Articles

Sampling Duration and Season Recommendations for Passive Acoustic Monitoring of Bats after White-Nose Syndrome

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Abstract

Since 2006, white-nose syndrome has caused drastic declines in populations of several hibernating bat species throughout eastern North America. Thus, there is a growing need to establish long-term monitoring programs to assess changes in bat populations over time. Information on the seasonal timing of species occurrence and the sampling effort required to acoustically detect individual bat species and obtain complete inventories will enable researchers to design and implement more effective monitoring programs. From April to October 2018 to 2021, we passively sampled for bats using full-spectrum detectors at eight permanent sites at Fort Indiantown Gap National Guard Training Center, Pennsylvania. We examined seasonal activity patterns and estimated bat species richness among sites and seasons using species accumulation curves. We also estimated probability of detection (p) and site occupancy (Ψ) using single-season occupancy models in PRESENCE software and then determined the minimum number of sampling nights needed to reliably infer the absence of each species. We identified 286,131 bat passes of eight species in 4,107 detector-nights. Seasonal patterns of activity varied among species. We needed approximately 20 sampling nights to detect 90% of the total bat species richness among sites, and we needed 4 to 10 nights to detect 90% of species richness among seasons. We needed relatively few nights ($\leq$12 nights) to detect most species during summer; however, we needed many more nights to detect acoustically rare species. Our results indicate that the acoustic sampling effort currently required to determine the presence or probable absence of Indiana myotis *Myotis sodalis*, northern long-eared myotis *M. septentrionalis*, and tricolored bats *Perimyotis subflavus* during summer may not be adequate for these species in some areas and that a considerable level of effort ($>$40 nights) is needed to detect little brown myotis *M. lucifugus*. Monitoring programs that incorporate efficient sampling methodologies will be critical for future conservation efforts as populations of several bat species continue to decline.

Keywords: bat detector; passive acoustic monitoring; sampling effort; species accumulation curves; white-nose syndrome

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Introduction

White-nose syndrome (WNS) is an emergent infectious disease of hibernating bats caused by the invasive fungal pathogen *Pseudogymnoascus destructans* (*Pd*; Lorch et al. 2011; Warnecke et al. 2012). Since it was first observed in New York in 2006 (Blehert et al. 2009), WNS has caused unprecedented declines in populations of several hibernating bat species throughout eastern North America (Thogmartin et al. 2012; Ingersoll et al. 2016; Cheng et al. 2021), threatening some species with regional extinction (Frick et al. 2010) and leading to shifts in species abundance and community structure (Moosman et al. 2013; Hauer et al. 2019; O'Keefe et al.

2019; Deeley et al. 2021a; Reynolds et al. 2021; Perry and Jordan 2022). In Pennsylvania, WNS became widespread by 2012 (Heffernan and Turner 2016), and winter counts of all hibernating bat species at known, large hibernacula declined by 99% (PGC 2014). Currently, 12 hibernating bat species have been confirmed with WNS in 40 of the U.S. states and 8 Canadian provinces (WNS Response Team 2023).

In April 2015, the U.S. Fish and Wildlife Service (USFWS) listed the northern long-eared myotis *Myotis septentrionalis* as threatened under the U.S. Endangered Species Act (ESA 1973, as amended), largely due to WNS-induced declines (USFWS 2015). More recently, the northern long-eared myotis was reclassified as endangered under the U.S. Endangered Species Act (ESA 1973) since WNS continues to spread across the species' range (USFWS 2022a). The tricolored bat *Perimyotis subflavus* was also recently proposed for federal listing as endangered (USFWS 2022b), and the little brown myotis *M. lucifugus* is currently undergoing a discretionary status review (USFWS 2022c) to determine if listing is warranted under the U.S. Endangered Species Act (ESA 1973).

Declines in bat populations have led to a greater reliance on acoustic survey methods, as traditional capture surveys (i.e., mist netting) have become increasingly costly and time consuming (Coleman et al. 2014). Acoustic surveys provide a noninvasive, cost-effective method for monitoring bats (Ford et al. 2011; Sugai et al. 2018), and recent technological advancements in ultrasound detectors and automated call identification software have made acoustic surveys more feasible (Parsons and Szewczak 2009; Frick 2013). Passive acoustic monitoring, which involves the deployment of detectors to automatically record bat echolocation calls in the absence of a researcher (Britzke et al. 2013; Fraser et al. 2020), allows for the collection of extensive datasets at large spatial and temporal scales (Froidevaux et al. 2014) and often results in higher species richness and detection probabilities than mist netting (Murray et al. 1999; O'Farrell and Gannon 1999) or other acoustic methods (Tonos et al. 2014; Teets et al. 2019). Data from passive acoustic monitoring of bats have been used to document activity patterns (Stahlschmidt and Bruhl 2012; Adams et al. 2015; Muthersbaugh et al. 2019b), estimate species richness (Skalak et al. 2012; Froidevaux et al. 2014; Barnett and Collins 2019) and occupancy rates (Baumgardt et al. 2022), and document population declines due to WNS (Dzal et al. 2011; Nocera et al. 2019; Reynolds et al. 2021). However, few studies have examined the sampling effort needed to detect different bat species and evaluate the completeness of acoustic inventories (Milne et al. 2004; Skalak et al. 2012; Lopez-Baucells et al. 2021), particularly in areas impacted by WNS (Deeley et al. 2021b).

In the eastern United States, USFWS survey guidelines are used to determine the presence or probable absence of Indiana myotis *M. sodalis*, northern long-eared myotis, and tricolored bats during the summer active season (15 May to 15 August; USFWS 2023). The sampling effort required to document the presence or absence of these species was derived using probability of detection (p) and site occupancy (Ψ) estimates from acoustic studies throughout the species' ranges (Niver et al. 2014; Armstrong et al. 2022). Currently, the USFWS requires a minimum of 4 detector-nights per 1 km of linear habitat for all three species, 10 detector-nights per 0.5 km^2 of nonlinear habitat for Indiana myotis, and 14 detector-nights per 0.5 km^2 of nonlinear habitat for northern long-eared myotis and tricolored bats (USFWS 2023). Additional occurrence data may help to refine existing survey guidelines for these species and inform similar guidelines for little brown myotis if the species becomes federally listed under the U.S. Endangered Species Act (ESA 1973) in the future.

Military installations can serve as important conservation areas for threatened and endangered species (Boice 2006; Stein et al. 2008; Zografou et al. 2017). Installations are required to monitor the effects of training activities to ensure compliance with federal regulations for endangered species management (Durant 2010) and thus have the potential to support long-term population monitoring efforts for bats (Ford et al. 2011; Nocera et al. 2020; Reynolds et al. 2021). Information on the seasonal timing of species occurrence and the level of sampling effort necessary to detect target bat species and completely inventory bat assemblages will enable researchers to design and implement more effective monitoring programs, especially when resources are limited and rare or declining species are expected. In this study, we used passive acoustic monitoring to assess the current bat assemblage at Fort Indiantown Gap National Guard Training Center, a military training installation in southeastern Pennsylvania where WNS has been established for >10 years. Our first objective was to document seasonal activity patterns and the timing of occurrence for bat species on the installation. Our second objective was to determine the minimum number of nights (sampling effort) required to provide a complete inventory of the bat assemblage and reliably document the presence (infer absence) of individual bat species at a given site. Because detection of bats varies seasonally (Skalak et al. 2012; Baumgardt et al. 2022), we predicted that the sampling effort required to detect species would differ among seasons.

Study Site

Fort Indiantown Gap National Guard Training Center is a 6,920-ha, live-fire military training installation located in Lebanon and Dauphin Counties in southeastern Pennsylvania, (40°26′13.15″N, 76°34′33.8″W; Figure 1). Fort Indiantown Gap lies within the Ridge and Valley physiographic province (PADCNR 2018) and supports a variety of habitat types, including warm-season grasslands, oak *Quercus* sp. and hickory *Carya* sp. forests, scrub oak *Q. ilicifolia* barrens, shrublands, and wetlands (PADMVA 2022). Elevations range from 122 to 439 m above sea level. The climate is humid continental, with an average annual temperature of 11.3°C and an average annual precipitation of 117.9 cm (PADMVA 2002). Fort Indiantown Gap is located approximately 90–130 km from the two largest remaining bat hibernacula in the state

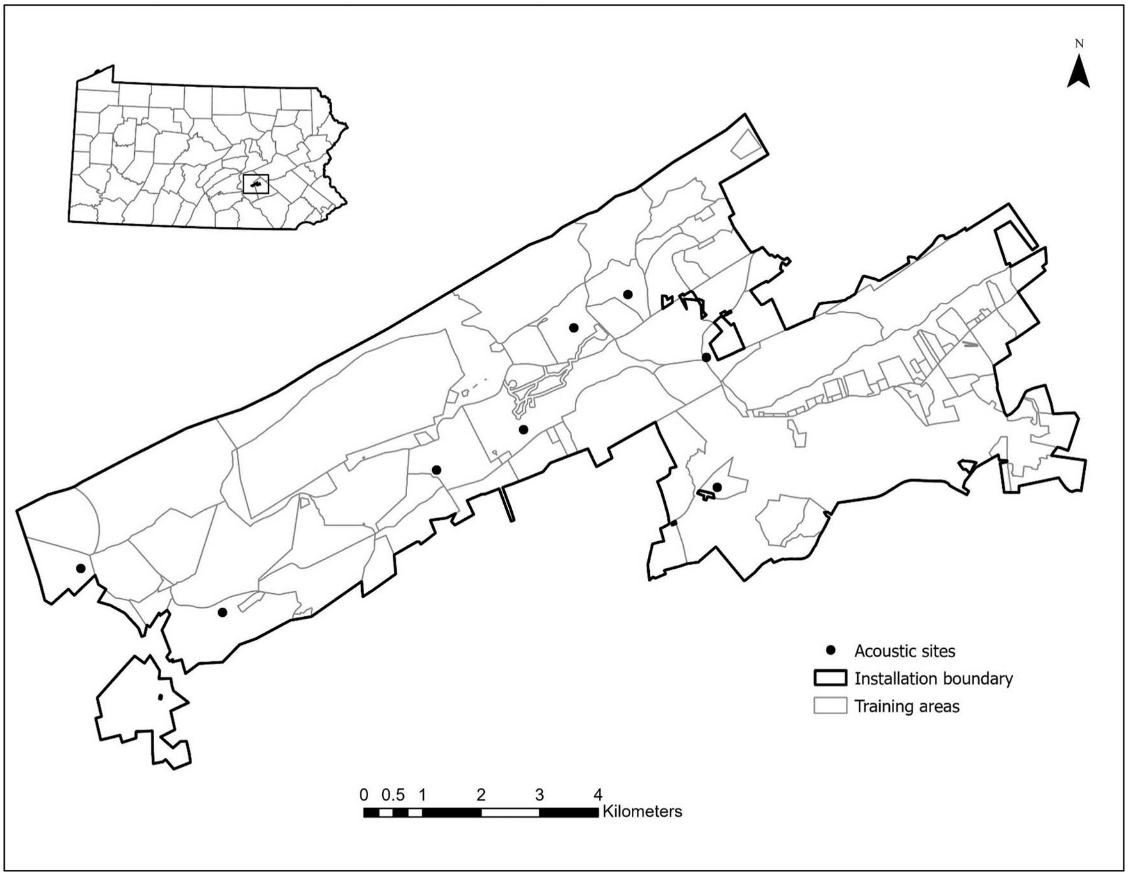

Figure 1. Map of permanent acoustic sampling sites at Fort Indiantown Gap National Guard Training Center in Annville, Pennsylvania, where we surveyed bats from April to October 2018 to 2021.

(G. Turner, Pennsylvania Game Commission, personal communication).

Methods

Study design

We selected sampling sites in areas that permitted regular access (limited military training) and included common habitat types found on the installation. Although we did not assess habitat use by bats in this study, we recognize that differences in habitat may contribute to variability in species richness and activity among sites (Skalak et al. 2012). We placed detectors along potential travel corridors for foraging and commuting bats, which included small streams, forested roads and trails, and forest canopy openings (Coleman et al. 2014; USFWS 2023). Each detector was located between 1.0 and 4.5 km from other detectors, and we maintained the location of each detector throughout the entire study. We deployed detectors at five sites in April 2018 and at two additional sites in May 2018 (seven total). We added one site in April 2019, and we maintained all eight sampling sites for the remainder of the study (Figure 1). Each year, detectors remained in the field and recorded continuously from 1 April to 31 October with few exceptions (in 2020, we initially deployed detectors at three sites in mid-April due to logistical constraints resulting from the coronavirus disease 2019 pandemic, and we retrieved the detector at one site in early September due to construction activities at that site).

Acoustic sampling

We passively recorded bat echolocation call sequences (hereafter "bat passes") using full-spectrum Pettersson D500x ultrasound detectors (Pettersson Electronik AB, Uppsala, Sweden). We powered detectors using 6-V deep-cycle batteries (PS-6200, Power-Sonic Corp., San Diego, CA) and stored them within weatherproof plastic containers. We secured external microphones (with directional horn attachment) to collapsible poles horizontal to the ground and elevated approximately 2.5 m above ground level. We deployed microphones at least 3 m from surrounding vegetation and in the direction with the least vegetative clutter, thereby increasing the number and quality of bat passes while reducing extraneous background noise and reflection (Weller and Zabel 2002; Loeb et al. 2015; Fraser et al. 2020). We programmed detectors to record continuously from sunset to sunrise each night and used the following settings for all detectors: 1) sampling frequency = 500 kHz, 2) pretrigger = off, 3) recording length = 5 s, 4) high pass filter = on, 5) autorecorder = on, 6) trigger sensitivity = high, 7) trigger level = 80, and 8) input gain = 80 (Reichert et al. 2017). Before and after field deployment, we ensured that detectors were functioning properly by producing ultrasound (e.g., snapping fingers and clapping hands) in front of the microphone. We georeferenced each sampling site using a global positioning system (Garmin Oregon 450, Olathe, KS).

Echolocation analysis

We stored digitally recorded full-spectrum (.wav) call files on compact flash cards within detectors and downloaded them to a computer once every 1 to 4 weeks. We uploaded call files to the SonoBat D500x File Attributer 2.7 (SonoBat Inc., Arcata, CA) and scrubbed them using a high-grade filter to remove noise and poor-quality files. We analyzed the remaining files using SonoBat analysis software (version 4.0.7, New York–Pennsylvania–West Virginia classifier, SonoBat Inc., Arcata, CA). SonoBat uses a decision engine based on quantitative machine learning and algorithms trained on a reference library of known recordings from species throughout eastern North America (Barnhart and Gillam 2014; Clement et al. 2014; Cox et al. 2016). SonoBat evaluates the mean value of 76 parameters (e.g., minimum frequency, maximum frequency, characteristic frequency, duration, and slope) of acceptable pulses and agreement among pulses within a bat pass to characterize call structure and make a species assignment (Cox et al. 2016). We used the default sequence decision threshold of 0.90 and acceptable call quality of 0.80 as well as a 20-kHz filter (Lemen et al. 2015; Cox et al. 2016; Reichert et al. 2018; Barnett and Collins 2019; Goodwin and Gillam 2021). To minimize errors in species identification, we only included search-phase bat passes with ≥3 pulses that were designated a consensus "SppAccp" classification.

Although widely used in bat acoustic studies (Gallagher et al. 2021; Baumgardt et al. 2022; Kunberger and Long 2023), SonoBat is considered a "candidate" program and is not currently approved by the USFWS for stand-alone use for Indiana myotis and northern long-eared myotis presence/absence surveys (USFWS 2019). In a recent study, Goodwin and Gillam (2021) found that average correct classification rates were similar between SonoBat (82.1%) and one of the USFWS-approved software programs (Kaleidoscope Pro; 85.3%). Although classification rates for northern long-eared myotis and little brown myotis were comparatively low when using SonoBat, the authors attributed this to a greater number of bat passes being left unidentified because they used settings adjusted for greater accuracy (e.g., decision threshold = 0.90; Lemen et al. 2015; Brabant et al. 2018). Moen et al. (2018) also found that SonoBat was more conservative than Kaleidoscope Pro in assigning species classifications and that SonoBat classifications were comparable to consensus classifications in which both programs agreed on the species identification of a bat pass. Therefore, by using conservative, high-accuracy settings in SonoBat, combined with manual verification of species identifications by a trained biologist (C.L.H.), we believe our approach successfully removed most false-positive species identifications.

We considered eight bat species as potential residents on the installation based on previous capture surveys (TNC 2001; BCM 2004; Hauer et al. 2019). These species included big brown bat *Eptesicus fuscus*, eastern red bat *Lasiurus borealis*, hoary bat *L. cinereus*, silver-haired bat *Lasionycteris noctivagans*, tricolored bat, northern long-eared myotis, eastern small-footed myotis *M. leibii*, and little brown myotis. Although Indiana myotis have not been captured during previous mist-netting surveys on the installation (TNC 2001; BCM 2004; Hauer et al. 2019), they are in surrounding areas (G. Turner, Pennsylvania Game Commission, personal communication). Thus, we deemed the presence of Indiana myotis as possible, and conservatively grouped bat passes identified as little brown myotis or Indiana myotis into a single phonic group (hereafter "MYLU-MYSO") due to similarities in their echolocation characteristics (Caldwell et al. 2019; Gorman et al. 2021). We felt confident in reliably separating northern long-eared myotis and eastern small-footed myotis passes from those of the MYLU-MYSO phonic group because of their steeper slope, higher maximum frequency (>90 kHz), higher characteristic frequency (>40 kHz), and shorter duration (<5 ms; Murray et al. 2001; Broders et al. 2004; Mukhida et al. 2004; White et al. 2016; Szewczak 2018). To identify northern long-eared myotis, we looked for passes that had a nearly vertical frequency-modulated sweep, a maximum frequency of >110 kHz, and a frequency bandwidth of >70 kHz (Caceres and Barclay 2000). To identify eastern small-footed myotis, we looked for passes with a steep frequency-modulated sweep that increased in curvature and ended in a well-defined terminal sweep or tail (Mukhida et al. 2004).

Data analysis

Seasonal activity patterns. We divided our sampling period into three distinct seasons: spring (1 April–14 May), summer (15 May–15 August), and fall (16 August–31 October). These time periods encompass the summer active season (USFWS 2023) and the spring and fall migratory periods when bats are presumed to be returning to or departing from their summer foraging grounds. We did not keep the number of deployed detectors consistent among nights or seasons due to periodic detector malfunction (e.g., power loss, equipment failure, and improper deployment) or access restrictions from military training. Thus, we only used data from detectors that operated successfully from sunset to sunrise (defined as one detector-night) in our analyses. Per USFWS survey guidelines (USFWS 2023), we also excluded data from sampling nights in which there was rainfall between sunrise and sunset, as precipitation can negatively impact bat activity (Erickson and West 2002; Yates and Muzika 2006; Muthersbaugh et al. 2019a). We examined seasonal activity patterns by dividing the total number of bat passes recorded for each species by the total number of successful detector-nights for each night of sampling (Johnson et al. 2011).

Species richness and sampling effort needed for a complete inventory. We estimated bat species richness and the number of nights needed to achieve a complete inventory of the bat assemblage using species accumulation curves (Soberon and Llorente 1993; Moreno and Halffter 2000; Froidevaux et al. 2014). Species accumulation curves are a class of linear dependence models that plot the cumulative number of species detected within a defined sampling area against increasing levels of sampling effort (Thompson and Thompson 2007). We used EstimateS (Colwell 2019) to calculate species accumulation curves for each site and for all sites combined during spring, summer, and fall. We used the number of sampling nights as a measure of sampling effort. Curves reached an asymptote when the probability of detecting a new species approached zero. We repeated and randomly reordered the sampling sequence 100 times in EstimateS to produce smoothed curves (Moreno and Halffter 2000).

To assess the completeness of our acoustic surveys, we calculated the proportion of the total number of bat species detected among seasons. We selected 90% of the total species richness detected during each season as a satisfactory level of survey completeness (Moreno and Halffter 2000; Shiu and Lee 2003; Thompson et al. 2007; Skalak et al. 2012; Froidevaux et al. 2014) because reaching 100% species richness is unlikely, as rare species may go undetected even with a substantial sampling effort. To evaluate the number of sampling nights needed to achieve this level of survey completeness, we estimated the average values of species richness for each site separately (between-site variation) and for all sites combined (between-season variation) using species accumulation curves (Si et al. 2014).

Sampling effort needed to infer species absence. We created nightly presence–absence detection histories for each bat species, where a value of 1 indicated a species detection and a value of 0 indicated a species nondetection. We considered a species to be present if we recorded and identified one or more bat passes at a site on a given night (Yates and Muzika 2006; Clement et al. 2014). For each bat species, we ran single-species, single-season occupancy models in the program PRESENCE (USGS 2021) to estimate the probability of detection (p) and site occupancy (Ψ) (MacKenzie et al. 2002). We examined the effects of minimum nightly temperature (°C), mean nightly relative humidity (%), mean nightly wind speed (m/s), and Julian date on probability of detection and survey year (2018, 2019, 2020, or 2021; categorical) on site occupancy of bat species. We obtained hourly weather data for each sampling night from a remote automated weather station (https://mesowest.utah.edu/cgi-bin/droman/meso_base_dyn.cgi?stn=RUNP1&unit=0&timetype=GMT) located on the installation. We constructed nine a priori models to examine single and additive combinations of the detection and occupancy covariates. We standardized all continuous survey-specific covariates using a z-score transformation before model fitting (Lombardi et al. 2018; Burns et al. 2019). To avoid multicollinearity, we calculated correlation coefficients of continuous covariates to ensure that highly correlated (Pearson's $|r| \geq 0.70$) covariates were not included in the same model (Hein et al. 2009; Burns et al. 2019; Barr et al. 2021).

We used Akaike's information criterion corrected for small sample sizes (AIC_c) to rank each model, and we examined relative support for each model using ΔAIC_c (the difference between the model with the lowest AIC_c and all other models) and model weights (w_i; Burnham and Anderson 2002). We considered models with the lowest ΔAIC_c and highest w_i to be the best-supported models (Armstrong et al. 2022). We examined parameter estimates and their 95% confidence intervals for the best-supported models and considered parameters with confidence intervals that did not overlap 0 to be informative (Burnham and Anderson 2002). We then used estimates of probability of detection and site occupancy from the best-supported model to calculate the number of sampling nights needed to infer absence of each bat species with 90% certainty at a given sampling site during each season (Niver et al. 2014; Law et al. 2015) using the following equation from Wintle et al. (2012):

$$n = \frac{\log\left(\frac{\alpha}{1-\alpha}\right) - \log\left(\frac{\Psi}{1-\Psi}\right)}{\log(1-\rho)},$$

where n is the number of sampling nights, α is the probability of committing a type I error (in this case, $\alpha = 0.1$), Ψ is the probability that a site is occupied, and p is the probability of detection.

Results

We passively monitored for bats at five to eight permanent sampling sites from 1 April to 31 October 2018, 2019, 2020, and 2021, resulting in a total of 4,107 detector-nights without precipitation: 110 detector-nights ($n = 5$ detectors) in the spring, 331 detector-nights ($n = 7$ detectors) in the summer, and 279 detector-nights ($n = 7$ detectors) in the fall of 2018; 205 detector-nights ($n = 8$ detectors) in the spring, 503 detector-nights ($n = 8$ detectors) in the summer, and 418 detector-nights ($n = 8$ detectors) in the fall of 2019; 202 detector-nights ($n = 8$ detectors) in the spring, 513 detector-nights ($n = 8$ detectors) in the summer, and 393 detector-nights ($n = 8$ detectors) in the fall of 2020; and 279 detector-nights ($n = 8$ detectors) in the spring, 508 detector-nights ($n = 8$ detectors) in the summer, and 366 detector-nights ($n = 8$ detectors) in the fall of 2021 (Table 1; Data S1, *Supplemental Material*). We recorded 507,342 bat passes, 56.4% ($n = 286{,}131$ passes) of which were of sufficient quality that we could identify them to species (Data S2, *Supplemental Material*). The remaining 221,211 bat passes were of poor quality or too ambiguous for confident species identifications, and we classified these as unknown. We documented all eight bat species presumed to occur on the installation, with big brown bats (78.8% of identified passes) and eastern red bats (16.6%) being the two most frequently detected species.

Each year, we initially detected six of the eight bat species in early April, and we continued to detect most species on the installation through the end of October (Figure 2). Tricolored bats and MYLU-MYSO were consistently the last species to arrive from late April to early

Table 1. Nightly bat activity (passes/detector-night) by season and year at Fort Indiantown Gap National Guard Training Center in Annville, Pennsylvania, from April to October 2018 to 2021 (the sampling effort per season is in parentheses). Species include big brown bat *Eptesicus fuscus* (EPFU), eastern red bat *Lasiurus borealis* (LABO), hoary bat *L. cinereus* (LACI), silver-haired bat *Lasionycteris noctivagans* (LANO), eastern small-footed myotis *Myotis leibii* (MYLE), little brown myotis *M. lucifugus*–Indiana myotis *M. sodalis* (MYLU-MYSO), northern long-eared myotis *M. septentrionalis* (MYSE), and tricolored bat *Perimyotis subflavus* (PESU).

	2018			2019			2020			2021		
Species	**Spring (n = 110)**	**Summer (n = 331)**	**Fall (n = 279)**	**Spring (n = 205)**	**Summer (n = 503)**	**Fall (n = 418)**	**Spring (n = 202)**	**Summer (n = 513)**	**Fall (n = 393)**	**Spring (n = 279)**	**Summer (n = 508)**	**Fall (n = 366)**
EPFU	8.22	102.12	22.99	2.08	113.71	8.35	0.94	126.64	28.54	1.20	83.73	10.69
LABO	0.48	34.32	1.14	2.26	28.12	0.78	1.73	26.17	2.33	0.75	11.11	0.47
LACI	0.01	0.53	0.05	0.04	0.33	0.11	0.06	0.37	0.10	0.12	1.48	0.42
LANO	1.36	1.84	1.05	0.97	0.87	0.84	1.67	1.28	0.64	1.23	1.59	1.73
MYLE	1.43	1.40	0.54	0.28	0.37	0.27	0.40	1.68	2.66	1.30	0.21	1.17
MYLU-MYSO	0.01	0.02	0.02	0.02	0.03	0.08	0.01	0.10	0.33	0.01	0.18	0.11
MYSE	1.90	0.42	0.21	0.97	0.26	0.36	0.29	0.24	0.32	0.02	0.15	0.12
PESU	0.03	0.58	0.12	0.01	0.40	0.09	0.03	0.56	0.04	0.04	0.37	0.02

May, whereas northern long-eared myotis were the first species to depart from late September to early October. Seasonal activity patterns varied by species but were relatively consistent for each species within the study period. Nightly activity of big brown bats and eastern red bats increased gradually through spring and early summer, peaked from mid-July to early August, and then declined by September each year (Figures 2a and 2b). Except for a few nights of particularly high activity in May 2018, hoary bats exhibited a similar pattern, with activity peaking from mid-July to early August (Figure 2c). Nightly activity of eastern small-footed myotis and northern long-eared myotis peaked in late spring and again in fall, whereas the activity of both species remained comparatively low during the summer (Figures 2e and 2g). Nightly activity of MYLU-MYSO also peaked in early fall but declined rapidly by October (Figure 2f). Nightly activity of tricolored bats and silver-haired bats remained relatively constant throughout the entire sampling period each year (Figures 2d and 2h).

We detected several bat species at all sampling sites within and among seasons ($\Psi = 1.0$), whereas we only detected some species at one or two sites. We found a range of five to eight (mean $\pm$ standard error [SE] = 5.9 $\pm$ 0.4) species detected among sites during the spring, five to eight (6.8 $\pm$ 0.4) species during the summer, and four to eight (6.4 $\pm$ 0.5) species during the fall. The number of sampling nights required to detect 90% of the total species richness across all eight sites (between-season variation) varied with season (Figure 3). We found that the sampling effort required was lowest during the summer (4 nights), followed by the fall (6 nights) and spring (10 nights). Species accumulation curves for each site (between-site variation) reached an asymptote at different rates within and among seasons (Figure 4). It took a mean $\pm$ SE of 17.7 $\pm$ 0.9 nights to detect 90% of the known species at a site during the spring, 24.1 $\pm$ 2.3 nights during the summer, and 23.0 $\pm$ 2.0 nights during the fall.

We found that site occupancy (Ψ) of bats was not influenced by survey year. Probability of detection (p) varied among bat species and seasons and was primarily influenced by Julian date, minimum nightly temperature, and mean nightly relative humidity. In spring, $\Psi(.)$, p(date + temp) was the best-supported model for six of the eight bat species, while $\Psi(.)$, p(temp) was the best-supported model for hoary bats and northern long-eared myotis (Table S1, *Supplemental Material*). Detection of all eight species was positively related to minimum nightly temperature, and detection of eastern red bats, silver-haired bats, eastern small-footed myotis, MYLU-MYSO, and tricolored bats was positively related to Julian date (Table S2, *Supplemental Material*).

In the summer, $\Psi(.)$, p(date + rh) was the best-supported model for five of the eight species, whereas $\Psi(.)$, p(date + temp) was the best-supported model for hoary bats and silver-haired bats (Table S3, *Supplemental Material*). The best-supported model for MYLU-MYSO contained a single covariate: temperature (Table S3, *Supplemental Material*). Detection of big brown bats, eastern red bats, hoary bats, northern long-eared myotis, and tricolored bats was positively related to Julian date, whereas detection of silver-haired bats and eastern small-footed myotis was negatively related to Julian date (Table S4, *Supplemental Material*). Detection of hoary bats and silver-haired bats was positively related to minimum nightly temperature (Table S4, *Supplemental Material*). Detection of big brown bats, eastern small-footed myotis, northern long-eared myotis, and tricolored bats was negatively related to mean nightly relative humidity (Table S4, *Supplemental Material*).

In the fall, $\Psi(.)$, p(date + temp) was the best-supported model for big brown bats and eastern red bats (Table S5, *Supplemental Material*). The best-supported model for hoary bats and northern long-eared myotis was $\Psi(.)$, p(date + rh), whereas the best-supported model for silver-haired bats, eastern small-footed myotis, MYLU-MYSO, and tricolored bats contained either temperature or date (Table S5, *Supplemental Material*). Detection of six of the eight species was negatively related to Julian date, and detection of big brown bats and silver-haired bats was positively related to minimum nightly temperature (Table S6, *Supplemental Material*).

The number of sampling nights required to have 90% certainty in inferring the absence of a species at a sampling site was lowest during summer for seven of the eight species, including big brown bats (2 nights; Figure 5a), eastern red bats (2 nights; Figure 5b), eastern small-footed myotis (4 nights; Figure 2e), silver-haired bats (6 nights; Figure 2d), hoary bats (12 nights; Figure 5c),

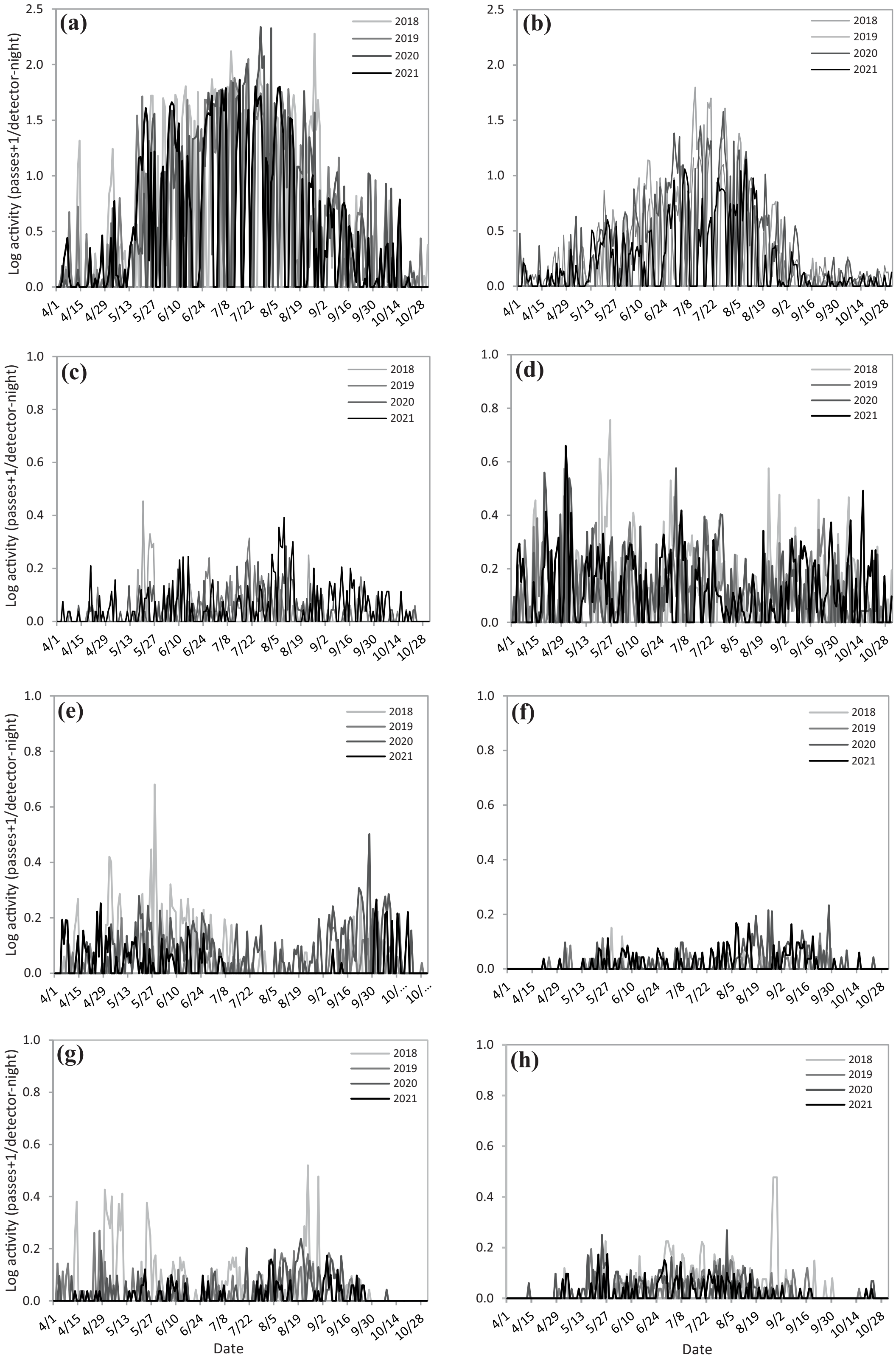

Figure 2. Seasonal activity of (**a**) big brown bats *Eptesicus fuscus*, (**b**) eastern red bats *Lasiurus borealis*, (**c**) hoary bats *L. cinereus*, (**d**) silver-haired bats *Lasionycteris noctivagans*, (**e**) eastern small-footed myotis *Myotis leibii*, (**f**) little brown myotis *M. lucifugus*–Indiana myotis *M. sodalis*, (**g**) northern long-eared myotis *M. septentrionalis*, and (**h**) tricolored bats *Perimyotis subflavus* at Fort Indiantown Gap National Guard Training Center in Annville, Pennsylvania. Data are cumulative from detectors (n = 5–8) that recorded continuously from April to October 2018 to 2021.

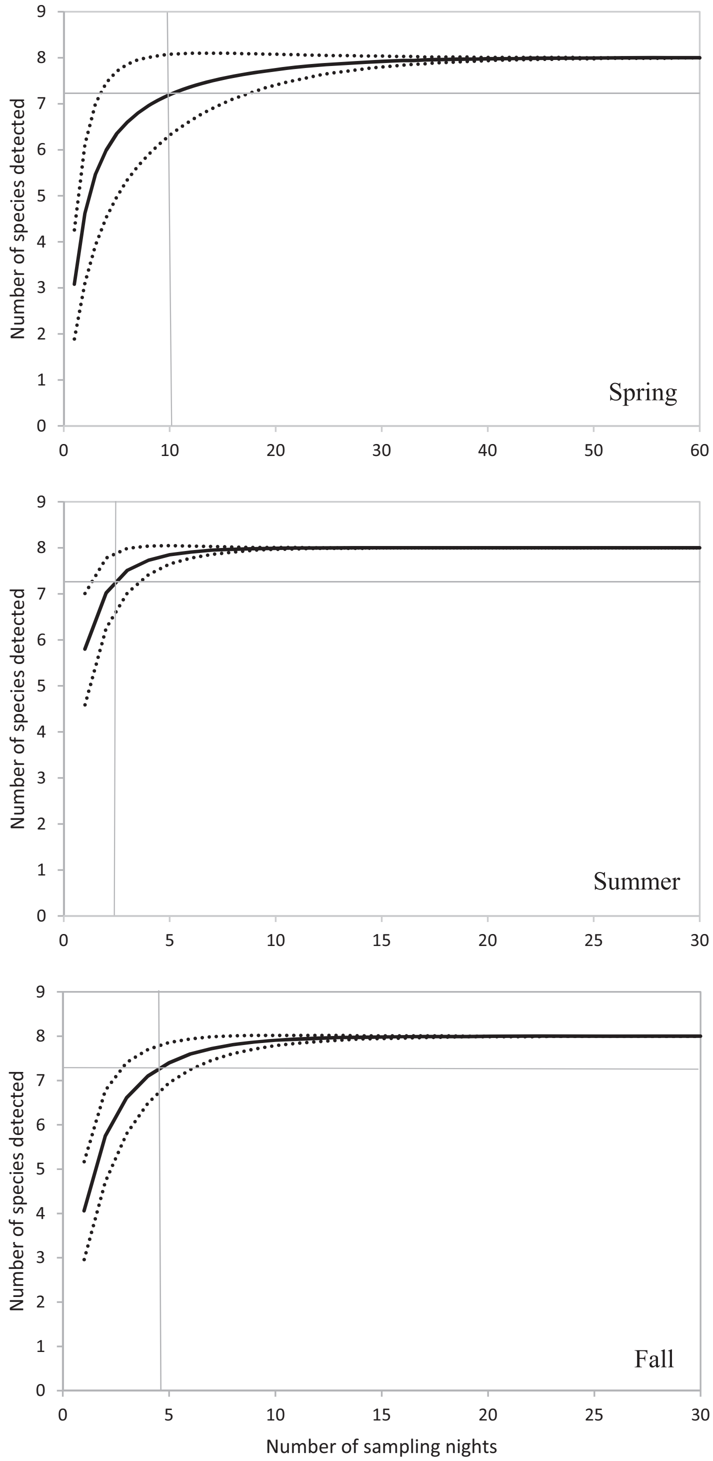

Figure 3. Bat species accumulation curves for the combined data from eight sampling sites at Fort Indiantown Gap National Guard Training Center in Annville, Pennsylvania, during the spring, summer, and fall 2018 to 2021. Dashed lines indicate 95% confidence intervals. Horizontal gray lines indicate the species richness threshold of 90%, and vertical gray lines indicate the corresponding number of nights (sampling effort) required to achieve that threshold.

northern long-eared myotis (19 nights; Figure 5g), and tricolored bats (31 nights; Table 2; Figure 5h). The sampling effort needed to infer the absence of MYLU-MYSO was lower in fall (36 nights) than in summer (41 nights) or spring (88 nights; Table 2; Figure 5f).

Discussion

Most bat species were present on the installation throughout the entire sampling period (April–October). Our results indicate that the seasonal occurrence of bats

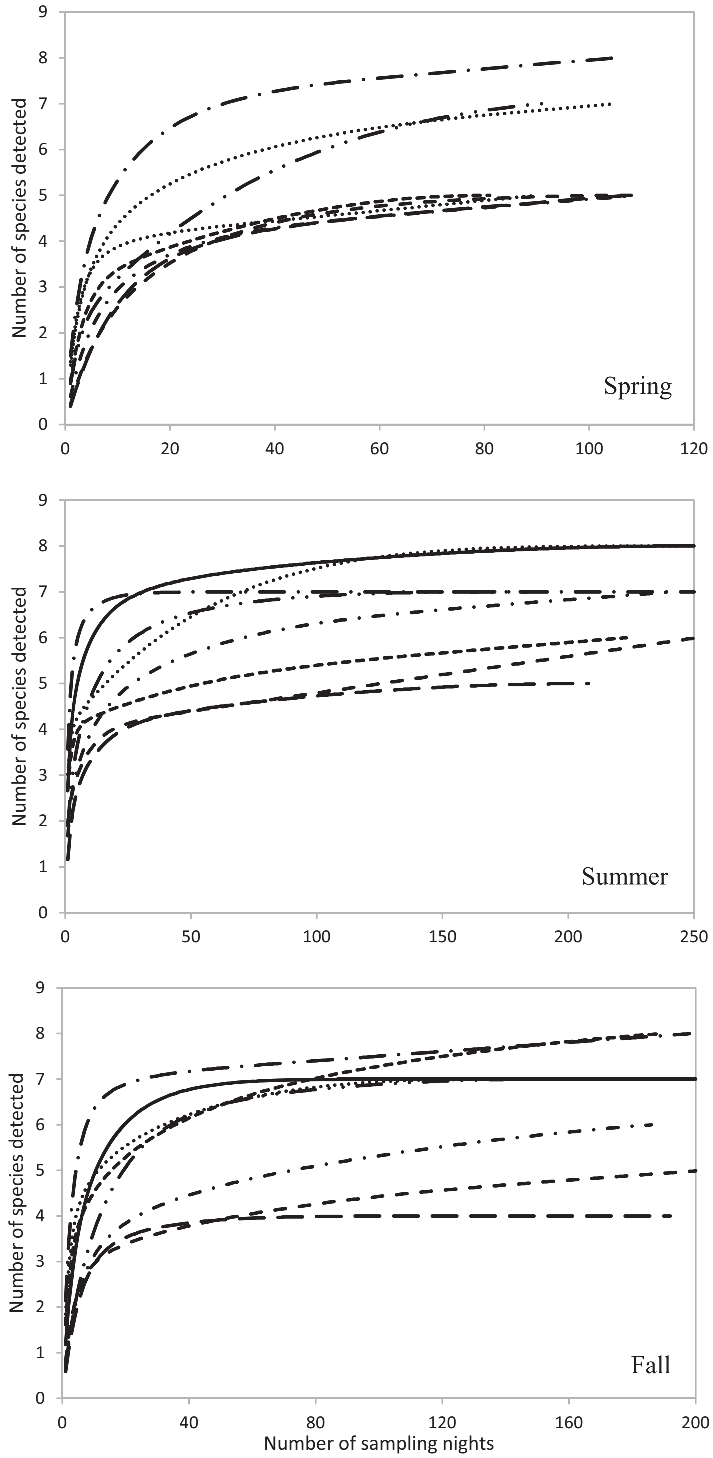

Figure 4. Bat species accumulation curves for each sampling site at Fort Indiantown Gap National Guard Training Center in Annville, Pennsylvania, during the spring, summer, and fall 2018 to 2021. Each curve represents the cumulative number of bat species detected at a site as a function of the number of nights.

on the installation was primarily influenced by temperature, with bats likely arriving earlier in spring and remaining on the installation later in fall in years when warmer nighttime temperatures favored foraging (Smith and McWilliams 2016; Pettit and O'Keefe 2017; Muthersbaugh et al. 2019a; Snively et al. 2021). Each year, MYLU-MYSO and tricolored bats were the last species to arrive on the installation from late April to early May, which was expected as they are among the last bat species to emerge from hibernation in spring (Fenton and Barclay 1980; Fujita and Kunz 1984; Merritt 1987). The first species to depart the installation each year was the northern long-eared myotis, with no passes

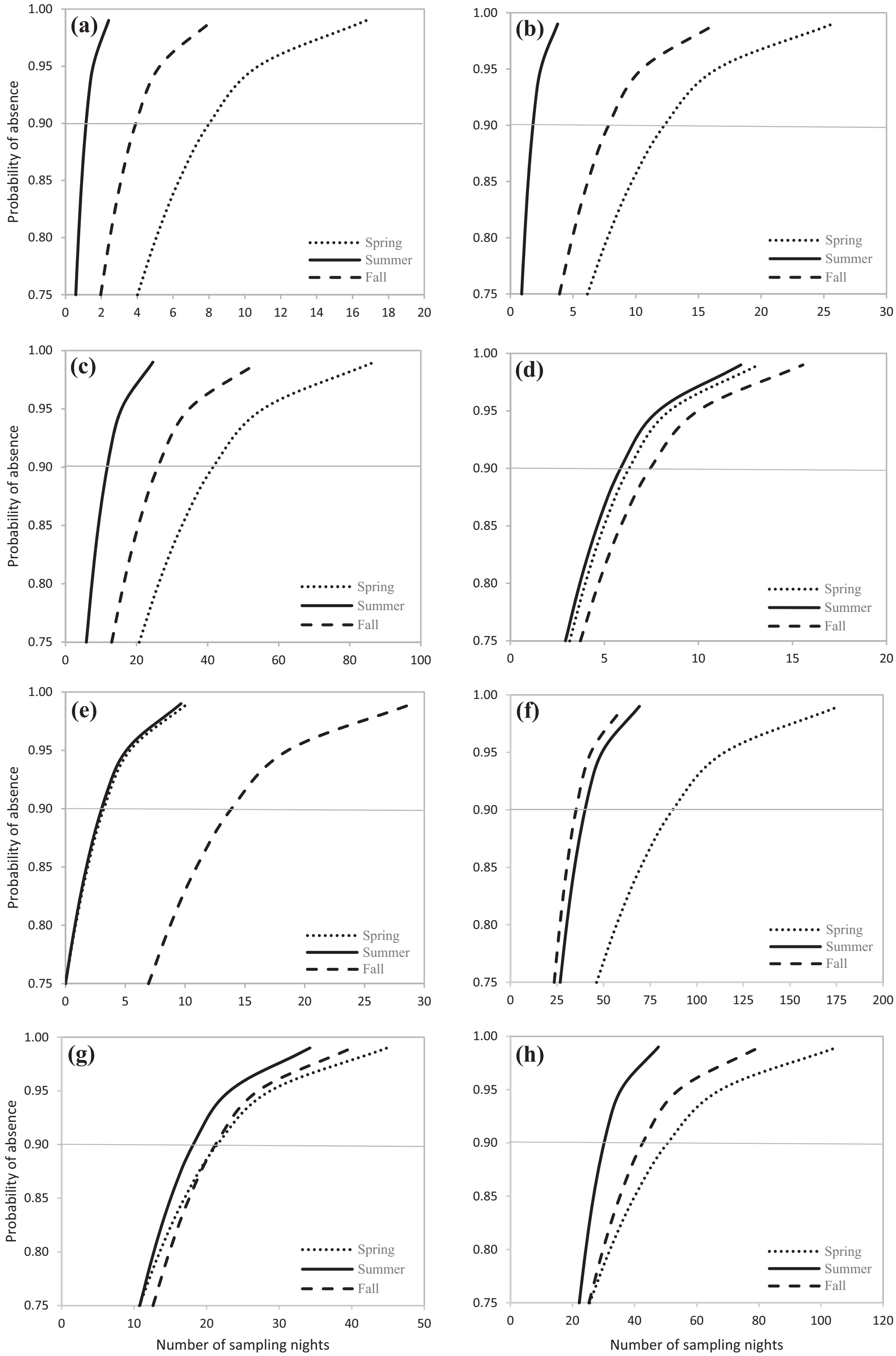

Figure 5. Number of sampling nights required to infer the absence of each bat species at a sampling site by season at Fort Indiantown Gap National Guard Training Center in Annville, Pennsylvania, 2018–2021. Species include (**a**) big brown bat *Eptesicus fuscus*, (**b**) eastern red bat *Lasiurus borealis*, (**c**) hoary bat *L. cinereus*, (**d**) silver-haired bat *Lasionycteris noctivagans*, (**e**) eastern small-footed myotis *Myotis leibii*, (**f**) little brown myotis *M. lucifugus*–Indiana myotis *M. sodalis*, (**g**) northern long-eared myotis *M. septentrionalis*, and (**h**) tricolored bat *Perimyotis subflavus*. Horizontal gray lines indicate the 90% confidence level for probability of absence.

Table 2. Level of acoustic sampling effort (detector-nights) to reach certainty of absence at given α levels using detection (p) and occupancy (Ψ) estimates from the best-supported model for eight bat species at Fort Indiantown Gap National Guard Training Center in Annville, Pennsylvania, during the spring, summer, and fall 2018 to 2021. Species include big brown bat *Eptesicus fuscus* (EPFU), eastern red bat *Lasiurus borealis* (LABO), hoary bat *L. cinereus* (LACI), silver-haired bat *Lasionycteris noctivagans* (LANO), eastern small-footed myotis *Myotis leibii* (MYLE), little brown myotis *M. lucifugus*–Indiana myotis *M. sodalis* (MYLU-MYSO), northern long-eared myotis *M. septentrionalis* (MYSE), and tricolored bat *Perimyotis subflavus* (PESU).

	Detection and occupancy				Detector-nights					
Species	***p***	**SE**	**Ψ**	**SE**	**0.25**	**0.20**	**0.15**	**0.10**	**0.05**	**0.01**
EPFU										
Spring	0.24	0.02	1.00	0.00	4.01	5.06	6.33	8.01	10.74	16.76
Summer	0.85	0.01	1.00	0.00	0.57	0.72	0.91	1.15	1.54	2.40
Fall	0.43	0.02	1.00	0.00	1.96	2.47	3.09	3.92	5.25	8.20
LABO										
Spring	0.16	0.02	1.00	0.00	6.14	7.74	9.69	12.27	16.45	25.67
Summer	0.70	0.02	1.00	0.00	0.90	1.14	1.42	1.80	2.41	3.77
Fall	0.24	0.02	1.00	0.00	3.91	4.93	6.17	7.82	10.48	16.35
LACI										
Spring	0.05	0.01	1.00	0.00	20.74	26.18	32.75	41.49	55.60	86.77
Summer	0.17	0.01	1.00	0.00	5.88	7.42	9.28	11.76	15.76	24.59
Fall	0.08	0.01	1.00	0.00	12.98	16.38	20.50	25.97	34.80	54.31
LANO										
Spring	0.29	0.03	1.00	0.00	3.15	3.98	4.98	6.30	8.45	13.18
Summer	0.31	0.02	1.00	0.00	2.93	3.70	4.62	5.86	7.85	12.25
Fall	0.26	0.02	1.00	0.00	3.72	4.69	5.87	7.43	9.96	15.54
MYLE										
Spring	0.29	0.05	0.25	0.15	0.00	0.84	1.85	3.20	5.38	10.20
Summer	0.30	0.03	0.25	0.15	0.00	0.79	1.76	3.03	5.09	9.65
Fall	0.15	0.02	0.50	0.18	6.94	8.75	10.95	13.87	18.59	29.01
MYLU-MYSO										
Spring	0.03	0.01	0.54	0.19	46.21	56.91	69.86	87.06	114.84	176.21
Summer	0.08	0.01	0.75	0.15	26.72	30.22	34.45	40.08	49.16	69.23
Fall	0.09	0.01	0.75	0.15	23.47	26.54	30.26	35.20	43.19	60.82
MYSE										
Spring	0.10	0.02	0.50	0.18	10.72	13.53	16.93	21.44	28.74	44.85
Summer	0.14	0.02	0.63	0.17	10.79	12.72	15.05	18.15	23.16	34.22
Fall	0.12	0.02	0.63	0.17	12.60	14.86	17.58	21.21	27.06	39.98
PESU										
Spring	0.04	0.02	0.50	0.18	25.48	32.06	40.03	50.60	67.69	105.43
Summer	0.13	0.01	0.88	0.12	22.18	24.27	26.81	30.18	35.62	47.65
Fall	0.06	0.01	0.63	0.17	25.28	29.80	35.27	42.53	54.27	80.20

recorded after 8 October. This timing coincides with dispersal toward hibernacula ahead of mating and hibernation (Barbour and Davis 1969).

Seasonal trends in activity varied among species. The activity of big brown bats and eastern red bats peaked from mid-July to early August, likely due to the addition of newly volant juveniles on the landscape (Ford et al. 2011; Nocera et al. 2019) or increased foraging activity of reproductive females to support the high energetic demands of lactation (Kurta et al. 1989). These assumptions are supported by increased captures (particularly of lactating females and juveniles) of both species during concurrent mist-netting surveys at the same sites (C.L. Hauer, Pennsylvania Department of Military and Veterans Affairs, unpublished data). Consistent with other studies (Baerwald and Barclay 2011; Johnson et al. 2011), we found a peak in activity of hoary bats in early August, suggesting fall migratory movements through the installation (Whitaker and Hamilton 1998; Cryan 2003). We did not observe any apparent peaks in activity of silver-haired bats during spring or fall, as has been previously reported in the eastern United States and Canada (McGuire et al. 2012; Muthersbaugh et al. 2019a). This may be because our sampling sites were located at relatively low elevations, and migratory species, including silver-haired bats, are known to use ridgelines as migratory corridors, particularly during the fall (Johnson et al. 2003; Reynolds 2006). Wieringa et al. (2021) also suggested that silver-haired bats undergo a partial or incomplete migration, with some individuals overwintering in the northern portion of the species' range rather than migrating to more southern latitudes.

The activity of eastern small-footed myotis and northern long-eared myotis initially peaked from May to early June, followed by a second peak in activity in September. We observed a single peak in activity of MYLU-MYSO from late August to early September. Although previous studies observed peaks in activity of *Myotis* species in June and July (Nocera et al. 2019; Gorman et al. 2021; Lewis et al. 2022), we observed relatively low activity levels of these species during mid-summer, likely resulting from low survivorship of these species due to WNS (Ford et al. 2011). Before WNS, northern long-eared myotis and little brown myotis were two of the most common bat species (along with big brown bats) in mist-netting surveys on the installation (TNC 2001; BCM 2004). However, surveys after WNS showed significant declines in captures of both species (Hauer et al. 2019).

When estimating between-season variation in bat species richness for the combined data from all eight sites, we found that a minimum of 10, 4, and 6 sampling nights were required to detect 90% of possible species present on the installation during spring, summer, and fall, respectively. When estimating between-site variation in bat species richness using species accumulation curves for each site separately, we found that relatively few sampling nights (three to five nights) were needed to the detect the four bat species that were commonly detected at most sites. However, many more nights of sampling were needed to detect 90% of possible species at some sites. For example, in summer, it took on average 25 nights to detect 90% of possible species at a site, which was slightly higher than in spring (18 nights) and fall (23 nights). The higher sampling effort needed in summer may be attributed to higher species richness during this period (Skalak et al. 2012). Skalak et al. (2012) found that approximately 30 nights were needed to detect 90% of bat species at a site when sampling seven to nine sites in a similarly sized (95 km^2) wildlife refuge in southern Nevada. The fact that we required nearly the same level of sampling effort as Skalak et al. (2012) despite lower bat species richness in our study area (8 versus 14 species), highlights the substantial sampling effort required to assess bat species richness in post-WNS landscapes, primarily due to the rarity of WNS-affected species.

Consistent with previous studies (Muthersbaugh et al. 2019a; Gorman et al. 2021), we found that temperature and date were important predictors of bat activity and detection. Across all seasons, the detection of bats was positively related to minimum nightly temperature, likely due to increased insect prey availability and the thermoregulatory costs incurred during flight in colder temperatures (McGuire et al. 2014; Wolbert et al. 2014; Muthersbaugh et al. 2019a). Detection of most species was positively related to Julian date during spring and summer but was negatively related to Julian date during the fall, consistent with the seasonal activity patterns that we observed (Figure 2). Interestingly, relative humidity was also an important predictor of detection for several species during the summer. Bats can modify their activity in response to air saturation levels (Lacki 1984), and Geluso and Geluso (2012) suggested that bats are more active on nights with higher humidity levels due to reduced evaporative water loss during flight. However, we were more likely to detect big brown bats, eastern small-footed myotis, northern long-eared myotis, and tricolored bats on nights with lower humidity levels. The negative association that we observed may be the result of increased atmospheric attenuation of calls at higher humidity levels (Goerlitz 2018), particularly for eastern small-footed myotis and northern long-eared myotis which emit high-frequency, low-amplitude calls.

The sampling effort needed to infer the absence of individual species varied considerably among species and was influenced by season. The number of sampling nights needed to infer absence was lowest during summer for big brown bats, eastern red bats, hoary bats, silver-haired bats, eastern small-footed myotis, northern long-eared myotis, and tricolored bats. During the summer, $\leq$12 sampling nights were needed to infer the absence of most species, but many more nights ($>$19 nights) were needed for northern long-eared myotis, tricolored bats, and MYLU-MYSO due to very low detection probabilities ($p = 0.08$–0.14) for these species (Table 2). Little brown myotis–Indiana myotis were the least documented species ($n = 388$ passes on 5.1% of detector-nights) in our study. The sampling effort needed to infer absence of MYLU-MYSO was lowest during the fall when probability of detection ($p = 0.09$) and site occupancy ($\Psi = 0.75$) were highest (Table 2). The sampling effort needed to infer absence of eastern small-footed myotis was similar between spring and summer (4 nights), and the sampling effort for northern long-eared myotis was similar between spring and fall (22 nights; Table 2).

In a large-scale acoustic survey across the mid-Atlantic United States, Deeley et al. (2021b) found that during the summer, a minimum sampling effort of 133 detector-nights was required to detect northern long-eared myotis, which was a slightly lower level of effort than we observed in our study (8 sites surveyed for 19 nights each = 152 detector-nights). Deeley et al. (2021b) also reported lower sampling effort for little brown myotis (51 detector-nights), Indiana myotis (153 detector-nights), and tricolored bats (43 detector-nights). Acoustic studies have consistently demonstrated that less effort is required to detect a species when more sites are surveyed for few nights than when sampling fewer sites for more nights (MacKenzie and Royle 2005; Fischer et al. 2009; Skalak et al. 2012; Froidevaux et al. 2014; Law et al. 2015; Deeley et al. 2021b). This is because sampling widely across the landscape maximizes the number of occupied sites sampled (Field et al. 2005; MacKenzie et al. 2018). Rare, less detectable species, such as those impacted by WNS, may go undetected if too few sites are sampled, resulting in biased estimates (Meyer et al. 2011; Deeley et al. 2021b). We acknowledge that the sampling effort needed to detect northern long-eared myotis, MYLU-MYSO, and tricolored bats in our study may have been lower if we had access to more detectors and could survey more sites.

Our results indicate that 14 sampling nights per site, as currently required by the USFWS to determine presence or probable absence of northern long-eared myotis and tricolored bats (USFWS 2023), may not be adequate to eliminate false absences of these species during the summer. USFWS guidelines may also not require enough sampling nights to infer the absence of Indiana myotis in some areas or under certain recording conditions. Because we grouped Indiana myotis and little brown myotis into a single phonic group, our ability to make conclusions regarding sampling effort for Indiana myotis was limited, especially if the species was truly absent from the installation. Our results also suggest that a considerable level of sampling effort may be needed to detect little brown myotis, especially if populations of the species continue to decline throughout the region from WNS (Cheng et al. 2021).

In addition to informing USFWS summer survey guidelines, our findings may have important implications for the North American Bat (NABat) monitoring program, a continent-wide project designed to track changes in the distributions and abundance of multiple bat species over broad spatial and temporal scales (Loeb et al. 2015). When conducting stationary acoustic surveys, NABat guidelines recommend sampling two to four sites for four nights each within grid cells of up to 100 km^2 (Loeb et al. 2015). Similar to Deeley et al. (2021b), our results indicate that NABat guidelines may not require enough sampling sites to detect rare or declining species, as we needed double the number of recommended sites (eight versus four) to detect 90% of species present when sampling each site for four nights. Also, we found that the recommended sampling duration (four sampling nights per site) is insufficient to eliminate false absences of all but the most common species. Additionally, NABat guidelines recommend sampling during the summer active period before young become volant (Loeb et al. 2015). This may reduce the ability to detect some species, as we found that most species, except for eastern small-footed myotis and silver-haired bats, were more likely to be detected later in the summer. However, our study was limited in scale, and more studies conducted across greater spatial scales are needed to determine if NABat sampling protocols are adequate for bat species impacted by WNS.

Conclusion

Given the increasing number of threats to bats (O'Shea et al. 2016; Frick et al. 2020), there is a growing need to establish long-term monitoring programs to assess changes in bat populations over time (Ford et al. 2011). This is especially the case for WNS-affected bat species that have become increasingly rare and patchily distributed on the landscape (Nocera et al. 2020; Deeley et al. 2021a). A greater understanding of patterns of activity and detectability of target species (Deeley et al. 2021b) and the subsequent sampling effort needed to achieve monitoring goals is essential for developing robust monitoring programs (Soberon and Llorente 1993; Dubos et al. 2021) and will likely lead to more effective management and conservation actions (Skalak et al. 2012). In this study, we found that activity and detection of bats varied seasonally; therefore, we recommend that surveyors consider local variation in the relative detectability of target species (Skalak et al. 2012; Deeley et al. 2021b) and then restrict sampling to periods of highest activity and detection probability of those species (Baumgardt et al. 2022). Our results also indicate that surveyors should account for the potential influence of temporal and weather conditions (particularly temperature) on detectability.

No sampling design will be most effective for all species, as there is a tradeoff between allocating monitoring effort to more sites and more repeat visits to those sites (Field et al. 2005). Species accumulation models can improve the efficiency of sampling protocols by producing reliable estimates of species richness and subsequent sampling effort (Soberon and Llorente 1993), and we suggest that natural resource managers use a similar approach when designing and implementing long-term monitoring studies in post-WNS landscapes. Although we needed relatively few nights to detect common species, longer sampling periods will likely be required to detect rare or declining species. Sampling for approximately 20 nights per site allowed us to confidently infer the absence of most bat species while also achieving a complete inventory of the entire bat assemblage at our study area. It is important to note that our results may have differed slightly had we sampled more sites or in areas with varying levels of species richness or years since WNS onset (Skalak et al. 2012; Barr et al. 2021). Our results may therefore be most applicable to researchers with limited resources or to those sampling in areas where access is restricted, such as other military installations. We also acknowledge that our sampling effort may have been slightly higher had we used a more conservative threshold (e.g., maximum likelihood estimator P value of <0.05; USFWS 2023) for determining species presence at a site.

Our analyses indicate that a considerable level of effort is required to detect WNS-affected *Myotis* species and tricolored bats in areas where the disease has been well established and that the sampling duration currently recommended by the USFWS and NABat guidelines may not be adequate to detect these species under certain conditions. Species occurrence and activity data from long-term acoustic studies may help to further refine existing survey guidelines for listed bat species and may inform guidelines for additional species in the future.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Passive acoustic monitoring efforts at Fort Indiantown Gap National Guard Training Center in Annville, Pennsylvania, from April to October 2018 to 2021. Each row represents a single detector deployment, and columns represent the year (YEAR), site (SITE_ID), date that we initially deployed (DEPLOYMENT) and retrieved (RETRIEVAL) each detector each year, number of successful detector-nights (EFFORT), geographic location information (latitude LAT and longitude LONG in decimal degrees), and habitat feature sampled (HABITAT).

Available: https://doi.org/10.3996/JFWM-23-021.S1 (16 KB XLSX)

Data S2. Bat acoustic detection records from Fort Indiantown Gap National Guard Training Center in Annville, Pennsylvania, from April to October 2018 to 2021. Each row represents a unique sampling (detector) night, and columns represent the date (DATE), site (SITE_ID), and number of detections for each bat species per night.

Available: https://doi.org/10.3996/JFWM-23-021.S2 (188 KB XLSX)

Table S1. Model with covariates, Akaike's information criterion adjusted for small sample size (AIC_c), difference in AIC_c between a model and the model with the lowest AIC_c value (ΔAIC_c), model weights (w_i), and number of model parameters (K) for the set of models used to predict site occupancy (Ψ) given the probability of detection (p) of eight bat species at Fort Indiantown Gap National Guard Training Center in Annville, Pennsylvania, during the spring (1 April to 14 May) 2018 to 2021. Species include big brown bat *Eptesicus fuscus*, eastern red bat *Lasiurus borealis*, hoary bat *L. cinereus*, silver-haired bat *Lasionycteris noctivagans*, eastern small-footed myotis *Myotis leibii*, little brown myotis *M. lucifugus*–Indiana myotis *M. sodalis,* northern long-eared myotis *M. septentrionalis*, and tricolored bat *Perimyotis subflavus*. Covariates were minimum nightly temperature (temp), mean nightly relative humidity (rh), mean nightly wind speed (wind), Julian date (date), and survey year (year).

Available: https://doi.org/10.3996/JFWM-23-021.S3 (29 KB DOCX)

Table S2. Parameter estimates, standard errors (SE), and 95% confidence intervals (CI) for covariates in the best-supported model that we used to predict site occupancy (Ψ) given the probability of detection (p) of eight bat species at Fort Indiantown Gap National Guard Training Center, Pennsylvania, during the spring (1 April to 14 May) 2018 to 2021. Informative covariates (95% confidence intervals that do not overlap 0) are denoted with an asterisk (*). Species include big brown bat *Eptesicus fuscus*, eastern red bat *Lasiurus borealis*, hoary bat *L. cinereus*, silver-haired bat *Lasionycteris noctivagans*, eastern small-footed myotis *Myotis leibii*, little brown myotis *M. lucifugus*–Indiana myotis *M. sodalis,* northern long-eared myotis *M. septentrionalis*, and tricolored bat *Perimyotis subflavus*.

Available: https://doi.org/10.3996/JFWM-23-021.S4 (22 KB DOCX)

Table S3. Model with covariates, Akaike's information criterion adjusted for small sample size (AIC_c), difference in AIC_c between a model and the model with the lowest AIC_c value (ΔAIC_c), model weights (w_i), and number of model parameters (K) for the set of models that we used to predict site occupancy (Ψ) given the probability of detection (p) of eight bat species at Fort Indiantown Gap National Guard Training Center in Annville, Pennsylvania, during the summer (15 May to 15 August) 2018 to 2021. Species include big brown bat *Eptesicus fuscus*, eastern red bat *Lasiurus borealis*, hoary bat *L. cinereus*, silver-haired bat *Lasionycteris noctivagans*, eastern small-footed myotis *Myotis leibii*, little brown myotis *M. lucifugus*–Indiana myotis *M. sodalis*, northern long-eared myotis *M. septentrionalis*, and tricolored bat *Perimyotis subflavus*. Covariates were minimum nightly temperature (temp), mean nightly relative humidity (rh), mean nightly wind speed (wind), Julian date (date), and survey year (year).

Available: https://doi.org/10.3996/JFWM-23-021.S5 (29 KB DOCX)

Table S4. Parameter estimates, standard errors (SE), and 95% confidence intervals (CI) for covariates in the best-supported model that we used to predict site occupancy (Ψ) given probability of detection (p) of eight bat species at Fort Indiantown Gap National Guard Training Center, Pennsylvania, during the summer (15 May to 15 August) 2018 to 2021. Informative covariates (95% confidence intervals that do not overlap 0) are denoted with an asterisk (*). Species include big brown bat *Eptesicus fuscus*, eastern red bat *Lasiurus borealis*, hoary bat *L. cinereus*, silver-haired bat *Lasionycteris noctivagans*, eastern small-footed myotis *Myotis leibii*, little brown myotis *M. lucifugus*–Indiana myotis *M. sodalis*, northern long-eared myotis *M. septentrionalis*, and tricolored bat *Perimyotis subflavus*.

Available: https://doi.org/10.3996/JFWM-23-021.S6 (29 KB DOCX)

Table S5. Model with covariates, Akaike's information criterion adjusted for small sample size (AIC_c), difference in AIC_c between a model and the model with the lowest AIC_c value (ΔAIC_c), model weights (w_i), and number of model parameters (K) for the set of models that we used to predict site occupancy (Ψ) given the probability of detection (p) of bat species at Fort Indiantown Gap National Guard Training Center in Annville, Pennsylvania, during the fall (16 August to 31 October) 2018 to 2021. Species include big brown bat *Eptesicus fuscus*, eastern red bat *Lasiurus borealis*, hoary bat *L. cinereus*, silver-haired bat *Lasionycteris noctivagans*, eastern small-footed myotis *Myotis leibii*, little brown myotis *M. lucifugus*–Indiana myotis *M. sodalis*, northern long-eared myotis *M. septentrionalis*, and tricolored bat *Perimyotis subflavus*. Covariates were minimum nightly temperature (temp), mean nightly relative humidity (rh), mean nightly wind speed (wind), Julian date (date), and survey year (year).

Available: https://doi.org/10.3996/JFWM-23-021.S7 (29 KB DOCX)

Table S6. Parameter estimates, standard errors (SE), and 95% confidence intervals (CI) for covariates in the best-supported model that we used to predict site occupancy (Ψ) given the probability of detection (p) of eight bat species at Fort Indiantown Gap National Guard Training Center, Pennsylvania, during the fall (16 August to 31 October) 2018 to 2021. Informative covariates (95% confidence intervals that do not overlap 0) are denoted with an asterisk (*). Species include big brown bat *Eptesicus fuscus*, eastern red bat *Lasiurus borealis*, hoary bat

L. cinereus, silver-haired bat *Lasionycteris noctivagans*, eastern small-footed myotis *Myotis leibii*, little brown myotis *M. lucifugus*–Indiana myotis *M. sodalis*, northern long-eared myotis *M. septentrionalis*, and tricolored bat *Perimyotis subflavus*.

Available: https://doi.org/10.3996/JFWM-23-021.S8 (22 KB DOCX)

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