Articles

Activity Patterns of Bats During the Fall and Spring Along Ridgelines in the Central Appalachians

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Abstract

Many central Appalachian ridges offer high wind potential, making them attractive to future wind-energy development. Understanding seasonal and hourly activity patterns of migratory bat species may help to reduce fatalities at wind-energy facilities and provide guidance for the development of best management practices for bats. To examine hourly migratory bat activity patterns in the fall and spring in Virginia in an exploratory fashion with a suite of general temporal, environmental, and weather variables, we acoustically monitored bat activity on five ridgelines and side slopes from early September through mid-November 2015 and 2016 and from early March through late April 2016 and 2017. On ridges, bat activity decreased through the autumn sample period, but was more variable through the spring sample period. In autumn, migratory bat activity had largely ceased by mid-November. Activity patterns were species specific in both autumn and spring sample periods. Generally, migratory bat activity was negatively associated with hourly wind speeds but positively associated with ambient temperatures. These data provide further evidence that operational mitigation strategies at wind-energy facilities could help protect migratory bat species in the Appalachians; substantially slowing or locking wind turbine blade spin during periods of low wind speeds, often below where electricity is generated, and warm ambient temperatures may minimize mortality during periods of high bat activity.

Keywords: Appalachians; eastern red bat *Lasiurus borealis*; hoary bat *Lasiurus cinereus*; migration; seasonal acoustic activity; silver-haired bat *Lasionycteris noctivagans*; wind energy

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Introduction

Most existing migratory tree bat data have come from recent research focusing on mortality associated with wind turbines (e.g., Arnett et al. 2008; Hayes 2013; Martin et al. 2017). Extensive increases in wind-energy developments across North America, particularly in the Appalachians, are expected in the coming decades (AWEA 2016) as regional electricity production shifts away from coal-generated power (McIlmoil and Hansen 2010). Wind energy is the fastest-growing form of energy production in the United States today. Over a decade ago when still in its infancy in the region, wind energy was recognized as a serious threat to bat populations (Kunz and Fenton 2006).

The vast majority of North American bat-associated wind turbine fatalities are the eastern red bat *Lasiurus borealis* (LABO), hoary bat *Lasiurus cinereus* (LACI), and silver-haired bat *Lasionycteris noctivagans* (LANO) (hereafter tree bats; Barbour and Davis 1969) and occur when these species are migrating (Fiedler 2004, Kunz and Fenton 2006, Arnett et al. 2008). There is a considerable degree of variation in bat fatality rates among wind farms. Turbine size has been associated with some of this disparity; however, much of this variation remains unexplained (Barclay et al. 2007). The highest rates of reported bat fatalities are at wind farms in the eastern United States, specifically in the Appalachians, where wind turbines are located along ridge tops (Kunz et al. 2007; Arnett et al. 2008; Lott 2008, Hayes 2013). As more wind-energy facilities are developed, it is imperative that land managers understand the relationships between migratory bats and wind energy to facilitate development of potential mitigation practices to curtail mortality events and reduce the risk of extinction (Frick et al. 2017).

Although most bat species in eastern North America hibernate in caves or mines during the winter, LABO, LACI, and LANO are migratory, moving from northern latitudes to southern portions of the continent, and day-roost in trees year round. Because of the difficulty of tracking these highly mobile species, little is known about the specific habits and activity of tree bats during the spring and fall migration periods when their mortality is highest, particularly in the central Appalachians where wind-energy production is increasing (Arnett et al. 2008; Holland and Wikelski 2009). Research to date has addressed large-scale seasonal occurrence and distribution patterns but smaller-scale, spatially explicit activity patterns in migratory bats are needed to assess potential wind-energy impacts (Cryan 2003; Kunz and Fenton 2006). In the central Appalachians, some LABO can remain in the region through the winter months, roosting in leaf litter (Davis and Lidicker 1956; Cryan 2003). However, it is unknown if these LABO wintering in the central Appalachians are resident year round or seasonal migrants that provide a source population for more northern latitudes in the summer (Dunbar and Tomasi 2006).

Migrating bats appear to concentrate along specific travel routes that are associated with landscape features, such as mountain ridges, coastlines, and large valleys. For example, in the eastern United States, the Appalachian Mountains and the Atlantic Coast are physiographic features that appear to concentrate migratory bat activity (Fiedler 2004; Baerwald and Barclay 2009; Cryan and Barclay 2009; Hamilton 2012; Smith and McWilliams 2016). Nonetheless, for the central Appalachians, it is unknown whether all or only certain ridges and valleys are important landscape features, or if patterns are consistent between physiographic subprovinces within the region (i.e., Blue Ridge, Ridge and Valley, and Allegheny Plateau). Furthermore, if ridges and valleys in the central Appalachians act as migratory corridors, it remains unclear how elevation of ridges in relation to proximal valley floors (local relief) affects migratory bat activity. Migratory bat activity patterns are variable within seasons, between seasons, and associated photoperiods and atmospheric conditions such as barometric pressure, wind, and precipitation (Cryan 2003; Baerwald and Barclay 2011; Weller and Baldwin 2012; Smith and McWilliams 2016). Autumn migratory bat activity patterns appear to be positively associated with storm-front passage and associated ambient conditions, resulting in periods with higher numbers of mortalities (Arnett et al. 2008; Baerwald and Barclay 2011; Smith and McWilliams 2016). Indeed, mortality rates among migratory bat species are higher in autumn compared with all other seasons (Arnett et al. 2008; Cryan and Barclay 2009). Lower mortality rates at wind turbines during spring and summer, compared with autumn, suggest that there exists important differences in migration behavior between seasons (Arnett et al. 2008; Grodsky et al. 2012). In eastern North America, patterns of migration in bats may be somewhat comparable with terrestrial bird migration, whereby different migratory pathways between seasons has been observed (La Sorte et al. 2014). Furthermore, these differences between seasons are influenced by differences in seasonal atmospheric conditions.

Numerous studies have documented a positive association between ambient temperatures and activity of migratory tree bats during the spring and autumn, with activity generally increasing with temperatures above 10°C (Fiedler 2004; Baerwald and Barclay 2011; Weller and Baldwin 2012; Bender and Hartman 2015; Smith and McWilliams 2016; Dechmann et al. 2017). The effect of barometric pressure on migratory bat activity has been less conclusive. Cryan and Brown (2007), Baerwald and Barclay (2011), and Dechmann et al. (2017) all observed that lower and dropping barometric pressures were correlated with increased activity, whereas others have found the opposite (Bender and Hartman 2015; Smith and McWilliams 2016). Indeed, barometric pressure may affect migratory bat activity positively or negatively: higher pressures are associated with easier flight conditions, whereas dropping pressure may indicate a passing storm front (Richardson 1978; Smith and McWilliams 2016). Previous research has also concluded that precipitation negatively affects migratory bat activity, likely due to a combination of attenuation of sound affecting echolocation, exposure on an individual level, associated atmospheric conditions (wind), and

reduced insect prey availability (Griffin 1971; Arnett et al. 2007; Lacki et al. 2007). Still, the effects of precipitation on bat activity may be negligible when compared with other atmospheric conditions. For example, Smith and McWilliams (2016) found that autumn migratory activity of bats in southern New England was less influenced by precipitation than by temperature, wind direction, and pressure change.

In addition to atmospheric conditions, landscape features including relief and elevation likely affect migratory bats differently between seasons and among species, and may depend on migratory pathways (Reynolds 2006; Baerwald and Barclay 2009). Also, geographic conditions, especially elevation, greatly influence atmospheric conditions in the Appalachians (Lindberg et al. 1988). Average temperatures are lower and precipitation amount and duration are greater at higher elevations (Lindberg et al. 1988). Furthermore, more precipitation occurs on windward slopes in the Appalachians, and because many weather fronts travel from west to east, the Allegheny physiographic subprovince is generally more mesic than the Ridge and Valley to the east (Soulé 1998). Ambient temperatures affect migratory bat activity, and temperature likely interacts with other conditions such as wind speed, wind direction, and elevation. Notably, Wolbert et al. (2014) found a significant interaction between the effects of relative elevation and ambient temperatures on bat activity such that ambient temperatures had greater effects on bat activity at higher elevations.

In areas where wind resources are high and commercially viable, bat mortality at wind turbines typically has been associated with lower wind speeds (Fiedler 2004; Arnett et al. 2008; Baerwald and Barclay 2011). The cut-in wind speed, whereby turbines begin to produce energy, is typically between 11 and 14.5 kph, whereas the rated wind speed (where maximum electricity is generated) is around 40 to 56 kph. Most bat mortality occurs around and below cut-in wind speed, when energy production is less than optimal (Fiedler 2004; Arnett et al. 2011; Martin et al. 2017). Furthermore, greater bat activity is associated with lower wind speeds regardless of geographic location or position (Cryan and Brown 2007; Smith and McWilliams 2016; Dechmann et al. 2017). Wind direction may also influence migratory bat activity in both the fall and spring migration periods as bats use steady tailwinds for long-distance movement (Smith and McWilliams 2016; Dechmann et al. 2017). Wind direction and wind speed likely have interactive effects on migratory bat activity (Smith and McWilliams 2016; Dechmann et al. 2017). As such, simply raising turbine cut-in speed may be an effective strategy to reduce a high proportion of bat mortality at wind facilities while still maintaining economic viability (Baerwald et al. 2009; Arnett et al. 2011, 2013; Weller and Baldwin 2012; Martin et al. 2017). Site-specific understanding of the effect of wind speed and wind direction on migratory behavior also could contribute to management practices that greatly reduce future wind-energy-associated bat mortality. By identifying important migratory pathways and geographic features associated with them, land managers could significantly reduce bat mortality associated with wind turbines through the development of better geographic-specific strategies, such as seasonal curtailment, that minimize wind-turbine activity in migratory pathways.

Our objectives were to describe activity patterns and define drivers thereof for migratory bat species during the autumn and spring migration periods along ridgelines and side slopes in the central Appalachians. We expected activity patterns to vary among migratory species both temporally and spatially. During the fall migratory period, we anticipated greater migratory bat activity at higher elevations than at lower elevations. Conversely, we expected the opposite during the spring migratory period. We also expected that ambient conditions influence migratory bat activity during the fall and spring migratory periods in the central Appalachians. Regardless of season, we expected decreased levels of activity during periods of high wind speed, low temperatures, and precipitation.

Methods

Study area

We conducted our study on five mountain massifs (ridges) and adjacent side slopes in the Ridge and Valley and Blue Ridge subprovinces of the central Appalachian Mountains in Virginia within George Washington and Jefferson National Forest lands in Bath and Giles counties and Shenandoah National Park in Madison and Rockingham counties (Figure 1). Although located on public land where the possibility of wind-energy development is low, we selected five ridgeline areas where the maximum elevations exceeded 1,000 m, the wind potential was rated as high, and the summits were topographically similar, that is, broad and relatively flat similar to existing wind farms in the central Appalachians (Virginia Center for Wind Energy 2018). The forests types throughout are generally xeric to moderately mesic oak associations on ridges with mixed mesophytic forest along drainages or sheltered north-facing slopes (Braun 1950). Multiple species of oak occur, with white oak *Quercus alba* and chestnut oak *Quercus pinus* being dominant. In lower elevations and along riparian corridors, mesic species such as eastern white pine *Pinus strobus*, tulip poplar *Liriodendron tulipifera*, and eastern hemlock *Tsuga canadensis* are common (Kniowski and Ford 2017).

Data collection

We collected acoustic data using Song Meter ZC detectors with SMM-U1 microphones, Song Meter SM2 detectors with SMX-U1 microphones, and Song Meter SM4 detectors with SMM-U1 microphones (Wildlife Acoustics, Maynard, MA). Our sampling occurred from early September to mid-November in 2015 and 2016, when migratory tree bats depart summer ranges and fly south, and in early March to late April in 2016 and 2017, when bats migrate northward and disperse across the

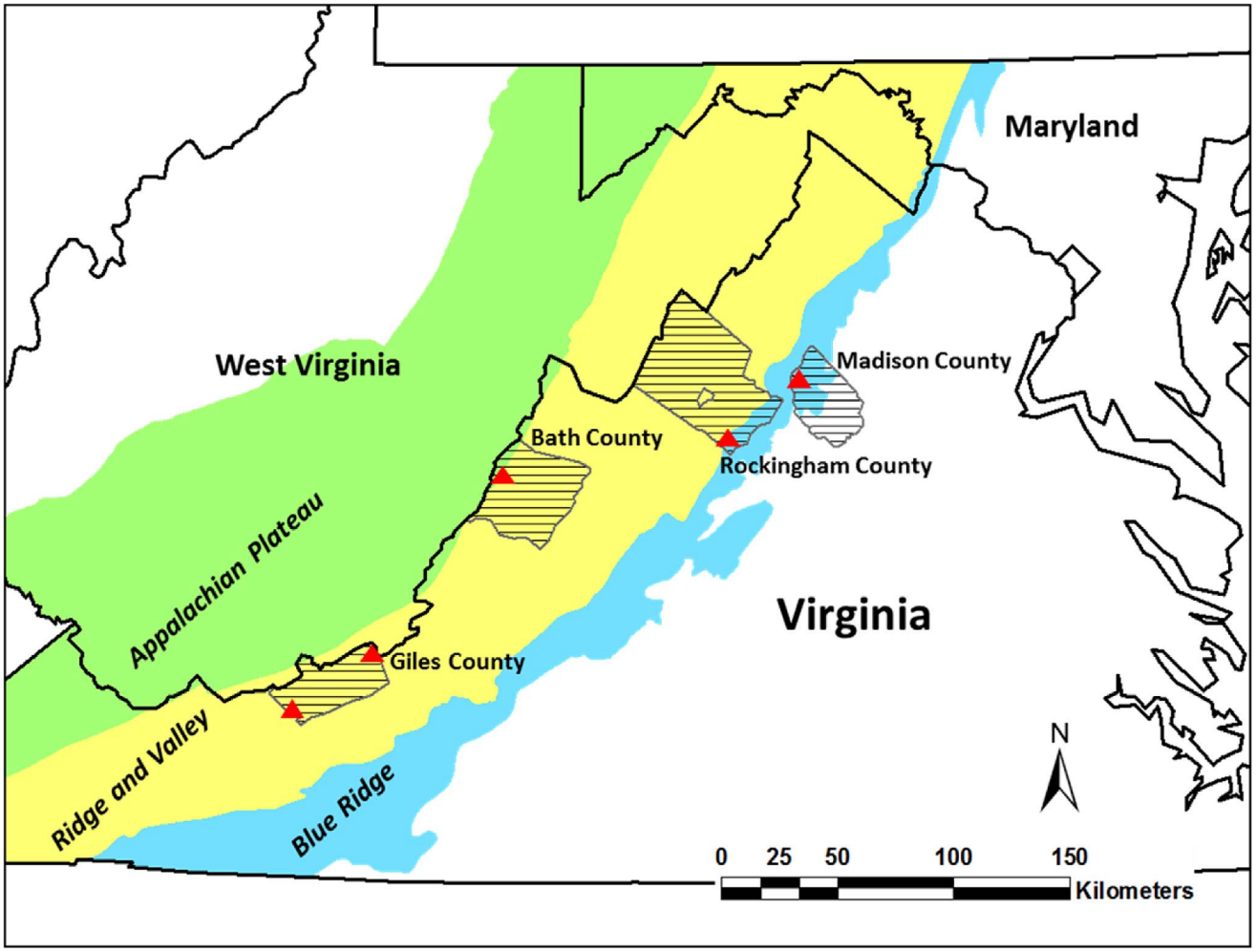

Figure 1. Approximate locations of five ridges sampled in central Appalachians of Virginia. The ridges sampled in Giles and Bath counties occur in the Ridge and Valley subphysiographic province, whereas the ridges sampled in Rockingham and Madison counties occur in the Blue Ridge subphysiographic province. Acoustic sampling occurred during autumn 2015 and 2016 and spring 2016 and 2017.

landscape to summer ranges (Cryan 2003; Baerwald and Barclay 2011). We deployed detectors longitudinally along ridgelines, with three detectors placed at high elevations (higher than 1,000 m where possible), one detector at mid-elevation (roughly halfway between the ridgetop elevation and the associated valley floor elevation, 500–750 m), and one detector at low elevation (generally less than 300-m elevation and proximal to a valley; Figure 2). We used digital elevation models in ArcMap 10.3.1® (ESRI, Redlands, CA) software to derive elevation, and chose potential general detector locations at each elevation category. We programmed detectors to record nightly from 1900 to 0700 hours, binning recordings into variable hourly blocks as sunset and sunrise times changed during seasons. Our precise detector locations were chosen on the basis of accessibility, likelihood of migratory bat presence, and site characteristics known to produce high-quality call recordings (i.e., low clutter such as a forest canopy gap/riparian corridor).

We collected hourly weather data such as temperature, precipitation (binary as occurring or absent), wind speed, wind direction, and barometric pressure from the airport nearest to each detector site (https://www.wunderground.com/2017). We created a wind profit variable by combining average wind speeds and average hourly wind directions to discern if bats use tailwinds for advantageous flight during migratory seasons (Smith and McWilliams 2016). Because bats use the linear arrangement of ridgelines to migrate north or south depending on season, we assumed that winds running parallel to ridgelines would have either a positive or negative effect on bat activity. In autumn, when bats are migrating southward, winds from the southwest (i.e., headwinds) were assigned a negative wind profit value and winds from the northeast (i.e., tailwinds) were assigned a positive wind profit value. In summer, when bats are migrating northward, winds from the northeast were assigned a negative wind profit value and winds from the southwest were assigned a positive wind profit value.

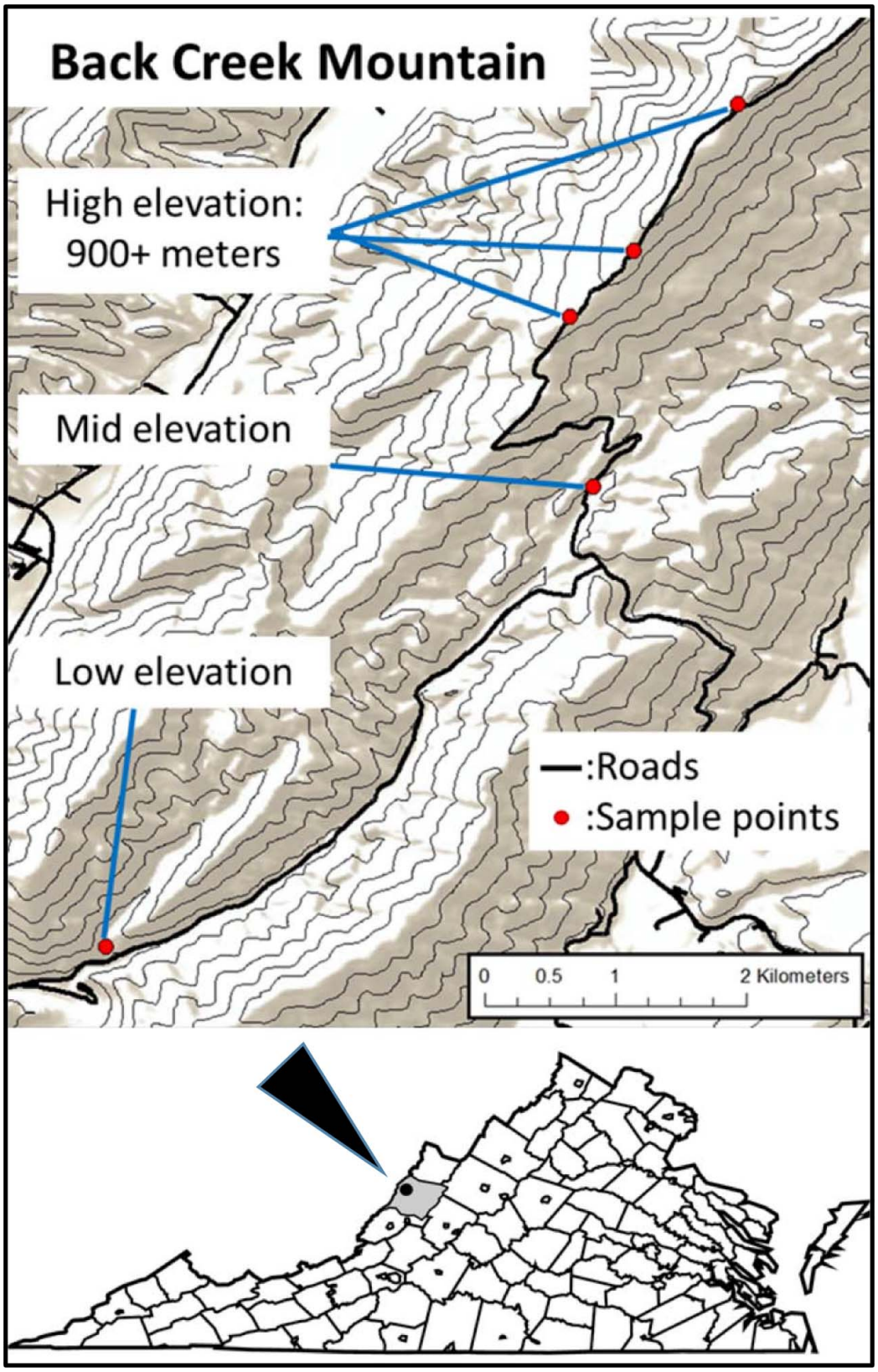

Figure 2. Example of acoustic sampling survey sites on ridgelines and adjacent side slopes on Back Creek Mountain, Bath County, Virginia. We deployed acoustic detectors in this manner along five ridgelines in the central Appalachians, Virginia during autumn 2015 and 2016 and spring 2016 and 2017.

Table 1. Variables used in candidate models representing hypotheses regarding migratory bat activity along five ridgelines and adjacent side slopes in the central Appalachians, 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	Variable type
Julian day: day of year for spring analyses	Continuous
Week of year: week of year for autumn analyses	Continuous
Hour: hour of acoustic recording; 0–11	Continuous
Avg. temp.: mean hourly temperature	continuous
Delta temp.: change in mean hourly temperature from 4 h prior	continuous
Avg. wind: mean hourly wind speed	continuous
Avg. wind profit: mean hourly wind profit; combination of wind speed and direction	continuous
Avg. pressure: mean hourly barometric pressure	Continuous
Delta pressure: change in mean hourly pressure from 6 h prior	Continuous
Relative elevation: proximal to valley floor or mid-slope with ridgetop as the reference condition	Discrete
Precipitation: amount of precipitation for each hour	Continuous

We identified acoustic call data to species using Kaleidoscope version 4.3.1 (Wildlife Acoustics), classifier 4.2.0 at the neutral setting, with default signal parameters (8–120-kHz frequency range, 500 maximum intersyllable gap, two minimum number of pulses, enhanced with advanced signal processing; USFWS [2017]: Indiana Bat Summer Survey Guidance—Automated Acoustic Bat ID Software Programs, Wildlife Acoustics—Overview of Kaleidoscope Pro 3 Analysis Software). We limited subsequent analyses to include only call data with a minimum of three call pulses to reduce automated species identification errors. We manually reviewed recorded files using program AnalookW version 4.1t (Titley Electronics, Columbia, MO) to validate automated species identification and check for systematic and systemic errors (Lemen et al. 2015).

Statistical analyses

We created a set of 18 a priori candidate generalized additive mixed models examining the relationships between atmospheric and habitat variables and hourly bat activity. We used the same variables and models for analyses of both fall and spring data. Candidate models included additive and two-way interactive combinations of date, hour, site, landscape characteristics, and ambient conditions (Tables 1 and 2). We assessed multicollinearity among predictors using package corrplot (Wei and Simko 2016) in program R version 3.2.3 (R Core Team 2013) to ensure that highly correlated ($r > 0.6$) variables were not included within the same model unless that potential interaction was deemed biologically relevant itself. We tested for serial correlation in hourly bat activity for each species using R package stats. We fit all generalized additive mixed models using the generalized additive mixed model function from R package mgcv, with an autoregressive random effects structure to account for the serial correlation of bat echolocation passes between hours at any given site (hour nested within each unique site-date), and with a negative binomial link function to account for overdispersion in bat pass counts (Wood 2017). We used generalized additive mixed models because migratory bat activity may display nonlinear responses to independent variables, and these models allow for curvilinear responses. Smoothing terms were applied to continuous covariates, that is, temperature, hour, and date, to account for a high degree of response variability. We used an information theoretic approach to select the best supported model, ranking models using Akaike's information criterion corrected for small sample size (AIC_c from package MuMIn, Bartoń 2015; Burnham and Anderson 2002). We centered and scaled all continuous predictors from −1 to 1 to aid model fitting and to facilitate assessment of main effects of interactions (Schielzeth 2010). All variables except hourly wind profit had nonzero effects. For each species, we only considered and report models that had empirical support ($\Delta AIC_c < 2$).

Results

We sampled 183 site-nights during autumn 2015 and 2016, and 109 site-nights during spring 2016 and 2017. Because of detector failure and inaccessibility due to weather, some detector recordings at specific sites were occasionally not wholly continuous over the 2 y. From the Kaleidoscope software, we identified 3,322 and 5,118 LANO acoustic passes, 2,657 and 2,512 LABO acoustic passes, and 2,051 and 892 LACI acoustic passes in data recorded during autumn 2015 and 2016, respectively. Similarly, we identified 3,178 and 10,851 LANO acoustic passes, 1,409 and 1,413 LABO acoustic passes, and 1,913 and 5,243 LACI acoustic passes in data recorded during spring 2016 and 2017, respectively. We were unable to model autumn LACI activity patterns because of limited nightly echolocation passes recorded.

Autumn activity patterns

The best supported model describing autumn LANO hourly activity contained Julian date, mean hourly temperature, hour of sampling, change in temperature from 4 h prior, mean hourly barometric pressure, change in barometric pressure from 6 h prior, mean hourly wind speed, and relative elevation (in order of decreasing effect sizes; Table 3). No other models were competing. Smoothers were supported for temperature, date, and

Table 2. Variables used in candidate models describing bat activity with hypothesized relationships and supporting literature for each parameter. Candidate models represented hypotheses regarding bat activity along five ridgelines and adjacent side slopes in the central Appalachians, Virginia during autumn 2015 and 2016 and spring 2016 and 2017.

Parameter	Hypothesis	Supporting literature
Date	Bat activity varies in intensity and spatially by date	Cryan (2003), Baerwald and Barclay (2009), Hamilton (2012)
Hour of night	Bat activity varies throughout each night	Kunz (1973), Kunz and Lumsden (2003), Kunz (2013)
Mean hourly temperature	Ambient temperatures affect bat activity	Reynolds (2006), Weller and Baldwin (2012), Smith and McWilliams (2016)
Change in mean temperature from hours prior	Bats likely can sense even small temperature changes and adjust behavior accordingly	Kunz (2013), Smith and McWilliams (2016)
Precipitation	Bat activity generally decreases with precipitation	Voight et al. (2011)
Mean hourly wind speed	Bat activity generally decreases with high wind speeds	Baerwald and Barclay (2011), Weller and Baldwin (2012), Smith and McWilliams (2016)
Mean hourly wind profit	Bats likely can sense wind direction and speed and adjust behavior accordingly	Smith and McWilliams (2016)
Mean hourly barometric pressure	Bats may respond to barometric pressure due to flight conditions or associated conditions	Baerwald and Barclay (2011), Bender and Hartman (2015), Smith and McWilliams (2016)
Change in mean pressure from hours prior	Bats may respond to changing pressure and associated changing conditions	Baerwald and Barclay (2011), Smith and McWilliams (2016)
Relative elevation	Bat activity varies along an elevational gradient	Wolbert et al. (2014)

hour (Table 3). All variables except elevation (low vs. high) displayed nonzero effects. Activity levels were variable over the season, with a pulse of activity in October; were negatively related to hour of sampling; and were positively related to mean hourly temperature, peaking around 20°C (Figures 3a–3c). Change in temperature from 4 h prior had the largest effect size, and activity was greater at lower temperatures (Figure 3d). Activity was greatest at low and high elevations and lowest at mid-elevation. Increased activity was weakly related to barometric pressure and change in pressure from 6 h prior, but negatively related to wind speed.

The best supported model describing LABO hourly activity included hour of sampling, mean hourly wind speed, change in barometric pressure from 6 h prior, mean hourly wind profit, and hourly precipitation (in order of decreasing effect sizes; Table 4). No other models were competing. A smoother on hour was supported, with LABO activity higher in the first few and last few hours of the night (Figure 4a). All variables except mean hourly wind profit displayed nonzero effects. Among remaining continuous predictors, wind speed had the largest effect size (Figure 4b). Activity of LABO was related negatively with wind speed and hourly binary precipitation (Figure 4c). Wind profit and change in barometric pressure from 6 h prior had minimal effect sizes.

Table 3. Relationship between hourly activity of silver-haired bats *Lasionycteris noctivagans* and regional hourly atmospheric conditions along five ridgelines and adjacent side slopes in the central Appalachians, Virginia during autumn 2015 and 2016. Covariates were scaled and centered on zero before analysis.

Variable	Estimate	SE	Lower CI	Upper CI
(Intercept)	−2.57	0.05	−2.67	−2.47
Delta temperature	−0.45	0.05	−0.56	−0.35
Mid-elevation vs. high?	−0.20	0.10	−0.40	0.01
Pressure	0.14	0.04	0.06	0.23
Delta pressure	0.12	0.04	0.03	0.20
Wind speed	−0.11	0.05	−0.21	−0.02
Low elevation vs. high?	0.03	0.10	−0.17	0.23
Smoothed terms	**Estimated *df***	**Reference *df***		
Temperature	7.19	7.19		
Hour	1.56	1.56		
Week	7.19	7.19		

Spring activity patterns

The best supported model describing LANO hourly activity contained Julian date, hour, mean hourly temperature, mean hourly wind speed, change in barometric pressure from 6 h prior, mean hourly wind profit, and hourly binary precipitation (in order of decreasing effect sizes; Table 5). No other models were competing. Smoothers were supported for both hour and date (Table 5). All variables except mean hourly wind profit displayed nonzero effects. Activity generally increased over the season, with a peak in mid-April, and activity was higher in the first few hours of the night (Figures 5a, 5b). Activity was related negatively to hourly binary precipitation. Spring LANO activity was related positively to temperature, and temperature had a large effect size (Figure 5c). Although contained in the best supported model, mean hourly wind speed only had a marginal negative effect on activity (Figure 5d), as did change in pressure from 6 h prior.

The best supported model describing LABO hourly activity contained Julian date, hour, mean hourly temperature, mean hourly wind speed, change in barometric pressure from 6 h prior, mean hourly wind

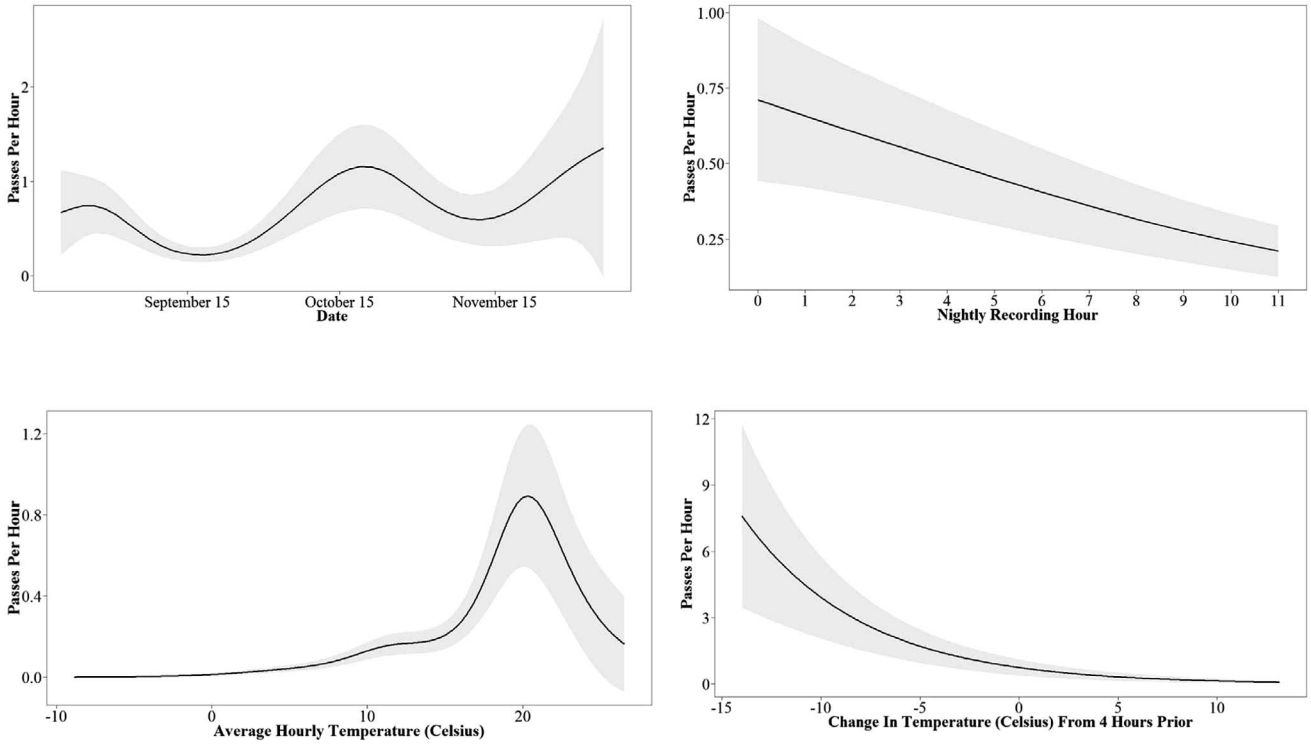

Figure 3. Partial-effects plots of the relationship among date (**a**), hour of sampling each night (**b**), mean hourly ambient temperature (°C; **c**), and change in ambient temperature from 4 h prior (**d**) with silver-haired bat *Lasionycteris noctivagans* echolocation passes per hour (with 95% confidence intervals; gray) along five ridgelines in the central Appalachians, Virginia during autumn 2015 and 2016. Other variables held constant.

profit, and precipitation (yes or no) (in order of decreasing effect sizes (Table 6). No other models were competing. Among smoothed terms, both hour and date had well-supported smoothers (Table 6). All variables except mean hourly wind profit displayed nonzero effects. Activity decreased slightly over the season, and activity peaked during the third and eighth hours of sampled nights (Figures 6a, 6b). Among other continuous predictors, temperature and wind speed had the largest effect sizes. Activity was related positively with temperature, but negatively with wind speed and hourly binary precipitation (Figures 6c, 6d). Although also included in the best supported model, wind profit and change in barometric pressure from 6 h prior had minimal effect sizes.

Table 4. Relationship between hourly activity of eastern red bats *Lasiurus borealis* and regional hourly atmospheric conditions along five ridgelines and adjacent side slopes in the central Appalachians, Virginia during autumn 2015 and 2016. Covariates were scaled and centered on zero before analysis.

Variable	Estimate	SE	Lower CI	Upper CI
(Intercept)	−2.33	0.04	−2.42	−2.25
Precipitation	−0.66	0.19	−1.03	−0.29
Wind speed	−0.49	0.04	−0.58	−0.41
Delta pressure	−0.10	0.04	−0.18	−0.01
Wind profit	0.06	0.04	−0.02	0.14
Smoothed terms	**Estimated *df***	**Reference *df***		
Hour	4.29	4.29		

The best supported model describing LACI hourly activity contained Julian date, hour of sampling, mean hourly temperature, an interaction between date and mean hourly temperature, and precipitation (yes or no) (in order of decreasing effect sizes; Table 7). No other models were competing (ΔAICc $<$ 2). Smoothers were supported for both hour and date (Table 7). All variables except hourly binary precipitation had nonzero effects. Activity generally increased over the season, with a peak in mid-April, and activity was higher in the first few hours of the night (Figures 7a, 7b). Activity was related negatively to hourly precipitation. Among other continuous predictors, mean hourly temperature had the largest effect size, and activity was related positively to temperature (Figure 7c). The interaction between date and temperature had minimal effect size.

Discussion

Our findings are similar to results from previous research that found a definitive positive relationship between migratory bat species' activity and ambient temperatures regardless of season (Reynolds 2006; Bender and Hartman 2015; Smith and McWilliams 2016; Bernard and McCracken 2017). In general, hourly temperatures and date had the largest effect on bat activity during the autumn and spring migration periods.

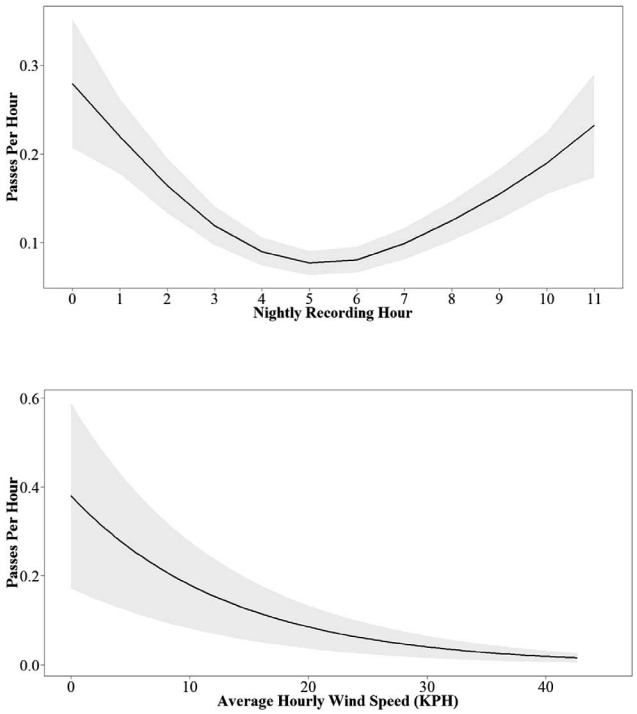

Figure 4. Partial-effects plot of relationship between hour of sampling each night (**a**) and mean hourly wind speed (kph;**b**) with eastern red bat *Lasiurus borealis* echolocation passes per hour (with 95% confidence intervals; gray) along five ridgelines in the central Appalachians, Virginia during autumn 2015 and 2016. Other variables held constant.

Moreover, hourly precipitation typically suppressed migratory bat activity during the autumn and spring (Griffin 1971; Smith and McWilliams 2016). However, some differences existed between the individual species' relationship to environmental conditions and intraseasonality, supporting prior research (Baerwald and Barclay 2011).

Date was not related closely to autumn LABO activity in our study, but in southern New England, outside the presumed wintering grounds (Cryan 2003), Smith and McWilliams (2016) observed a stronger relationship as later dates and lower temperatures were more closely correlated. It is possible that some LABO activity we observed was indicative of individuals present in their northernmost wintering range in the central Appalachians (Davis and Lidicker 1956; Cryan 2003; Figure 8). Thus, recorded LABO activity potentially could be attributable to resident individuals throughout the autumn sampling period, rather than to migrating individuals. Furthermore, Bernard and McCracken (2017) found that migratory bat species were active throughout the winter months in Tennessee, across a range of ambient temperatures; similarly, temperature did not substantially affect autumn LABO activity at our study sites. Depending on ambient conditions, LABO likely restricted activity because of metabolic/thermal trade-offs, balancing insect prey availability with energy expenditures associated with active foraging behavior (Bender and Hartman 2015, Bernard and McCracken 2017). Unsurprisingly, LABO activity was lower during hours with precipitation, likely due to reducing foraging efficiency with decreased insect activity and increasing metabolic costs associated with flight and exposure (Griffin 1971; Voigt et al. 2011). Although date and hourly ambient temperatures appeared to have little effect on autumn LABO activity, they remained important predictors of activity for autumn LANO and grouped migrant species. The observed peak of autumn LANO activity in mid-October may correspond to a final migratory push or "wave" as suggested by McGuire et al. (2012). Furthermore, LANO and LACI activity was positively related to mean hourly temperature, likely due to insect prey availability and metabolic costs of activity or migration in cold temperatures (Reynolds 2006; McGuire et al. 2014; Wolbert et al. 2014).

Table 5. Relationship between hourly activity of silver-haired bats *Lasionycteris noctivagans* and regional hourly atmospheric conditions along five ridgelines and adjacent side slopes in the central Appalachians, Virginia during spring 2016 and 2017. Covariates were scaled and centered on zero before analysis.

Variable	Estimate	SE	Lower CI	Upper CI
(Intercept)	−1.77	0.06	−1.89	−1.66
Precipitation	−1.97	0.27	−2.49	−1.44
Temperature	1.02	0.07	0.87	1.16
Wind speed	−0.26	0.08	−0.41	−0.11
Delta pressure	−0.13	0.07	−0.26	0.01
Wind profit	0.05	0.08	−0.10	0.20
Smoothed terms	**Estimated *df***	**Reference *df***		
Hour	4.05	4.05		
Julian day number	8.31	8.31		

Our results generally corroborate previous research on the seasonal distribution and migratory timing of migratory bat species (Cryan 2003; Johnson et al. 2003). It appears that much of the migratory bat activity in the central Appalachians occurs somewhat later in the year compared with more northern regions where most activity (and hence wind-related mortality) occurs in August and early September (Johnson et al. 2003; Baerwald and Barclay 2011; McGuire et al. 2012; Arnett et al. 2016). In Ontario, Canada, a final autumn LANO migration wave occurred in mid-September (McGuire et al. 2012), nearly 4 wk earlier than the final wave we observed in the central Appalachians. Geographic variation in the timing of major migratory pulses also has important implications regarding future wind-energy development and potential bat mortality mitigation policies in the central Appalachians. Understanding timing of major waves of activity at multiple regions also could provide data inputs to managers to further adjust or modify wind-energy best-management practices.

Contrary to our expectations, some bat species such as LANO were related negatively to mid-elevation sites. Migratory bat species may use the linear arrangement of the Ridge and Valley and Blue Ridge subprovinces to navigate during autumn migration in the central Appalachians (Baerwald and Barclay 2009; Furmankie-

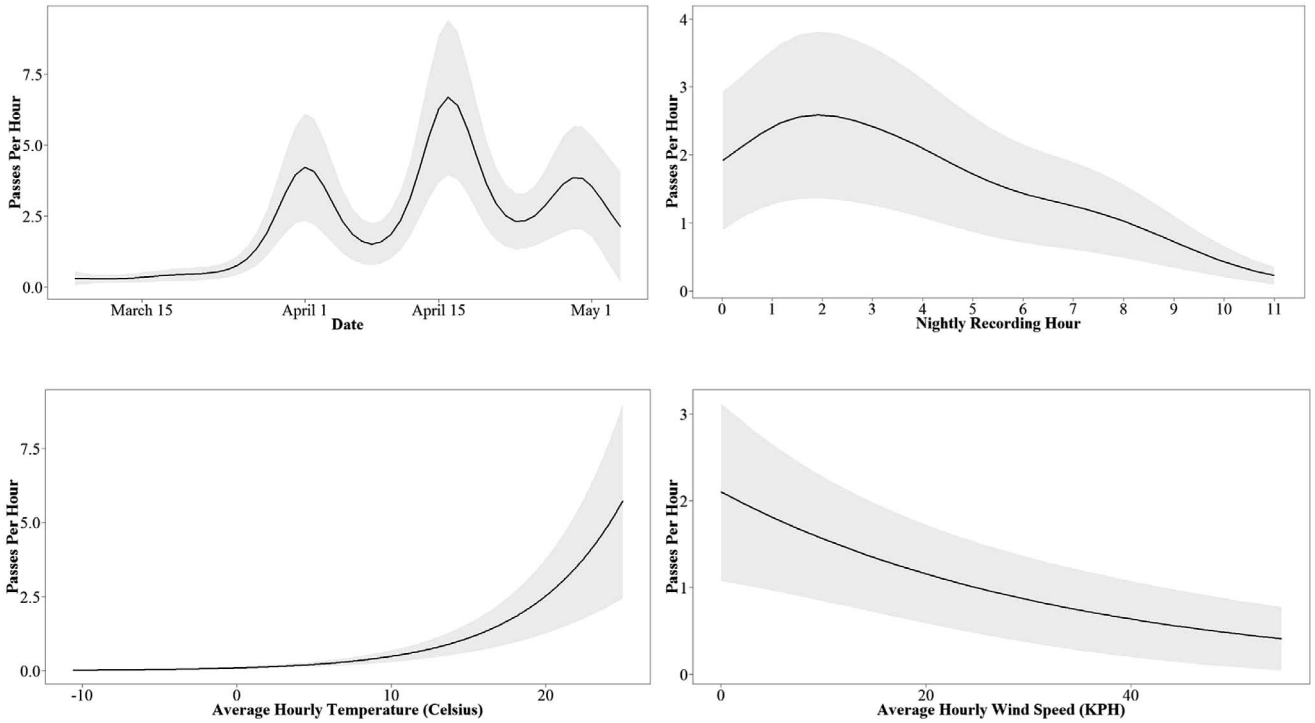

Figure 5. Partial-effects plot of the relationship among date (**a**), sampling hour of night (**b**), hourly ambient temperature (°C; **c**), and hourly wind speed (kph; **d**) with silver-haired bat *Lasionycteris noctivagans* echolocation passes per hour (with 95% confidence intervals; gray) along five ridgelines in the central Appalachians, Virginia during spring 2016 and 2017. Other variables held constant.

wicz and Kucharska 2009), but our results provide evidence that valleys are used as much as or more as preferred migratory corridors in this region than ridgetops. In the central Appalachians of Virginia, valleys have a higher prevalence of cleared habitats such as pasture, whereas ridgetops typically are forested (Kniowski and Ford 2017). Many bat species utilize linear landscape features such as riparian areas for foraging and movement between foraging/roosting areas (Limpens and Kapteyn 1991; Ford et al. 2005). Migratory bats in the central Appalachians may be more active in areas with these features because of proximity to roosting habitat or improved migrating and foraging conditions due to lack of environmental clutter (Brigham et al. 1997; Kunz et al. 2007; Drake et al. 2012; Wolbert et al. 2014; Brooks et al. 2017).

Table 6. Relationship between hourly activity of eastern red bat *Lasiurus borealis* and regional hourly atmospheric conditions along five ridgelines and adjacent side slopes in the central Appalachians, Virginia during spring 2016 and 2017. Covariates were scaled and centered on zero before analysis.

Variable	Estimate	SE	Lower CI	Upper CI
(Intercept)	−2.76	0.06	−2.87	−2.64
Precipitation	−0.95	0.26	−1.46	−0.45
Wind speed	−0.72	0.07	−0.87	−0.58
Temperature	0.66	0.07	0.52	0.79
Delta pressure	−0.12	0.07	−0.25	0.01
Wind profit	0.07	0.07	−0.08	0.21
Smoothed terms	**Estimated *df***	**Reference *df***		
Hour	6.11	6.11		
Julian day number	1.00	1.00		

Although the general seasonality of bat migrations is known, patterns of bat activity on an hourly basis are less understood (Kunz 1973; Baerwald and Barclay 2011). Hour (of sampling) each night generally had a negative effect on bat activity during autumn, with most activity occurring within the first few hours of the night, similar to previous findings (Kunz 1973). However, LABO displayed a unimodal response to hour of nightly sampling in autumn, suggesting that these bats are likely foraging in the first hours after sunset and the last few hours before sunrise (Kunz 1973, 2013; Kunz and Lumsden 2003). This species is known to forage early in the evening (sometimes before sunset), and may be active at slightly different times of day because of differences in prey availability, day-roost selection and proximity to foraging areas, or even interspecific temporal niche partitioning (Kunz 1973).

Spring migratory bat activity was related to date, and ambient temperature was an important driver of activity (Reynolds 2006; Bender and Hartman 2015; Smith and McWilliams 2016; Bernard and McCracken 2017). Spring migratory bat activity, similar to autumn activity, is related positively with ambient temperature likely due to insect prey availability and metabolic costs of migration/flight in cold temperatures (Reynolds 2006; McGuire et al. 2014; Wolbert et al. 2014). Bat activity increased through the spring sample season, but displayed defined peaks of activity, again suggesting that bats may migrate in waves

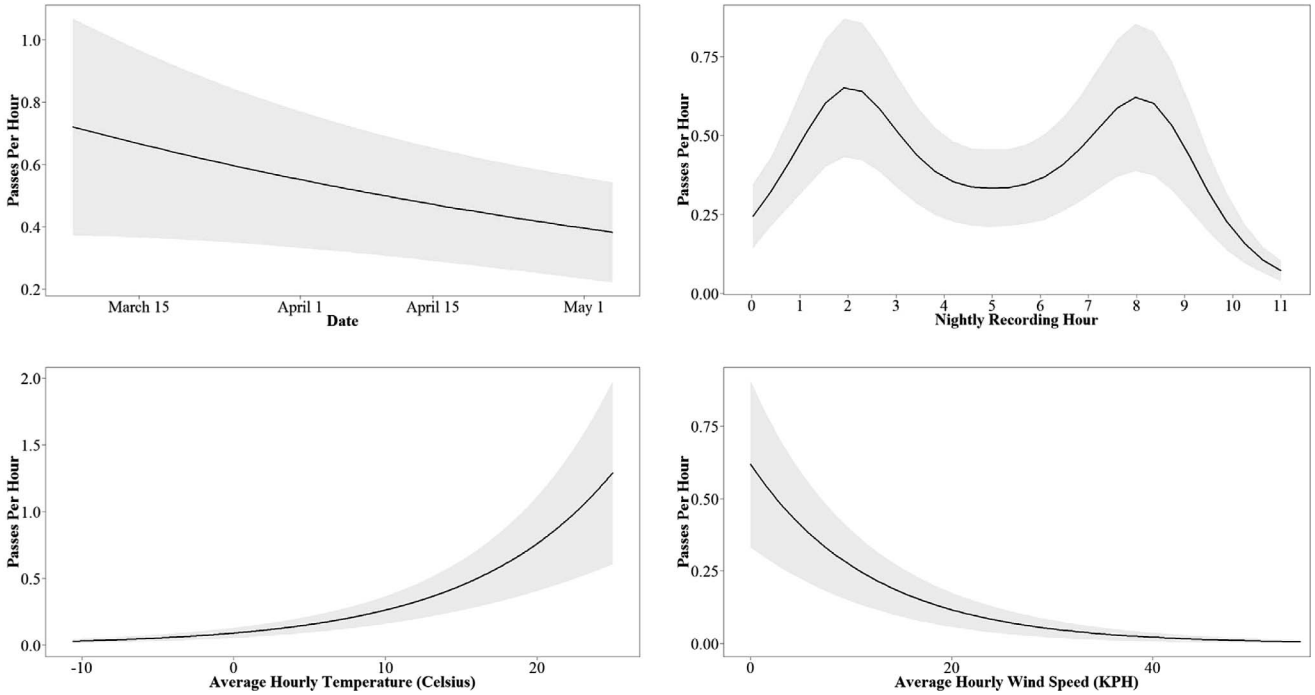

Figure 6. Partial-effects plot of the relationship among date (**a**), sampling hour of night (**b**), hourly ambient temperature (°C; **c**), and hourly wind speed (kph; **d**) with eastern red bat *Lasiurus borealis* echolocation passes per hour (with 95% confidence intervals; gray) along five ridgelines in the central Appalachians, Virginia during spring 2016 and 2017. Other variables held constant.

during the spring months, as they do in autumn. These spring waves also may be correlated with ambient conditions such as temperatures. Activity of LACI and LANO individually peaked in mid-April in the central Appalachians of Virginia. However, spring activity of LABO decreased slightly through time, in contrast to what we expected. These data may suggest that LABO wintering in the central Appalachians may migrate (likely northward) in spring, and a subsequent wave of LABO had yet to arrive before late April. Pulses or waves of activity in the spring season may be caused by differences in migration timing between sexes, or differences in wintering grounds between sexes (Cryan 2003; Cryan and Wolf 2003; Jonasson and Guglielmo 2016). Similar timing and patterning of activity has been observed north of our study area (Cryan 2003; Reynolds 2006; Grodsky et al. 2012).

Table 7. Relationship between hourly activity of hoary bats *Lasiurus cinereus* and regional hourly atmospheric conditions along five ridgelines and adjacent side slopes in the central Appalachians, Virginia during spring 2016 and 2017. Covariates were scaled and centered on zero before analysis.

Variable	Estimate	SE	Lower CI	Upper CI
(Intercept)	−2.23	0.06	−2.35	−2.12
Temperature	0.91	0.06	0.79	1.03
Precipitation	−0.41	0.23	−0.87	0.05
Temp. × Julian day number	0.17	0.06	0.06	0.29
Smoothed terms	**Estimated *df***	**Reference *df***		
Hour	1.00	1.00		
Julian day number	5.03	5.03		

Contrary to our expectations, elevation was not included within the best supported model describing spring activity for any migratory species. Greater recorded mortality rates during fall migration at wind-energy sites suggest that migratory bats use higher elevations/ridgelines more during the fall and lower elevations/valleys during spring migration (Johnson et al. 2003; Reynolds 2006; Grodsky et al. 2012). Our results indicate that migratory bat activity is more evenly dispersed across the landscape in the spring compared with autumn (Johnson et al. 2003). Sex and reproductive condition may contribute to different migration patterns between autumn and spring as suggested by Jonasson and Guglielmo (2016). Female migratory bats leave wintering grounds earlier than males (Cryan 2003), and likely use torpor less than males during the spring because of pregnancy (Ford et al. 2002; Turbill and Geiser 2006; Dzal and Brigham 2013). Without extensive use of torpor during spring migration, female migratory bats need to forage more to cope with thermoregulatory costs incurred by low ambient temperatures (Ford et al. 2002, Cryan and Wolf 2003; Jonasson and Guglielmo 2016). Increased foraging behavior of female migratory bats during spring migration compared with autumn migration may explain why our results suggest more widespread migratory bat activity on the landscape, with relative elevation having little influence on activity.

Wind speed was not included in the best supported model describing spring LACI activity, suggesting that other ambient conditions may have greater influence on

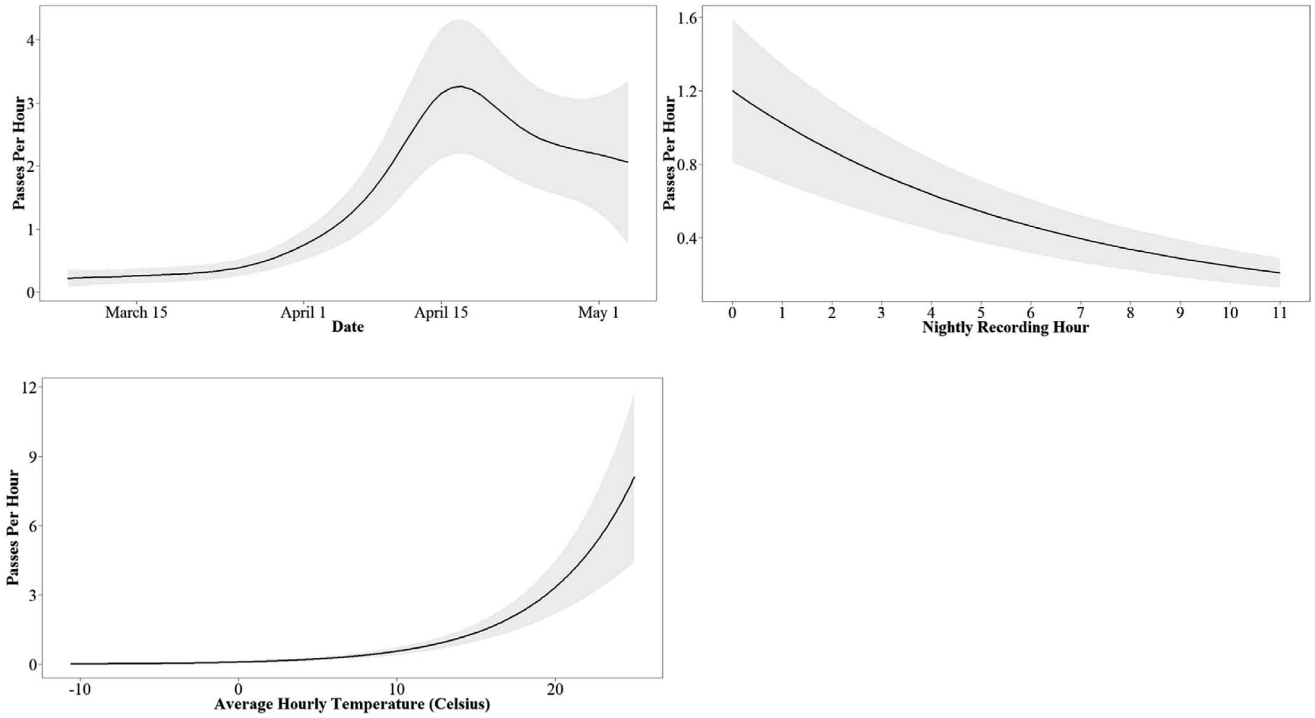

Figure 7. Partial-effects plot of the relationship among date (**a**), sampling hour of night (**b**), and hourly ambient temperature (°C; **c**) with hoary bat *Lasiurus cinereus* echolocation passes per hour (with 95% confidence intervals; gray) along five ridgelines in the central Appalachians, Virginia during spring 2016 and 2017. Other variables held constant.

their behavior, possibly due to larger bodies and more powerful flight compared with other migratory species (Barbour and Davis 1969; Salcedo et al. 1995; Riskin et al. 2010). However, LACI may be affected by wind speeds, but the relationship could be difficult to identify because data were limited. For instance, actively migrating bats may fly outside the range of detection (higher or during different atmospheric conditions) or they do not forage during migration flight.

Migratory bat activity was related closely to temporal (date) and weather variables, notably hourly wind speed, in both autumn and spring. However, the relationship of autumn and spring activity to other environmental conditions varied among migratory bat species. Although we found little evidence that wind profit

Figure 8. Photograph of an eastern red bat *Lasiurus borealis* roosting in litter (**left**), and approximate location of roost on hillside (**right**) at Pandapas Pond Recreational area, George Washington and Jefferson National Forest, Montgomery County, Virginia on March 8, 2015. Photograph credit: Andrew Kniowski.

substantially affected migratory species' activity patterns in the central Appalachians as was noted in southern New England (Smith and McWilliams 2016), our results suggest that wind speed may be the best overall predictor of migratory bat activity in the central Appalachians exclusive of LACI. Corroborating previous research from other geographic regions, our data do indicate that migratory bat species are more active at lower wind speeds (Fiedler 2004; Reynolds 2006; Baerwald and Barclay 2011; Weller and Baldwin 2012). The majority of migratory bat activity occurred at winds speeds lower than the 11 to 14.5 kph, cut-in wind speed common for most industrial wind turbines (Fiedler 2004). Wind turbine blades often continue to free spin below cut-in wind speeds and are capable of causing bat mortality at these speeds (Arnett et al. 2013). Bat mortality rates can be significantly reduced at higher cut-in speeds for blade unlocking or at minimum, directionally feathering blades to reduce blade speed if below production cut-in wind levels (Arnett et al. 2011, 2013). Mortality reduction rates vary among operational mitigation experiments, but 50% or greater reduction in bat mortality is commonly achieved (Arnett et al. 2013). Projections for the economic costs of operational mitigation and annual output lost vary greatly because of differences in exact mitigation treatment implemented (i.e., seasonal duration), associated turbine technology/limitations, and geographic locations/wind patterns (Arnett et al. 2013).

However, wind speeds are not the only predictor of migratory bat activity, and our results suggest that migratory bats appear to respond to other atmospheric conditions as well. Specifically, ambient temperature and precipitation appear to influence migratory bat activity in the central Appalachians. For instance, while variable, ultimately there is very little migratory bat activity at ambient temperatures below 10°C, and activity typically ceases during periods of precipitation. Using a combination of conditions to inform operational mitigation at wind-energy facilities may further reduce migratory bat fatality rates while optimizing energy production. Accordingly, our findings could inform energy producers and regulators about potential migratory bat mortality factors to aid in the development or modification of industry best-management practices relative to bats (Frick et al. 2017). Because of the nature of acoustic data, it is not possible to distinguish between a bat that is foraging and a bat that is migrating. We assumed that more acoustic activity inherently was related to greater numbers of migrating bats, but this actual relationship is unknown. Previous research in the Midwest has suggested that actively migrating bats may occasionally use visual cues as an alternative to echolocation and therefore are less likely to be detected during acoustic surveys (Timm 1989). Therefore, our results may be underestimating the number of bat passes at our sampled sites. However, in Europe, migratory bat species use echolocation during migration periods (Furmankiewicz and Kucharska 2009); therefore, our acoustic detectors likely recorded at least some bats engaged in migratory activity (Cryan et al. 2014; Smith and McWilliams 2016). Our detailed, regional understanding of the effects of atmospheric conditions, date, and landscape features on migratory bat activity should aid land managers' risk assessments of bat mortality at future wind-energy development sites, as well as offering potential pathways to maximize power output while reducing bat mortality at existing wind-energy sites. However, further monitoring of migratory bat activity patterns, especially earlier in the spring and autumn periods, and perhaps at more southern sites in the central Appalachians where overwintering might also be occurring, such as southwest Virginia, eastern Kentucky, and southern West Virginia, could inform wind-turbine mitigation regimens that allow maximum power generation while minimizing bat mortality (Arnett et al. 2013; Martin et al. 2017).

Supplemental Material

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Reference S1. Arnett EB, Huso MM, Reynolds DS, Schirmacher M. 2007. Patterns of pre-construction bat activity at a proposed wind facility in northwest Massachusetts. An annual report submitted to the Bats and Wind Energy Cooperative. Bat Conservation International. Austin, Texas.

Found at DOI: https://doi.org/10.3996/082018-JFWM-072.S1 (1.9 MB PDF); also available at http://batsandwind.org/wp-content/uploads/precon_ma.pdf.

Reference S2. Arnett EB, Johnson GD, Erickson WP, Hein CD. 2013. A synthesis of operational mitigation studies to reduce bat fatalities at wind energy facilities in North America. A report submitted to the National Renewable Energy Laboratory. Bat Conservation International. Austin, Texas.

Found at DOI: https://doi.org/10.3996/082018-JFWM-072.S2 (866 KB PDF); also available at https://www.energy.gov/sites/prod/files/2015/03/f20/Operational-Mitigation-Synthesis-FINAL-REPORT-UPDATED.pdf.

Reference S3. Lindberg SE, Silsbee D, Schaefer DA, Owens JG, Petty W. 1988. A comparison of atmospheric exposure conditions at high- and low- elevation forests in the southern Appalachian Mountain Range. Pages 321–344 in Unsworth MH, Fowler D, editors. Acid deposition at high elevation sites. NATO ASI Series, Dordrecht, the Netherlands: Springer.

Found at DOI: https://doi.org/10.3996/082018-JFWM-072.S3 (2.43 MB PDF); also available at https://link.springer.com/content/pdf/10.1007%2F978-94-009-3079-7_17.pdf.

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Data S1. Acoustic site survey locations; survey dates by year, month, day, and hour; bat species acoustic passes by year, month, day, and hour; and associated weather and habitat variables for ridges, side slopes, and valley floors in the Ridge and Valley and Blue Ridge physiographic provinces of the central Appalachians in western Virginia. Archived at: https://www.sciencebase.gov/catalog/item/5b5a0904e4b0610d7f4dcb60.

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