures and a peak predicted around 10 °C (Fig. 3). This could indicate residency early in the year and dispersal by late summer when temperatures could be more consistently higher than 10 °C. Francl et al. (2012) noted a narrowing in reproductive windows for northern long-eared bats and little brown bats post-WNS. Considering the Day of year or year interaction with temperature, it is likely that WIFL does not support active maternity colonies in close proximity. Therefore, for our data, the little brown/Indiana bat activity relationship with temperature is relative to season; foraging during temperatures that are high for April nights (10 °C) but that would not be considered high in August. These species' presence early in the spring and later in the fall reduced the direct strength of the relationship between activity and temperature when all other values were held constant (Table 4, Fig. 2).

In general, at WIFL, northern long-eared bats and Eastern red bats are more active later in the night, with hourly activity occurring earlier in the night as the year progresses (Table 4). This pattern indicates these species forage earlier in the night as decreasing nighttime temperatures likely cause insects to be more active earlier in the night. Alternatively, the big brown bat/silver-haired bat phonic group was more acoustically active closer to sunset, suggesting they forage primarily closer to sunset or are emerging from roosts within the park close to sunset and foraging elsewhere until returning to roost in the park again close to sunrise. As the year progressed that pattern shifted, suggesting that as the summer proceeds, these bats may exhibit longer or more numerous foraging bouts later in the night.

Hoary bats were the only species analyzed where Day of year alone was a positive predictor of activity, indicating that WIFL area

Table 4
Model outputs for top generalized linear mixed model for each species. Coefficient values (β), standard errors (*SE),* lower 95% confidence limits (LCL), and upper 95% confidence limits (UCL) for best supported generalized linear mixed models predicting species hourly activity during the maternity season at the William Floyd Estate, Fire Island National Seashore, New York, 2018 and 2019. Models are written out under the species/group name, and an * denotes an interaction. "Mean hourly temp" is mean hourly temperature, and "Time since sunset" is time (in hours) since sunset that a particular call sequence occurred. Big brown bats (*Eptesicus fuscus*) and silver-haired bats (*Lasionycteris noctivigans*) were combined into one phonic group; likewise, little brown bats (*Myotis lucifugus*) and Indiana bats (*M. sodalis*) were combined into one phonic group.

Big brown bat/silver-haired bat phonic group				
Calls ~ Mean hourly temp + Day of year * Year * Time since sunset + Detector (random variable)				
	β	***SE***	**LCL**	**UCL**
(Intercept)	1.79	0.34	1.12	2.45
Mean hourly temp	0.08	0.004	0.08	0.09
Day of year	-0.62	0.05	-0.71	-0.53
Year	0.99	0.24	0.52	1.47
Time since sunset	-0.42	0.04	-0.49	-0.35
Day of year * Year	-0.31	0.07	-0.45	-0.18
Day of year * Time since sunset	0.07	0.01	0.05	0.09
Year * Time since sunset	0.10	0.05	0.001	0.20
Day of year * Year * Time since sunset	-0.03	0.01	-0.05	0.003
Eastern red bat				
Calls ~ Mean hourly temp + Day of year * Year * Time since sunset + Detector (random variable)				
	β	***SE***	**LCL**	**UCL**
(Intercept)	-0.61	0.53	-1.65	0.44
Mean hourly temp	0.08	0.01	0.07	0.09
Day of year	-0.26	0.06	-0.37	-0.15
Year	0.05	0.33	-0.60	0.71
Time since sunset	0.18	0.04	0.11	0.25
Day of year * Year	-0.27	0.10	-0.47	-0.07
Day of year * Time since sunset	-0.06	0.01	-0.08	-0.04
Year * Time since sunset	-0.14	0.06	-0.26	-0.02
Day of year * Year * Time since sunset	0.04	0.02	0.004	0.08
Hoary bat				
Calls ~ Mean temp * Day of year * Year + Detector (random variable)				
	β	***SE***	**LCL**	**UCL**
(Intercept)	-20.06	1.36	-22.73	-17.39
Mean hourly temp	31.33	2.14	27.14	35.53
Day of year	4.13	0.35	3.45	4.80
Year	19.59	1.40	16.86	22.33
Mean hourly temp * Day of year	-6.95	0.57	-8.07	-5.83
Mean hourly temp * Year	-30.19	2.26	-34.62	-25.75
Day of Year * Year	-5.01	0.38	-5.76	-4.26
Mean hourly temp * Day of year * Year	7.56	0.63	6.33	8.80
Little brown bat/Indiana bat phonic group				
Calls ~ Mean hourly temp * Day of year * Year + Detector (random variable)				
	β	***SE***	**LCL**	**UCL**
(Intercept)	3.58	0.86	1.90	5.26
Mean hourly temp	-6.75	1.32	-9.34	-4.16
Day of year	-1.20	0.20	-1.58	-0.81
Year	-6.29	1.12	-8.49	-4.09
Mean hourly temp * Day of year	1.71	0.34	1.03	2.38
Mean hourly temp * Year	10.85	1.89	7.14	14.55
Day of year * Year	1.28	0.31	0.67	1.88
Mean hourly temp * Day of year * Year	-2.44	0.52	-3.47	-1.42
Northern long-eared bat				
Calls ~ Mean hourly temp + Day of year * Year * Time since sunset + Detector (random variable)				
	β	***SE***	**LCL**	**UCL**
(Intercept)	-0.85	0.62	-2.06	0.37
Mean hourly temp	-0.04	0.01	-0.06	-0.02
Day of year	-0.56	0.13	-0.81	-0.30
Year	2.97	0.56	1.88	4.06
Time since sunset	0.37	0.09	0.20	0.53
Day of year * Year	-0.71	0.17	-1.05	-0.37
Day of year * Time since sunset	-0.12	0.03	-0.17	-0.07
Year * Time since sunset	0.05	0.11	-0.17	0.27
Day of year * Year * Time since sunset	0.0003	0.04	-0.07	0.07

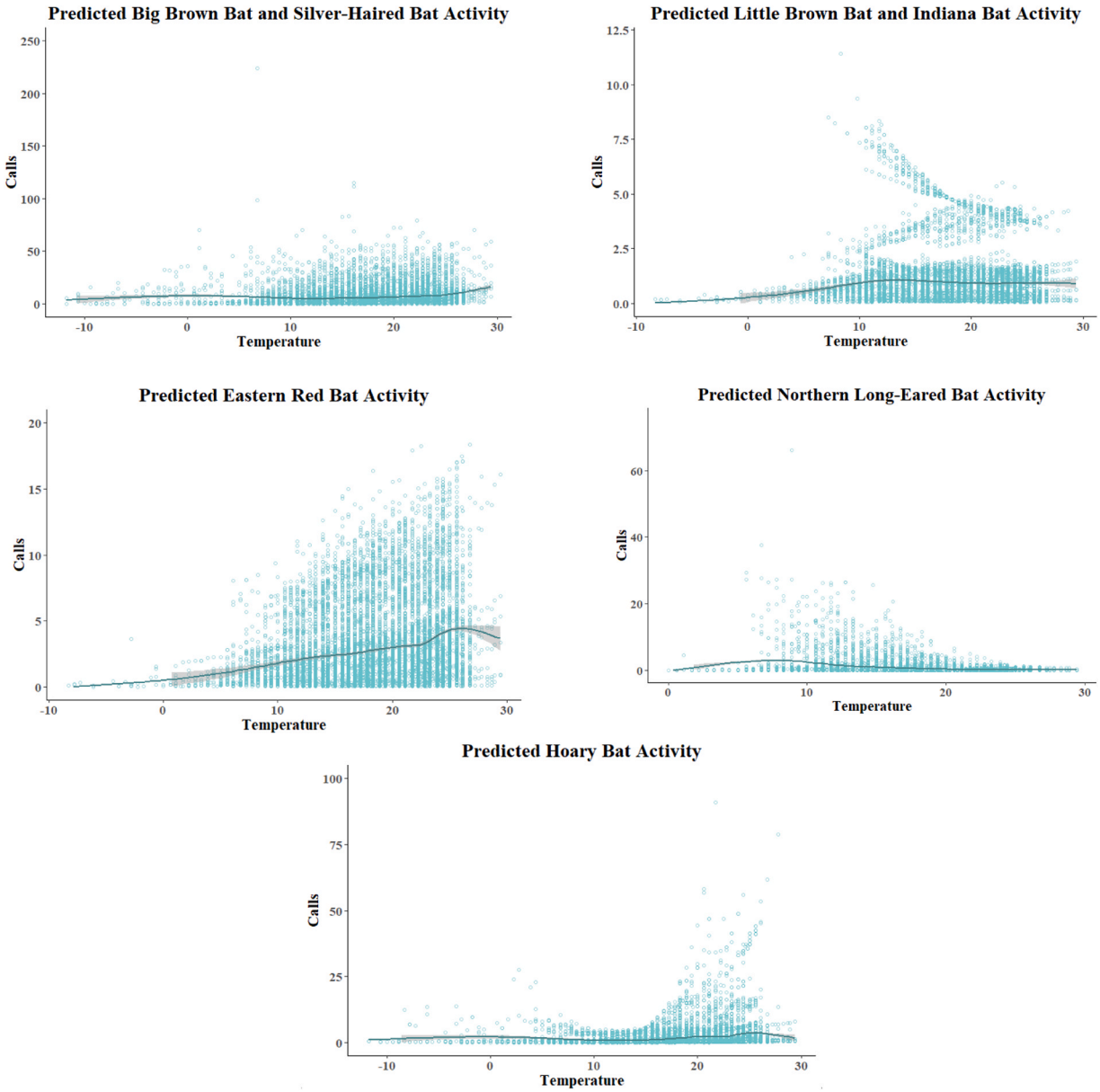

Fig. 3. Modeled effects on hourly activity for each bat species based on best supported generalized linear mixed models (points), smoothed with generalized additive models for illustrative purposes (blue lines), with 95% confidence intervals (gray), William Floyd Estate, Fire Island National Seashore, New York, maternity season, 2018 and 2019. Note the variable x-axes and y-axes across species; x-axes reflect activity window for each species or group. Big brown bats (*Eptesicus fuscus*) and silver-haired bats (*Lasionycteris noctivigans*) were combined into one phonic group; likewise, little brown bats (*Myotis lucifugus*) and Indiana bats (*M. sodalis*) were combined into one phonic group. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

was used as a late summer-fall southward migration corridor but less so in the spring during northward migration. Whether this was a function of a northward migration more diffuse in space and time (Cryan, 2003), or use of a non-coastal route is unknown. It is possible these positive relationships were sampling artifacts, i.e., more detectors deployed in the fall of the second year. Unfortunately, our initial April start date in 2018 may have missed the initial hoary bat pulse that year if migration occurred prior to that date, therefore masking our ability to document a strong spring migration signal.

A long-term study to confirm the viability of the bat communities at WIFL using in-hand confirmations of all species being recorded and their reproductive condition, as well as recording subtle corresponding meteorological changes across several years, could further elucidate these patterns across species. Increased researcher participation in large-scale, long-range monitoring projects such as the Motus Wildlife Tracking System (Motus.org) would allow us to pinpoint migratory windows for certain species, and late-season radio-tagging of cave bats would provide opportunities for identifying local hibernation sites.

Table A1
Top three competing generalized linear mixed models, associated number of parameters (K), Akaike's information criterion values (AIC), model rankings (ΔAIC), and Akaike weights (ω_i) for predicting species activity during the maternity season at the William Floyd Estate, Fire Island National Seashore, New York, 2018 and 2019. Models are written out under the species/group name, and an * denotes an interaction. Temp is mean hourly temperature (°C), wind is mean hourly wind speed (KPH), precip is total hourly precipitation (mm), day is Day of year, and hour is time (in hours) since sunset that a particular call sequence occurred. Site is detector site and was included as a random variable. Big brown bats (*Eptesicus fuscus*) and silver-haired bats (*Lasionycteris noctivigans*) were combined into one phonic group; likewise, little brown bats (*Myotis lucifugus*) and Indiana bats (*M. sodalis*) were combined into one phonic group.

Big brown bat/silver-haired bat phonic group					
Model	**K**	**AIC**	**ΔAIC**	**ω_i**	**R^2**
Temp + Day * Year * Hour + Site (random)	12	56,475.79	0.00	1.00	0.13
Temp + Day + Year + Hour + Site (random)	8	56,587.87	112.08	4.59e-25	0.14
Wind + Precip + Year * Day * Hour + Site (random)	13	56,807.40	331.61	9.81e-73	0.07
Eastern red bat					
Temp + Day * Year * Hour + Site (random)	12	39,091.74	0.00	1.00	0.08
Temp * Day * Year + Site (random)	11	39,095.53	0.15	0.13	0.06
Temp + Day + Year + Hour + Site (random)	8	39,129.78	38.04	4.77e-09	0.07
Hoary bat					
Temp * Day * Year + Site (random)	11	24,604.16	0.00	1.00	0.05
Temp + Day * Year * Hour + Site (random)	12	24,757.33	153.17	5.48e-34	0.08
Temp + Day * Year + Site (random)	8	24,808.39	204.23	4.48e-45	0.08
Little brown bat/Indiana bat phonic group					
Temp * Day * Year + Site (random)	11	25,980.05	0.00	1.00	0.06
Wind + Precip + Year * Day * Hour + Site (random)	13	26,005.15	25.10	3.55e-06	0.07
Temp + Day * Year * Hour + Site (random)	12	26,012.90	32.85	7.36e-08	0.07
Northern long-eared bat					
Temp + Day * Year * Hour + Site (random)	12	12,757.44	0.00	0.86	0.11
Wind + Precip + Year * Day * Hour + Site (random)	13	12,761.11	3.67	0.14	0.14
Day * Year * Hour + Site (random)	11	12,773.53	16.09	2.76e-04	0.13

Consistently rising temperatures due to climate change could shorten the hibernation windows for cave bats and allow for greater relative body mass either by increased prey abundance or smaller energetic costs, making them less susceptible to WNS-mediated mortality (Warnecke et al., 2012; Loeb and Winters, 2013; Grider et al., 2016; Haarsma et al., 2019; Faure-Lacroix et al., 2020). Entering torpor for shorter duration, with higher fitness, or in local, aberrant hibernacula (such as anthropogenic structures or trees), may decrease the temporal exposure to fungal loads. In our own research on Long Island at WIFL – as well as that of Dowling and O'Dell (2018) in Massachusetts – remaining northern long-eared bats along the northeastern coast are showing little physical evidence of WNS, despite occasionally testing positive for *Pseudogymnoascus destructans* spores (the causative agent of WNS). Nonetheless, in a coastal environment lacking typical hibernacula such as caves and mines, temperatures in available "aberrant" hibernacula may be less stable (Zahn, 1999); this may lead to a higher likelihood of mortality via exposure to freezing temperatures (Humphrey, 1975; Tuttle and Stevenson, 1982, Brack, 2007), or frequent arousals from torpor encouraged unseasonably warm temperatures, depleting fat reserves during a time when successful foraging is unlikely (Speakman and Rowland, 1999; Ruczyński et al., 2005, Cryan et al., 2010, Perry and Jordan, 2020).

Ongoing climate change has already affected evolutionary shifts in the distribution of plant species (Fitter and Fitter, 2002; Franks et al., 2007; Perry, 2018) as well as range expansions and changes in migration and reproductive timing for insects and birds (Parmesan and Yohe, 2003; Hitch and Leberg, 2006; Zuckerberg et al., 2009; Thomas, 2010; Chen et al., 2011), raising expectations for ecological shifts among other communities (Perry, 2018, Faure-Lacroix, 2020). With climate change, the migratory distances from maternity areas to overwinter areas may decrease for areas such as WIFL that are expected to shift to the transition between temperate and warm-temperate environments (Odom and Ford, in press). Future climates may allow tree bats to remain in the region with shorter and more moderate winters, or at a minimum allow for a delay in the costly energetic and physiological demands of migration if there are consistent food supplies locally (Cryan, 2003; Cryan et al., 2014; Grider et al., 2016). If they forego migration altogether and range extents are modified (Humphries et al., 2002; Jones et al., 2009; Andersen et al., 2017; Perry, 2018), this could have cascading effects on reproductive timing, their ecosystem service role (Rydell et al., 2010; Boyles et al., 2011; Maas et al., 2013), or as bioindicators (Jones et al., 2009; Bender and Hartman, 2015). It could also increase the chance that these bat species are caught in unseasonable, severe cold snaps that may still occur in future warmer climates at these higher latitudes (Newton, 2007). Regardless, because some elements of climate change in terms of warmer temperatures and changes in potential vegetation are predicted to occur more rapidly along the coast, near-term responses of bats at Northeast USA sites such as WIFL may provide insights for longer term changes in inland, continental regions (Zuckerberg et al., 2009; Chen et al., 2011).

Although temperature can fluctuate between years, variability in temperature (especially extremes) is predicted to occur more frequently and be greater due to climate change processes (Bell et al., 2004; Viceto et al., 2019). Our research at WIFL may suggest a need to foster more discussion about management guidelines designed to minimize impact to bats, especially when considering land management restrictions that are date-based such as the 4(d) Rule for northern long-eared bats (USFWS, 2016). The 4(d) Rule provides guidelines for allowable activities that might impact a threatened species in order to maximize protections during sensitive life stages and minimize requirements for those implementing the conservation actions, i.e., avoiding a "take" designation that would otherwise occur under an Endangered listing. However, our observations from WIFL may indicate that in coastal areas, and perhaps in the future

Table A2
All candidate models tested in analyses; null model also tested but not included in table. An * denotes an interaction. Temp is mean hourly temperature (°C), wind is mean hourly wind speed (KPH), precip is total hourly precipitation (mm), day is Day of year, and hour is time (in hours) since sunset that a particular call sequence occurred. Site is detector site and was included as a random variable.

Model
Day + Site (random)
Day + Year + Site (random)
Temp + Site (random)
Wind + Day + Year + Site (random)
Precip + Day + Year + Site (random)
Temp + Wind + Site (random)
Temp * Wind + Site (random)
Temp + Precip + Site (random)
Temp * Precip + Site (random)
Wind + Precip + Site (random)
Wind * Precip + Site (random)
Temp + Wind + Precip + Site (random)
Day * Year + Site (random)
Wind + Year + Site (random)
Wind + Precip + Year + Site (random)
Wind * Precip + Year + Site (random)
Wind + Precip + Day + Year + Site (random)
Wind + Precip + Day * Year + Site (random)
Precip + Year + Site (random)
Wind * Year + Site (random)
Temp + Day + Year + Site (random)
Temp + Day * Year + Site (random)
Temp * Day * Year + Site (random)
Wind + Site (random)
Precip + Site (random)
Day + Hour + Site (random)
Day + Year + Hour + Site (random)
Day * Year * Hour + Site (random)
Wind + Precip + Year + Day + Hour + Site (random)
Wind + Precip + Year * Day * Hour + Site (random)
Wind + Day + Year + Hour + Site (random)
Precip + Day + Year + Hour + Site (random)
Temp + Day + Year + Hour + Site (random)
Temp + Day * Year * Hour + Site (random)
Temp + Wind + Precip + Day + Year + Hour + Site (random)

for inland areas as climate change proceeds, shifts in activities such as timber harvesting, prescribed burning or development and current curtailment windows (which are designed to protect maternity activity and non-volant juveniles from harm) may need to be considered. The peak activity window calculated with the GAM trend lines suggests that we may need to monitor for species of concern earlier in the year than we initially thought. Similarly, for migratory tree bats, less seasonally-predictable temperatures, i.e., higher early spring temperatures or later fall temperatures in the future, could make anticipating migratory pulses more difficult and thus complicate seasonal-based efforts to match wind-energy mortality mitigation standards with dates.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

See Appendix Tables A1 and A2.

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