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Activity Patterns of Cave-Dwelling Bat Species during Pre-Hibernation Swarming and Post-Hibernation Emergence in the Central Appalachians

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Abstract: In North America, bat research efforts largely have focused on summer maternity colonies and winter hibernacula, leaving the immediate pre- and post-hibernation ecology for many species unstudied. Understanding these patterns and processes is critical for addressing potential additive impacts to White-nose Syndrome (WNS)-affected bats, as autumn is a time of vital weight gain and fat resources are largely depleted in early spring in surviving individuals. Our study sought to examine autumn and spring bat activity patterns in the central Appalachian Mountains around three hibernacula to better understand spatio-temporal patterns during staging for hibernation and post-hibernation migration in the post-WNS environment. From early September through November 2015 and 2016, and from early March through April 2016 and 2017, we assessed the effects of distance to hibernacula and ambient conditions on nightly bat activity for *Myotis* spp. and big brown bats (*Eptesicus fuscus*) using zero-crossing frequency division bat detectors near cave entrances and 1 km, 2 km, and 3 km distant from caves. Following identification of echolocation calls, we used generalized linear mixed effects models to examine patterns of activity across the landscape over time and relative to weather. Overall bat activity was low at all sample sites during autumn and spring periods except at sites closest to hibernacula. Best-supported models describing bat activity varied, but date and ambient temperatures generally appeared to be major drivers of activity in both seasons. Total activity for all species had largely ceased by mid-November. Spring bat activity was variable across the sampling season, however, some activity was observed as early as mid-March, almost a month earlier than the historically accepted emergence time regionally. Current timing of restrictions on forest management activities that potentially remove day-roosts near hibernacula when bats are active on the landscape may be mismatched with actual spring post-hibernation emergence. Adjustments to the timing of these restrictions during the spring may help to avoid potentially additive negative impacts on WNS-impacted bat species.

Keywords: bat activity; caves; central Appalachians; emergence; swarming

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1. Introduction

Prior to hibernation, many temperate cave-dwelling bat species “swarm” around hibernacula to mate and choose suitable hibernation sites [1–3]. This time is vital for weight gain and fat deposition, a necessity to survive the energetic demands of hibernation [4–7] which have been exacerbated by the impacts of White-nose Syndrome (WNS) impacts [8,9]. During the late summer and early autumn, hundreds to thousands of individual bats may engage in swarming behavior outside a hibernaculum [3,10], with males being most active throughout the night and for a longer period into the autumn at or near hibernacula compared to females [11–13]. Still, prior to entering hibernation in mid- to late-autumn, bats continue to roost on the landscape, in trees, snags, emergent rocks, and human structures [12,14]. Effects of ambient conditions on bat activity, regardless of sex, during the autumn swarming period, and specifically around known hibernacula, are unknown for the central Appalachian Mountains. A greater examination of how ambient conditions affect the timing of autumn swarm activity and subsequent hibernation phenology could help natural resource managers better define and manage critical autumn swarm habitat on the landscapes surrounding hibernacula being used by bats. These insights may help prevent accidental 'take', as defined under Section 3 of the Endangered Species Act, as amended [15], especially with regard to the federally-endangered Indiana bat (*Myotis sodalis*; hereafter MYSO) from activities which constitute a forest disturbance, i.e., forest harvesting or prescribed burning.

During the spring emergence/staging period, cavernicolous bats emerge from hibernacula and disperse across the landscape, with reproductively-active females establishing maternity colonies [16,17]. Post-emergence, bats often do not re-enter hibernacula and will instead roost across the landscape. However, observations of spring roost sites are limited compared to well-studied summer roosts [18]. Foraging success and prey availability around hibernacula during the spring, when energetic demands are high post-hibernation, are important factors affecting subsequent movement to maternity areas and subsequent reproductive success [9,19]. Spring emergence may not be triggered by prey availability *per se*, but it is probably linked directly to temperature and pressure changes, photoperiod, reproductive phenology and circannual rhythms [19]. Meyer et al. [19] suggested that female bat arrival at colony areas coincides with increasing insect abundance, even if prey availability was low at first emergence.

Some cave-dwelling bat species, such as MYSO, may migrate great distances (as far as 500 km) to maternity areas upon emergence in the spring, a behavior which consumes valuable energy stores in species already experiencing WNS-related impairment [9,18,20]. Similarly, spring movement data are lacking for the threatened northern long-eared bat (*Myotis septentrionalis*; hereafter MYSE) that while not considered a migratory bat, may still travel > 150 km to summer foraging/maternity colony habitat [21,22]. Because energetic demands of migration are high, foraging may be an important activity immediately post-emergence. Foraging success, however, is tied closely to prey availability, which in turn is affected by weather conditions [19,23]. Spatio-temporal assessments of bat activity post-emergence may better allow managers to recognize vital habitat and time periods, thus encouraging conservation actions and habitat management that provide maximum benefit to dwindling bat populations regionally.

Critical to understanding the effects of WNS on emergence timing and dynamics [8,9] is the influence of the disease on reproductive output [24]. Female bats emerge earlier than males regardless of WNS-related impacts [24,25], and WNS causes bats (regardless of sex) to emerge earlier in the spring [8,25], which may prove detrimental to species' recruitment. Clearly, WNS compromises female bats' physiological condition during hibernation [9]. To this effect, Francl et al. [26] proposed that female bats may abort pregnancy if crucial energy sources are too limited to provide ample energy required for fetal or juvenile development during the maternity season. Bats may not be able to withstand the danger of unseasonably cold temperatures in the early spring. Furthermore, WNS increases overwinter energy consumption, and reproductive failure may negate any physiological benefits of emerging earlier. Females lacking the physiological energy demands of pregnancy may have fewer behavioral/roosting constraints. Therefore, they could conceivably emerge from hibernation very early with less deleterious effects, though this remains speculative. Non-reproductive females may have a better chance of surviving through the spring and summer.

Under the Indiana Bat Protection and Enhancement Plan Guidelines [27], hibernacula where MYSO exist in the central Appalachians are afforded protective buffer zones, whereby tree clearing activities are seasonally restricted. Within an 8-km radius of Priority 3 and Priority 4 MYSO hibernacula [22], tree clearing can only occur between November 15 and March 31 to avoid disturbing MYSO day-roosting in trees during the autumn swarm or spring emergence [27]. A regional understanding of bat activity patterns around hibernacula during spring and autumn could help determine the sufficiency of these protective cave buffers, especially for the federally-listed species such as MYSE and MYSO.

Accordingly, our primary objective was to determine activity patterns in cave-hibernating bats during the pre-hibernation staging period and the spring emergence period around caves in the central Appalachians several years after the onset of WNS regionally. Secondly, we sought to define drivers of acoustic activity during these understudied seasons. We hypothesized that activity would vary both temporally and spatially around caves, but activity would occur throughout the sampling season, specifically proximal to cave entrances [28]. Furthermore, we hypothesized that ambient conditions such as temperature or precipitation act as indicators and cause bats to restrict or increase activity during autumn and spring in habitats around caves.

2. Methods

2.1. Study Area

We conducted our study adjacent to three known bat hibernacula in the central Appalachians Mountains, two caves in the Ridge and Valley sub-province in Virginia and one cave in West Virginia in the unglaciated Appalachian Plateau sub-province (Figure 1). These karst-solution caves were chosen because of similar numbers of hibernating Indiana bats pre-WNS along with multi-year cave-count records [29] and a south to north gradient on the regional landscapes. Each of the three caves sampled were considered MYSO Priority 3 hibernacula based on cave count data [22], prior to the advent of WNS and contained similar numbers of hibernating bats. The two Virginia caves were located in Bath and Bland counties (hereafter Caves A and B, respectively), and the West Virginia cave was located in Tucker County (hereafter Cave C; specific names withheld to protect locations of federally-listed species' hibernacula). The forests surrounding Caves A and B are generally xeric-to moderately mesic oak (*Quercus* spp.) associations on ridges and other areas with well-drained soils, and mixed mesophytic forest along riparian areas and north-facing aspects [30]. The predominant forest surrounding Cave C is a northern/Allegheny hardwood association [31]. The landscape immediately surrounding both Cave A and Cave C primarily was forested, whereas the landscape surrounding Cave B is a matrix of forest and agricultural land. Ford et al. [31] and Powers et al. [29] provide a description of the extant bat community at these locations.

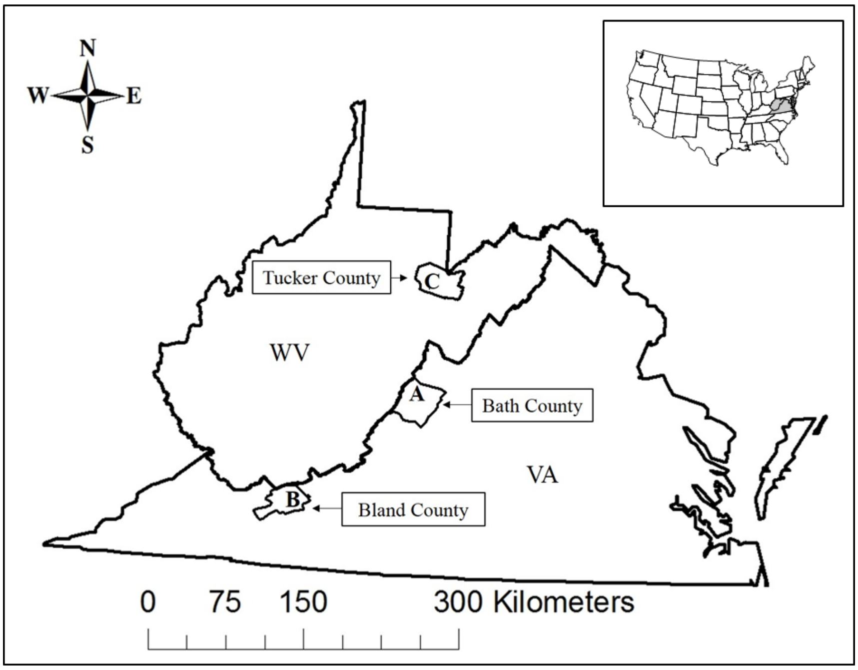

Figure 1. Approximate locations of central Appalachian Mountain caves acoustic sampling was conducted for bat species during autumn 2015 and 2016 and spring 2016 and 2017; two are located in the Ridge and Valley physiographic sub-province of Virginia (**A**,**B**), and the third is in the unglaciated central Appalachian Plateau physiographic sub-province of West Virginia (**C**). Inset shows position of Virginia and West Virginia within the continental United States.

2.2. Data Collection

For autumn, we monitored bat activity at the main entrance of each cave and at sampling points located generally one km, two km, and three km distances from cave entrances (Figure 2) from early September to mid-November in 2015 and 2016, when cave bats swarm and mate around hibernacula. For spring, we monitored bat activity in early March to late April in 2016 and 2017, when bats were leaving hibernacula and dispersing across the landscape prior to the summer maternity season [32]. For each cave, one detector was placed near the cave entrance (away from acoustically reflective surface), and two were deployed at each radii distance. We deployed an additional detector at the three km radii at Cave C, as the detector was opportunistically available for study. We chose detector locations based on accessibility (landowner permission and topography), likelihood of MYSE and MYSO presence [31] and site characteristics known to produce high-quality call recordings (i.e., low clutter such as a forest canopy gap/riparian corridor). We spaced the two detectors at each radii > 100 m apart to ensure that individual bats were not sampled on two detectors simultaneously and to maintain quasi-independent sampling units [31]. We recorded acoustic data using Song Meter ZC detectors (SMM-U1 microphones), Song Meter SM2 (SMX-U1 microphones), and Song Meter SM4 detectors (SMM-U1 microphones, Wildlife Acoustics, Maynard, Massachusetts. The use of any trade, product or firm names does not imply endorsement by the US government. We attached detectors to trees, however, omni-directional microphones were placed on 3 m poles 2–4 m away from the boles. We programmed detectors to record nightly from 1900 to 0700 hours. We collected local weather data in Meteorological Terminal Aviation Routine format from Weather Underground digital records, from the airport nearest to each detector site (Supplementary Materials).

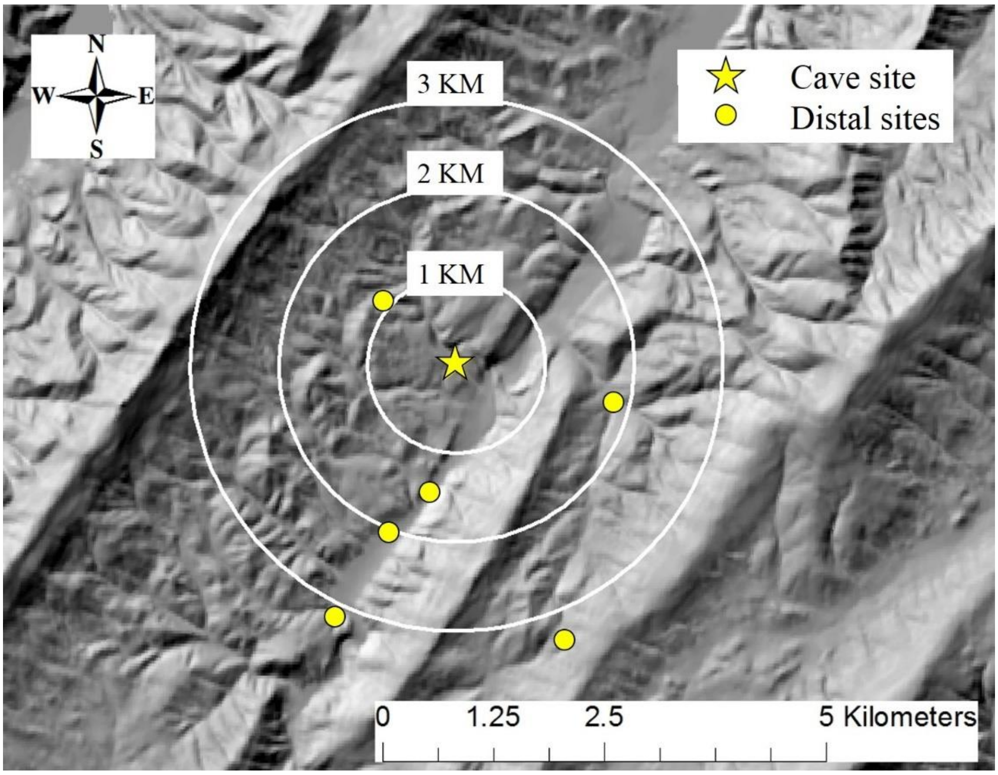

Figure 2. Generalized example of acoustic sampling setup around cave sites. Acoustic detector locations were chosen based on land ownership, access, and proximity to the 'km rings', in habitats where *Myotis sodalis* (Indiana bat) and *Myotis septentrionalis* (northern long-eared bat) presence was known, and where habitat physical features supported high-quality recordings. Acoustic detectors were deployed in this manner around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016 and spring 2016 and 2017.

We identified acoustic call data to species using the United States Fish and Wildlife Service (USFWS) approved Kaleidoscope version 4.3.1 (Wildlife Acoustics, Maynard, MA, USA) classifier 4.2.0 at the neutral setting for big brown bats (*Eptesicus fuscus*; hereafter EPFU), eastern red bats (*Lasiurus borealis*), hoary bats (*Lasiurus cinereus*), silver-haired bats (*Lasionycterus noctivigans*), eastern small-footed bats (*Myotis leibii*), little brown bat (*Myotis lucifugus*; hereafter MYLU), MYSE, MYSO and tri-colored bats (*Perimyotis subflavus*) with default signal parameters at 8–120 kHz frequency range, 500 maximum inter-syllable gap, minimum of three pulses, and enhanced with advanced signal processing. We manually checked recorded files using program Analook (Titley Electronics, Columbia, Missouri) to ensure there were no major misclassification errors (e.g., noise files consistently classified as bat echolocation pass). We were not concerned with overall accuracy of the program to assess levels of activity, as all bat species examined were known to be present at our sites, therefore we assumed constant bias in automated file identification [33]. Nonetheless, because of the precipitous declines of *Myotis* spp. post-WNS and subsequent difficulty in obtaining enough species-specific calls to overcome maximum likelihood estimator identification confidence thresholds [34], along with, known poor echolocation call quality near hibernacula, we grouped all *Myotis* spp. (MYLE, MYLU, MYSE, and MYSO) as one category [26,35].

2.3. Statistical Analyses

We created a set of *a priori* candidate models representing specific hypotheses about the relationship between habitat variables and bat activity, using the variables and models for analyses of both autumn and spring data. Candidate models included combinations of date, site (caves A, B, and C) cave proximity, and ambient conditions (Table 1). To evaluate potential curvilinear relationships between relative bat activity and date, we included polynomial terms on date, we assessed the multi-collinearity among predictors to ensure highly correlated variables ($r > 0.6$) were not included within the same model using package corrplot [36] in program R version 3.2.3 [37]. We tested for autocorrelation in daily bat activity, for each species using R package nlme, but found little evidence to warrant the use of an autoregressive term in modelling [38]. We modelled nightly acoustic bat activity per detector site using negative binomial mixed models, with nested random effects to account for the correlated nature of sites around caves and repeated measures at sites. We fit negative binomial mixed models using R package glmmADMB [39]. We used negative binomial mixed models because bat activity data are counts, and variance was greater than the mean. Because we expected nonlinear changes in bat activity over the sampling period, we compared fully parameterized models with different polynomial structures on date for each species and species group. We used a two-step information theoretic approach; first ranking models with polynomial structures on date using Akaike's Information Criterion corrected for small sample size (AIC_c) from package MuMIn [40,41], then using the best-supported polynomial structure for all subsequent candidate models representing *a priori* hypotheses. If models were competing ($\Delta AIC_c < 2$) we used the model with the lowest polynomial order, to avoid overfitting. We centered and scaled all continuous predictors to allow us to assess main effects of interactions [42].

We included a set of models for all *Myotis* bat species (hereafter *Myotis* spp.) and also for big brown bat (*Eptesicus fuscus*; hereafter EPFU) individually because we expected differences in activity patterns for this species. For example, EPFU represent a cave-dwelling species with somewhat different life history than most *Myotis* spp.; notably, EPFU are impacted less from WNS due to their larger body size and, in much of our study area, tend to prefer human structures for roost sites [43,44]. We compared constructed models using AIC_c [41]. To test for the existence of interacting effects of date and distance to hibernacula on bat activity, we additionally fit *post hoc* models for each species/group for both autumn and spring. We fit models using a distance to hibernacula variable (0 km, 1 km, 2 km, 3 km), but due to convergence issues in some species or groups, we had to revert to a binary variable (at cave, not at cave).

Table 1. Variables used in candidate models representing hypotheses regarding bat activity around three caves in the central Appalachians, Virginia, and West Virginia, during autumn 2015 and 2016, and spring 2016 and 2017. Variables were used in different combinations, and highly correlated variables were not included within a single candidate model.

Variable	Explanation
Date	date
Year	sampling year
Avg. Temp	mean daily temperature
Max. Temp	maximum daily temperature
Min. Temp	minimum daily temperature
Δ Avg. Temp	change in mean daily temperature from previous day
Δ Max. Temp	change in maximum daily temperature from previous day
Δ Min. Temp	change in minimum daily temperature from previous day
Max Wind	maximum daily wind speed
Avg. Wind	mean daily wind speed
Δ Max. Wind	change in maximum daily wind speed from previous day
Δ Mean. Wind	change in mean daily wind speed from previous day
Binary Precipitation	binary precipitation
Δ Binary Precipitation	change in binary precipitation from previous day
Cave Proximity	at cave or distance from cave along radii

3. Results

3.1. Total Activity

Overall, we acoustically sampled 22 sites around the three caves, in autumn 2015, spring 2016, autumn 2016, and spring 2017. We sampled for 68 and 97 nights over autumn 2015 and 2016, and for 49 and 56 nights during spring 2016 and 2017, respectively. This effort accounted for 98,979 of identified bat echolocation passes. Among the total identified echolocation passes, 49,737 (50% of total) were identified as *Myotis* spp. and 6543 (6.6% of total) were identified as EPFU, whereas the remainder were non-hibernating species such as eastern red bat. Though our objective was to sample continuously across each season, due to detector failure, and inaccessibility due to weather, some detectors did not record continuously for a few nights through the sampling periods.

3.2. Autumn Activity Patterns

We recorded 23,430 *Myotis* spp. echolocation passes during the autumn sample period. Our best supported model describing *Myotis* spp. activity received 88 percent of the overall model support and contained the following variables: date, a 2nd order polynomial term on date, year, mean daily temperature, change in mean daily temperature, mean daily wind speed, change in mean daily wind speed, change in binary precipitation, distance to cave, and an interaction between date and mean daily temperature (Table 2). No other models were competing. Among continuous predictors, date and mean daily temperature had the largest effect sizes (Table 2). *Myotis* spp. activity was substantially greater proximal to cave entrances relative to distal sites (Table 2) and decreased over the season. However, these relationships were related positively to mean daily temperature. Temperature and date interacted, such that temperature had a stronger impact on activity later in the season (Figure 3). Although contained in the best supported model, change in mean daily temperature, mean daily wind speed, change in mean daily wind speed, and change in binary precipitation had minimal effect sizes (Table 2). Overall *Myotis* spp. activity was lower in 2016 than 2015 (Figure 3). *Post-hoc* modelling indicated that there was no substantial interaction between date and distance to hibernacula (Table 3).

Table 2. Estimates and 95% confidence intervals (CI) from the best supported *a priori* model predicting combined Myotis species (*Myotis leibii*, eastern small-footed bat; *Myotis lucifugus*, little brown bat; *Myotis septentrionalis*, northern long-eared bat; *Myotis sodalis*, Indiana bat) activity around three caves in the central Appalachians, Virginia, and West Virginia, during autumn 2015 and 2016. An asterisk (*) between predictors indicates an interaction.

Variable	β	Lower CI	Upper CI
(Intercept)	3.848	2.046	5.651
Date	−0.810	−0.958	−0.661
Date^2	−0.057	−0.186	0.072
Year 2016	−0.516	−0.717	−0.316
Avg. Temp	0.493	0.336	0.650
Δ Avg. Temp	−0.204	−0.300	−0.107
Avg. Wind	−0.143	−0.305	0.020
Δ Mean. Wind	−0.143	−0.265	−0.022
Δ Binary Precipitation	−0.302	−0.489	−0.116
Distal Sites	−3.095	−4.609	−1.582
Date*Avg. Temp	0.466	0.315	0.616

Table 3. Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting combined Myotis species (*Myotis leibii*, eastern small-footed bat; *Myotis lucifugus*, little brown bat; *Myotis septentrionalis*, northern long-eared bat; *Myotis sodalis*, Indiana bat) activity around three caves in the central Appalachians, Virginia, and West Virginia, during autumn 2015 and 2016. An asterisk (*) between predictors indicates an interaction.

Variable	β	Lower CI	Upper CI
(Intercept)	3.881	2.068	5.694
Date	−0.661	−0.927	−0.394
Date^2	−0.061	−0.190	0.068
Year 2016	−0.519	−0.720	−0.318
Avg. Temp	0.499	0.341	0.657
Δ Avg. Temp	−0.205	−0.302	−0.107
Avg. Wind	−0.144	−0.306	0.019
Δ Mean. Wind	−0.141	−0.263	−0.020
Δ Binary Precipitation	−0.303	−0.490	−0.117
Distal Sites	−3.129	−4.647	−1.610
Date*Avg. Temp	0.477	0.325	0.630
Date*Cave Proximity	−0.181	−0.451	0.088

We recorded 2485 EPFU echolocation passes during the autumn sample period. The best supported model describing EPFU activity contained the following variables: date and its 4th order polynomial term, year, maximum daily temperature, change in maximum daily temperature, maximum daily wind speed, change in maximum daily wind speed, binary precipitation, and change in binary precipitation (Tables 4 and 5). Only maximum daily temperature had a large effect size (Figure 4, Table 5). Neither date nor year had a substantial effect on activity level (Table 5). Although also contained in the best supported model, change in maximum daily temperature, maximum daily wind speed, change in maximum daily wind speed, binary precipitation, and change in binary precipitation had minimal effect sizes (Table 5). *Post-hoc* modelling indicated that an interaction between date and distance to hibernacula had a substantial effect on EPFU activity, such that activity levels decreased at distal sites more rapidly than those proximal to hibernacula (Figure 5, Table 6).

Table 4. Rankings of models predicting *Eptesicus fuscus* (big brown bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during autumn 2015 and 2016, with k (number of parameters), Akaike's information criteria (AIC) value, Akaike's information criteria (AIC$_c$) value corrected for small sample size, difference in AIC$_c$ value between best supported model and ith model (ΔAIC$_c$), w_i (model weight), and ER_i (evidence ratio).

Variable	k	AIC	AIC$_c$	ΔAIC$_c$	w_i	ER_i
Date + Date^2 + Date^3 + Date^4 + year + Max. Temp + Δ Max. Temp + Max Wind + Δ Max. Wind + Binary Precipitation + Δ Binary Precipitation	12.0	3699.4	3699.6	0.0	0.5	1.0
Date + Date^2 + Date^3 + Date^4 + year +Date*Max. Temp + Min. Temp + Δ Max. Temp + Δ Min. Temp + Max Wind + Δ Max. Wind + Binary Precipitation + Δ Binary Precipitation + Cave Proximity	16.0	3700.5	3700.9	1.3	0.2	1.9
Date + Date^2 + Date^3 + Date^4 + year + Max. Temp + Δ Max. Temp + Max Wind + Δ Max. Wind + Binary Precipitation + Δ Binary Precipitation + Cave Proximity	13.0	3701.0	3701.2	1.6	0.2	2.3

Table 5. Estimates and 95% confidence intervals (CI) from the best supported *a priori* model predicting *Eptesicus fuscus* (big brown bat) activity around three caves in the central Appalachians, Virginia, and West Virginia, during autumn 2015 and 2016.

Variable	β	Lower CI	Upper CI
(Intercept)	−1.298	−2.049	−0.547
Date	0.071	−0.222	0.364
$Date^2$	0.139	−0.257	0.534
$Date^3$	−0.114	−0.243	0.016
$Date^4$	−0.056	−0.182	0.070
Year 2016	−0.038	−0.340	0.264
Max. Temp	1.222	0.983	1.462
Δ Max. Temp	0.165	0.012	0.318
Max Wind	0.296	0.109	0.483
Δ Max. Wind	−0.068	−0.240	0.104
Binary Precipitation	−0.201	−0.509	0.108
Δ Binary Precipitation	−0.230	−0.549	0.089

Table 6. Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting *Eptesicus fuscus* (big brown bat) activity around three caves in the central Appalachians, Virginia, and West Virginia, during autumn 2015 and 2016. An asterisk (*) between predictors indicates an interaction.

Variable	β	Lower CI	Upper CI
(Intercept)	−0.704	−2.541	1.132
Date	0.941	0.509	1.373
$Date^2$	0.006	−0.378	0.390
$Date^3$	−0.131	−0.262	0.000
$Date^4$	−0.028	−0.151	0.094
Year 2016	0.010	−0.283	0.303
Max. Temp	1.213	0.977	1.449
Δ Max. Temp	0.140	−0.009	0.290
Max Wind	0.202	0.018	0.386
Δ Max. Wind	−0.094	−0.263	0.075
Binary Precipitation	−0.197	−0.500	0.106
Δ Binary Precipitation	−0.247	−0.561	0.067
Distance to Cave1km	−1.380	−3.609	0.849
Distance to Cave2km	−0.611	−2.825	1.604
Distance to Cave3km	−0.245	−2.384	1.894
Date*Distance to Cave1km	−0.821	−1.245	−0.397
Date*Distance to Cave2km	−0.728	−1.108	−0.348
Date*Distance to Cave3km	−1.230	−1.610	−0.850

3.3. Spring Activity Patterns

We recorded 26,307 *Myotis* spp. echolocation passes during the spring sample period. The best supported model describing *Myotis* spp. activity contained the following variables: date and its 3rd order polynomial term, year, mean daily temperature, change in mean daily temperature, mean daily wind speed, change in mean daily wind speed, change in binary precipitation, distance to cave, and an interaction between date and mean daily temperature (Table 7). Among those, mean daily temperature, mean daily wind speed, and distance to cave had the largest effect sizes (Table 7). *Myotis* spp. activity was substantially greater proximal to cave entrances relative to distal sites (Table 7). *Myotis* spp. activity was consistently low over the season relative to summer pre-WNS values [35], only increasing slightly later in the spring, but neither date nor year had a substantial effect on activity level. *Myotis* spp. activity was related positively to mean daily temperature, but negatively related to mean daily wind speed. Temperature and date interacted, and temperature had a stronger impact early in the season (Figure 6). Although also contained in the best supported model, change in mean daily temperature, change in mean daily wind speed, and change in binary precipitation had minimal effect sizes (Table 7). *Post-hoc* modelling indicated that there was no substantial interaction between date and distance to hibernacula (Table 8).

Table 7. Estimates and 95% confidence intervals (CI) from the best supported *a priori* model predicting combined Myotis species (*Myotis leibii*, eastern small-footed bat; *Myotis lucifugus*, little brown bat; *Myotis septentrionalis*, northern long-eared bat; *Myotis sodalis*, Indiana bat) activity around three caves in the central Appalachians, Virginia, and West Virginia, during spring 2016 and 2017. An asterisk (*) between predictors indicates an interaction.

Variable	β	Lower CI	Upper CI
(Intercept)	3.624	1.746	5.501
Date	−0.216	−0.442	0.010
Date^2	−0.003	−0.104	0.099
Date^3	0.243	0.141	0.345
Year 2017	−0.010	−0.239	0.219
Avg. Temp	0.904	0.761	1.047
Δ Avg. Temp	−0.266	−0.373	−0.158
Avg. Wind	−0.507	−0.670	−0.343
Δ Mean. Wind	0.068	−0.064	0.201
Δ Binary Precipitation	−0.125	−0.331	0.080
Distal Sites	−3.384	−5.391	−1.377
Date*Avg. Temp	−0.471	−0.591	−0.351

Table 8. Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting combined Myotis species (*Myotis leibii*, eastern small-footed bat; *Myotis lucifugus*, little brown bat; *Myotis septentrionalis*, northern long-eared bat; *Myotis sodalis*, Indiana bat) activity around three caves in the central Appalachians, Virginia, and West Virginia, during spring 2016 and 2017. An asterisk (*) between predictors indicates an interaction.

Variable	β	Lower CI	Upper CI
(Intercept)	3.629	1.708	5.549
Date	−0.195	−0.635	0.245
Date^2	−0.194	−0.384	−0.005
Date^3	0.110	−0.067	0.287
Year 2017	−0.070	−0.307	0.168
Avg. Temp	0.891	0.743	1.039
Δ Avg. Temp	−0.275	−0.387	-0.163
Avg. Wind	−0.458	−0.629	-0.288
Δ Mean. Wind	0.075	−0.061	0.212
Δ Binary Precipitation	−0.059	−0.269	0.152
Distance to Cave1km	−3.462	−5.804	−1.120
Distance to Cave2km	−4.251	−6.620	−1.881
Distance to Cave3km	−2.754	−5.001	−0.507
Date*Distance to Cave1km	0.129	−0.486	0.743
Date*Distance to Cave2km	−0.082	−0.735	0.570
Date*Distance to Cave3km	0.153	−0.460	0.765
Date^2*Distance to Cave1km	0.293	0.034	0.552
Date^2*Distance to Cave2km	0.187	-0.080	0.454
Date^2*Distance to Cave3km	0.003	-0.259	0.264
Date^3*Distance to Cave1km	−0.030	−0.287	0.227
Date^3*Distance to Cave2km	0.170	−0.099	0.440
Date^3*Distance to Cave3km	−0.120	−0.381	0.140

We recorded 4058 EPFU echolocation passes during the spring sample period. The best supported model describing EPFU activity contained the following variables: date and its 3rd order polynomial, year, maximum daily temperature, minimum daily temperature, change in maximum daily temperature, change in minimum daily temperature, maximum daily wind speed, change in maximum daily wind speed, binary precipitation, change in binary precipitation, distance to cave, and an interaction between date and maximum daily temperature (Table 9). Among those, maximum daily temperature, binary precipitation, and distance to cave had the largest effect sizes (Table 9). Big brown bat activity was positively related to maximum daily temperature and negatively related to daily precipitation (Figure 7). Activity was higher proximal to cave entrances relative to distal sites (Table 9). Neither date nor year had a substantial effect on EPFU activity level. Although also contained in the best supported model, minimum daily temperature, change in maximum daily temperature, change in minimum daily temperature, maximum daily wind speed, change in maximum daily wind speed, change in binary precipitation, and the interaction between date and maximum daily temperature had minimal effect sizes (Table 9). *Post-hoc* modelling indicated that an interaction between date and distance to hibernacula had a substantial effect on EPFU activity, such that activity levels increased at sites one km and two km away from hibernacula throughout the spring while activity proximal to hibernacula displayed a unimodal peak early in the season (Table 10, Figure 8).

Table 9. Estimates and 95% confidence intervals (CI) from the best supported *a priori* model predicting *Eptesicus fuscus* (big brown bat) activity around three caves in the central Appalachians, Virginia, and West Virginia, during spring 2016 and 2017. An asterisk (*) between predictors indicates an interaction.

Variable	β	Lower CI	Upper CI
(Intercept)	0.040	−2.346	2.427
Date	−0.087	−0.404	0.231
Date^2	−0.213	−0.336	−0.089
Date^3	0.160	0.033	0.287
Year 2017	−0.440	−0.767	−0.114
Max. Temp	1.501	1.155	1.847
Min. Temp	0.381	0.104	0.657
Δ Max. Temp	0.008	−0.201	0.217
Δ Min. Temp	−0.072	−0.223	0.080
Max Wind	−0.122	−0.305	0.062
Δ Max. Wind	0.119	−0.068	0.305
Binary Precipitation	−0.516	−0.819	−0.214
Δ Binary Precipitation	−0.079	−0.383	0.225
Distal Sites	−0.654	−3.184	1.876
Date*Max. Temp	−0.077	−0.269	0.115

Table 10. Estimates and 95% confidence intervals (CI) from the best supported *post hoc* model predicting *Eptesicus fuscus* (big brown bat) activity around three caves in the central Appalachians, Virginia and West Virginia, during spring 2016 and 2017. An asterisk (*) between predictors indicates an interaction.

Variable	**β**	**Lower CI**	**Upper CI**
(Intercept)	0.048	−2.212	2.308
Date	−0.633	−1.016	−0.249
Date^2	−0.220	−0.343	−0.098
Date^3	0.185	0.060	0.311
Year 2017	−0.447	−0.773	−0.122
Max. Temp	1.535	1.191	1.878
Min. Temp	0.398	0.116	0.679
Δ Min. Temp	−0.058	−0.212	0.095
Δ Max. Temp	0.001	−0.209	0.211
Max Wind	−0.075	−0.259	0.110
Δ Max. Wind	0.150	−0.033	0.334
Binary Precipitation	−0.536	−0.837	−0.236
Δ Binary Precipitation	−0.104	−0.406	0.198
Distance to Cave1km	−1.418	−4.138	1.302
Distance to Cave2km	−1.152	−3.874	1.570
Distance to Cave3km	0.143	−2.459	2.746
Date*Distance to Cave1km	0.979	0.597	1.361
Date*Distance to Cave2km	0.718	0.358	1.079
Date*Distance to Cave3km	0.424	0.079	0.770
Date*Max. Temp	−0.122	−0.312	0.068

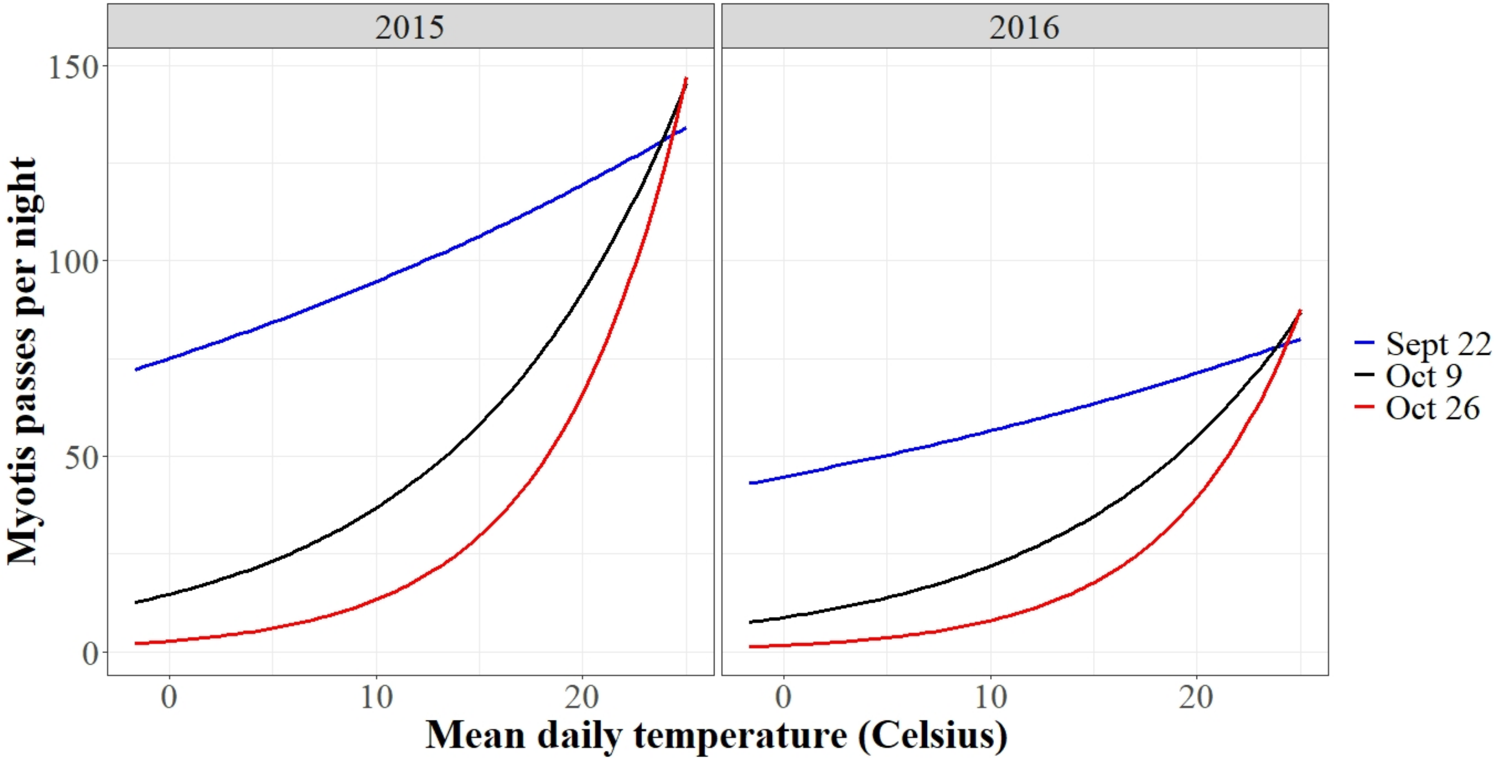

Figure 3. Partial effects plot of the interacting relationship between mean daily temperatures, date, and combined Myotis species (*Myotis leibii*, eastern small-footed bat; *Myotis lucifugus*, little brown bat; *Myotis septentrionalis*, northern long-eared bat; *Myotis sodalis*, Indiana bat) echolocation passes per detector night around three caves in the central Appalachians, Virginia, and West Virginia, during autumn 2015 and 2016. Panels show differences in number of passes between sampling years. Predicted activity from an early-(blue), mid-(black), and late-season (red) date are shown. Confidence intervals not shown for clarity.

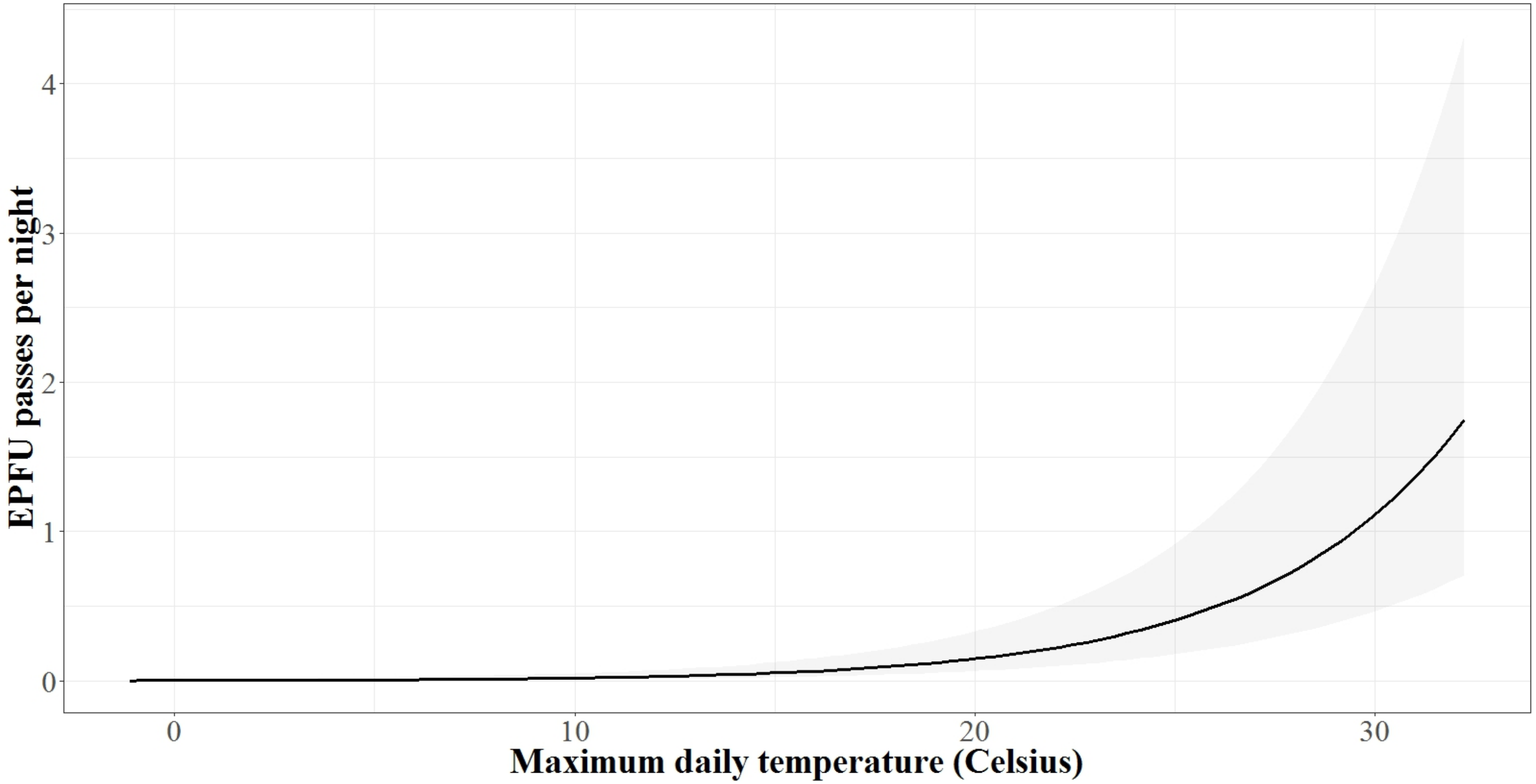

Figure 4. Partial effects plot of the relationship between maximum daily temperature and *Eptesicus fuscus*, big brown bat (EPFU), echolocation passes per detector night (with 95% confidence intervals) around three caves in the central Appalachians, Virginia, and West Virginia, during autumn 2015 and 2016.

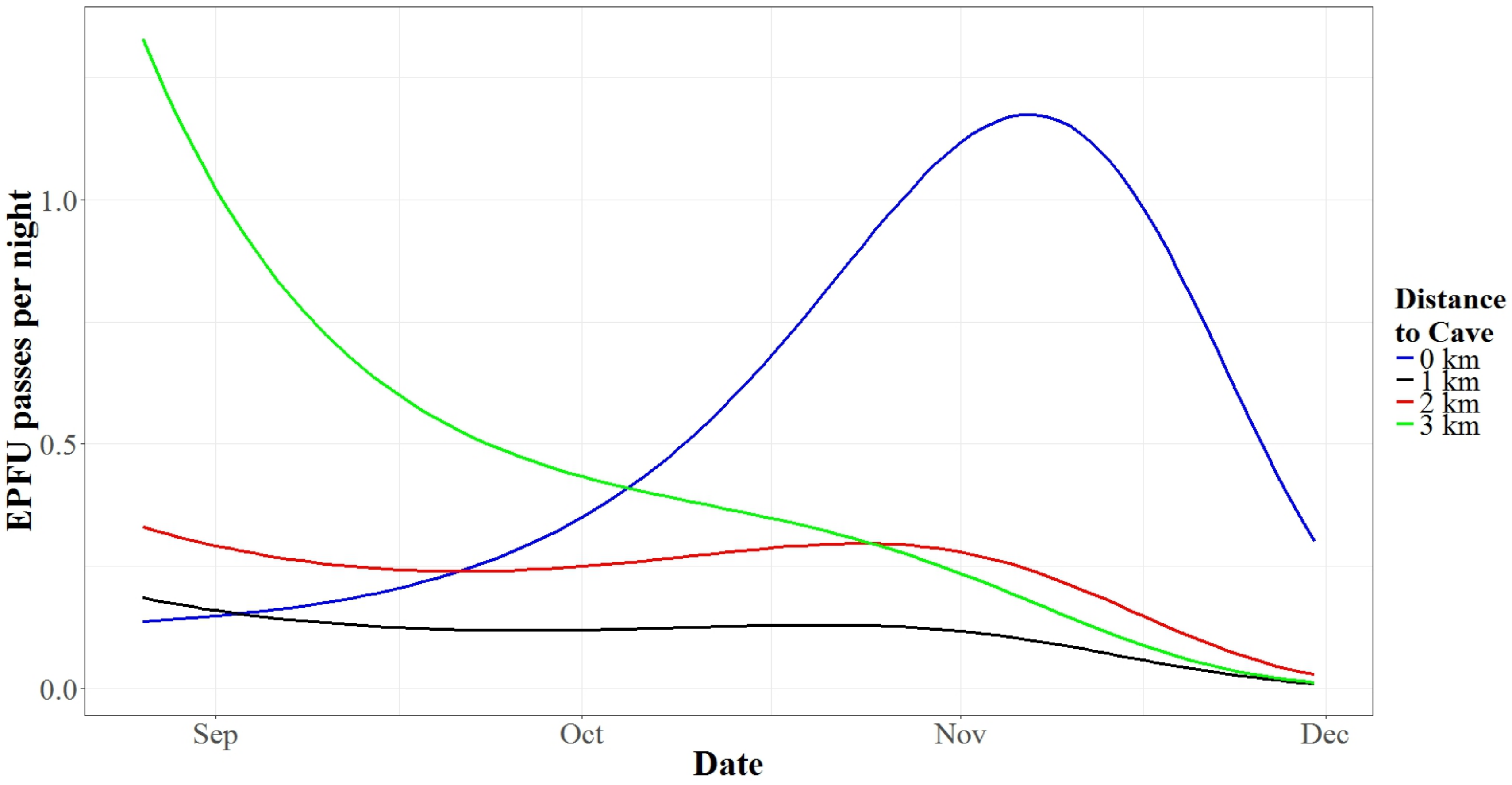

Figure 5. Partial effects plot of the interacting relationship between date and distance to hibernacula, and *Eptesicus fuscus*, big brown bat (EPFU), echolocation passes per detector night around three caves in the central Appalachians, Virginia, and West Virginia, during autumn 2015 and 2016. Confidence intervals not shown for clarity.

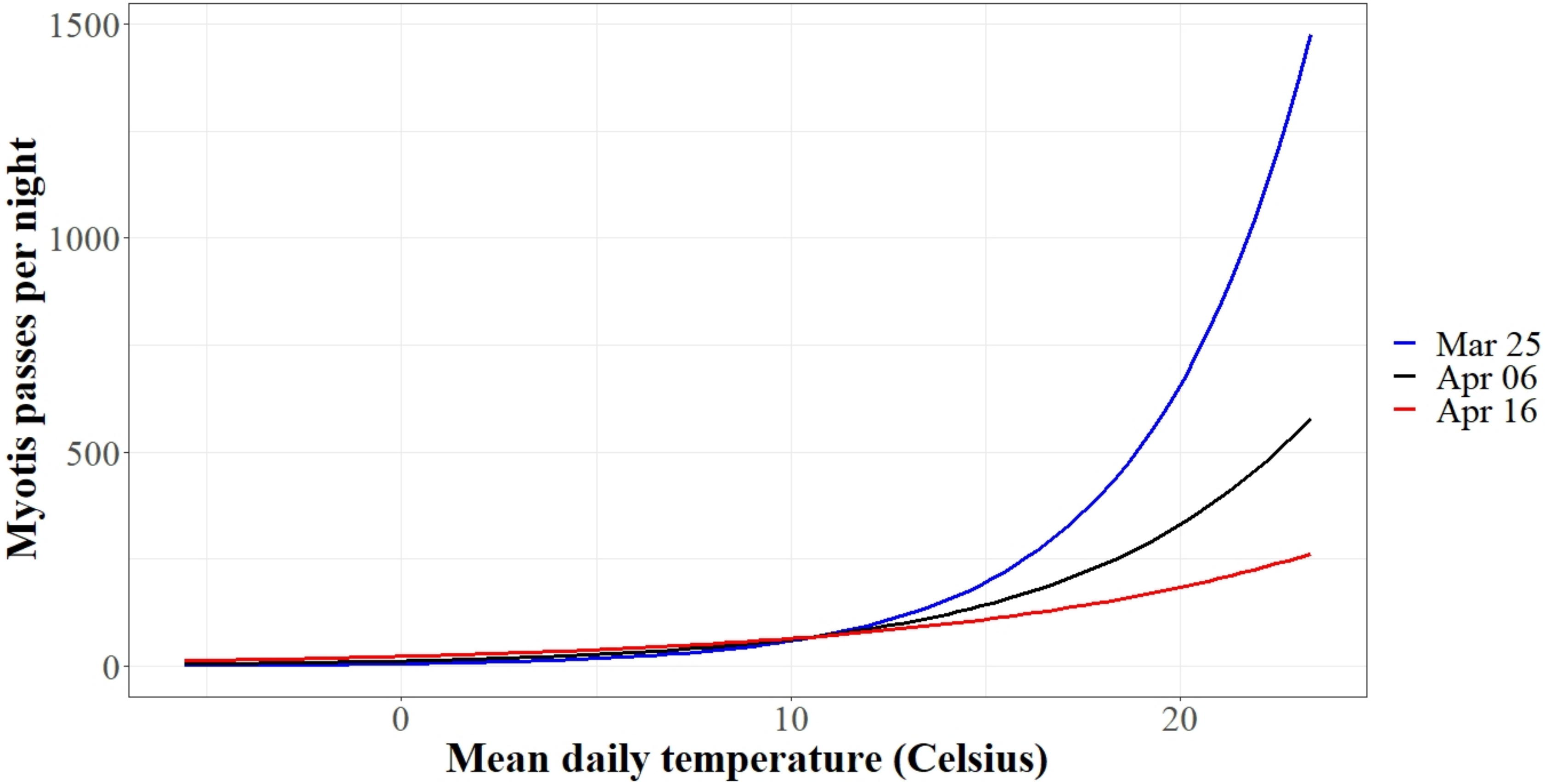

Figure 6. Partial effects plot of the relationship between mean daily temperatures, date, and combined Myotis species (*Myotis leibii*, eastern small-footed bat; *Myotis lucifugus*, little brown bat; *Myotis septentrionalis*, northern long-eared bat; *Myotis sodalis*, Indiana bat) echolocation passes per detector night around three caves in the central Appalachians, Virginia, and West Virginia, during spring 2016 and 2017. Predicted activity from an early- (blue), mid-(black), and late-season (red) date are shown. Confidence intervals not shown for clarity.

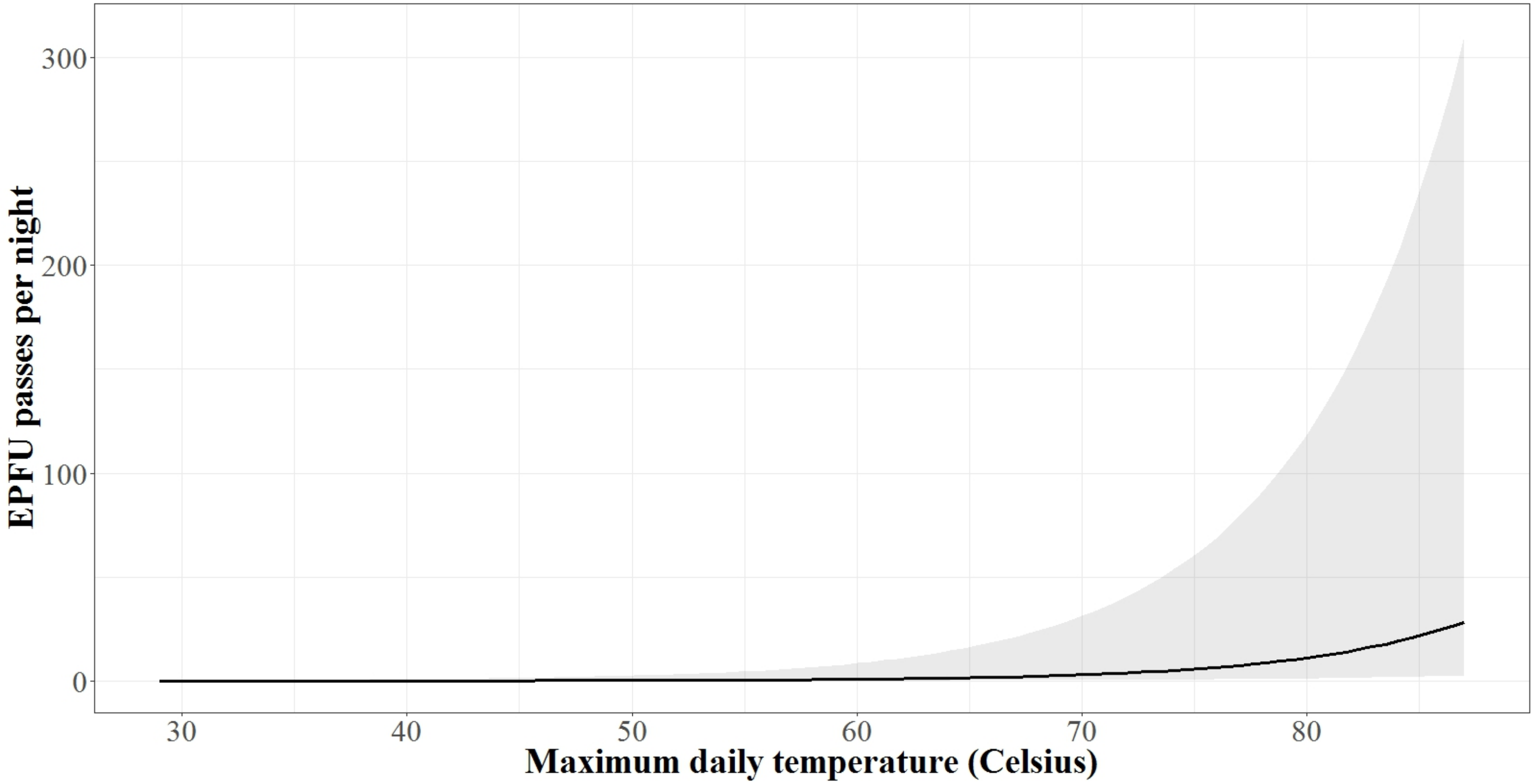

Figure 7. Partial effects plots of the relationship between maximum daily temperatures and *Eptesicus fuscus*, big brown bat (EPFU), echolocation passes per detector night (with 95% confidence intervals) around three caves in the central Appalachians, Virginia, and West Virginia, during spring 2016 and 2017.

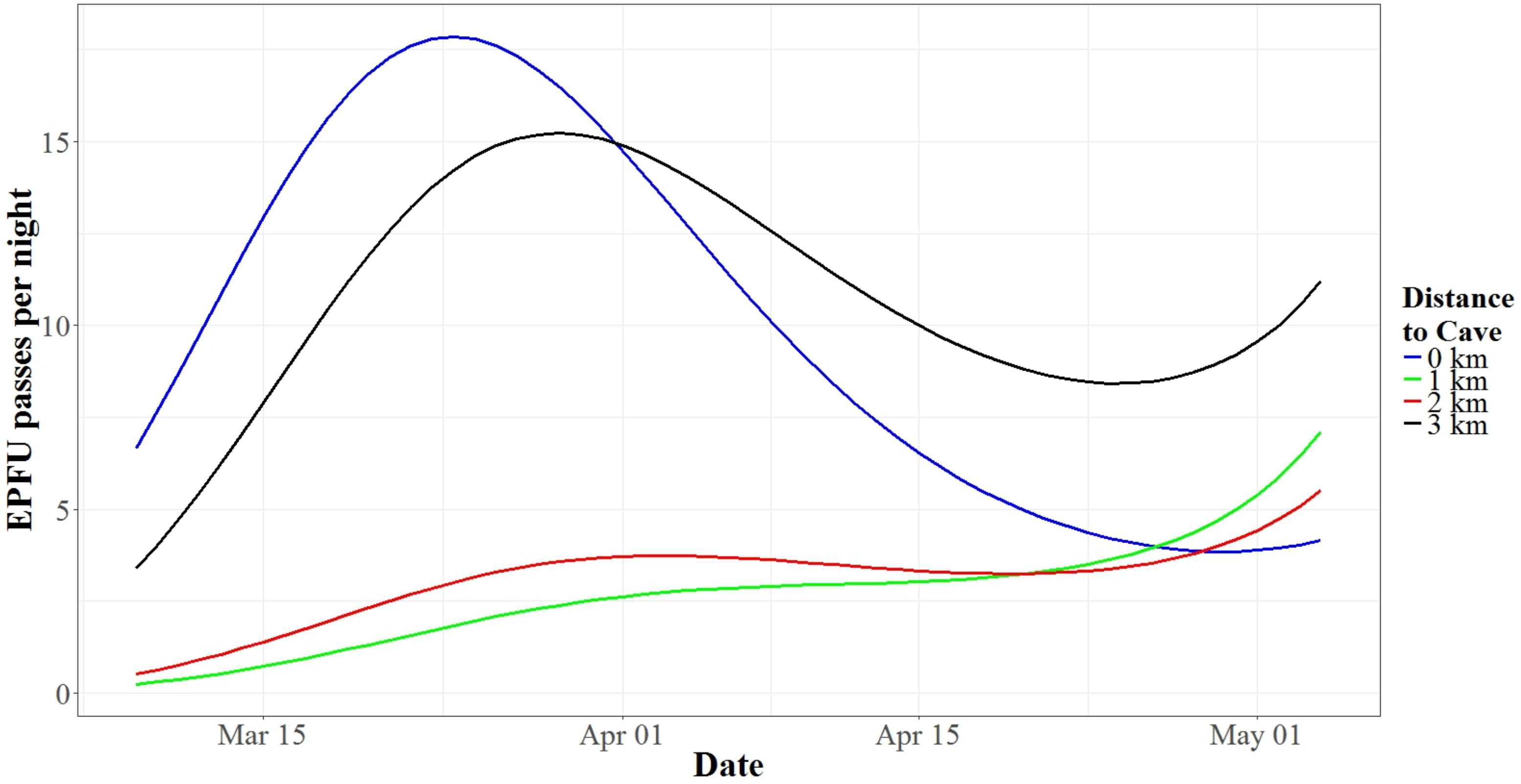

Figure 8. Partial effects plot of the interacting relationship between date, distance to cave, and *Eptesicus fuscus*, big brown bat (EPFU), echolocation passes per detector night around three caves in the central Appalachians, Virginia, and West Virginia, during spring 2016 and 2017. Confidence intervals not shown for clarity. The EPFU relative activity increased at distal sites faster than at cave sites later in the spring.

4. Discussion

Autumn activity varied among EPFU and the *Myotis* spp. group, but our results largely were consistent with *a priori* expectations. In general, bat activity was most related to ambient temperatures during autumn. In spring, bat activity was most related to ambient temperatures, but also related to date. Based on different life histories, we expected species-specific responses to ambient conditions and distance to caves in temperate environments [25,45–47]. The results corroborate previous research indicating ambient temperatures are positively related to general bat activity across seasons [19,28,43,48,49], and specifically show this relationship exists around hibernacula in the central Appalachians.

Although temperature and date generally had effects on overall bat activity, not all species/groups followed this exact pattern. We expected *a priori* that activity of cave-dwelling species would contract and concentrate around cave entrances through autumn, and our results indicated this pattern existed for EPFU. The substantial interacting effects of temperature and date on *Myotis* spp. and autumn activity likely exist due to metabolic/thermal costs and/or benefits relating to prey availability [49,50]. Prey resources of insectivorous bats become scarce at lower ambient temperatures [19,23]. Autumn activity of EPFU largely depended on maximum daily temperature, a finding similar to previous research indicating EPFU activity through the winter months is influenced by temperature [50]. Research has found that unlike *Myotis* spp., EPFU appear to be less impacted by WNS [26] and may have fewer physiological constraints due to larger body sizes, allowing for greater proportional late autumn and winter energy expenditures during the hibernation season. Indeed, we found no evidence of interacting effects of temperature and date on EPFU autumn activity. It is possible that EPFU can also return to typical summer-type roosts (human structures/barns) during autumn and winter activity, which may afford different thermal and metabolic benefits than caves [51]. The best supported model did not include the at-cave variable, indicating that EPFU activity was generally more widespread across the landscape during autumn in contrast with activity patterns of *Myotis* spp. These differences likely are a result of species-specific foraging strategies, but also could be attributed to species-specific roost selection and preference; EPFU may often fly > 2 km to foraging areas from roost sites, further, on average, than the *Myotis* spp. that occurred at our study sites [52,53]. The verified [29,54] and speculative [55] existence of other hibernacula in close proximity (within 3 km) to our study sites might have had an influence on each of the species and species groups through the autumn swarm period whereby activity estimates distal from sampled caves may have been positively biased.

The majority of bat echolocation calls occurred in early autumn and declined through mid-October, yet some activity continued to occur through the autumn swarm season at warmer conditions, suggesting that ambient conditions may partially regulate swarm activity and cave entry dynamics. Furthermore, by influencing bat activity and prey availability, ambient temperature may ultimately influence the body condition of bats entering hibernation [6,56]. In any given year, above-average ambient temperatures may delay bats' entry into hibernation by allowing bats to remain active later in autumn. This could presumably lead to shorter hibernation periods, potentially reducing fungal loads and therefore WNS-related mortality [7,57]. Warmer temperatures are linked to increased prey availability [23] and may lead to better body condition for bats entering hibernation, which in turn also may affect overwinter survival as well as reproductive output in the following seasons [58]. Conversely, it may be that colder ambient temperatures during the pre-hibernation period lead to improved fat reserves, as observed for the brown long-eared bat (*Plecotus auritus*) in Europe [59]. Prior to hibernation, warmer temperatures lead to longer activity on the landscape, but this could cause bats to be susceptible to other threats such as wind energy development or forest management on the landscapes we studied, if day-roost loss occurred later into autumn than previously anticipated. Furthermore, the exact biological triggers for immergence into hibernation are not fully understood for bats, and these triggers may be more closely linked to fat reserves than to ambient conditions and/or prey availability [6]. Although cave-dwelling bats, and specifically MYSO, usually hibernate where they swarm [3,60], pre-hibernation long-distance movements between hibernacula/swarming sites are not uncommon [48,61]. Ambient temperatures could certainly affect the movement patterns of bats between hibernacula/swarming sites, and thus may affect mating dynamics and immergence phenology. Further understanding the effects of temperature on swarming behavior may allow managers to determine the most crucial swarming periods, and thus plan protective measures around hibernacula more efficiently.

In general, spring activity was less related to date than in autumn activity. Daily temperature was the driving climatic variable that impacted activity for all species and groups in the spring, supporting *a priori* expectations. Findings also agreed with previous research that showed bat emergence from hibernacula in the spring was related positively to ambient temperatures and, to a lesser extent, photoperiod [23]. Czenze and Willis [24] found MYLU spring emergence was correlated most with a drop in barometric pressure, rather than temperatures outside hibernacula. Furthermore, Meyer et al. [23] found that timing of emergence was not associated with temperatures inside hibernacula. However, we found that ambient temperatures substantially affect bat activity post-emergence, across species/groups. Temperatures at roost sites within hibernacula change very little regardless of changing outside ambient temperatures [23,24], but temperatures and temperature fluctuations at roost sites outside hibernacula are readily perceived by bats [62,63]. Ambient temperatures post-emergence likely are the principal indicators for bats' activity in the spring. Although the effect size of date in spring was smaller than in autumn, there was an interaction between date and distance to hibernacula for EPFU. Spring activity of EPFU increased faster at distant sites than at sites more proximal to caves. Although the interaction between date and distance to hibernacula had large effect sizes, confidence intervals for estimates of EPFU activity were large and overlapping, suggesting small trends.

Even though the USFWS seasonal tree removal/forest harvesting window in the central Appalachians allows clearing activities through March 31st, we recorded a substantial amount of *Myotis* spp. activity well before the end of March. Furthermore, many hibernacula are used by both MYSO and MYSE during the winter months, and summer ranges overlap significantly [64–66]. Combined, these results suggest that tree-clearing activities in the spring could affect MYSO and MYSE in the central Appalachians, especially when early spring temperatures are unseasonably warm. Tree-clearing activities during the spring near hibernacula prior to March 31 may have the potential, albeit small, to be an additive stressor to the WNS-related population declines in the central Appalachians. Alternately, our data support the adequacy of the spatial and temporal extent of these buffers during the autumn swarm season, as activity had declined to negligible levels prior to the November 15th clearing date. Currently, guidelines provide for flexibility and adjustments to tree clearing restriction dates based on localized autumn swarming and spring emergence data within the range of MYSO [27]. However, data documenting bat activity around hibernacula during these seasons are limited, offering few insights to inform establishment of clearing restriction dates. Due to the physiological vulnerability of bats following hibernation when their fat reserves are critically depleted and prey resources are less abundant or highly variable in availability, maintaining habitat quality surrounding hibernacula can ensure adequate foraging and roosting opportunities.

5. Conclusions

Despite much reduced numbers of bats using central Appalachian hibernacula post-WNS, autumn entrance patterns remained consistent with those from pre-WNS. Spring emergence, however, was variable. With smaller extant populations, monitoring efforts are best served by concentrating near hibernacula entrances. Still, current land use and/or active land management around hibernacula may impact *Myotis* spp. during the autumn and spring. Prior to WNS, many of these impacts could have been considered negligible, but additive mortality factors may further imperil already diminutive populations following the impacts of WNS. Our data suggest that concluding tree-clearing activities by early March could more adequately protect physiologically-stressed MYSO as they resume behaviors on the landscape. Streamlining management strategies may contribute to population persistence and recovery by avoiding additive stress in seasons critical for successful reproduction. Extending these protections to a number of hibernacula also may benefit other imperiled bat species' populations not considered here. Finally, a better regional comprehension of the effects of ambient conditions on autumn and spring bat activity could enhance surveys to further understand post-WNS ecology of bats.

Supplementary Materials: Bat acoustic echolocation activity data at and surrounding known hibernacula in Virginia and West Virginia portion of the central Appalachians during the fall swarm and spring emergence, 2015–2017 are available online at https://www.sciencebase.gov/catalog/item/5b634dc4e4b006a11f71823e.

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