High Rates of Winter Activity and Arousals in Two New England Bat Species: Implications for a Reduced White-nose Syndrome Impact?

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Abstract - We studied the winter activity of bats at a site where long-term summer monitoring data has documented the presence of a diverse and abundant bat community. Acoustic monitoring at multiple locations over 4 winters (2010–2011 through 2013–2014) documented some level of activity in every species, but *Myotis leibii* (Eastern Small-footed Myotis) and *Eptesicus fuscus* (Big Brown Bat) were the only 2 species with consistent activity throughout the hibernation period. We modeled winter activity as a function of meteorological variables and the distance to both a presumed local hibernaculum and an important foraging site that we had previously documented at the New Boston Air Force Station. Based on our Random Forest model, ambient temperature was the strongest predictor of winter activity for both species; the highest rate of activity occurred when temperatures were above 12 °C. Although most of the activity occurred during the evening, we detected diurnal activity by both species throughout the winter. The fact that the 2 most abundant species during this winter study are also the 2 most common species captured during the summer suggest that these species are hibernating in close proximity to their summer range.

Introduction

Hibernation is a behavioral adaptation that generates energetic savings through dramatic reductions in both body temperature and metabolic rate (Speakman and Thomas 2003). Hibernating bats can reduce their metabolic rate to as little as 4% of their euthermic levels by lowering their body temperature throughout the winter months in response to long periods of low food availability (Geiser 2013). Temperate bats are the smallest and most energetically constrained hibernators because they rely exclusively on stored fat as an energy source during hibernation but can store only small amounts of body fat due to the loading constraints of flight (French 1988, Webb et al. 1996).

A universal feature of all hibernating mammals is periodic arousal throughout the winter (French 1988, Lyman et al. 1982, Thomas and Geiser 1997). Although the purpose of these arousal events is still debated, researchers have suggested 3 main hypotheses to explain the phenomenon: (1) metabolic stabilization, (2) water balance, or (3) endogenous rhythms (Thomas and Geiser 1997). During arousal

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events, bats return to their euthermic state by using energy reserves to elevate body temperature from deep torpor (generally in the range of 2–8 °C) up to their normal active range of 36–40 °C (Salcedo et al. 1995). These arousal events are initially powered by non-shivering thermogenesis within the brown adipose tissue (Eddy et al. 2006, Hayward 1965). Once at euthermia, which usually takes less than 45 minutes (Salcedo et al. 1995, Thomas et al. 1990), the bats become physically active and often leave the hibernaculum to drink water (Thomas and Geiser 1997), feed (Avery 1985, Rysgaard 1942), copulate (Daan 1973, Fenton and Barclay 1980), and even switch hibernacula (Daan 1973). Although bats seldom stay at euthermic temperatures for more than a few hours at a time (Beer 1955, French 1988, Twente and Twente 1987), arousal events can account for up to 90% of the total metabolic demand of hibernation (Daan 1973, Mrosovsky 1976). Given that the cost and the frequency of arousal events are the 2 key factors that determine the energy expenditure of hibernators (Thomas et al. 1990), there is likely to be strong selective pressure to maximize the benefits of these costs.

Despite the obvious importance of hibernation to the life history and phenology of temperate bats, researchers know relatively little about the seasonal timing of entry into hibernation or the patterns of activity that occur during the winter months. Bats of hibernating species have been observed flying during the winter in Europe (Avery 1985, Hope and Jones 2012), Canada (Lausen and Barclay 2006), and the western (Falxa 2007) and midwestern (Dunbar et al. 2007, Whitaker and Rissler 1992) US, but there has been relatively little research on the winter activity of bats in the eastern US.

Long-term monitoring of the bat community at the New Boston Air Force Station (NBAFS) has documented the presence, either acoustically or through mist-net capture, of all 8 bat species found in New Hampshire (Table 1). The impetus for the long-term monitoring at this site was the observation that the abundance and diversity of bat species at the NBAFS was being markedly impacted by the onset of White-nose Syndrome (WNS), an emergent infectious disease that has caused the widespread decline of multiple hibernating bat species throughout the eastern US and Canada (WNS 2016). WNS is caused by the psychrophilic fungus

Table 1. Bat species of New Hampshire. FE THR = federally threatened, NH ES = New Hampshire endangered, NH THR = New Hampshire threatened, NH SOC = New Hampshire species of concern (NHFG 2014, USFWS 2016).

Common name	Species name	Winter status	Conservation status
Little Brown Myotis	*Myotis lucifugus* (LeConte)	Hibernator	
Northern Myotis	*Myotis septentrionalis* (Trouessart)	Hibernator	Fed THR NH THR
Eastern Small-footed Myotis	*Myotis leibii* (Audubon and Bachman)	Hibernator	NH ES
Tricolored Bat	*Perimyotis subflavus* (Cuvier)	Hibernator	NH SOC
Big Brown Bat	*Eptesicus fuscus* (Palisot de Beauvois)	Hibernator	
Silver-haired Bat	*Lasionycteris noctivagans* (LeConte)	Migratory	NH SOC
Eastern Red Bat	*Lasiurus borealis* (Müller)	Migratory	NH SOC
Hoary Bat	*Lasiurus cinereus* (Palisot de Beauvois)	Migratory	NH SOC

Pseudogymnoascus destructans (Blehert & Gargas) Minnis & D.L. Lindner (Lorch et al. 2011). The disease first appeared in New York State in 2006 and, as of 2016, it had spread to 29 states and 5 of the eastern Canadian provinces (WNS 2016). In the Northeast, WNS has caused declines of 45–98% of hibernating bat populations across the region (Turner et al. 2011). *Myotis lucifugus* (Little Brown Myotis) has declined by well over 90% in affected areas (USFWS 2016). Data collected from the NBAFS site during the summer months suggested that 2 species of hibernating bats (Little Brown Myotis and *M. septentrionalis* [Northern Myotis]) were impacted much more severely than Eastern Small-footed Myotis and the Big Brown Bat. These findings are consistent with regional models on the impact of WNS that suggest Eastern Small-footed Myotis and the Big Brown Bat show the least decline among the hibernating bat species (Langwig et al. 2012).

Compared to most other bat species in the Northeast, we know relatively little about the summer or winter ecology of Eastern Small-footed Myotis. Data collected throughout its range suggest that the Eastern Small-footed Myotis is a saxicolous species whose distribution is limited primarily to exposed rocky habitat, including cliffs, talus slopes, and even crevices in rock slabs (Best and Jennings 1997, Czaplewski et al. 1979, Erdle and Hobson 2001, Johnson et al. 2011), although they appear to forage in a variety of forested and open habitats (Fenton et al. 1980). Winter surveys of hibernating bat populations show that Eastern Small-footed Myotis use a variety of hibernacula, but they are generally found in very low numbers, and they are often roosting alone low on the walls near the entrance (Thomas 1993).

Our research at NBAFS first documented a summer population of Eastern Small-footed Myotis in 2001, and radiotelemetry work has confirmed a stable population of Eastern Small-footed Myotis roosting and foraging within the NBAFS, with day roosts located along the southern rock slope of Joe English Hill and under cedar shakes on a house located just outside the NBAFS (D.S. Reynolds, unpubl. data). Eastern Small-footed Myotis are considered to have a summer distribution that is constrained by the proximity of a winter hibernaculum (Erdle and Hobson 2001, Thomas 1993). The closest known hibernaculum containing Eastern Small-footed Myotis is over 150 km north of the study area, and Eastern Small-footed Myotis are known to hibernate in rock crevices (Roble 2004). Thus, we suspected that these individuals may be spending the winter near Joe English Hill, using this geological feature as both a summer maternity roost and a winter hibernaculum.

In contrast, the Big Brown Bat is one of the most thoroughly researched temperate bats in North America, and is documented from every state except Hawaii, all of Canada west of New Brunswick, and all of Mexico outside of the Yucatan Peninsula (Kurta and Baker 1990). During the summer months, Big Brown Bats are habitat generalists (Agosta 2002, Furlonger et al. 1987) that use a wide variety of roost types, including trees, crevice roosts, and a diversity of human structures (Brigham 1991, Feldhamer et al. 2009, Whitaker and Gummer 1992). Although the Big Brown Bat appears to be both spatially and temporally flexible during foraging (Agosta 2002), most individuals generally forage within a few kilometers of their roost (O'Shea et al. 2011). During the winter months, Big Brown Bats can be found in cave and mine hibernacula, but it is likely that most of the population overwinters in unheated sections of buildings (Whitaker and Gummer 1992). There are also multiple records of Big Brown Bats overwintering in rock crevices (Krutzsch 1946, Lausen and Barclay 2006, O'Shea et al. 2010). Given that mark–recapture data from Big Brown Bats suggest that many individuals hibernate within 5 km of their summer range (Hitchcock 1965, Whitaker 1997), we suspected that some individuals would be hibernating at the NBAFS site, possibly even using rock crevices near Joe English Hill.

The long-term summer monitoring at NBAFS has documented a shift in the bat community in response to WNS, and it is likely that the winter ecology of both Eastern Small-footed Myotis and the Big Brown Bat is playing a major role in their persistence on the landscape. It is likely that the type and location of the hibernaculum, as well as the behavioral physiology of hibernation, are factors in minimizing the impact of WNS on these populations. The goal of this study was to monitor the level of winter bat-activity at the NBAFS site. We predicted that (1) bats hibernating near NBAFS would remain active throughout the winter, (2) bat activity during the winter months would be dominated by Eastern Small-footed Myotis and Big Brown Bats because they were hibernating in proximity to the NBAFS site, and (3) winter bat activity outside of the hibernaculum would be influenced more by climate than intrinsic factors (such as a circadian rhythm).

Methods

Study area

The NBAFS is a 1114-ha remote military and communications-satellite–tracking facility located in south-central Hillsborough County, NH (42°56"N, 71°38"W; Fig. 1). Elevation at the NBAFS is variable, ranging from a minimum of 104 m in the southeast corner of the site to a maximum of 389 m at the summit of Joe English Hill in the northwestern corner of the site (LaGory et al. 2002). Precipitation at NBAFS averages 111 cm annually and is distributed relatively evenly throughout the year. Average annual temperature is 8.0 °C with monthly averages ranging from -5.2 °C in January to 21.0 °C in July (LaGory et al. 2002). Although the central operations area is highly developed, the habitat outside this core area is typical for the surrounding region, with a rural land-use pattern of residential areas interspersed with agricultural lands and forests. The NBAFS is approximately 90% forest; the dominant vegetative community is a mixed New England maple–beech forest. There are a total of 228 wetlands and open-water areas within the boundaries of NBAFS, with a combined area of ~80 ha (LaGory et al. 2002). There are 24 open-water sources and 17 intermittent and perennial streams located within the site. The largest water body within NBAFS is Joe English Pond, a 17-ha open pond located at the center of the site.

Acoustic monitoring

We established acoustic monitoring stations at 3 sites within the NBAFS (Campsite, Laurel Lane, and Shooting Field; Fig. 1), but did not monitor all stations every year. The Campsite monitoring station was located in open habitat adjacent to a small (0.12 ha) pond immediately south of Joe English Hill. The Laurel Lane monitoring station was placed parallel to a tree-lined gravel road east of Joe English Hill. The Shooting Field monitoring station was located parallel to the edge of a deciduous woodland and early successional field.

We used remote Anabat II and SD1 acoustic detectors (Titley Electronics, Ballina, Australia) with a compact flash ZCA interface or integrated compact flash data storage, respectively. Each monitoring station was enclosed in a NEMA-4 watertight housing (Fibox, Inc., Glen Burnie, MD) powered with a 35-A–hr battery maintained by a 30-W solar panel and set to continuously monitor for bat activity. We attached each detector to a pre-amplified stainless steel microphone housed within a protective shroud (Bat Hat, EME Systems, Berkeley, CA) using a 3-m shielded cable. Each detector sampled at 2-m altitude with a Lexan plate reflecting sound into the shroud while protecting the microphone from rain, snow, and ice. Each microphone was oriented so that maximum sensitivity of the microphone was in uncluttered space and at least 180° of the sampling area had a >5-m band of non-vegetated habitat. We employed EchoClass v3.1 (Britzke 2015) to filter all data files and for species identification analysis.

We accepted all species identifications made by EchoClass, and D.S. Reynolds manually reviewed all files that were categorized as "unknown" by EchoClass. We limited our initial reclassification to files that had at least 3 pulses that EchoClass identified to species. Other researchers have used similar filtering criteria (Gannon et al. 2003, Law and Chidel 2002), but our filter was more conservative because it

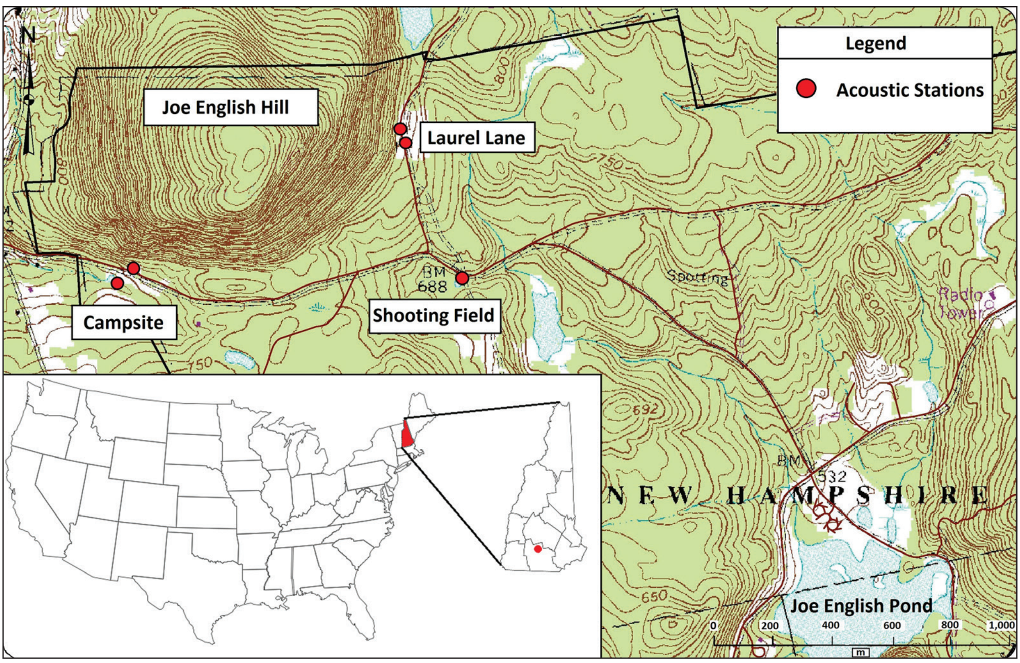

Figure 1. Map of acoustic sampling locations at New Boston Air Force Station, New Boston, NH.

restricted the analysis to pulses that were identified to species. Next, we generated a probable species identification for each file using the pulse identification based on 2 criteria: >50% of the pulses were categorized as "high" frequency, and ≥67% of the pulses were categorized within a single myotine species (MYLE, MYLU, MYSE, and MYSO). Files that met the "high" criterion but not the species criterion were assigned as *Myotis* spp. We classified as "unknown" all files that met neither criterion and eliminated them from further analysis. To validate this approach, D.S. Reynolds visually vetted a subsample of 10 re-assigned files for each myotine species from the 2011–2012 winter sampling period. Although we later excluded some of these files from analysis because they fell outside of the winter sampling period, all of the files had frequency and slope characteristics that were consistent with the assigned value.

We defined the winter monitoring season as 15 November–15 March for each of the sampling years (2010–2014). Limiting the start of the winter season to mid-November minimized the likelihood of late-autumn foraging and swarming behavior that was not related to hibernation. We computed total hourly detections for each bat species at each acoustic station. To minimize multiple consecutive detections of the same individual at a microphone (and thereby reduce serial autocorrelation), we rarefied detection records to ensure a minimum 15-min time interval between consecutive observations. Similar approaches have been used in other bat acoustic surveys to reduce the autocorrelation of acoustic monitoring data and to ensure that counts more closely represent the true number of individuals in the vicinity of each monitoring station (Downs and Racey 2006, Miller 2001, Williams et al. 2006).

Predictive model of winter bat-activity

We extracted all meteorological covariates (Table 2) for predicting winter bat-activity from data for Manchester airport (Manchester, NH; located ~15.5 km from the study site) using the R package 'weatherData' (Narasimhan 2014), which accesses the Weather Underground® database). These covariates included air temperature, wind speed, precipitation, and overall weather conditions (Table 2). We employed the R package 'maptools' to compute solar altitude on the basis of time and location (Bivand and Lewin-Koh 2014). Moon phase was computed in the R package 'oce' (Kelley 2014). We also included the specific acoustic monitoring station as a covariate (3 monitoring stations in total).

We quantified relationships between potential geographic and weather factors (hereafter "predictor variables"; see Table 2) and winter activity of the 2 focal bat species (Eastern Small-footed Myotis and Big Brown Bat) using a Random Forest (RF) algorithm implemented in R package 'party' (Hothorn et al. 2006). RF is a machine-learning algorithm that combines the predictions from multiple independent classification or regression trees into a robust composite predictive model. RF models are commonly used by ecologists for their high predictive accuracy and the ability to detect non-linear, context-dependent interactions among multiple, correlated predictor variables (Cutler et al. 2007). We used a distribution-free RF model ("conditional inference forests") that relies on nonparametric permutation tests to perform recursive partitioning. Recursive partitioning selects criteria that maximize the internal similarity of the resulting groups. This type of criteria selection has been shown to reduce bias in variable selection with respect to conventional recursive partitioning methods (Strobl et al. 2007).

For each focal bat species or species group, the RF model comprised 500 conditional inference trees, with each tree fitted with a random subset of 75% of the data sampled without replacement; each split criterion formed the nodes of each regression tree. These criteria were chosen from a random subset of 4 (out of 11 total) predictor variables. We selected these RF control parameters based on recommendations from the literature (Cutler et al. 2007) and multiple trials using cross-validation metrics to select the highest predictive accuracy. We computed the relative importance of predictor variables with respect to winter bat-activity as the degree to which prediction error increased when observation indices for a predictor variable were randomly permuted to eliminate information content for a particular predictor variable. Therefore, importance values computed using this method account for both main effects and interactions. We assessed model performance and predictive ability using a standard 10-fold cross-validation scheme. We converted the response variable (hourly bat activity) to binary form, where any hour having 1 or more bats detected was labeled a "1" and all other observation periods were labelled "0". We then measured predictive performance in 2 ways: first, we computed the root mean-square error (RMSE) using only the validation data; second, we used the binary data to construct receiver operating characteristic (ROC) plots and computation of "area under the curve" (AUC) statistics.

We generated partial-dependence plots to visualize and interpret the univariate relationships between each predictor variable and the winter-activity rates of Eastern Small-footed Myotis and Big Brown Bats. To construct these plots, we used

Table 2. Description of variables hypothesized to influence winter bat-activity at New Boston Air Force Station, NH.

Predictor variable	Abbreviated name	Description
Month	MONTH	Month of the year (categorical).
Acoustic monitoring station	SITE	Acoustic monitoring station (3 stations were deployed in total).
Temperature (C)	TempC	Hourly temperature at Manchester Airport, °C.
Wind Speed (mps)	WindMPS	Average hourly wind speed recorded at Manchester Airport, in meters per second (mps).
Precipitation (cm)	PrecipCM	Total hourly precipitation recorded at Manchester Airport, in cm.
Weather conditions	Condition	Weather category, classified as one of the following: clear, cloudy, rain, snow.
Solar altitude (degrees)	SunHeight	Solar altitude, in degrees (representing the height of the sun above or below the horizon).
Moon Fullness	MoonFrac	Fraction of the moon that is illuminated.
Dawn hour	SUNRISE	Binary indicator of the dawn period, within 1 h of sunrise.
Dusk hour	SUNSET	Binary indicator of the dawn period, within 1 h of sunset.

the RF model to predict winter bat-activity across the range of observed variation for a focal predictor variable, holding all other predictor variables at their mean value. Similarly, we assessed bivariate interactions following 3 steps. First, we divided each of the 2 focal predictor-variables into 10 bins, resulting in 100 bins in a 2-D parameter slice, and winter bat-activity for each bin was predicted using the random RF model while all other predictor variables were held constant at mean values. Second, we modeled the predictions from step 1 (n = 100) as an additive but otherwise unconstrained function of the 2 focal variables, with 1 free parameter for each of the 10 bins for each focal predictor variable, with no interaction terms. Finally, we calculated the total predictive error (RMSE) under the additive model from step 2 to represent an index of the strength of interaction, and, therefore, the degree to which the additive model was inadequate for predicting the results from the full RF model. We plotted the top 3 bivariate interactions in 3-D to enable further interpretation.

Results

We detected each of the 8 bat species known to occur in New Hampshire at least once in 4 years of winter acoustic surveys at NBAFS from 2010 to 2014 (Table 3). Eastern Small-footed Myotis was the most commonly observed bat species, followed by the Big Brown Bat and unidentified *Myotis* spp. Most species were detected at least once during each month of the winter except for January, and activity for most species was highest in late fall and early spring (Fig. 2). We observed low levels of activity of all migratory tree bats (*Lasiurus borealis* [Eastern

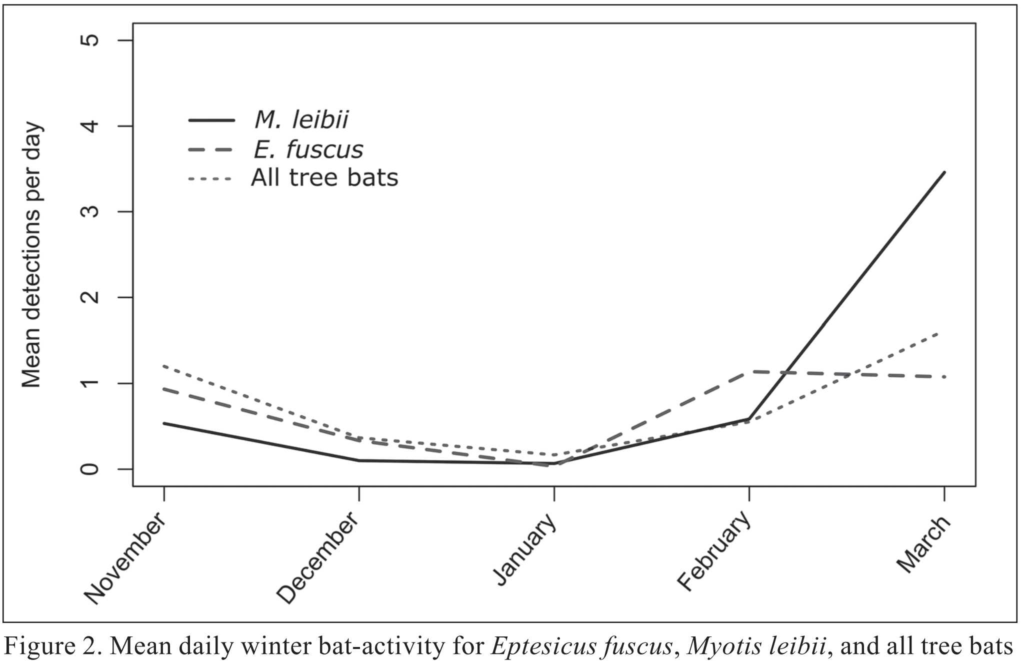

Figure 2. Mean daily winter bat-activity for *Eptesicus fuscus*, *Myotis leibii*, and all tree bats (*L. borealis*, *L. cinereus*, and *Lasionyscteris noctivagans*) computed per month for acoustic-monitoring stations located at the New Boston Air Force Station, NH, from 2010 to 2014.

Table 3. Winter bat-activity rates recorded at New Boston Air Force Station, NH, 2010–2014.

	Little Brown Myotis	Northern Myotis	Eastern Small-footed Myotis	*Myotis* spp.	Tricolored Bat	Big Brown Bat	Silver-haired Bat	Eastern Red Bat	Hoary Bat
Detections	7	38	472	210	1	277	18	155	14
Detection intervals (rarefied)	4	15	75	56	1	72	11	52	8
Detection intervals per day									
November	0.07	0.00	0.53	0.60		0.93	0.40	0.67	0.13
December	0.03	0.00	0.10	0.17		0.33	0.07	0.23	0.07
January	0.00	0.00	0.07	0.03		0.03	0.00	0.13	0.03
February	0.03	0.24	0.59	0.41		1.14	0.10	0.41	0.03
March	0.08	0.62	3.46	2.23		1.08	0.00	1.46	0.15

Red Bat], *L. cinereus* [Hoary Bat], and *Lasionycteris noctivagans* [Silver-haired Bat]) throughout the winter, with greatest detection frequency for Eastern Red Bat (Table 3; Fig. 2).

Predictive model of winter bat-activity

RF performed well in cross validation for both the Eastern Small-footed Myotis model and the Big Brown Bat model (see Figs. S1 and S2 in Supplemental File 1, available online at http://www.eaglehill.us/NENAonline/suppl-files/n24-sp7-N1468P-Reynolds-s1, and, for BioOne subscribers, at http://dx.doi.org/10.1656/N1468P.s1). The Eastern Small-footed Myotis model had an AUC of 0.97 (0.98 for training data) and the Big Brown Bat model had an AUC of 0.98 (0.98 for training data). The error estimates (RMSE) were 0.09 bats per hour for Eastern Small-footed Myotis and 0.07 bats per hour for the Big Brown Bat, with 18% of the deviance explained (analogous to R^2 statistic) for Eastern Small-footed Myotis (37% for training data) and 29% of the deviance explained for the Big Brown Bat (39% for training data).

Ambient temperature was by far the most important variable for predicting the winter activity of both Eastern Small-footed Myotis and the Big Brown Bat, followed by solar altitude, acoustic monitoring site, and month (Fig. 3). Solar altitude was an important predictor of winter activity for both Eastern Small-footed Myotis and the Big Brown Bat; winter activity for both species was very low during daylight hours (positive solar altitude) and was highest when the sun was well below the horizon (angles of -20° or less). Sampling site was also an important predictor of winter bat-activity for both species, with the site closest to Joe English Hill

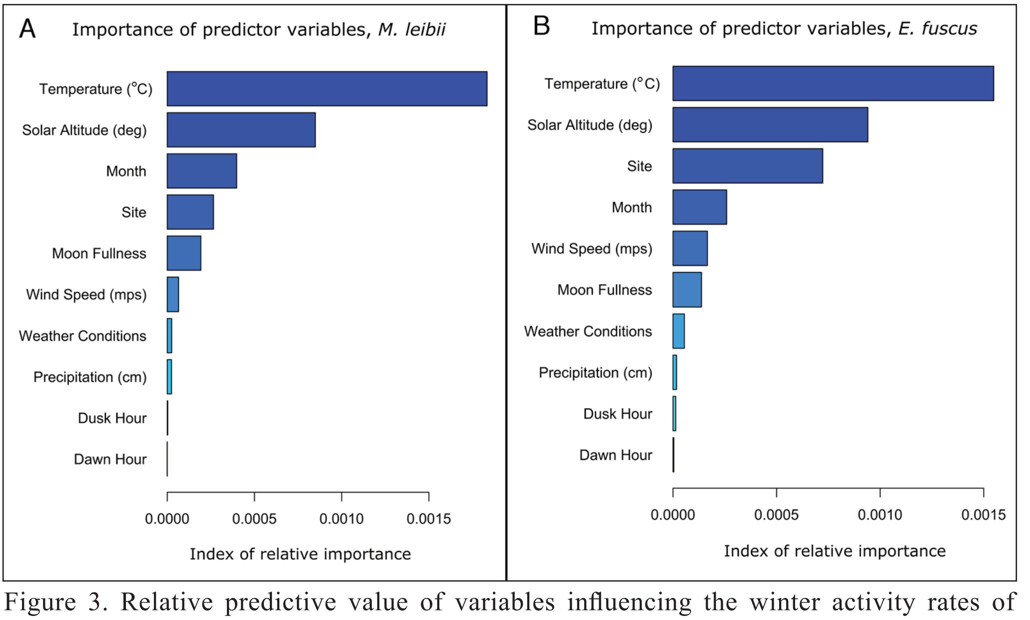

Figure 3. Relative predictive value of variables influencing the winter activity rates of (a) *Myotis leibii* (Eastern Small-footed Myotis) and (b) *Eptesicus fuscus* (Big Brown Bat) at the New Boston Air Force Station (NBAFS), N from 2010 to 2014. Relative importance values of each variable were derived from a Random Forest algorithm.

(Campsite) showing more bat activity than the other 2 sites. There was a slight but significant effect of moon phase on activity for both Eastern Small-footed Myotis and Big Brown Bats, with more activity as the moon approached full phase.

Based on univariate-plot analysis of the relationship between winter bat-activity and ambient temperature (with all other variables held constant), winter activity of Eastern Small-footed Myotis was very low at air temperatures <10 °C, but increased rapidly up to temperatures of ~15 °C, and remained high at temperatures >15 °C (Fig. 4). For the Big Brown Bat, winter activity was very low at air temperatures <3 °C, but increased approximately linearly up to temperatures of 20 °C (Fig. 5). Based on the RF model, winter activity in Eastern Small-footed Myotis was highest at Campsite on nights when ambient temperatures were at least 12 °C (see Fig. S3 in Supplemental File 1, available online at http://www.eaglehill.us/NENAonline/

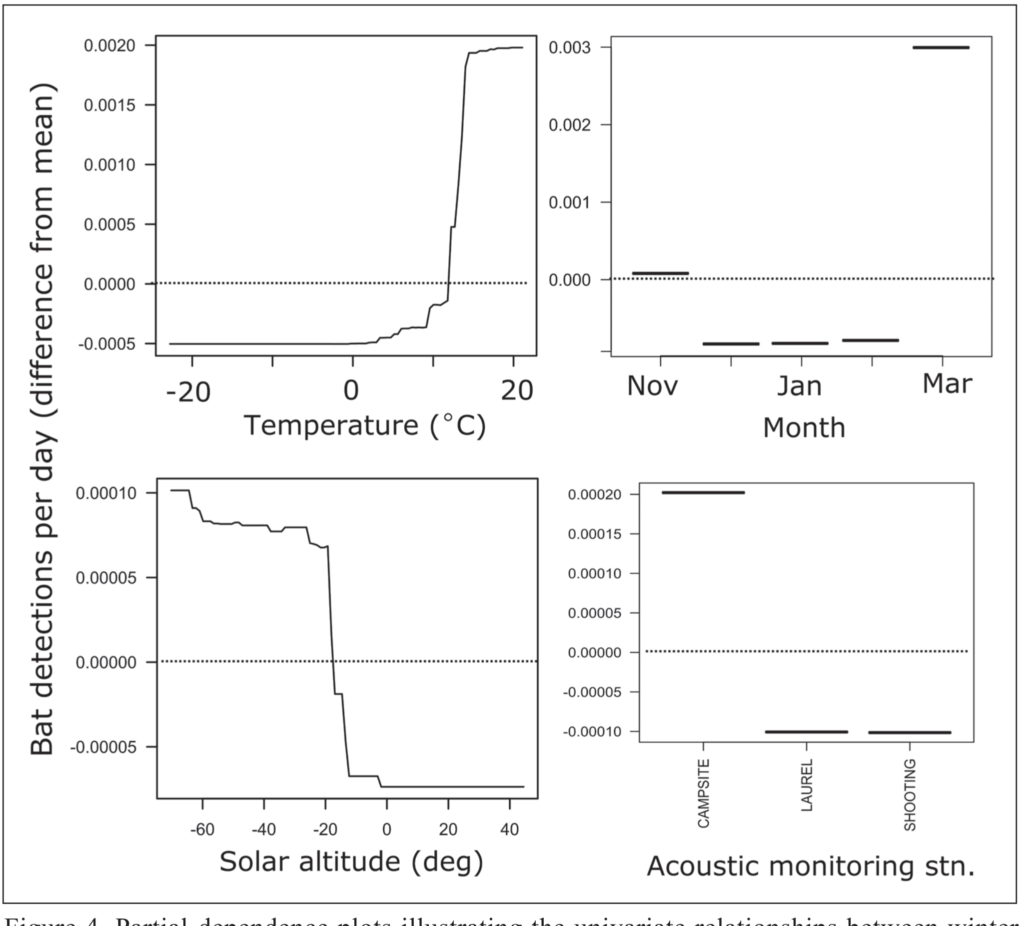

Figure 4. Partial-dependence plots illustrating the univariate relationships between winter activity of *Myotis leibii* (Eastern Small-footed Myotis) for the variables with the highest predictive value in a random forest (RF) model. These figures were constructed by making predictions from the RF model across a univariate slice of parameter space, holding all other predictor variables constant at mean values. The *y*-axis represents the difference from the mean daily detection rate (indicated by stippled horizontal line).

suppl-files/n24-sp7-N1468P-Reynolds-s1, and, for BioOne subscribers, at http://dx.doi.org/10.1656/N1468P.s1). Winter activity of Big Brown Bats was highest at Campsite on nights when ambient temperatures were at least 3 °C (see Fig. S4 in Supplemental File 1, available online at http://www.eaglehill.us/NENAonline/suppl-files/n24-sp7-N1468P-Reynolds-s1, and, for BioOne subscribers, at http://dx.doi.org/10.1656/N1468P.s1). For Eastern Small-footed Myotis, but not Big Brown Bats, the effect of temperature on winter activity was more pronounced in the month of March than in other months.

Discussion

Relatively little is known about the winter ecology of hibernating bats beyond the general phenology that bats enter a hibernaculum in the late fall, arouse

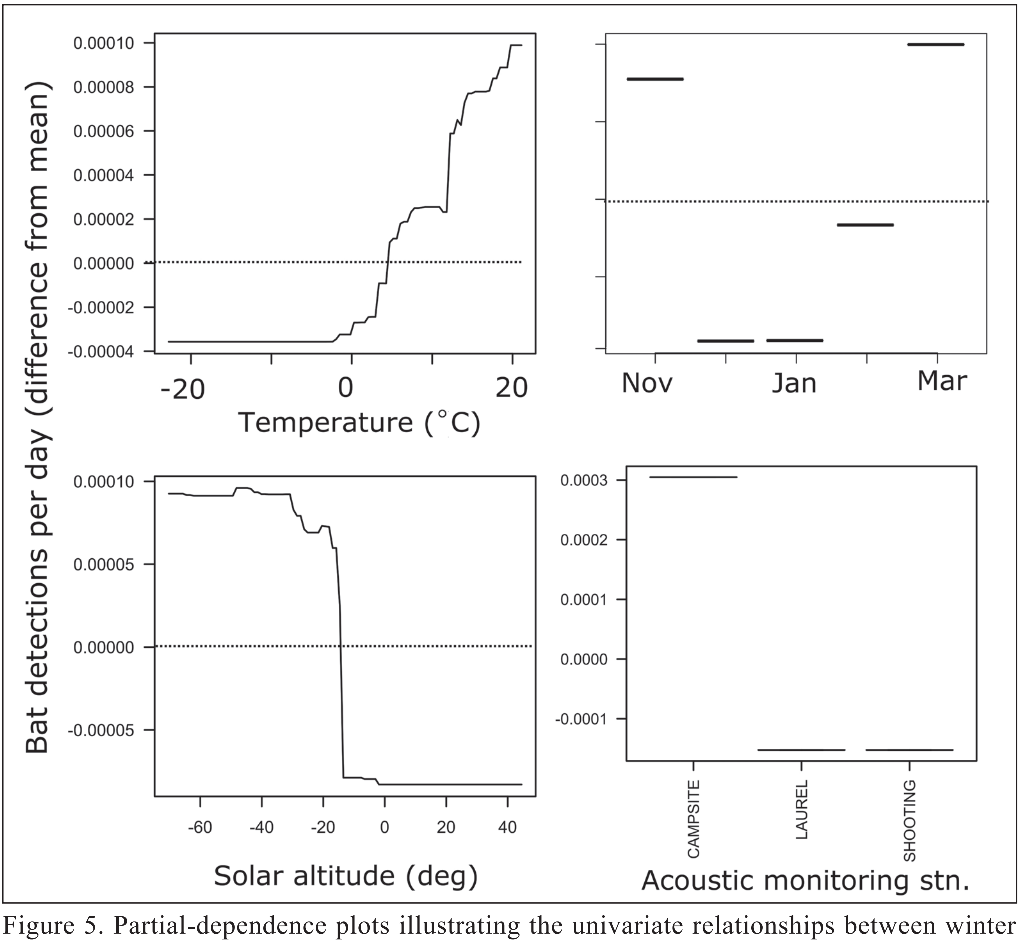

Figure 5. Partial-dependence plots illustrating the univariate relationships between winter activity of *Eptesicus fuscus* (Big Brown Bat) for the variables with the highest predictive value in a random forest (RF) model. These figures were constructed by making predictions from the RF model across a univariate slice of parameter space, holding all other predictor variables constant at mean values. The *y*-axis represents the difference from the mean daily detection rate (indicated by stippled horizontal line).

periodically throughout the winter, and emerge in the spring to return to their summer foraging area. As predicted, the Big Brown Bat and Eastern Small-footed Myotis were the 2 most frequently documented bat species throughout the winter. However, all 8 species of bats that are known to occur in New Hampshire were documented at least once during the winter months. Although the tree bats (Eastern Red Bat, Hoary Bat, and Silver-haired Bat) generally migrate out of the Northeast during the winter, previous research from Missouri (Dunbar et al. 2007) and North Carolina (Whitaker et al. 1997) have documented winter activity in Eastern Red Bat. The current study is the first to clearly document sustained winter activity of this species within the Northeast. Although it remains unclear where these bats roost during the winter months, the frequency of activity at NBAFS suggest that at least some individuals remain in the area year-round.

Hibernation is a remarkably efficient adaptation to low resource-availability, but it comes with physiological costs, including the buildup of metabolic waste, dehydration, and decreased immune function (Burton and Reichmann 1999, Thomas and Geiser 1997). Periodic arousals appear to be a universal response to these demands, although the frequency of arousal is highly variable within and between species (Johnson et al. 2012, Menaker 1964, Twente et al. 1985). The cost of arousal events and the frequency of arousals are the 2 key factors that determine the energy expenditure of hibernators (Thomas et al. 1990); thus, there is likely strong selective pressure to optimize these costs. One approach would be to lower the cost of each arousal event by becoming euthermic when the ambient temperature is high. Body temperature tracks ambient temperature during typical hibernation conditions (Lyman et al. 1982), and rewarming rates are generally linear (in °C/min: Halsall et al. 2012). Timing arousal events to coincide with high ambient temperatures reduces the total energy expense of reaching euthermia. Relying on increased ambient temperature to elevate body temperature (passive rewarming) can save 20% of the energetic cost of arousal (Halsall et al. 2012). Passive rewarming may be even more beneficial for species that hibernate at the coldest temperatures, such as Eastern Small-footed Myotis and the Big Brown Bat, because the energetic gains from hibernating at colder ambient temperatures would be more than offset by the additional costs of arousal (Kokurewicz 2004). This balance is likely why the strongest predictor of arousal frequency, and therefore winter bat-activity, is ambient temperature (Avery 1985, Brack and Twente 1985, Erkert 1982, Menaker 1962). Prior to this study, there was no evidence for any adaptive response to ambient temperature in Eastern Small-footed Myotis.

Most of the energetic cost of each arousal event involves obtaining a euthermic state; thus, one would also predict that bats should optimize their time in euthermia by using each arousal event as an opportunity to recover from the metabolic and physiological burdens of hibernation. This recovery may include drinking, urinating, and even foraging on available insects. One prediction of this resetting function is that arousal events maintain the circadian rhythm of bats so that they can emerge from hibernacula during the evening and thus avoid an increased risk of predation. The existing data suggest that hibernating bats do indeed arouse in a manner that is consistent with their nocturnal ecology (Halsall et al. 2012, Hope and Jones 2012, Johnson et al. 2012, Twente and Twente 1987). The results of this study are also consistent with the maintenance of circadian cycles in bats because the majority of winter activity in both Eastern Small-footed Myotis and Big Brown Bat occurred between sunset and sunrise.

Both Eastern Small-footed Myotis and Big Brown Bats are known to use rock crevices as transitional roosts between the summer active season and winter hibernation (Neubaum et al. 2006, Roble 2004). Within larger hibernacula, both species are relatively cold-tolerant and roost closer to the entrance than other hibernating bat species (Best and Jennings 1997, Hitchcock et al. 1984, Twente 1955, Veilleux 2007). These hibernating conditions are likely very similar to the environment found in small rock-crevices because these habitats are within a heterothermic zone that has both seasonal and daily fluctuations in microclimate caused by direct exchange with ambient conditions (Perry 2013). If these species were staying close to their summer foraging range and hibernating in relatively unstable microclimatic conditions, it would explain some of the unique aspects of their hibernation ecology. Both Eastern Small-footed Myotis and Big Brown Bats tend to enter hibernation later and remain in hibernation for a shorter period of time than other species (Best and Jennings 1997, Hitchcock et al. 1984). We would expect this situation if the bats were able to remain on their summer foraging range longer and return to it earlier than migratory hibernators. In addition, both species appear to be more tolerant of cold conditions than species that rely on the homothermic conditions found deep within large hibernacula; in the case of the Big Brown Bat, individuals have been documented surviving subfreezing temperatures for 7 days without evidence of injury (Goehring 1972). Hibernating within the heterothermic zone of a hibernaculum allows these bats to be more responsive to environmental conditions, thereby minimizing the energetic demands of hibernation, as evidenced by the fact that both species arouse more frequently than other hibernating bats (Hitchcock et al. 1984).

White-nose Syndrome has had a devastating impact on bat populations throughout the eastern US. The hyphae of *P. destructans* cause lesions on the skin of infected bats that ultimately invade the underlying dermal tissue with little to no immune response (Meteyer et al. 2012, Wibbelt et al. 2010). Although the exact mechanism of mortality has yet to be confirmed, infected bats appear to suffer from starvation and electrolyte imbalance that result from frequent arousal from deep torpor throughout the winter period (Blehert et al. 2009, Warnecke et al. 2013). Some species of hibernating bats have experienced declines of over 90% of their populations. However, Eastern Small-footed Myotis and the Big Brown Bat have experienced lower levels of decline. Since the onset of WNS, it has become critical that we understand species-specific differences in winter ecology that may be influencing mortality risk to hibernating bats. Although some effort has been made to understand why species such as *Myotis sodalis* Miller & Allen (Indiana Bat) and *M. lucifugus* (LeConte) (Little Brown Bat) have been so devastated by WNS (Langwig et al. 2012, Thogmartin et al. 2013), very little research has focused on why species such as Eastern Small-footed Myotis and Big Brown Bat have experienced significantly less mortality. Specifically, it is important to understand whether aspects of their ecology and behavior are minimizing their exposure to *P. destructans* or whether their hibernation phenology is protecting them from severe levels of WNS-related mortality. The results of this study are consistent with the assumption that these 2 species are utilizing small hibernacula within or adjacent to their summer foraging range. Small hibernacula, particularly rock crevices, are typically colder than large hibernacula and therefore maintain seasonal temperatures that are below the thermal optima needed for the growth of *P. destructans* (Verant et al. 2012). Our results also suggest that these 2 species are more active throughout the winter, and this higher rate of periodic arousal would allow the bats to groom more frequently, and thus, prevent germinating *P. destructans* conidia from invading into the dermis and developing into WNS (Moore et al. 2011). Coinciding this higher level of winter activity during periods of warm weather may also allow bats to rehydrate and replenish depleted fat reserves enough to survive the effects of WNS.

Despite the fact that overwinter survival is the dominant factor influencing population recruitment in hibernating bat species such as the Little Brown Bat (Frick et al. 2010), winter activity in hibernating bats is a poorly studied phenomenon. Data from NBAFS suggest that ambient temperature was the strongest predictor of winter bat-activity at the site, with both Eastern Small-footed Myotis and Big Brown Bat activity higher on warmer days. Although the temperature threshold identified by the model differed for the 2 species (12 °C and 3 °C, respectively), they both appeared to synchronize their arousal events with warmer weather. The lower temperature threshold observed for Big Brown Bat may be a function of their larger body size, which provides them additional insulation and allows them to store more body fat than myotine bats (Frank et al. 2014). Hibernating in shallow rock crevices with direct exposure to ambient conditions would simplify this synchrony and therefore maximize the benefits of the arousal event (Kokurewicz 2004).

Although there have been multiple studies of the physiology, energetics, and demography of hibernating bat species, there has been relatively little research on intraspecific and interspecific differences on where and how bats hibernate. In the context of WNS, the choice of where and how to hibernate has the potential to influence both individual and population-level survivorship, and ultimately determine whether a species becomes regionally extirpated. The results of this study support that both Big Brown Bats and Eastern Small-footed Myotis are hibernating in proximity to their summer habitat and are probably using nearby attics and rock crevices along Joe English Hill, respectively. These 2 species appear to be the least impacted by WNS of all hibernating bat species in the northeast (Langwig et al. 2012); thus, it is likely that using isolated hibernacula reduces their exposure to *P. destructans* and, therefore, accounts for the lower level of overwinter mortality.

The Big Brown Bat is one of the most abundant species in the northeast and within our study site at NBAFS. Our results show that Big Brown Bats remain active on the landscape well into November and likely hibernate in close proximity to the NBAFS. Historically, ecologists have focused their research on endangered and rare bats. However, after the appearance and rapid spread of WNS, more attention needs to be given to the Big Brown Bat because it plays a more dominant role in the ecosystem than any other bat species in terms of ecosystem services (Agosta 2002).

The Eastern Small-footed Myotis has been described as one of the rarest bats in North America (Best and Jennings 1997). Recent data, including from this study, suggest that the species is more abundant than previously estimated. Our lack of knowledge of Eastern Small-footed Myotis has been identified as a research priority in the eastern US for a decade (Barclay and Kurta 2007), but relatively little research has been focused on this species. The data we collected in the present study and related research at NBAFS represent one of the most comprehensive surveys of Eastern Small-footed Myotis conducted in the Northeast, and confirm the reliance of these bat populations on rocky habitat during both summer and winter. Eastern Small-footed Myotis distribution on the landscape is highly heterogeneous; thus, broad population surveys across random habitats, including summer acoustic transects (Whitby et al. 2014), are unlikely to accurately represent their abundance. Similarly, hoping to conserve and study this species as we manage endangered species such as Indiana Bat or Northern Myotis is unlikely to be successful because the 2 groups of species do not occupy similar core habitat. It is also becoming increasingly clear that winter hibernacula surveys do not provide an accurate estimate of their abundance because a significant proportion of Eastern Small-footed Myotis hibernate in isolated and unknown hibernacula. We hope that our surveys at NBAFS will increase awareness of the unique research and conservation challenges posed by the patchy distribution and reliance on rocky habitat of Eastern Small-footed Myotis populations.

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