

Post-white-nose syndrome passive acoustic sampling effort for determining bat species occupancy within the mid-Atlantic region

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ABSTRACT

We assessed the sampling effort requirements for detecting the presence of extant bat species following the impact of white-nose syndrome in the mid-Atlantic region of the United States. We acoustically sampled 27,796 nights across 846 sites between 15 May and 15 August 2016–2018 within the District of Columbia, Maryland, Pennsylvania, Virginia, and West Virginia. We developed simulations to determine the number of sites required to document bat species when each site was sampled different numbers of nights. We examined these simulations with respect to land cover, physiographic region, and time period. We generally found that sampling a greater number of sample sites within a survey area increased detection more than increasing the number of nights at individual sampling sites. The sampling effort required to detect a given bat species varied by species, as well as land-cover type and physiographic region. Our results suggest that land managers and researchers should use caution in using protocols developed with other objectives, e.g., the U.S. Fish and Wildlife Service endangered and threatened bat species and the North American Bat monitoring programs' methods are designed relative to their specific needs. Unfortunately, neither protocol may be adequate for accurately detecting bat communities within all mid-Atlantic areas.

1. Introduction

Since white-nose syndrome (WNS) was first observed in New York in 2006, evidence of the causative fungal agent, *Pseudogymnoascus destructans* has spread to 33 U.S. states and 7 Canadian provinces (U.S. Fish and Wildlife Service, 2019). In the District of Columbia (D.C.), Maryland, Virginia, and West Virginia, WNS has greatly reduced or locally extirpated Indiana (*Myotis sodalis*), little brown (*M. lucifugus*), northern long-eared (*M. septentrionalis*), and tricolored (*Perimyotis subflavus*) bat populations (Deeley et al., in press; Turner et al., 2011; Franci et al., 2012; Powers et al., 2015). Although the Indiana bat's U.S. Fish and Wildlife Service (USFWS) endangered status predates WNS, the USFWS listed northern long-eared bats as threatened based on WNS-caused declines (U.S. Fish and Wildlife Service, 2011), and the little brown and tricolored bats currently are undergoing a listing review.

Many research and monitoring efforts have moved from mist-netting approaches to use of passive acoustic techniques as ever-increasing mist-netting survey efforts are required to capture bats in light of population

declines (Coleman et al., 2014; Loeb et al., 2015; U.S. Fish and Wildlife Service, 2020). In bat communities affected by WNS, determining occupancy of rare species requires extended acoustic detector deployments at multiple sites (Coleman et al., 2014). Additionally, because landscape structure affects bat occupancy and activity within an area (Mills et al., 1996; Gehrt and Chelvig, 2003), habitat type may influence the number of sites required to reach the asymptote of bat species richness (Hourigan et al., 2010). In previous research, higher numbers of echolocation calls were recorded along forest edges and within uncluttered, open environments (Loeb and O'Keefe, 2006; Brooks, 2008; Jantzen and Fenton, 2013). In particular, big brown (*Eptesicus fuscus*), hoary (*Lasiurus cinereus*), and little brown bat echolocation calls have been positively associated with edges (Jantzen and Fenton, 2013). Echolocation calls from large-bodied bat species (big brown, hoary, and eastern red bats [*Lasiurus borealis*]) have been more frequently documented in open than in cluttered habitats (Ford et al., 2005; Loeb and O'Keefe, 2006; Brooks, 2008; Brooks et al., 2017). Conversely, calls from smaller-bodied, clutter-adapted species', such as the northern long-eared bat, are often

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recorded in closed-canopy forests (Ford et al., 2005; Starbuck et al., 2015). Large-scale bat acoustic surveys have identified some influence of urbanization and habitat fragmentation on community structure (Deeley et al., in press; Loeb and O'Keefe, 2006; Johnson et al., 2008; Loeb et al., 2009), and in some cases, it appears that broad-scale habitat features influence roost selection more than fine-scale habitat features (O'Keefe, 2009).

In the mid-Atlantic United States, the USFWS Indiana bat survey guidelines (U.S. Fish and Wildlife Service, 2020) and the North American Bat (NABat) monitoring program (Loeb et al., 2015) provide guidance on passive acoustic sampling methodologies for different objectives. USFWS Indiana bat survey guidelines are used to determine presence or absence of Indiana and northern long-eared bats prior to possible land management activities that may impact known or potential habitat, i.e., forest harvesting, prescribed burning, highway construction or mining, (U.S. Fish and Wildlife Service, 2020). The NABat program's primary objective is to track population indices of multiple species over broad temporal and spatial scales (Loeb et al., 2015).

Despite their different scales of interest, both protocols provide a recommended number of sampling sites and nights for bat surveys (Loeb et al., 2015; U.S. Fish and Wildlife Service, 2020). Within areas impacted by WNS, current USFWS guidance requires that for every 0.5 km² of a study area, 8 acoustic sample nights minimum should be distributed on ≥ 2 sites for non-linear management projects and 2 detector-nights per 1 km of linear habitat for activities such as highway construction (U.S. Fish and Wildlife Service, 2020). The NABat program recommends that 2–4 sites be sampled for 4 nights each within areas of up to 100 km² (Loeb et al., 2015). Additionally, both protocols provide recommendations as when to sample for bats in terms of time of year and weather conditions (Loeb et al., 2015; U.S. Fish and Wildlife Service, 2020).

Use of generic study designs are intended to allow comparisons among studies, but using the same methods across broad scales and different ecosystems can be uninformative for many research objectives (Lindenmayer and Likens, 2010). A survey should account for variable detectability by taking detection covariates into account or estimating detectability (Pollock et al., 2002; Meyer et al., 2011). In Switzerland, for example, Froidevaux et al. (2014) determined that the most effective acoustic sample design to document the entire bat community within a 1 km² area required sampling all microhabitats and that surveys restricted to small spatial extents or a single habitat type would fail to document the entire community.

In the context of these two widely-used bat monitoring standards, our intent was to provide insight into the impact of passive acoustic sample design on the detection of species of interest, based on commonly-used acoustic identification software. Our main objective was to identify the sample effort required to reliably document the presence of bat species in the mid-Atlantic region. We predicted that coarse sampling categories (e.g., physiographic region, land cover types) would impact the sample effort required to detect species. Our second objective was to determine how sample effort for the northern long-eared bat varied between areas with recent mist net capture records and the study area overall. For example, we expected that sample effort for the northern-long eared bat would be lower in areas with recent capture records than in the study area overall.

2. Material and methods

2.1. Study area

Data were collected from multiple research efforts with variable objectives and methods that acoustically surveyed for bats across 41 counties in 4 mid-Atlantic states and D.C., within 19 National Park Service (NPS) units, U.S. Army Ft. George G. Meade, and National Aeronautics and Space Administration Wallops Flight Facility (Fig. 1). Sites included highly-fragmented, agricultural areas in the Piedmont of southern Pennsylvania, Maryland, and Virginia; urban and suburban

NPS units within and surrounding D.C.; and montane contiguous, forested habitat within the Blue Ridge Mountains and Ridge and Valley regions (Fig. 1).

As northern long-eared bats are of particular interest regionally due to their conservation status, we identified areas with capture data that overlapped with our acoustic data. Female northern long-eared bats were captured within Prince William Forest Park (PRWI), Rock Creek Park (ROCR), Shenandoah National Park (SHEN), and Gettysburg National Battlefield (GETT) within the acoustic sampling periods (Deeley and Gorman, 2018; Kalen, 2018; Deeley et al., in press). These units consist of all habitat types described above: GETT (in Pennsylvania) is a highly-fragmented, agricultural area; both PRWI (in Virginia) and ROCR (in D.C.) are forested NPS units within urban and suburban landscapes, and SHEN spans a large portion of Virginia's rural mountains (Fig. 1).

2.2. Data collection and preparation

We sampled 846 sites within the study area from 2016 to 2018 (between 15 May and 15 August), in accordance with USFWS time-of-year recommendations for northern long-eared bat surveys (Fig. 1; U.S. Fish and Wildlife Service, 2018). Acoustic sites in PRWI were within 10 km proximity and spread across the unit, including areas with northern long-eared bat captures and roosts (Deeley et al., in press; Fig. 1). Acoustic sites in ROCR were all within 10 km of each other, with most sites within a 1-km² area of northern long-eared bat captures and roosts (Deeley et al., in press; Fig. 1). The SHEN sites spanned almost 80 km, including the portions of the park with 2016 northern long-eared bat captures (Kalen, 2018; Fig. 1).

We used frequency division/zero-crossing SongMeters (ZC, 2+, 3, and 4) and full-spectrum SongMeter 4 acoustic recorders (Wildlife Acoustics, Inc., Concord, MA, USA¹) programmed to record, at a minimum, from sunset to sunrise to collect bat echolocation calls. Due to individual project criteria, sample site selection and sampling duration at each site varied greatly within and between years. Most sites were within forest, forest edge, and wetland habitats, but some sites were within open habitat (e.g., agricultural fields). To improve the probability of recording bat calls, we placed the omnidirectional detector microphones on 3.66 m high telescoping poles that were >3 m from any tree bole (Loeb et al., 2015), except for sites in central Virginia, where they were tree-mounted.

To identify echolocation pulses to species, we used the Kaleidoscope 4.5.0 Bats of North America 4.2.0 classifier (Wildlife Acoustics, Inc., Concord, MA, USA) per USFWS standards (Ford, 2017). Automatic software species identification is imperfect, particularly with identifying *Myotis* species (Lemen et al., 2015; Russo and Voigt, 2016; Custer et al., 2017; Ford, 2017; Austin et al., 2019; Nocera et al., 2019). However, the software provides a level of repeatability in analysis that visual verification does not (Nocera et al., 2019). Given that automatic software identifications are being used in agency assessments (Loeb et al., 2015; U.S. Fish and Wildlife Service, 2020), acoustic software misclassifications are congruent with error rates that would be observed in other acoustics-based survey work. For our purposes of identifying relative sampling efforts, we used the software-provided nightly maximum likelihood estimate (MLE) value < 0.05 as the acceptance threshold to determine nightly presence of bat species at each site, thereby attempting to control for false positive identifications (U.S. Fish and Wildlife Service, 2020).

Temperature, wind, and precipitation can impact acoustic detection rates, whether by affecting equipment or reducing bat activity, as inclement weather is associated with reduced prey availability and increased energetic requirements to maintain body temperature (Erickson and West, 2002; Voigt et al., 2011; Muthersbaugh et al.,

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

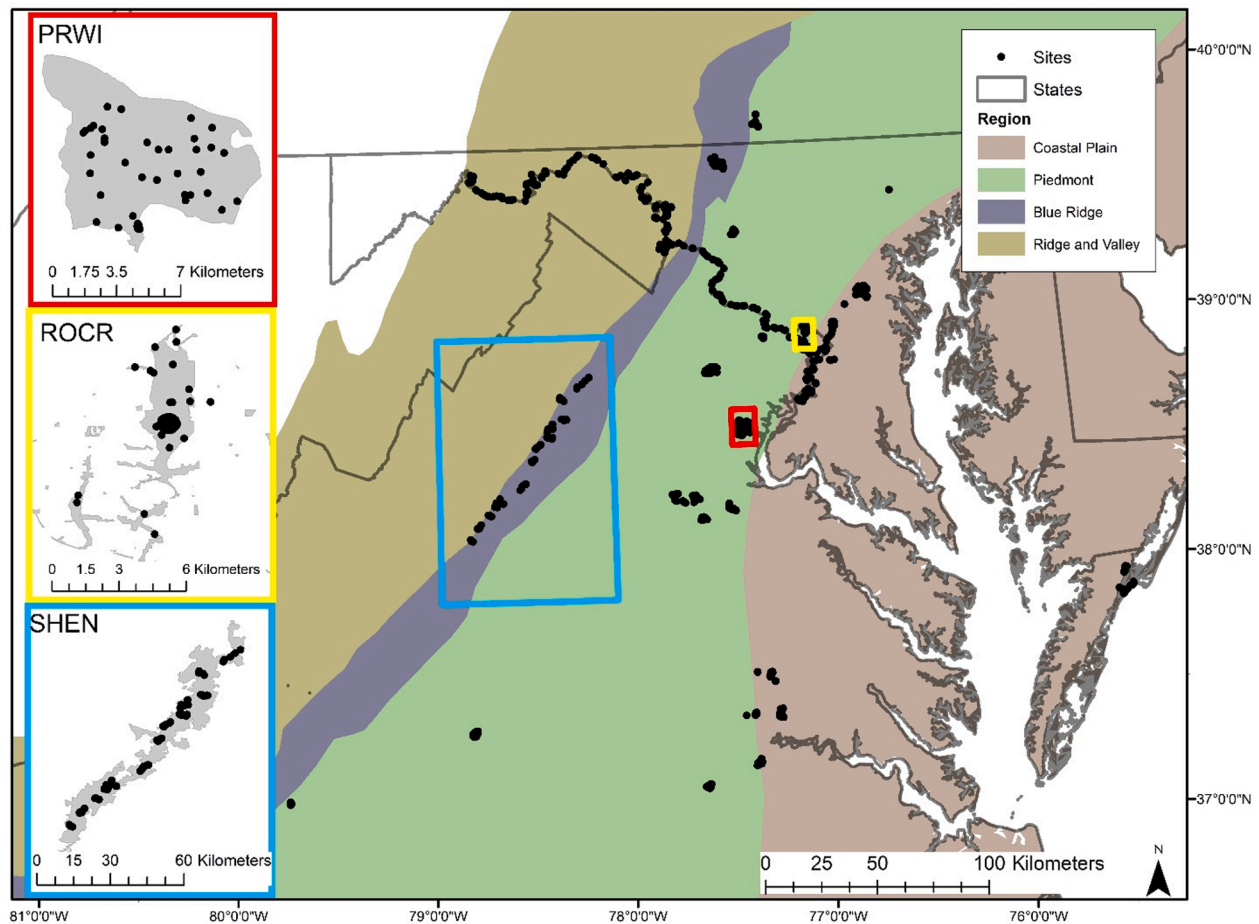


Fig. 1. Passive bat acoustic survey sites within 41 counties in the District of Columbia, Maryland, Pennsylvania, Virginia, and West Virginia, 2016–2018. Sample areas include 21 National Park Service, U.S. Fish and Wildlife Service, Department of Defense, and National Aeronautics and Space Administration lands units and four physiographic regions (Coastal Plain, Piedmont, Blue Ridge, and Ridge and Valley). Insets contain sites on National Park Service (NPS) parks where northern long-eared bats were captured: a) Prince William Forest Park, Virginia; b) Rock Creek Park, District of Columbia; and c) and Shenandoah National Park, Virginia. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2019). USFWS guidelines stipulate that sampling should not occur during precipitation or temperatures $<10^{\circ}\text{C}$ during the first five hours of the survey (U.S. Fish and Wildlife Service, 2020). Because of the potential for these factors to influence bat activity, we identified samples that may have received precipitation and/or had minimum temperatures $<10^{\circ}\text{C}$ (PRISM Climate Group, 2019). Because these nightly weather data included 24-hour data from the afternoon prior to through the morning after a sample event, our exclusion criteria likely excluded more samples than needed.

To determine whether broad- or fine-scale habitat categorization would influence the sample effort required to detect species, we associated sites with physiographic region and land-cover type (U.S. Geological Survey, 2004; Fig. 1). We selected physiographic region and land-cover type as examples of general but environmentally-meaningful categories on which researchers or government agencies could base sample effort. In this sample area, physiographic region was also a coarse surrogate for urbanization, fragmentation, and landscape features. Generally, elevation and proximity to karst decreased while urbanization and forest fragmentation increased along a west-east gradient across physiographic provinces. Based on field observations at each site, we determined if a site was in a forest stand, wetland (i.e. within a wetland or adjacent to a water body), edge (along a forest stand with one side exposed to open fields or developed area), or open area. We categorized sites that were identified as wetland and any another land-cover type as being wetland.

2.3. Simulations

Species with historic distribution within the entire study area include big brown bat, eastern red bat, hoary bat, silver-haired bat (*Lasionycteris noctivagans*), little brown bat, northern long-eared bat, Indiana bat, and tricolored bat (Whitaker and Hamilton, 1998; St. Germain et al., 2017). We note that despite a large number of netting events within the study region, Indiana bats have been confirmed at only one location in the region via mist-netting, i.e., at Fort A.P. Hill in Caroline County, Virginia on the Piedmont-Coastal Plain Fall Line (St. Germain et al., 2017). To determine the sample effort required to document each species, we developed simulations based on species accumulation curves (SACs; Fig. 2). We conducted all SACs with the Program R *vegan* package using random sampling and 100 permutations (Oksanen et al., 2015). Each species accumulation curve calculated the number of species a researcher would expect to find based upon the numbers of sites sampled.

Each simulation consisted of combining results from multiple SAC iterations: the mean number of species, standard deviation and standard error of species richness per site (Step 3 in Fig. 2). For each SAC iteration, we randomly selected n nights (where n was between 1 and 60) within each site and combined all n nightly species detections to create new site-level presence or absence values (Fig. 2). For example, when $n = 3$, we randomly selected 3 nights out of all nights a site was sampled and determined whether the species of interest was present or absent within those 3 nights.

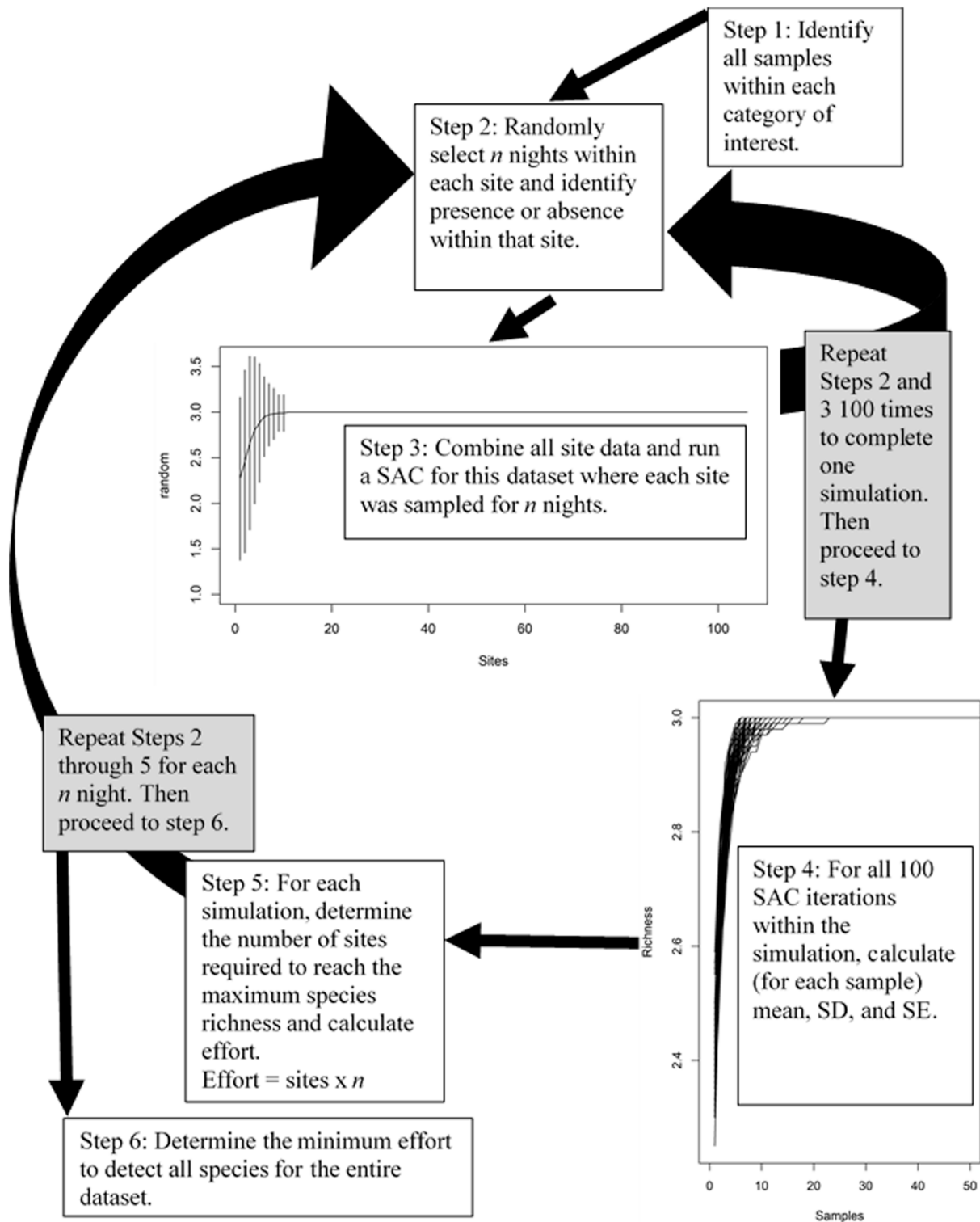


Fig. 2. Conceptualization of the simulation process used to identify the number of sites required to detect a bat species within the mid-Atlantic region when each survey site is sampled a particular number of nights. Abbreviations include SAC = species accumulation curve, SD = standard deviation, SE = standard error.

We created a new dataset of these site-level presence or absence values, where each site was sampled for n nights. We ran the SAC based on this dataset. We repeated the random night selection within each site and calculation of a SAC 100 times for each n , documenting mean and standard error of species richness for each iteration.

For each n simulation, we determined the effort (sites \times nights) required to detect the species of interest. As SACs require the presence of

at least 2 species within a sample community to run, we added 2 “dummy” species that were present within each sample. Therefore, detection of 1 species of interest was indicated by the accumulation of 3 species. We used effort until detection (number of sample sites where all SACs accumulated to 3 species) as a surrogate measure of sampling effort across categories. Minimum sample effort was the lowest effort value(s) for all n simulations, excluding n simulations where mean

Table 1

Passive acoustic sample nights between Julian days 135 and 227, 2016–2018, wherein bat echolocation data were recorded. Samples were collected in the District of Columbia, Maryland, Pennsylvania, Virginia, and West Virginia and only included nights with no precipitation and minimum nightly temperatures $>10^{\circ}\text{C}$.

		Samples within each land cover type				Sites
		Edge	Forest	Open	Wetland	
Samples within each physiographic region	Coastal Plain	227	1339	118	459	122
	Piedmont	460	6507	257	1214	180
	Blue Ridge	125	1999	320	347	135
	Ridge and Valley	64	630	143	220	408
Sites		80	523	72	170	

species <3 and detection was not reached within every simulation.

We conducted a study area-wide simulation with all sampled nights. With the truncated dataset of only samples with no precipitation and temperatures $\geq 10^{\circ}\text{C}$, we ran simulations for the entire study area and for each physiographic region and land-cover type sampled. To evaluate northern long-eared bat detectability within areas with recent captures, we also ran simulations for northern long-eared bats within PRWI, ROCR, and SHEN. We did not run the area simulation for GETT based on low sample size. To determine whether samples collected in the earliest and latest sampling days impacted detection of the northern long-eared bat, we conducted simulations for each NPS unit and based on USFWS and NABat guidance ideal sampling periods: 1 June–1 August, after 1 June (i.e. 1 June–15 August), and before 1 August (i.e. 15 May–1 August).

To further explore detection of northern long-eared bats, we used the *unmarked* package in R to run single-season occupancy models in PRWI, ROCR and SHEN for northern long-eared bats (Fiske and Chandler, 2011). One model included only nights within acceptable USFWS weather conditions and the other included all nights. We used null models to calculate the probability of detection (p) for northern long-eared bats, which was the ability of the survey to detect the true presence of a species.

3. Results

Between 15 May and 15 August, we collected data on 27,796 sample nights (2016 = 5063; 2017 = 10,159; 2018 = 12,574). We recorded big brown bat calls on 12,010 nights; eastern red bats on 7007 nights; hoary bats on 5542 nights; silver-haired bats on 4076 nights; little brown bats on 3750; northern long-eared bats on 2749; Indiana bats on 1260 nights; and tricolored bats on 3994 nights. We identified 14,429 sample nights (2016 = 2657, 2017 = 5573, 2018 = 6199) without precipitation and temperatures $\geq 10^{\circ}\text{C}$ (Table 1). We recorded 6834 nights with acoustic observations of big brown bats; 4038 nights with eastern red bats; 3131 nights with hoary bats; 2270 nights with silver-haired bats; 2088 nights with little brown bats; 1513 nights with northern long-eared bats; 654 nights with Indiana bats; and 2287 nights with tricolored bats. As most sites were sampled <15 nights, we determined that including simulations ≥ 15 nights introduced spatial biases. We note that some PRWI, ROCR and SHEN temporal simulations ran <14 nights due to sample size.

At PRWI, we sampled 36 sites (mean nights per site = 37.3 ± 1.7 ; Table 2). We sampled 29 nights along edges; 1101 nights in forests; and 214 nights in wetlands. Northern long-eared bats were present in 114 sample nights (8.5%). Within ROCR, we sampled 119 sites, with a mean of 37.5 ± 1.3 nights per site (Table 2). We sampled for 18 nights along edges; 4107 nights in forest; 57 nights in open areas and 276 nights in or near wetlands. Northern long-eared bats were present within 526 sample nights (11.8%). For SHEN, data included 76 sites, with a mean of 31.37 ± 3.2 nights per site (Table 2). We sampled for 341 nights in or near wetlands; 102 nights along edges; 1666 nights in forest; and 275 nights in open areas. Northern long-eared bats were present in 664 sample nights (11.3%).

Generally, the minimum effort to detect a species occurred when many sites were sampled for 1 night each. Increasing the number of nights sampled at each site did not linearly decrease the number of sites required, and increasing the number of sample nights per site did not increase the detection of all species similarly. In simulations comparing the number of sites required to detect species within the entire study area, the minimum effort required to detect any species was the big brown bat with 15 sites sampled for 1 night each (Table 3). The study area simulations indicated that the inclusion of nights with precipitation or low temperatures had little to no impact on detecting the most common species (big brown and eastern red bats). Increasing the number of nights sampled decreased the impact of precipitation and low temperature samples for hoary, and silver-haired bats (Table 3). The all-weather models required more individual survey sites for northern long-eared bats but fewer for Indiana bats (Table 3). Some species, such as the little brown and Indiana bat, had increases in the number of sites as the number of nights increased that likely reflected the inclusion of more poor-weather nights or perhaps the exclusion of sites with a low number of sample nights.

Land cover type did appear to impact the number of site-nights required to detect species (Table 4). For most species, the highest effort occurred within forest areas and the lowest effort within open areas (Table 4). However, land-cover type had minimal influence on big brown bat detection. Edge and open site categories tended to require similar minimum efforts for detecting eastern red, hoary, silver-haired, little brown, and tricolored bats (Table 4). Open sites required the least effort for Indiana and northern long-eared bats, followed by wetland for northern long-eared bats and edge for Indiana bats (Table 4).

Physiographic region influenced the minimum effort required to

Table 2

Passive acoustic sample sites and nights between 15 May and 15 August 2016–2018, wherein bat echolocation data were recorded at three areas where northern long-eared bats (*M. septentrionalis*) were captured. We identified samples as falling between or outside 1 June and 1 August (Julian day [JD] 152–213), after 1 June (JD 152), or before 1 August (JD 213). Samples include only nights with no precipitation and minimum nightly temperatures $>10^{\circ}\text{C}$ and include sites within the National Park units of Prince William Forest Park (PRWI), Virginia; Rock Creek Park (ROCR), District of Columbia; and Shenandoah National Park (SHEN), Virginia.

Area	Covariate	Category	Sites	Samples
PRWI	JD 152–213	Between	36	1122
		Outside	31	222
ROCR	JD 152–213	After	36	1224
		Before	36	1242
		Between	119	3322
		Outside	105	1136
SHEN	JD 152–213	After	119	3793
		Before	199	3987
		Between	64	1824
SHEN	JD 152–213	Outside	59	560
		After	71	2243
		Before	69	1965

Table 3

Minimum number of acoustic sampling sites required to detect bat species when each site was sampled between 1 and 14 nights. Samples were collected Julian days 135 to 227 in 2016–2018 within the District of Columbia, Maryland, Pennsylvania, Virginia, and West Virginia. Calls were identified to species by using the Kaleidoscope 4.5.0 Bats of North America 4.2.0 classifier (Wildlife Acoustics Inc., Concord, MA, USA) with the following species: big brown bat (*Eptesicus fuscus*; EPFU), eastern red bat (*Lasiurus borealis*; LABO), hoary bat (*Lasiurus cinereus*; LACI), silver-haired bat (*Lasionycteris noctivagans*; LANO), little brown bat (*Myotis lucifugus*; MYLU), northern long-eared bat (*Myotis septentrionalis*; MYSE), Indiana bat (*Myotis sodalis*; MYSO), and tricolored bat (*Perimyotis subflavus*; PESU). Abbreviations are: N = no precipitation and minimum nightly temperatures > 10C and All = All data.

Nights	EPFU		LABO		LACI		LANO		MYLU		MYSE		MYSO		PESU	
	N	All	N	All	N	All	N	All	N	All	N	All	N	All	N	All
1	15	15	23	26	32	27	49	62	51	65	133	162	153	135	43	52
2	13	18	16	19	27	22	33	29	31	31	76	81	93	109	32	27
3	10	11	14	16	16	16	33	28	30	24	60	79	79	88	24	19
4	10	9	13	13	17	20	18	26	28	24	44	77	91	71	19	22
5	8	9	13	11	16	14	17	23	24	21	44	58	67	64	19	22
6	6	8	12	10	14	11	18	17	17	17	36	43	60	55	18	14
7	8	7	10	8	11	11	14	18	19	18	27	33	61	46	13	14
8	7	7	10	9	9	10	16	18	17	19	27	38	61	47	12	12
9	6	7	9	10	13	11	14	14	19	15	26	30	50	40	10	13
10	7	6	13	8	11	11	15	15	17	14	17	35	50	48	11	11
11	5	6	10	11	7	12	13	12	15	14	23	24	53	39	13	10
12	6	6	11	10	10	9	13	14	16	15	16	26	45	45	10	10
13	6	6	12	10	9	7	15	11	14	17	16	19	62	32	9	11
14	5	6	8	9	7	7	12	12	13	17	12	17	50	39	14	10

Table 4

Minimum sampling effort (sites × nights) required to detect each bat species for the entire study area within different land-cover types and physiographic regions. Some categories included two minimum sampling efforts. Data were collected with passive acoustic sampling from 2016 to 2018 within the District of Columbia, Maryland, Pennsylvania, Virginia, and West Virginia. Values are derived from simulated sampling of sites between 1 and 15 nights. Calls were identified to species by using the Kaleidoscope 4.5.0 Bats of North America 4.2.0 classifier (Wildlife Acoustics Inc., Concord, MA, USA) with the following species: big brown bat (*Eptesicus fuscus*; EPFU), eastern red bat (*Lasiurus borealis*; LABO), hoary bat (*Lasiurus cinereus*; LACI), silver-haired bat (*Lasionycteris noctivagans*; LANO), little brown bat (*Myotis lucifugus*; MYLU), northern long-eared bat (*Myotis septentrionalis*; MYSE), Indiana bat (*Myotis sodalis*; MYSO), and tricolored bat (*Perimyotis subflavus*; PESU).

Species	Land cover type				Physiographic Region			
	Forest	Open	Wetland	Edge	Coastal Plain	Piedmont	Blue Ridge	Ridge and Valley
EPFU	14 × 1	14 × 1	13 × 1	16 × 1	14 × 1	14 × 1	16 × 1	19 × 1
LABO	25 × 1	10 × 1	23 × 1	12 × 1	20 × 1	23 × 1	24 × 1	15 × 1
LACI	42 × 1	13 × 1	38 × 1	16 × 1	45 × 1	39 × 1	21 × 1	25 × 1
LANO	38 × 2	15 × 1	46 × 1	16 × 1	26 × 1	56 × 1	51 × 1	49 × 1
MYLU	50 × 1	26 × 1	43 × 1	31 × 1	41 × 1	58 × 1	31 × 1	22 × 1
MYSE	119 × 1	49 × 1	92 × 1	80 × 2	103 × 3	157 × 1	37 × 1	135 × 1
MYSO	225 × 1	33 × 1	118 × 1	80 × 1	173 × 1	220 × 1	49 × 1	84 × 1
PESU	51 × 1	33 × 1	30 × 1	36 × 1	51 × 1	52 × 1 / 26 × 2	47 × 1	34 × 1 / 17 × 2

detect every species (Table 4). Big brown bats required more effort in the Ridge and Valley where eastern red bats required the smallest effort (Table 4). For hoary, little brown, Indiana, northern long-eared, and tricolored bats, the least effort needed for detection was within the Ridge and Valley and Blue Ridge Mountains (Table 4). Silver haired bats were most readily detected within the Coastal Plain.

Sample effort required to detect northern long-eared bats in the entire study area was higher than in PRWI, ROCR, and SHEN individually, areas where their presence was confirmed with mist-netting captures (Tables 3 and 5). Far less sample effort was required to detect northern long-eared bats in SHEN than either PRWI or ROCR (Table 5). PRWI and ROCR required almost three times as many sites as SHEN to detect northern long-eared bats with 8 nights per site (Table 5). Though sample period influenced minimum efforts for all three locations, ROCR and SHEN had similar minimum efforts (<=10 site-nights differences; Fig. 3). Because of the long sampling periods at many sites at SHEN, PRWI, and ROCR, we had high naïve occupancy. Naïve occupancy was higher in the entire dataset (SHEN = 0.92, PRWI = 0.75, and ROCR = 0.86) than in the dataset with precipitation and low temperature (SHEN = 0.88, PRWI = 0.67, and ROCR = 0.82). The probability of detection estimates were lower for the models including all samples versus those excluding precipitation and low temperatures models (SHEN = 0.25, 0.29; PRWI = 0.08, 0.12; and ROCR = 0.10, 0.12).

4. Discussion

Unsurprisingly, the sampling effort required to detect individual species varied greatly. Our finding that forested sites required higher sampling effort for most species may be due to issues with forest clutter impacting detection (Loeb et al., 2015), software misclassifications (Ford, 2017), or that forest was the most common land cover type sampled. The breadth of the forest habitat category in our study area may be concealing pertinent habitat features that may have influenced detection or reflect habitat use, such as stand composition, structure, and terrain of forested sites. The lower effort required to document northern long-eared bats during our study in open areas was unexpected, as they are typically associated with closed canopy forest, forest riparian or forest/edge habitats (Caceres and Barclay, 2000; Owen et al., 2003, 2004; Ford et al., 2005).

Even within areas of known northern long-eared bat presence, the number of sample nights required to detect this rare species was highly variable. For example, in simulations involving 4 nights of effort per site, ROCR required twice the number of sites as SHEN, and occupancy model detection probabilities for SHEN were over twice as high as within ROCR. Perhaps disconnects between acoustic and netting results emanate from their spatial context: PRWI and ROCR are smaller, mostly-contiguous forests surrounded by urban and suburban landscape, whereas SHEN has a greater diversity of terrain and is surrounded by other contiguous forests. If northern long-eared bats' roosting and

Table 5

Number of sample sites required to detect northern long-eared bat (*Myotis septentrionalis*), when each site is sampled for 1 to 14 nights, based on simulated species accumulation curves. Simulations were based on passive acoustic data collected in the District of Columbia, Maryland, Pennsylvania, Virginia, and West Virginia, 2016–2018. Simulations in which not all runs detected northern long-eared bats include the mean and standard deviation (SD). Abbreviations are: Prince William Forest Park (PRWI), Rock Creek Park (ROCR) and Shenandoah National Park (SHEN).

Nights	PRWI	PRWI mean (SD)	ROCR	SHEN	Forest	Open	Wetland	Edge	Edge mean (SD)	Coastal plain	Coastal Plain mean (SD)	Piedmont	Blue Ridge	Ridge and Valley
1	36	2.98 (±0.14)	65	26	119	49	92	80	2.73 (±0.44)	180	2.99 (±0.01)	157	37	135
2	34		43	13	90	33	81	80		166	3	85	25	94
3	28		27	11	51	29	52	71	2.88 (±0.33)	103	3	67	24	65
4	27		23	12	49	27	50	64	2.94 (±0.24)	93	3	48	18	65
5	27		18	9	41	29	45	57	2.97 (±0.17)	96	3	43	14	69
6	19		17	9	28	31	41	50	3	73	3	33	16	47
7	21		16	8	26	25	26	43	3	60	3	32	14	34
8	17		16	6	21	18	27	33	3	54	3	25	10	20
9	17		13	8	20	17	23	28	2.94 (±0.24)	57	3	21	10	20
10	18		11	6	14	15	22	23	2.99 (±0.10)	58	3	19	9	18
11	14		10	6	16	15	17	18	3	38	3	17	9	17
12	14		11	6	14	12	15	12	2.88 (±0.33)	39	3	16	6	18
13	13		10	6	14	12	13	12	2.92 (±0.27)	35	3	14	7	16
14	14		7	5	11	12	12	12	2.93 (±0.26)	30	3	15	7	17

foraging options are bounded by surrounding urban and suburban habitat, capture rates may be higher in PRWI and ROCR, even if populations are similar or smaller than in the SHEN landscape overall. Relatedly, we cannot discount sampling bias, as PRWI and ROCR sites were much closer in intra-park proximity than many sites within SHEN, which may have impacted detection. Again, bat community compositions (i.e. eastern small-footed bat [*Myotis leibii*] prevalence at SHEN) may be leading to disproportionate misclassifications of echolocation calls or calculations of MLEs (Lemen et al., 2015; Russo and Voigt, 2016; Kalen, 2018; Nocera et al., 2019), which should be another consideration for sample design.

The high variance in minimum effort to detect individual bat species highlights the importance of researchers developing *a priori* determination of relative detectability with the intended survey methods and species of interest's rarity and habitat associations. Comparing acoustics, mist-netting, and day-roost observations in West Virginia, Ford et al. (2016) found that modeled northern long-eared bat habitat associations greatly differed based on the presence-only data collection techniques. In Australia, combinations of survey designs worked best to document the entire bat community (Meyer et al., 2011). European bat monitoring guidelines provide species-specific sampling methodology (Battersby, 2010).

Additionally, surveys with sample sizes too small to detect low densities can lead to incorrect conclusions about habitat associations (Kunin and Gaston, 2012; Moll et al., 2016). Bat species that were common throughout much of the eastern United States but have since experienced large population declines due to WNS, such as the northern long-eared bat, may have very low acoustic detection rates because they can occupy many habitat conditions. As habitat availability is likely no longer a limited factor following WNS declines, high sampling effort may be required to identify remnant and very patchily distributed populations.

We found that the sampling effort required to detect a species within an area, is lower when several sites are surveyed for few nights versus sampling fewer sites for more nights. This conclusion is well documented in other evaluations of survey design (Mackenzie and Royle, 2005; Fischer et al., 2009; Froidevaux et al., 2014; Andersen and Steidl,

2019; Luymes and Chow-Fraser, 2019). Financial and logistical calculations for increases in sites versus nights can be used to determine optimal survey effort (Froidevaux et al., 2014; Tarugara et al., 2019); although impacts upon detection within naïve surveys would be unknown, power estimates based on variable detection may aid in survey design (Guillera-Aroita and Lahoz-Monfort, 2012).

Our analyses emphasize that the USFWS and NABat protocols were designed with specific objectives that may not align with all research or management objectives. The intent of USFWS regulatory requirements is to detect Indiana or northern long-eared bats once within an area (U.S. Fish and Wildlife Service, 2020), not to determine habitat associations or parameterize occupancy models based on site-level data. The NABat program uses call-level data (not MLE) to determine total bat activity as a surrogate for species abundance and to track bat population trends over broad spatial and temporal scales not site-level or area-level presence (Loeb et al., 2015). If researchers were using these standards to evaluate occupancy within finer scales, they may miss some species detections. For example, for northern long-eared bats, our results indicate that sampling for 4 nights at 4 sites would be inadequate within PRWI, ROCR, and SHEN, where mist-net captures had verified presence in years where sampling occurred.

If researchers are basing survey methods on USFWS regulatory guidelines (U.S. Fish and Wildlife Service, 2020) or NABat minimum survey requirements (Loeb et al., 2015), our simulations indicate that their results may be biased based on sample location choice (e.g., not sampling within open areas, per USFWS guidelines), assuming that equal effort will have equal detection (e.g., directly comparing community results from different regions), or biased against rare species (e.g., by not sampling enough sites and/or nights within an area). Location-specific detectability also must be incorporated into sample design, especially for rare species; otherwise, combining data across a large geographic range could contain large biases that limit inference (Meyer et al., 2011; Meyer, 2015). Our simulations indicate that USFWS-mandated Indiana bat surveys or NABat recommended sampling may not require enough sample sites to detect the full suite of rare species in certain recording conditions, and our occupancy model detection values indicate that 8 sampling nights per site would likely still not be adequate

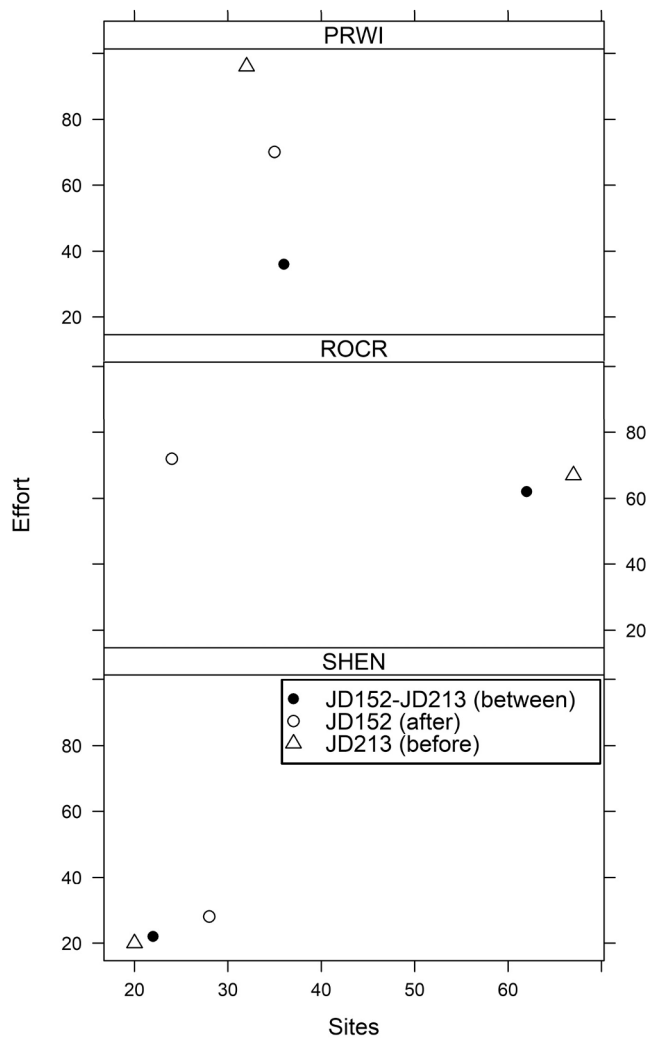


Fig. 3. Minimum sampling effort (sites \times nights) and number of sites required to detect northern long-eared bats (*Myotis septentrionalis*) within Prince William Forest Park (PRWI), Virginia; Rock Creek Park (ROCR), District of Columbia; and Shenandoah National Park (SHEN), Virginia. Samples were collected 15 May–15 August (JD 135–227), 2016–2018 and include nights with no precipitation and minimum nightly temperatures $>10^{\circ}\text{C}$. We identified samples as falling between 1 June and 1 August (Julian day [JD] 152–213), after 1 June (JD 152), or before 1 August (JD 213). Y-axes are the total effort (sites \times nights) and x-axes are the total number of sites needed to achieve the minimum effort for each simulation 1 to 60 nights for ROCR and SHEN. Calls were identified to species by using the Kaleidoscope 4.5.0 Bats of North America 4.2.0 classifier (Wildlife Acoustics Inc., Concord, MA, USA).

to eliminate false absences in areas of known northern long-eared bat presence. In the context of our intensive surveys of areas of known northern long-eared bat presence, a naïve acoustic survey would likely require even more sites than the simulations recommend.

5. Conclusions

The USFWS and NABat survey guidelines were developed with specific objectives that may not align with land manager or research objectives, with suitability dependent on bat species of interest, study area, and analysis or objective. Surveyors should ensure that they are accounting for variable detection based on the features of the study area and habitat use of the species of interest. Additionally, we suggest that acoustic bat surveys optimize effort by adding sites versus adding additional nights at individual sites.

Declaration of Competing Interest

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

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