Bat activity during autumn relates to atmospheric conditions: implications for coastal wind energy development

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The cryptic behavior of migrating bats leaves us largely uninformed of their seasonal distribution and abundance, important movement corridors, and migration behaviors. However, models of avian migration in relation to meteorological variables may prove useful in describing seasonal patterns of coastal bat activity. We pursued 2 primary objectives regarding regional autumn bat activity along the Atlantic Coast of southern New England, United States, inferred from continuous acoustic monitoring: 1) to evaluate hypotheses regarding the association of regional atmospheric conditions and coastal bat activity and 2) to construct and evaluate models that predict regional bat activity on a given night using meteorological data accessed ahead of the activity. Acoustic bat activity was attributable primarily to 2 species of migratory tree bats, red bat and silver-haired bat, but also the short-distance migrant tricolored bat and generally sedentary big brown bat. *Myotis* spp. and hoary bat detections were relatively uncommon among classified calls. Coastal bat activity varied with regional wind conditions indicative of cold front passage and expected to induce a more coastal flight path, but associations with other atmospheric conditions from models of songbird migration were typically weak. Bat acoustic activity also was associated strongly with various aspects of temperature. Predictive models of regional nightly bat activity were reasonably accurate in anticipating nights of the highest and lowest bat activity, particularly for low-frequency bats such as silver-haired and big brown bat. The ability to anticipate high bat activity may help reduce adverse interactions with forthcoming wind energy development in coastal and offshore areas along the western Atlantic Ocean.

Key words: acoustic monitoring, bats, migration, New England, weather, wind energy

As predators of flying insects, most North American bats occupying temperate and cold climates (sensu Peel et al. 2007) exhibit seasonal movements to avoid food scarcity and poor environmental conditions (Griffin 1970; Fleming and Eby 2003). The scale and termini of these movements vary among species and individuals. For example, bats may move tens to hundreds of kilometers to regional hibernacula or many hundreds of kilometers to warmer climates (Fleming and Eby 2003; Cryan 2011). Unlike most migratory songbirds which forage during the day and migrate at night, bats forage and migrate nocturnally, typically remaining inactive and inconspicuous during the day. These cryptic habits leave us almost completely uninformed about their seasonal distribution and abundance, important movement corridors, and migration behaviors (Cryan 2003; Cryan and Barclay 2009). Nonetheless,

migratory bats likely experience similar challenges and selection pressures to migrating birds, providing some justification for applying models of avian migration to bat migration (Larkin 2006; Holland 2007; McGuire and Guglielmo 2009; Willis et al. 2010). Certainly, regional similarities in patterns of bat activity during migration (Kerns et al. 2005; Lott 2008; Johnson et al. 2011b) and the consistent association between bat activity and cold front passage evoke the comparison to bird migration (Erickson and West 2002; Cryan and Brown 2007; Arnett et al. 2008; Johnson et al. 2011a; Weller and Baldwin 2012).

In the northeastern United States, the Atlantic Coast represents an obvious topographic barrier to and concentrator of migratory movements. Indeed, many southbound avian migrants orient and concentrate along the Atlantic Coast and

on offshore land masses under specific weather conditions (Drury and Keith 1962; Drury and Nisbet 1964; Richardson 1972; Ralph 1978). Coastlines might similarly influence and concentrate the activity of migratory bats (Barclay 1984; Timm 1989; Ahlén et al. 2009; Dzal et al. 2009) and their potential insect prey (Drake and Farrow 1988; Pedgley 1990; Rydell et al. 2010). Moreover, the long-distance migrants among North American bats—the so-called "tree bats," specifically eastern red bats (hereafter, red bats; *Lasiurus borealis*), hoary bats (*Lasiurus cinereus*), and silver-haired bats (*Lasionycteris noctivagans*)—possibly employ coastal navigation during fall migration (Cryan 2003; Johnson et al. 2011a). It remains largely unexplored, however, whether the use of the Atlantic Coast by migratory bats (especially tree bats) varies strongly with atmospheric conditions (e.g., front passage, westerly winds, and the coastal effect), as it does for birds.

Understanding the seasonal bat use of the Atlantic Coast and its atmospheric correlates has direct conservation implications given that migration may figure prominently in wind turbine-related bat fatalities (Cryan 2003; Johnson 2005; Kunz et al. 2007b; Arnett et al. 2008; Cryan et al. 2012) and the expansion of wind energy into the nearshore and offshore environments of New England and the mid-Atlantic appears imminent (Mahan et al. 2010; United States Department of Energy 2011). Whether migratory activity per se causes turbine-related fatalities or simply concentrates bats in proximity to turbines where other factors induce the bat–turbine interaction warrants evaluation (Cryan and Barclay 2009), but bat activity clearly increases during the autumn migratory season and fatalities often correspond with bat activity (Johnson et al. 2004; Kunz et al. 2007a; Baerwald and Barclay 2011; Johnson et al. 2011b; Jain et al. 2011; Young et al. 2011; Weller and Baldwin 2012). Identifying periods of high bat activity and associated atmospheric and meteorological conditions can assist the development of predictive tools to guide the operation of wind turbines, perhaps preempting bat fatalities, and thus represents a potentially valuable conservation tool (Reynolds 2006; Horn et al. 2008; Loew et al. 2013). We pursued 2 primary objectives regarding regional bat activity along the Atlantic Coast of southern New England: 1) to evaluate hypotheses regarding the association of regional atmospheric conditions with coastal bat activity, and 2) to construct and evaluate models that predict regional bat activity on a given night using meteorological data accessed ahead of the activity. We discuss the use of these predictive models as a potential tool for mitigating the risks to bats at future nearshore and offshore wind facilities (e.g., via the adjustment of turbine operations).

MATERIALS AND METHODS

Study area and acoustic monitoring.—During fall 2010–2012, we recorded the nocturnal acoustic activity of bats at 7 locations on the Rhode Island National Wildlife Refuge Complex in southern Rhode Island (Fig. 1). At each location, we recorded bat activity (i.e., number of bat passes; see below) with an ultrasonic microphone (SMX-US; Wildlife Acoustics,
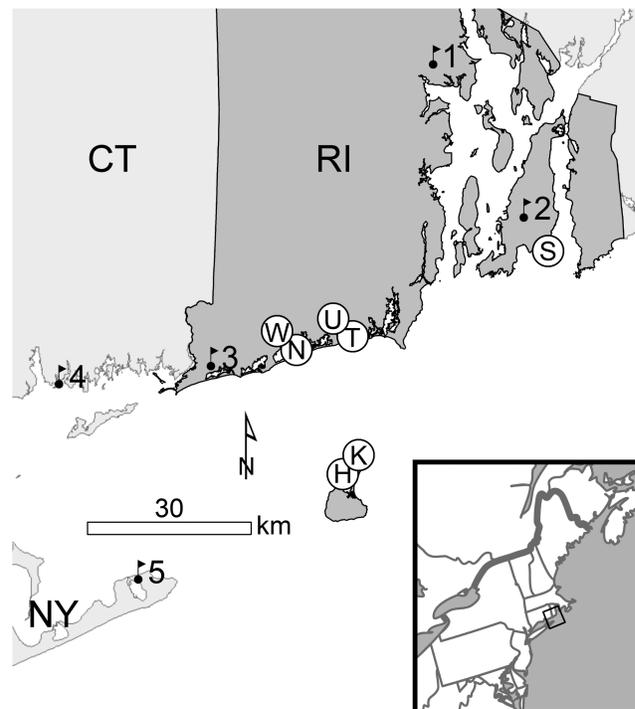
Fig. 1.—Locations of ultrasonic microphones (circles) and National Weather Service Automated Surface Observing System (ASOS) stations (flags) used to examine relationships between atmospheric conditions and migrating bat acoustic activity in southern Rhode Island (RI), Connecticut (CT), and New York (NY), United States, from August through October, 2010–2012. Microphone location abbreviations: S = Sachuest; T = Trustom (pond site); U = Trustom (upland site); N = Ninigret; W = Watchaug; K = Kurz; H = Wash. ASOS stations: 1 = Providence/T. F. Green State Airport; 2 = Newport State Airport; 3 = Westerly State Airport; 4 = Groton-New London Airport; 5 = Montauk Airport.

Inc., Concord, Massachusetts) attached to a passive full-spectrum ultrasonic recorder (SM2BAT, 192 or 384 kHz sampling rate; Wildlife Acoustics, Inc.). We installed microphones where we expected foraging bat activity (see Supporting Information S1). We mounted microphones horizontally 5–5.5 m above ground level, oriented northward, and above the canopy with limited obstructions within 50 m of the microphone. We recorded from evening civil twilight to morning civil twilight (i.e., sun elevation approximately 6° below the horizon), from 8 September to 31 October in 2010 and 2011 and from 2 August to 31 October in 2012. Coverage was not complete during these periods due to equipment malfunctions and poor weather, nor did we record at all sites in each year, and we changed our ultrasonic recorder settings after the 1st year of the study based on the manufacturer's suggestions (see Supporting Information S1). The sensitivity and detection range of microphones varies with call frequency, but based on controlled tests (Adams et al. 2012), we expect that our microphones sampled high- and low-frequency bats within a 3-dimensional airspace of approximately 30- and 50-m radius around the microphone, respectively, although at reduced efficiencies as distance from the microphone increased.

Bat classification.—Nine bat species inhabit or potentially migrate through Rhode Island in autumn, most making at least regional movements from or through the state (Table 1). We used the commercially available sound analysis software SonoBat (version 3.02, NNE suite; SonoBat, Arcata, California) to classify recorded bat passes. Recorded files were truncated to a maximum length of 8 s, the longest file the classification software could process. We defined bat passes as ≥ 2 call pulses of at least 2 ms duration or a single call pulse of at least 5 ms (Weller and Baldwin 2012) in each file. We considered each file to have only 1 pass of a given species. On those occasions that we detected multiple species in a single file, we counted a single pass for each represented species or frequency groups (see below). We vetted each call file manually to confirm the presence of at least a single unequivocal bat pulse.

A relatively small percentage of bat passes contained at least 2 call pulses (median = 4, range 2–12 pulses) that met SonoBat's default quality threshold (0.80) and achieved a 0.90 consensus species classification (see "Results"). We summarize the classification of these calls to estimate the species composition of our recordings (assuming classified calls are reasonably representative of unclassified calls) and seasonal activity patterns among species. However, we use all recorded bat passes, most classified only as high or low frequency, in the statistical analyses related to our 2 objectives. Indeed, it was this preponderance of calls identified only as high or low frequency that dictated our analysis (see below) and resulted in each frequency group containing species with mixed migratory strategies (Table 1).

Bat activity in relation to regional atmospheric conditions: testing hypotheses versus predicting forthcoming activity.—We evaluated how coastal bat activity related to regional atmospheric conditions in 2 distinct contexts and time frames. For objective 1, we evaluated hypotheses regarding the influence of regional atmospheric conditions on temporal variation in coastal bat activity (Table 2) by comparing total nightly bat activity with relevant weather variables averaged over the period of activity monitoring (i.e., nightly averages from evening civil twilight to morning civil twilight). In contrast, for objective 2, we attempted to anticipate the magnitude of bat activity in the forthcoming night using the regional average of pertinent weather variables (Table 2) from single observations reported approximately 30 min prior to sunset supplemented with NEXRAD radar data collected 1 h after sunset.

We derived atmospheric conditions primarily from weather data collected at 5 National Weather Service Automated Surface Observing System (ASOS) stations occurring within 50 km of the centroid of microphone locations (Fig. 1). While all atmospheric and derived variables are defined and described elsewhere (Table 2), 2 variables warrant more detail. We calculated wind profit, a variable combining wind direction and wind speed (Erni et al. 2002; Table 2) to associate positively with winds blowing towards the coast. Specifically, we formulated wind profit to give positive values for wind directions that 1) indicated the recent passage of cold fronts, 2) might have forced more coastal movements or activity, or 3) possibly induced the coastal effect (Ralph 1978) in migrating bats. Two variables did not represent nightly averages—the deviation of the daily high

Table 1.—Classification of ultrasonic bat passes (call sequences) recorded in southern Rhode Island, United States, during autumn 2010–2012. We report the classification of those bat passes using SonoBat 3.02 comprising at least 2 calls that met the software's default quality threshold and a 0.90 consensus discriminant probability threshold. We visually inspected classified calls to affirm software classifications. We placed all *Myotis* spp. into a collective species group. We categorized unclassified bat passes by their characteristic frequency (high: typically > 35 kHz; low: < 35 kHz).

Classification[a]	Migratory status[b]	Migratory period[c]	# passes	% of identified passes	% of frequency activity[d]	% of all activity[d]
High frequency						
Eastern red bat	L	Aug.–Oct.	2,677	33.4	66.6	48.6
Tricolored bat	S	Jul.–Aug.	1,098	13.7	27.3	19.9
Myotis spp.	S	Jul.–Sep.	246	3.1	6.1	4.5
Unknown			30,757			
Low frequency						
Silver-haired bat	L	Aug.–Oct.	1,905	23.8	47.8	12.9
Big brown bat	N		1,829	22.8	45.9	12.4
Hoary bat	L	Jul.–Sep.	250	3.1	6.3	1.7
Unknown			8,849			

[a] Scientific names: eastern red bat (*Lasiurus borealis*), tricolored bat (*Perimyotis subflavus*), silver-haired bat (*Lasionycteris noctivagans*), big brown bat (*Eptesicus fuscus*), and hoary bat (*Lasiurus cinereus*).
[b] Migratory status (L = long-distance; S = short-distance; N = nonmigratory) based on Fleming and Eby (2003). Tricolored bats (*Perimyotis subflavus*) may also exhibit long-distance movements (Fraser et al. 2012). *Myotis* spp. may include some nonmigratory species, but the predominant *Myotis* spp. in our identified calls is a short-distance migrant (little brown bat; *Myotis lucifugus*).
[c] Expected migratory period through southern New England is not well established in any species. Estimated periods are based on: Cryan 2003; Johnson et al. 2011a, 2011b (red, hoary, and silver-haired bat); McGuire et al. 2012 (silver-haired bat); Dzal et al. 2009 (hoary bat); Fujita and Kunz 1984; Winchell and Kunz 1996 (tricolored bat); Davis and Hitchcock 1965; Arnett et al. 2007 (*Myotis* spp.).
[d] Estimated assuming that the composition of identified passes is representative of unidentified passes of the same characteristic frequency. This percentage thus represents the sum of identified passes for each species and the estimated number of passes of each species present in the unidentified passes of the corresponding characteristic frequency, divided by the total number of passes of the corresponding characteristic frequency (frequency activity) or all frequencies (all activity).

Table 2.—Atmospheric variables used to explore relationships with patterns of bat activity in southern Rhode Island, United States, from 2010 to 2012. For most variables, we calculated the regional average over 2 time frames: 1) the nightly average from evening civil twilight to morning civil twilight and 2) based on single observations occurring approximately 30 min prior to local sunset. Expected associations apply only to the migratory season as defined by the period of monitoring in this study, 2 August to 31 October.

Variable	Units	Description	Expected association with bat activity
Day of year	day	Seasonality; day of the year	Negative; the expected decrease in bat activity through the season, however, is likely driven by other climatic and ecological variables (e.g., temperature and prey abundance, respectively) that decrease as migration progresses
Temperature	°C	Dry bulb surface temperature; centered by weather station to account for systematic differences among station	Positive; bats tend to be more active at warmer temperatures within a given season (Weller and Baldwin 2012, and citations therein); not evaluated due to high collinearity, particularly with day of year
Temperature deviation	°C	Deviation of daily high temperature from the 30-year (1982–2012) average high temperature	Positive; we suggest that above/below average temperatures may stimulate/suppress bat activity, particularly later in the migration season, suggesting a positive interaction with day of year
Δ Temperature	°C	24-h increment in temperature	Mostly positive; we suggest that an increase/decrease in nightly temperature relative to the prior night may stimulate/suppress bat activity, particularly later in the migration season, suggesting a positive interaction with day of year
Wind speed	m/s	Wind speed measured approximately 10 m above ground level; centered by weather station to account for systematic differences among stations	Negative; high wind speeds consistently associated with decreased migratory bat activity (Reynolds 2006; Baerwald and Barclay 2011; Weller and Baldwin 2012)
Wind profit	m/s	A variable combining wind direction and wind speed (Erni et al. 2002). The distance a bat is drifted toward a specified destination (in the present case, due southeast), in a fixed time interval, only through the effect of wind; calculated prior to centering wind speed	Positive; we expect positive wind profits as calculated to indicate combinations of wind speeds and directions that induce a more coastal flight path for migrating bats and perhaps the coastal effect (Ralph 1978) in inexperienced migrants
Barometric pressure	mb	Station barometric pressure; centered by weather station to account for systematic differences among stations	Positive or negative; higher pressure is typically associated with improved conditions for flying (e.g., clear skies and calmer winds), but relatively low pressure is also associated with the passage of cold fronts; reviewed in Richardson (1990)
Δ Pressure	mb	24-h increment in atmospheric pressure; for the pre-sunset variable, we used a 6-h increment	Positive; an increase in average nightly pressure from the prior night may indicate the recent passage of a cold front and improving conditions for flying; reviewed in Richardson (1990), but see Baerwald and Barclay (2011)
Relative humidity	%	Calculated from temperature and dew point according to the August-Roche-Magnus formula (Lawrence 2005)	Negative, but complicated due to correlations with other variables; in general, lower humidity is expected after the passage of cold fronts; reviewed in Richardson (1990); not evaluated due to high collinearity with several variables
Δ Relative humidity	%	24-h increment in relative humidity	Negative, but complicated; in general, falling humidity may be indicative of a recently passed cold front; reviewed in (Richardson 1990)
Rain (night only)	n/a	Proportion of the hours in a night with at least 1 station reporting the occurrence of precipitation	Negative; precipitation is likely to limit the ability of bats to acquire prey by either discouraging insect activity or interfering with echolocation (e.g., Griffin 1971; Parsons et al. 2003)
Visibility	mi	Sensor-derived value of air clarity converted to the corresponding visibility of the human eye	Positive; we expect the relationship is due largely to reduced activity during periods of low visibility, which is often indicative of inclement weather (e.g., fog, rain, high humidity) or conditions that may inhibit echolocation (e.g., high particulate matter)
Radar reflectivity (pre-sunset only)	Z	Sum of linearized radar reflectivity factors within 150 km of the KBOX radar	Positive in the absence of precipitation as increased reflectivity should reflect increased bioscatter (i.e., migrating animals—Gauthreaux and Belser 1998; Frick et al. 2012); level or negative in the presence of precipitation, suggesting an interaction with rain near the radar
Rain near radar (pre-sunset only)	n/a	Indicator of precipitation (1) or no precipitation (−1) within 150 km of the KBOX radar	Negative; the presence of regional precipitation is expected to suppress migratory bat activity

temperature from the long-term (30-year) average and the proportion of each night with measurable precipitation (Table 2). For Objective 2, we also incorporated weather surveillance radar data (NEXRAD; KBOX, Boston, Massachusetts), which provided information on the presence and magnitude of migratory animal activity in the atmosphere (Gauthreaux and Belser 1998). We selected radar scans approximately 1 h after sunset, at which time nocturnal migration should be well underway (Gauthreaux 1971). We proved additional detail on the acquisition and handling of weather and radar data in Supporting Information S1.

Analysis.—We used generalized additive mixed models (GAMMs—Wood 2006; Zuur et al. 2009) to evaluate the association between bat activity and regional atmospheric conditions. These GAMMs were essentially generalized linear models that accommodated potential nonlinear changes in bat activity with predictor variables (e.g., seasonal patterns of activity) if supported by the data, and also incorporated random effects and serial correlation (Wood 2006). We defined bat activity as the count of bat passes summed across all microphones active on a given night of monitoring, using only those nights with at least 3 operational microphones (162 of 197 nights). We modeled nightly bat activity with a negative binomial distribution to accommodate overdispersion (see Supporting Information S2). Nightly effort varied, so we used the number of active microphones on a given night as an offset in the analysis (i.e., a fixed covariate that allows us to model rates of activity among nights with different numbers of active microphones). We estimated separate GAMMs for high- and low-frequency bats using the GAMM function of the mgcv package (Wood 2012) within R (R Core Team 2012; version 2.15.2).

Despite broad similarities, our objectives required slightly different GAMM approaches. In our evaluation of hypotheses (objective 1), for example, we did not eliminate any variables from the models to avoid biased parameter estimates and *SE*s when evaluating hypotheses (Harrell 2001). We allowed for potential nonlinearity only in seasonal effects (i.e., nonlinear patterns of bat activity as a function of the day of year) using the default thin plate regression spline. We included interactions between a linear specification of day of year and 2 temperature variables—temperature deviations from normal and changes in nightly temperature (relative to the previous night)—which we expected to be more important later in the season. When predicting nightly bat activity (objective 2), we opted for a more flexible model specification (i.e., potential nonlinearity in all continuous effects). However, we used shrinkage-penalized thin plate splines for each variable, which could penalize (exclude) irrelevant variables from the model. Model complexity precluded the simultaneous fitting of multiple penalized splines, so we evaluated the penalized spline for each variable in turn while specifying all other variables in linear form. We also considered nonlinear interactions between day of year and temperature deviations from normal and changes in nightly temperature and explored separate splines for radar reflectivity depending on the presence or absence of precipitation within 150 km of the radar.

We expected variation in bat activity among years due to the vagaries of animal migration and therefore included year as a random effect. The changes in detector settings after 2010, which decreased the sensitivity of the microphones, were also absorbed by this random effect specification. Despite only 3 levels, we did not experience any difficulties in the estimation of random effect variances. We centered and scaled by 1 *SD* all continuous model input variables (fixed effects—Gelman 2008; Schielzeth 2010; definitions in Table 2). We also recoded (to −1 or 1) and then centered binary indicator variables to correspond to scaled continuous variables. We excluded temperature and relative humidity due to collinearity (i.e., variance inflation factors > 3). We evaluated model predictive ability using leave-one-out cross-validation (i.e., omitting data from a single night, refitting the model, and comparing the predicted bat activity on the omitted night to actual bat activity). We provide the data and code necessary to reproduce this analysis (including assessments of model adequacy and potential bias in parameter estimates) at https://github.com/adamdsmith/Bat_migration_acoustics.

RESULTS

Acoustic summary.—We recorded 47,611 bat passes during the 775 detector nights of the 3 autumns of this study. Although 15,368 passes (32.2% of all passes) contained at least 2 pulses of sufficient quality to facilitate classification to species, SonoBat reached a consensus classification on only 8,005 passes (16.8% of all passes). Most classified passes belonged to the 3 species of tree bats (Table 1), in particular red and silver-haired bat. We also detected significant acoustic activity from big brown bats and tricolored bats. We recorded *Myotis* spp. (mostly little brown bats) and hoary bats infrequently (Table 1). Bat passes classified with high confidence suggest seasonal differences in the activity of certain species (Fig. 2).

Some species or species groups may produce a higher proportion of unusable, fragmented sequences (Barclay 1999). For example, red bats and, to a lesser extent, *Myotis* spp. call sequences may be more likely to be of insufficient quality for automated identification compared to other northeastern species (see SonoBat documentation). Thus, red bats and *Myotis* spp. were likely overrepresented in the unidentified calls. Indeed, relaxing the quality (from 0.80 to 0.70) and consensus discriminant probability (from 0.90 to 0.75) thresholds required for classification increased the estimated contribution of red bats, hoary bats, and *Myotis* spp. (approximately 14% increase on average) to the acoustic data, but did not substantively change the seasonal phenology of species activity (i.e., Fig. 2—Adam D. Smith, pers. obs.).

Nightly bat activity and concurrent regional atmospheric conditions.—We based GAMM models on 162 nights with at least 3 active microphones (714 detector nights). High- and low-frequency bat models indicated some degree of support for most of the expected associations between bat activity and atmospheric conditions, although the magnitude of this support varied (Table 3). The fixed effects in our high- and
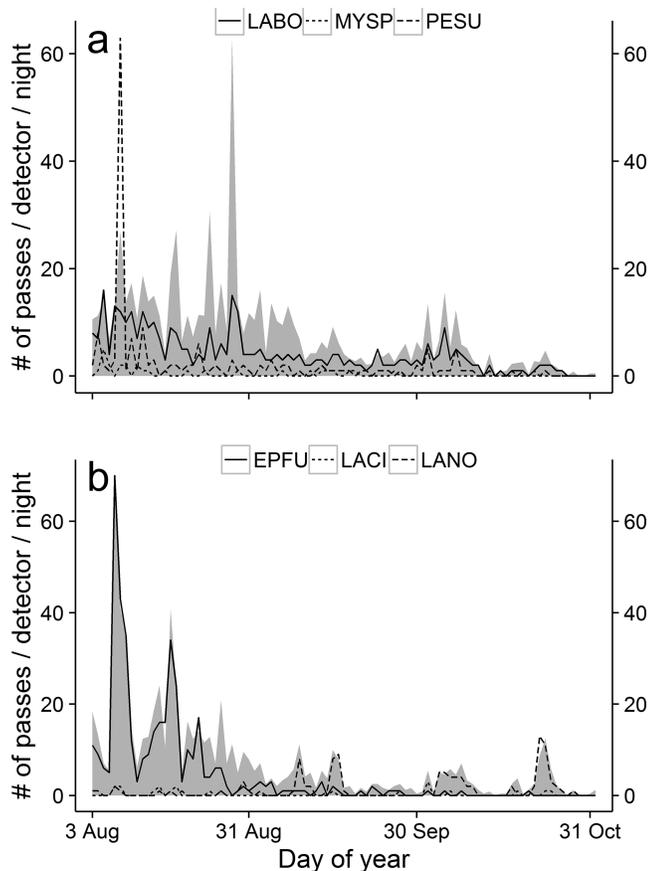
Fig. 2.—Comparison of nightly regional activity among a) high- and b) low-frequency bats recorded by ultrasonic recorders in southern Rhode Island, United States, during autumn 2010–2012. Patterns of activity over time within a species are of primary interest, as comparisons among species are complicated by unknown differences in behavior, call rates, and detectability. Gray shading indicates temporal patterns in bat passes not identified to species (scale on right vertical axis). High-frequency bats: LABO (eastern red bat; *Lasiurus borealis*), PESU (tricolored bat; *Perimyotis subflavus*), and MYSP (*Myotis* sp.); low-frequency bats: EPFU (big brown bat; *Eptesicus fuscus*), LACI (hoary bat; *Lasiurus cinereus*), and LANO (silver-haired bat; *Lasionycteris noctivagans*).

low-frequency models (i.e., atmospheric conditions; Table 2) explained roughly 19% and 35% of the variation in bat activity, respectively (marginal R^2—Nakagawa and Schielzeth 2013). We report average changes in bat activity relative to a per unit change in the independent variable to facilitate interpretation. High- and low-frequency bat activity exhibited similar associations with atmospheric conditions, although the associations were typically much stronger in low-frequency bats (Fig. 3). Bat activity declined approximately 2–3% per day over the course of the recording window, although in high-frequency bats this decrease occurred mostly after 1 October (Fig. 3a). Among atmospheric conditions, wind profit exhibited the strongest association with bat activity. High- and low-frequency bat activity increased approximately 19% and 51% for each m/s increase, respectively (Fig. 3b). Bat activity was positively associated with temperature deviation from normal, changing about 5% per °C in high-frequency bats and 11% per °C in low-frequency

bats in mid-September (Fig. 3c). In low-frequency bats, however, this association varied strongly over the course of the season, with below average temperatures apparently suppressing activity more strongly as the season progressed (Fig. 3c). Each °C change in average nightly temperature from the prior night was associated with an approximately 6% and 14% change in mid-September high- and low-frequency bat activity, respectively (Fig. 3d). However, night-to-night changes in temperature were less important for high-frequency bats as the season progressed (Fig. 3d). We found some indication that bat activity varied positively, although weakly, with pressure changes relative to the prior night (Fig. 3e).

Predicting regional nightly bat activity.—Roughly one-half of the input variables were retained in the predictive pre-sunset GAMMs, although not all were identified as important in the final models (Fig. 4; Table 4). All retained variables were penalized to linear specifications. High- and low-frequency bat activity exhibited associations with atmospheric conditions that were collected 30 min prior to sunset (Fig. 4) similar to those from nightly regional averages (Fig. 3). Expected bat activity declined approximately 2–3% per day over the course of the season (Fig. 4a). Wind profit varied positively with forthcoming regional bat activity—expected high- and low-frequency bat activity changed 10% and 24% per m/s of wind profit, respectively (Fig. 4b). The association between bat activity and daily high temperatures relative to normal changed as the season progressed for all bats—cooler than normal temperatures were associated with increasing activity early in the season and decreased activity late in the season (Fig. 4c). The change in temperature in the previous 24 h was positively associated with forthcoming low-frequency bat activity (9% change in activity per °C; Fig. 4d) but not high-frequency bat activity. Changes in atmospheric pressure in the 6 h prior to sunset were positively associated only with forthcoming high-frequency bat activity (11% change in activity per mb change; Fig. 4e) and not low-frequency bat activity. Visibility prior to sunset was related modestly and positively to forthcoming low-frequency bat activity (15% change in activity per mi of visibility; Fig. 4f).

Predictive models best captured low- and high-frequency bat activity and, in general, predictions from the low-frequency bat model were more accurate (Fig. 5). To help visualize, we categorized the continuous predictions of bat activity (Fig. 5) at their quartiles to generate 4 ordered classes of predicted bat activity to compare with the corresponding classes of observed pass rates (Fig. 6). We refer to these activity classes (with their associated percentiles) as low (≤ 25%), low-medium (26–50%), medium-high (51–75%), and high (> 75%) activity. Using low-frequency bats as an example (Fig. 6b), predictions of the highest bat activity class for a given night (rightmost group in Fig. 6b) corresponded to actual bat activity in the highest class about 65% of the time and in the highest 2 classes about 90% of the time. Similar levels of accuracy occurred when predicting the nights of lowest bat activity (leftmost group). Predictions for the middle classes of low-frequency bat activity were marginally better than random, although predictions favored the correct end of the activity spectrum.

Table 3.—Relationships between regional nightly activity of high- and low-frequency bats and average regional nightly atmospheric conditions derived from generalized additive mixed models. Input variables were centered and scaled, thus 1) exponentiation of parameter estimates provides the average change in bat activity per *SD* change of the input variable, and 2) comparisons of parameter estimates within a model convey information about the relative magnitude of a variable's association with bat activity.

Variable[a]	Expected association	High frequency			Low frequency		
		Estimate (*SE*)[b]	t[c]	P	Estimate (*SE*)[b]	t[c]	P
Day of year	−	−0.46 (0.10)	−4.76	< 0.001	−0.70 (0.12)	−6.08	< 0.001
Wind profit	+	0.26 (0.09)	2.95	0.002	0.59 (0.11)	5.28	< 0.001
Δ Temperature	+	0.16 (0.08)	1.99	0.05	0.37 (0.10)	3.59	< 0.001
Δ Temperature × day of year	+	−0.17 (0.07)	−2.50	0.01	0.07 (0.09)	0.76	0.45
Temperature deviation	+	0.16 (0.08)	1.87	0.06	0.32 (0.10)	3.09	0.002
Temperate deviation × day of year	+	0.08 (0.09)	0.86	0.39	0.32 (0.12)	2.74	0.007
Δ Pressure	+	0.19 (0.10)	2.00	0.05	0.15 (0.12)	1.24	0.22
Δ Relative humidity	−	0.00 (0.08)	0.01	0.99	0.12 (0.10)	1.22	0.23
Wind speed	−	−0.01 (0.09)	−0.08	0.93	−0.11 (0.11)	−0.96	0.34
Rain	−	−0.04 (0.08)	−0.51	0.61	−0.05 (0.10)	−0.44	0.66
Pressure	+/−	0.09 (0.10)	0.86	0.39	0.00 (0.12)	0.00	1.00
Visibility	+	0.05 (0.08)	0.64	0.52	0.02 (0.10)	0.18	0.86

[a] *SD*s of input variables: day of year (22.45 days), wind profit (1.58 m/s), Δ temperature (3.10°C), temperature deviation (3.44°C), Δ pressure (5.50 mb), wind speed (1.33 m/s), rain (0.21), pressure (6.17 mb), visibility (1.63 mi), Δ relative humidity (12.32%); use the *SD*s with parameter estimates to evaluate the effect of a variable on bat activity. For example, all else being equal, high-frequency bat activity on a night with an average wind profit of 1.58 m/s was approximately 30% higher ($e^{0.26}$) than nights with an average wind profit of 0 m/s.

[b] Day of year estimate from high-frequency model using linear fit only for comparison with other variables. All other estimates for high-frequency model that fitted day of year with a smooth term. In low-frequency mode, day of year smooth term was penalized to a linear term.
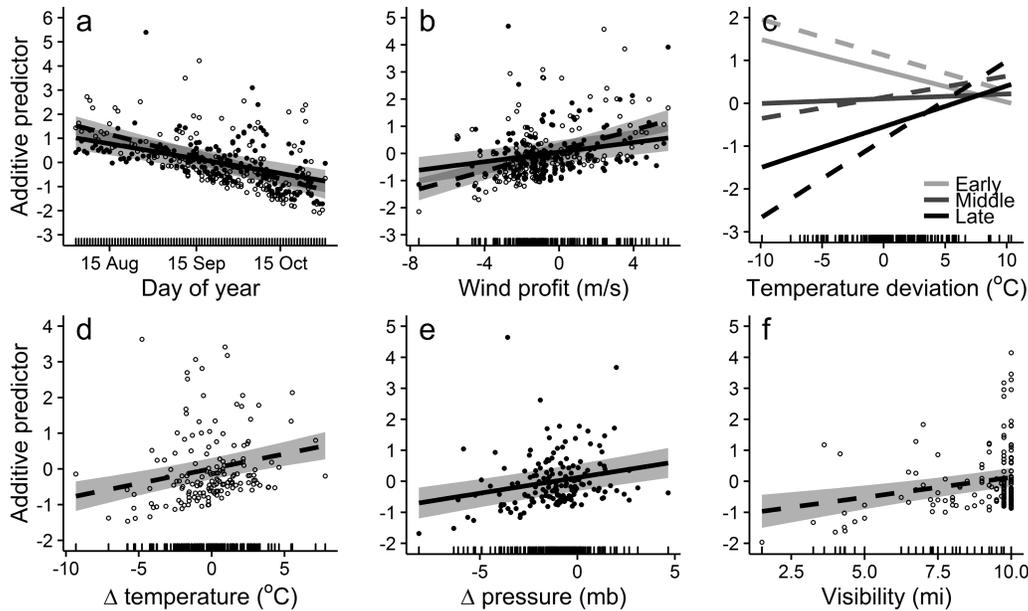
[c] 148 residual degrees of freedom.
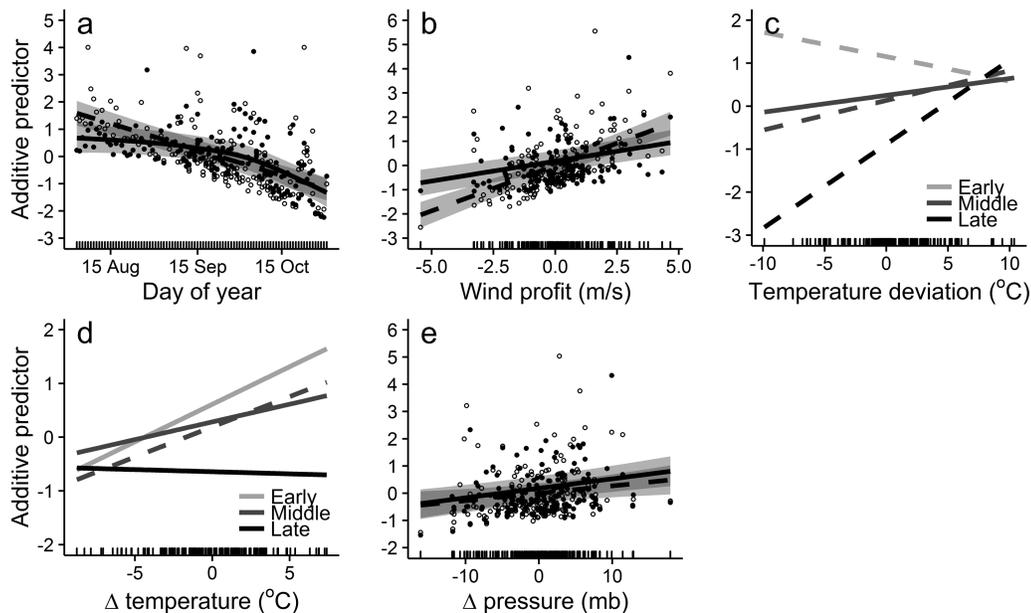
Fig. 3.—Changes in regional high-frequency (solid line, filled circles) and low-frequency (dashed line, open circles) bat acoustic activity a) over the course of autumn (day of year) and as a function of nightly regional averages of relevant atmospheric conditions including b) wind profit, c) the deviation in daily high temperature from the 30-year average and 24-h changes in d) temperature, and e) atmospheric pressure. Variable associations with bat activity are illustrated while holding all other variables at their mean. Shading illustrates the pointwise *SE* and circles the deviations of the observed data from the fitted association, respectively. A 1 unit change in the additive predictor (essentially the centered logarithm of expected bat activity) reflects approximately a 3-fold change in bat activity. When interactions with day of year are present (e.g., temperature and low-frequency bat acoustic activity [dashed lines in c], change in temperature and high-frequency bat acoustic activity [solid lines in d]), we separately illustrate the effect for early (15 August), middle (15 September), and late (15 October) in the season. *SE*s and observed data are not shown for these interactions (c, d) to preserve clarity. Rug plots illustrate the distribution of the independent variables in the original data.

DISCUSSION

Most detected bat activity during autumn along the Atlantic Coast of southern New England was attributable to the 3 species of tree bats, with significant contributions from big brown bats and tricolored bats (particularly in August). Bat activity varied most strongly with regional atmospheric conditions expected to induce a more coastal flight path and various aspects of

Fig. 4.—Changes in regional high-frequency (solid line, filled circles) and low-frequency (dashed line, open circles) bat acoustic activity a) over the course of autumn (day of year) and as a function of regional averages of relevant atmospheric conditions collected approximately 30 min prior to sunset. Atmospheric variables include b) wind profit, c) the deviation in daily high temperature from the 30-year average, d) 24-h change in temperature, e) 6-h change in atmospheric pressure, and f) visibility. Variable associations with bat activity are illustrated while holding all other variables at their mean. Shading illustrates the pointwise *SE* and circles, the deviations of the observed data from the fitted association, respectively. A 1 unit change in the additive predictor (essentially the centered logarithm of expected bat activity) reflects approximately a 3-fold change in bat activity. Temperature deviation interacted with day of year for both high- and low-frequency bat acoustic activity (c), so we separately illustrate the effect for early (15 August), middle (15 September), and late (15 October) in the season. *SE*s and observed data are not shown for these interactions to preserve clarity. Some variables were retained only in a single model (d–f). Rug plots illustrate the distribution of the independent variables in the original data.

Table 4.—Relationships between regional nightly activity of high- and low-frequency bats and average regional atmospheric conditions approximately 30 min prior to sunset derived from generalized additive mixed models. Input variables were centered and scaled, thus 1) exponentiation of parameter estimates provides the average change in bat activity per *SD* change of the input variable and 2) comparisons of parameter estimates within a model convey information about the relative magnitude of a variable's association with bat activity.

Variable[a]	Expected association	High frequency			Low frequency		
		Estimate (*SE*)	t^{b}	*P*	Estimate (*SE*)	t^{b}	*P*
Day of year	−	−0.45 (0.10)	−4.58	< 0.001	−0.68 (0.11)	−6.40	< 0.001
Wind profit	+	0.21 (0.08)	2.69	0.008	0.44 (0.09)	4.68	< 0.001
Δ Temperature	+				0.21 (0.08)	2.69	0.008
Δ Temperature × day of year	+				0.09 (0.09)	0.97	0.33
Temperature deviation	+	0.09 (0.08)	1.09	0.28	0.26 (0.10)	2.63	0.01
Temperature deviation × day of year	+	0.21 (0.09)	2.33	0.02	0.35 (0.11)	3.07	0.003
Δ Pressure (6 h)	+	0.19 (0.07)	2.76	0.007			
Visibility	+				0.22 (0.10)	2.26	0.03
Wind speed	−	0.11 (0.07)	1.65	0.10			
Δ Relative humidity	−				0.14 (0.09)	1.50	0.13

[a] *SD*s of input variables: day of year (22.45 days), wind profit (2.35 m/s), Δ temperature (2.55°C), temperature deviation (3.44°C), Δ pressure (1.92 mb), visibility (1.65 mi), wind speed (1.44 m/s), and Δ relative humidity (18.07%); use the *SD*s with parameter estimates to evaluate the effect of a variable on bat activity. For example, all else being equal, expected high-frequency bat activity on a night with a wind profit of 2.35 m/s at sunset will be approximately 23% higher ($e^{0.21}$) than on nights with a wind profit of 0 m/s at sunset.

[b] 154 residual degrees of freedom.

temperature. Predictive models of regional nightly bat activity based on pre-sunset meteorological data reasonably predicted nights of the highest and lowest bat activity. The ability to anticipate the nights of highest bat activity may help reduce adverse interactions with impending wind energy development in coastal and offshore areas along the western Atlantic Ocean.
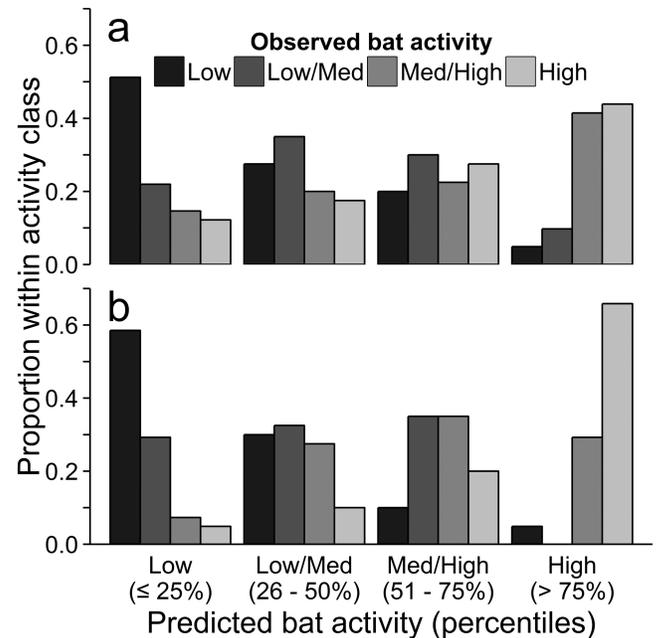
We emphasize that we have no means of using acoustics to distinguish local or resident foraging individuals from actively migrating individuals. Thus, the data set likely represents both processes, particularly towards the beginning of the sampling period. Nonetheless, we expect that a majority of recorded bat activity was associated with dispersing, relocating, or migrating
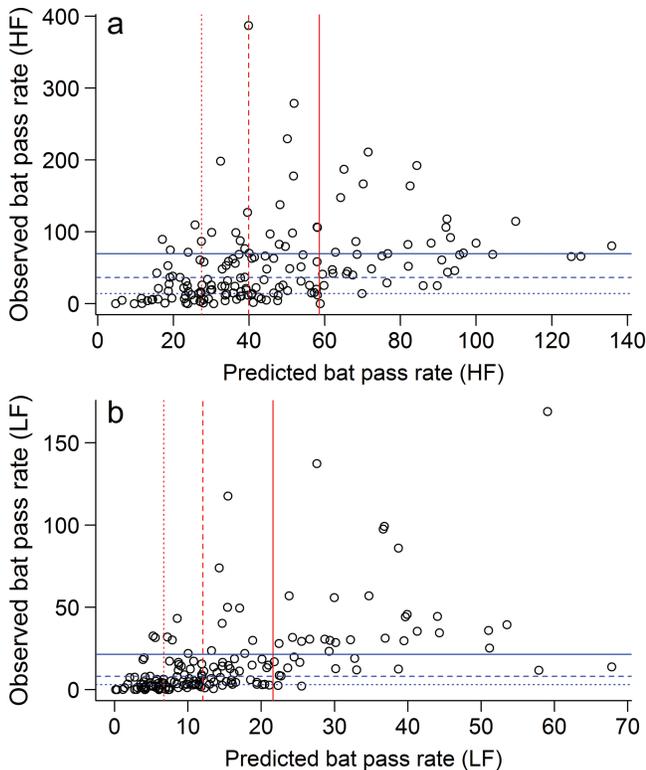
Fig. 5.—Observed nightly bat activity rates (number of bat passes divided by number of active microphones) against predicted bat activity rates from the predictive pre-sunset models for a) high-frequency and b) low-frequency bats. Vertical and horizontal lines represent the location of quartiles used to categorize observed and predicted bat activity into the 4 ordered classes of bat activity described in the text. HF = high frequency; LF = low frequency.

Fig. 6.—Regional a) high-frequency and b) low-frequency bat acoustic activity and corresponding predictions from models based on regional atmospheric conditions collected approximately 30 min prior to sunset. We illustrate 4 ordered classes of predicted and actual bat activity (and their associated percentiles): low (≤ 25%), low-medium (26–50%), medium-high (51–75%), and high (> 75%).

bats, even in August. For example, Johnson et al. (2011a) documented most migratory bat activity of a similar group of species in August at a coastal (beach) site in Maryland. Similarly to Johnson et al. (2011a), we placed our microphones in locations that generally lacked suitable roosting habitat within 1–2 km. Additionally, the activity of tree bats in the inland northeast was highest in August (Johnson et al. 2011b), and Cryan (2003) suggested that range expansion of tree bats in August (often towards the east coast) may be associated with breeding activity, dispersing juveniles, or exploratory migration. Even for the relatively sedentary big brown bat, the dispersal of maternity colonies (including associated juveniles) in August ahead of reproduction (swarming) or hibernation (Barbour and Davis 1969) suggests the large contribution of big brown bats in August may reflect a substantial contribution from regionally mobile individuals in addition to local foragers.

Patterns of bat activity along the northeastern Atlantic Coast.—Evaluating the importance of the northeastern Atlantic Coast as a flyway for migrating bats is complicated. While we necessarily assume the number of bat passes and associated pass rates correlate with abundance, the strength of this correlation is uncertain and likely variable. As such, acoustic activity is most appropriately considered an index of absolute bat activity (Miller 2001). Furthermore, differences among

ultrasonic detectors (Adams et al. 2012), monitoring context (Cryan and Barclay 2009), and analysis methods (e.g., bat pass definition, filtering, manual versus automatic classification—Britzke et al. 2013) complicate comparisons with activity levels in other acoustic studies in the eastern United States (e.g., Arnett et al. 2006, 2007; Hein et al. 2011; Johnson et al. 2011a, 2011b; Young et al. 2011). Long-term, cross-seasonal acoustic monitoring of bats in coastal as well as inland sites would further clarify the relative importance of certain areas for migrating bats, the relative contributions of resident and migrant bats, and whether bats, like birds, concentrate along ecological barriers such as the Atlantic Ocean.

Bat activity and temperature.—Bat activity commonly varies with temperature (e.g., Reynolds 2006), often as a result of concurrent changes in prey availability (Taylor 1963; Taylor and O'Neill 1988; Hickey and Fenton 1996). The strong association between bat activity and temperature was likewise apparent in this study. For example, the expected and steady seasonal decrease in bat activity from August through October likely reflected the general pattern of decreasing temperatures (with which day of year was very strongly correlated) and related changes in prey availability. But additional variables captured temperature context (departure from normal temperature) or temperature dynamics (24-h temperature increment) on a nightly basis and, perhaps with them, the relative likelihood of encountering insect prey. For instance, departures from normal temperature mattered little early in the season when average nightly temperatures remained relatively warm (i.e., always above 15°C). However, later in the season, particularly late in

September and through October, below-average temperatures increasingly inhibited bat activity. Although we cannot distinguish general bat activity from migratory activity in this study, these different aspects of temperature might reasonably influence migratory activity if the decision to migrate is based in part on the ability to forage concurrently with migration (e.g., Šuba et al. 2012; Voigt et al. 2012).

Bat activity and wind.—The strong positive association between bat activity and wind profit suggests that actively migrating individuals represent an important component of our bat activity data. We formulated wind profit in this study to give positive values for wind directions that 1) indicated the recent passage of cold fronts, 2) forced a more coastal migratory course, or 3) possibly induced the coastal effect (Ralph 1978) in migrating bats. The 1st condition is valid by our definition of wind profit given typical wind conditions behind cold fronts in the northeast (e.g., Richardson 1990), although we could not directly evaluate the applicability of the 2nd or 3rd conditions in this study. Note, however, that positive wind profit values are not a necessary condition for significant migratory activity along the Atlantic Coast. For example, northeast and east winds also provide favorable tailwinds to migrating songbirds (and presumably bats—Richardson 1990), but we expect they diminish any concentrating influence of the Atlantic Coast on migrant activity.

The absence of an association between bat activity and wind speed in this study contrasts notably with the nearly universal negative association between wind speed and migrating bat activity reported elsewhere (Fiedler 2004; Arnett et al. 2006; Redell et al. 2006; Reynolds 2006; Horn et al. 2008; Baerwald and Barclay 2011; Weller and Baldwin 2012). This discrepancy may relate to our use of regional rather than site-specific wind speed measurements, although regional nightly average wind speeds were strongly correlated with the corresponding nightly measurements near the 2 Block Island microphones ($R = 0.86$, $n = 102$—Adam D. Smith, pers. obs.). Given the low canopy of our sites, we used wind speeds measured at approximately 10 m above ground level (AGL), resulting in consistently slower average nightly wind speeds than those measured 30–50 m AGL in other studies. Negative associations between bat activity and wind speed seem disproportionately influenced by high average wind speeds (≥ 6 m/s), which represented only approximately 4% of nights in our study (compared to 20% to over 50% in other studies). Thus, we perhaps monitored activity at heights and wind speeds below which an influence on bat behavior was realized.

Predictive models of bat activity.—Wind profit and temperature best predicted forthcoming bat activity, particularly for low-frequency bats. This is not surprising given their importance in the nightly activity models and the strong autocorrelation of atmospheric conditions on short time scales. High-frequency bats apparently responded to short-term (6 h) changes in atmospheric pressure as well. Rising pressure typically indicates the recent passage of a cold front and increasingly favorable weather for flying (Richardson 1990). Its lack of importance in the nightly models may have to do with our switch from a 24-h increment in the nightly models to a 6-h increment in the predictive pre-sunset models to better capture short-term pressure trends associated with passing cold fronts (Richardson 1990). The lack of association between radar reflectivity and bat activity was disappointing, but perhaps not surprising. Reflectivity must be used with radial velocity and wind conditions to distinguish vertebrate from invertebrate activity (Gauthreaux and Belser 1998; Buler and Diehl 2009), and radar contamination (e.g., anomalous propagation, sea breeze clutter) must also be considered (Buler and Diehl 2009). We expect that an assessment of vertebrate migratory activity based on expert review would increase the utility of radar data in predictive models.

Example application of the predictive model.—Predictive models for both frequencies of bat calls performed best when anticipating nights of the highest and lowest bat activity. But how good are the predictions? Adverse interactions between bats and wind facilities are perhaps best mitigated by anticipating the nights of highest bat activity (Reynolds 2006; Horn et al. 2008). Consider, then, an example application using the predictive model for low-frequency bats in which a hypothetical coastal wind facility's protocol is to curtail turbine operation on autumn nights when the model anticipates high regional bat activity. Such a protocol might avoid substantial negative interactions on about 90% of those nights, when bat activity occurs at a medium-high or high level. On 10% of these nights, however, energy production is curtailed on nights of relatively low bat activity. Additionally, this protocol does not prescribe turbine curtailment on 34% of the nights with high regional bat activity. For high-frequency bats, the numbers are less favorable—bats are active at a medium-high or high level on 78% of nights but relatively inactive on 22% of nights with curtailed production, and turbines are not curtailed on 56% of the nights with the highest regional bat activity. While there is certainly a benefit to knowing with some probability that bats will be very active (or inactive) on a given night, considerable room remains for predictive improvement.

Atmospheric dynamics influence animal migration in complex ways and on different temporal and spatial scales (Shamoun-Baranes et al. 2010). We generated predictions of bat activity at a regional scale, but bat activity also varies on local scales, often considerably, and conditions important at any given location may differ from those at the regional level (Erickson and West 2002). Our predictive models used atmospheric variables that were readily accessible at the regional level and with clear expectations for their influence on bat activity. While the importance of these variables may fluctuate in informative ways at any given location (wind speed seems a reasonable candidate, as does wind profit for offshore locations), other variables may also prove useful and more accessible on a site-by-site basis (e.g., prey availability or habitat types—Horn et al. 2008; Santos et al. 2013).

Conservation implications.—Recent work emphasizes that effective landscape planning of wind power development and a comprehensive assessment of its risk depend fundamentally on high-quality baseline data concerning the behavior, habitat associations, distribution, and regional and continental activity

trends of migratory animals (Johnson et al. 2011b; Strickland et al. 2011; Carrete et al. 2012; Santos et al. 2013). We thus attempted to understand the atmospheric conditions that presumably influence the autumn distribution and activity of bats along the New England Atlantic Coast in advance of increased offshore and nearshore wind development. Additionally, we suggest that our predictive models provide a regional context for bat activity along the Atlantic Coast within which site-specific (i.e., wind generation facility) applications will be important to explore agreement with or, more informatively, departures from these regional expectations. Modeling bat activity at multiple scales improves our ability to anticipate nights or periods of high bat activity, thus informing turbine operations and reducing adverse interactions and fatalities considerably with potentially modest reductions in power production. Similarly, anticipating nights of low activity could prevent unnecessary turbine curtailment, further reducing lost power generation (Weller and Baldwin 2012). Finally, the efficacy of predictive models will undoubtedly benefit from an understanding of whether the activity of resident and migrating bats is associated differently with atmospheric conditions as well as the ultimate causes of fatalities at wind turbines (Cryan and Barclay 2009; Loew et al. 2013).

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

The Supporting Information document is linked to this manuscript and is available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The material consists of data provided by the author that is published to benefit the reader. The posted material is not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.— Additional methodological information.
Supporting Information S2.— Overview of the analysis of coastal bat acoustical activity.

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