

Temporal and spatial changes in *Myotis lucifugus* acoustic activity before and after white-nose syndrome on Fort Drum Army Installation, New York, USA

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Changes to bat distribution and habitat associations at the local to sub-landscape scale in the post white-nose syndrome (WNS) environment have received little attention to date despite being critical information for managers. To better understand the spatial nature of bat population declines, we modelled both activity patterns and occupancy from acoustic surveys for the *Myotis lucifugus* (little brown bat) on Fort Drum Military Installation in New York, USA over 15 summers (2003–2017) that span the pre-WNS, WNS-advent (2008) and post-WNS periods, using a set of generalized linear mixed models and geospatial analysis. Our best supported model indicated significant differences between years with significant declines in activity post-WNS. *M. lucifugus* activity was most closely associated with woody wetland habitats over the study period, however, the spatial patterns of high activity areas were variable over years, with the areal extent of these high activity areas decreasing post-WNS. Our best supported occupancy model varied by year. However, the null occupancy model [$\Psi(\cdot)$] was either competing (within 2 Δ AIC units) or was the best supported model. Meaning that none of our environmental variables seemed to impact occupancy, and when they did, these differences were not significant. There was high disagreement between our relative activity models and predictions compared to our occupancy models, suggesting that geographic spatial scale and the resolution of the data impacts model outcome. Our results indicate that continued acoustic monitoring of bat species in the Northeast to assess ongoing temporal and spatial changes in habitat associations and to provide direction for future mist-netting studies should rely more on relative activity as the metric of choice rather than site occupancy.

Key words: acoustic monitoring, GIS, *Myotis lucifugus*, occupancy model, relative activity, white-nose syndrome

INTRODUCTION

The fungal pathogen, *Pseudogymnoascus destructans*, causative agent of white-nose syndrome (WNS), was first documented in the United States in 2006 in upstate New York, U.S.A (Blehert *et al.*, 2009). Since then, the disease agent has moved rapidly throughout the Northeast, mid-South and Midwest, as well as throughout much of eastern and south-central Canada (U.S. Geological Survey, 2019). WNS has been found to infect eight species of cave-dwelling bats in eastern North America: the federally endangered *Myotis sodalis* (Indiana bat), the federally threatened *M. septentrionalis* (Northern long-eared bat), *M. leibii* (Eastern small-footed bat), *M. lucifugus* (little brown bat), the federally

endangered *M. grisescens* (gray bat), *M. austroriparius* (Southeastern bat), *Eptesicus fuscus* (big brown bat), and *Perimyotis subflavus* (tri-colored bat). Infecting the epidermis of hibernating bats, the fungus causes abnormal frequent arousal through winter leading to loss of critical fat reserves and disruption of water balance (Cryan *et al.*, 2010; Frick *et al.*, 2010; Meteyer *et al.*, 2012).

Among impacted species, *M. lucifugus*, *M. septentrionalis*, *M. sodalis*, and *P. subflavus* have had the most dramatic changes in activity patterns, abundance, and distribution (Blehert *et al.*, 2009; Frick *et al.*, 2010; Brooks, 2011; Ford *et al.*, 2011). Prior to the onset of WNS, populations of *M. lucifugus* were either stable or increasing, and was one of the most common and abundant bats in North

America. Yet, since the discovery of WNS, populations of *M. lucifugus* have declined precipitously, with estimates of loss being greater than 90% in the Northeast (Frick *et al.*, 2010; Dzal *et al.*, 2011; Jachowski *et al.*, 2014a; Ingersoll *et al.*, 2016). Some individuals of *M. lucifugus* do show healed wing membranes, post-winter survival, and reproduction after infection by *P. destructans* (Dobony *et al.*, 2011; Dobony and Johnson, 2018). However, significant mortality throughout the winter, poor female physiological condition, and energetic demands to repair dermal tissue have resulted in reproductive rates to become variable, limiting population recovery (Dzal *et al.*, 2011; Francel *et al.*, 2012; Langwig *et al.*, 2012). As a result, pre-WNS trends of activity levels increasing in mid-summer that are consistent with summer recruitment and reproduction, post-WNS often have declined (Ford *et al.*, 2011). Moreover, WNS impacts have been shown to significantly modify the spatial and temporal niche partitioning among bat communities, resulting from the elimination in interspecific competition of WNS-impacted bat species with those unaffected. Specifically, the reduction in *M. lucifugus* has been followed by an activity increase of non-WNS affected species that can utilize the spatial and temporal conditions that *M. lucifugus* favor (Jachowski, 2014a). This dramatic change in population size in a relatively short time frame makes *M. lucifugus* a good model species to evaluate inter- and intraspecific interactions, and their relationship with environmental conditions.

The scarcity of data encompassing pre-WNS and post-WNS years for most positive WNS regions has made it difficult to compare the relative change in bat activity and occupancy between the two periods. However, extensive long term, mist-netting and acoustic monitoring of bat activity, occupancy, and distribution at Fort Drum Military Installation (Fort Drum) in northern New York is an exception (Ford *et al.*, 2011). Much of this monitoring began in response to both known hibernacula nearby to the Installation and the presence of the federally endangered *M. sodalis* on the installation during the summer (Jachowski *et al.*, 2014b). Continuous monitoring from 2003 to present has allowed researchers to document changes in bat numbers, activity, and physiological status between pre- and post-WNS time periods (Dobony *et al.*, 2011; Ford *et al.*, 2011; Coleman *et al.*, 2014a, 2014b, 2014c; Dobony and Johnson, 2018). Previous acoustic surveys and mist-netting has shown that overall activity patterns have shifted among all species between pre- and

post-WNS years at Fort Drum. However, the significance of these changes is based on the species-specific susceptibility to WNS, with *M. septentrionalis*, *M. sodalis*, and *M. lucifugus* bat activity patterns decreasing the most in the years subsequent to WNS presence (Dobony *et al.*, 2011; Ford *et al.*, 2011). In response to the rapid expansion of WNS, and the steep declines in several of these bat species, this long-term monitoring program has provided a unique opportunity to observe and understand the ecological dynamics of a novel invasive disease. Secondly, these data have implications for understanding the impact to threatened and endangered species, how additional species might become endangered, and how land managers could enhance day-roosting and foraging habitat for remaining bats to compensate for WNS impacts.

Understanding the abiotic and biotic processes that affect how and why species are distributed across a landscape is central for researchers and managers studying biological organisms (Miller, 2010). This importance is exacerbated when dealing with rare or declining species, where changing environmental conditions, such as an outbreak of disease, imply ecological consequences to certain species (Rodhouse *et al.*, 2012). Thus, modelling species abundance, occurrence, distribution, and the metrics associated with changes in distribution have been used extensively to address changing populations within a landscape, especially in bats (Jaberg and Guisan, 2001; O'Shea *et al.*, 2003; Ford *et al.*, 2011; Rodhouse *et al.*, 2012). There are two uses of a model: to explain aspects of the real world, i.e., biological processes, and to predict across space and time (Nally, 2000; Borcard *et al.*, 2011; Sainani, 2014). Species distribution models are widely used as predictors of species presence, habitat suitability and range distribution. This technique often is required for natural resource research, management, and conservation (Franklin, 2010). At its basic form, species distribution can be categorized by the presence of a species and the space in which a species occupies (Franklin, 2010; Borcard *et al.*, 2011). This presents challenges to modeling distribution, activity, and occupancy, as communities and individuals exist in complex spatial arrangements and structures. Whereas models may try to predict the distribution, activity, or occupancy of wildlife populations onto a landscape, it is assumed that biotic distributions across different sampling sites are independent from each other (Franklin, 2010; Borcard *et al.*, 2011). This assumption rarely holds true. In reality, neighboring sites share both biotic and

abiotic factors, i.e., competition, weather events, and dispersal, where upon similarities between sites become more dependent with the decrease in distance between them (Dray *et al.*, 2006; Dormann *et al.*, 2007; Franklin, 2010; Borcard *et al.*, 2011). This spatial autocorrelation can lead to erroneous conclusions about how certain parameters influence species distributions (Franklin, 2010; Borcard *et al.*, 2011). As an example, in modeling species distributions using environmental conditions, without considering spatial autocorrelation, estimates for such covariates may be either over- or underrepresented, diminishing the accuracy of models (e.g., insects — González-Megías *et al.*, 2005; birds — Diniz-Filho and Bini, 2005; and mammals — Peakall *et al.*, 2003). As such, components such as scale, size of sampling units, distance between sites, and extent of the study site can interact with ecological processes and patterns that complicate occupancy and distribution modeling efforts (Borcard *et al.*, 2011).

Effective conservation planning at relatively large scales, such as at Fort Drum, require the understanding of the distribution and relative activity of a species, as well as the topographic and land cover characteristics influencing species presence at an individual site (Erickson and West, 2003; Ford *et al.*, 2005). We used *M. lucifugus* as a model species to study disease dynamics impacts as it relates to local and regional distribution, and in turn, develop practical research and management techniques appropriate for assessing the spatio-temporal changes in bat activity. We predicted that *M. lucifugus* would show marked declines in activity across Fort Drum over the duration of the study, that residual activity would become increasingly concentrated along riparian systems and that traditional occupancy analysis for a rare, but still widespread species would fail to convey full information on WNS-caused declines.

Accordingly, our major objectives were to 1) identify suitable site characteristics that affect *M. lucifugus* relative activity; 2) assess spatio-temporal changes in activity across the landscape; 3) develop predictive occurrence models for the wider Fort Drum landscape; and 4) determine how relative activity models and predictions compare to standard occupancy analysis and predictions using a highly mobile species as the model organism.

MATERIALS AND METHODS

Study Area

We conducted our study at Fort Drum Military Installation in Jefferson and Lewis counties in northwestern New York,

USA. Fort Drum is a 43,750 ha U.S. Military Installation situated where the Eastern Ontario Plains, St. Lawrence Valley, Western Adirondack Transition, Indian River Transition, and Black River Valley ecoregions converge. The Niagara Escarpment, which lies 10–15 km west, contains limestone (Karst) formation caves used as winter hibernacula by bats (Ford *et al.*, 2011). Approximately 57% of the installation (ca. 25,000 ha) was forested with associations of mature northern hardwood types of *Acer saccharum* (Sugar Maple), *Fagus grandifolia* (American beech), *Fraxinus americana* (white ash), and *Pinus strobus* (white pine). Early successional habitat was dominated by *Acer rubrum* (red maple), *Betula populifolia* (gray birch) and *Populus tremuloides* (quaking aspen). Beaver (*Castor canadensis*) ponds, small lakes, wet meadows and other wetland systems comprised approximately 20% of the land cover (ca. 8,000 ha). Extensive development was concentrated within the cantonment area and certain firing ranges encircling the main impact area; only scattered training facilities and other structures were found throughout the relatively undeveloped maneuver areas in the remainder of the installation. Elevations ranged from 125–278 m a.s.l.

The bat fauna of Fort Drum consists of nine species including: *E. fuscus*, *M. leibii*, *M. lucifugus*, *M. septentrionalis*, *M. sodalis*, and *Perimyotis subflavus* along with three species unaffected by WNS, *Lasiurus borealis* (Eastern red bat), *Lasiorycteris noctivagans* (silver-haired bat), and *Lasiurus cinereus* (hoary bat) (Ford *et al.*, 2011; Coleman *et al.*, 2014a, 2014b).

Acoustic Sampling

To assess *M. lucifugus* presence and activity, we examined a long-term collection of echolocation recordings from Fort Drum from the summers of 2003–2017 that has been collected by installation managers for ongoing monitoring tasks (Fig. 1). As such, our site selections were not random, but were systematically chosen to represent the range of habitat conditions encountered on Fort Drum and to provide data for regulatory clearance of land management and training activities. Sampling intensity varied across years with repeat site visits for 98% of locations across the years (Table 1). We excluded individual nights when detectors at individual sites failed to operate completely from sundown to sunrise. From May through early September for all years, we used Anabat II detectors connected to a compact flash-storage zero-crossings analysis-interface module (ZCAIM), as well as SD1 and SD2 detectors using the same transducer model (Titley Electronics, Ballina, NSW, Australia). From 2003–2011, we placed Anabat units in weatherproof boxes, but left the microphone exposed. In 2012 and onwards, we attached a PVC tube to protect the microphone from rain to the weatherproofing boxes (Britzke *et al.*, 2013). Following Ford *et al.* (2011) and Coleman *et al.* (2014b, 2014c), we placed each unit on a 1.5 m tripod and adjusted it so that sound could enter the exposed microphone or later the PVC tube at an angle of 45° (Weller and Zabel, 2002). Our survey sites primarily were located near features associated with known higher bat activity, such as interior forest canopy gaps, open water, streams, and wetland habitats (Ford *et al.*, 2005, 2006). Additionally, some sites were located along linear features that bats favor for travel (Verboom and Huitema, 1997), such as unimproved, gravel, secondary roads used for regular vehicular traffic or defined dirt, grass, and/or gravel trails used for military training and recreational use. Detectors were positioned to face road/trail corridors, forest canopy gaps or towards more

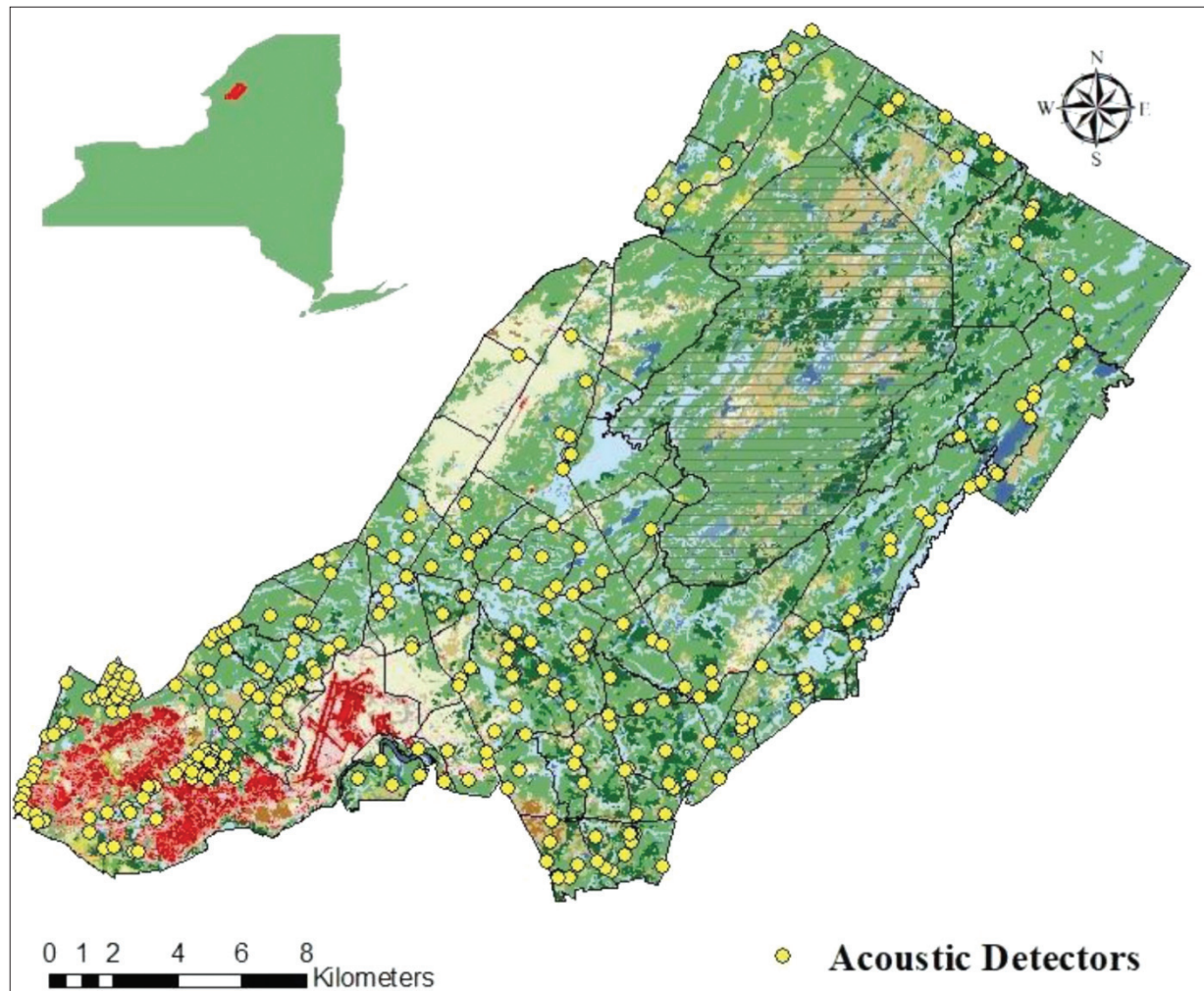


FIG. 1. Acoustic detector locations on Fort Drum, New York, USA during the summer, 2003–2017. Two hundred eighty-nine individual sites were sampled across 15 years within a variety of habitats and patch configurations, with a total of 8,373 detector nights. Hash marks indicate impact zone where no sampling occurred. Inset of New York State on right upper corner, with Fort Drum outlined in red

open water to maximize acoustic recording quality. Following acoustic data acquisition, we visually assessed recorded echolocation passes and scanned in Analog W (Titely Scientific Inc., Columbia MO) to remove extraneous non-bat noise. Cleaned files were then analyzed using Kaleidoscope Pro classifier 4.2.0 (Wildlife Acoustics Inc., Maynard MA), under the recommended settings of the U.S. Fish and Wildlife Service using 0 for the program sensitivity setting, and 3 pulse minimum (U.S. Fish and Wildlife Service, 2017a). However, for these analyses, we did not exclude nights with inclement weather, i.e., precipitation, as would be recommended for *M. sodalis* surveys for regulatory clearance work (U.S. Fish and Wildlife Service, 2017a).

Predictive Mapping

Previous research has shown that topographic characteristics (i.e. elevation), land cover variables (i.e. canopy cover, habitat, and water bodies), and presence of linear features (i.e. trails and roads) are important determinants of bat activity and occupancy (Humes *et al.*, 1999; Law and Chidel, 2001; Erickson and West, 2003; Brooks and Ford, 2005; Ford *et al.*, 2005; Wolbert

et al., 2014). We calculated elevation (m a.s.l.), percent canopy cover, land cover, distance to water (m), and distance to road/trail (m) to include as variables in our *M. lucifugus* occupancy and relative activity models for Fort Drum. We derived elevation data from U.S. Geological Survey 1/3 arc-second (10 m resolution) digital elevation models (DEM). We estimated elevation for each point by extracting the values of the DEM to our sample locations. We derived percent canopy cover and land cover from the Multi-Resolution Land Characteristics Consortium (MRLC) National Land Cover Database (MRLC, 2017) at 30 m. Because our acoustic locations varied through time, we estimated percent canopy cover for each detector and for each year by extracting the values of the most recent canopy cover layer respective to the sample year from the MRLC at 2003, 2006, and 2011, or by substituting those in later years where canopy cover was physically recorded at the site. Additional land cover data was also obtained from Fort Drum to improve the accuracy of our derived MRLC layer. We used Spatial Analyst Toolbox to reclassify our Fort Drum land cover data into five general categories (forest, shrub land, wetland, development, and barren). We acquired wetland data from the

TABLE 1. Acoustic sampling intensity and variation by year across Fort Drum, New York, during the summer, 2003–2017, with minimum and maximum number of nights, mean number of nights, and total number of sites sampled for each year

Year	Number of detector nights/site			Number of sites
	Minimum	Maximum	Mean	
2017	64	83	77.8	5
2016	8	28	15.0	81
2015	2	118	11.0	129
2014	81	131	103.6	5
2013	2	187	29.6	49
2012	1	223	38.9	55
2011	1	128	17.8	57
2010	1	6	2.6	19
2009	2	2	2.0	13
2008	1	2	1.8	12
2007	2	2	2.0	15
2006	2	2	2.0	18
2005	1	2	1.8	21
2004	1	3	1.9	17
2003	1	1	1.0	5

National Wetlands Inventory (U.S. Fish and Wildlife Service, 2017b) along with road/ trail layers from Fort Drum Military Installation. We then used the Euclidean Distance in Spatial Analyst Toolbox in ArcGIS 10.5 (ESRI, Inc., Redlands, CA), in conjunction with derived land cover road/trail, and NWI to calculate and assign variable distances to survey sites. We used the observed cell values for each raster layer at Fort Drum to predict relative bat activity levels. We used Program R (ver. 3.5.1 — R Core Team, 2018) to rearrange the individual raster layers into vectors and conversely centered and scaled each value with respect to the mean and standard deviation of our sampled covariates. We combined the associated vectors into a data frame and used the predict function in R to predict our global relative activity model onto the new data frame, encompassing all of Fort Drum, for each year. Due to differences in resolution between layers, we used ArcGIS 10.5 to visualize the predicted relative activity for each year across Fort Drum at 30 m resolution, as all other layers could be scaled to this resolution.

Activity Analysis

To assess *M. lucifugus* activity relative to environmental characteristics on Fort Drum, we fit a generalized linear mixed model (GLMM) package glmmADMB in program R (Bolker *et al.*, 2012; R Core Team, 2018) using a negative binomial distribution on our data from 2003–2017 (Fournier *et al.*, 2012). We used site as a random effect to account for repeated samples at individual sites, and included percent canopy cover, elevation, distance to road/trail, distance to water, land cover (both at a fine scale, 12 land cover types using NLCD (mixed forest, evergreen forest, deciduous forest, open water, emergent wetland vegetation, woody wetland, scrub/shrub, grass, barren rock, cultivated crop, pasture/hay, and developed) and broad scale (our reclassified land cover types from the Fort Drum land cover dataset)), day, and year as fixed effects (Tables 2 and 3). We included year and date to explain variations in relative activity across time. This allowed for predicting relative activity across Fort Drum for each year. We fit a set of a priori models representing individual hypotheses about activity patterns relative to our four objectives (Tables 2 and 3). We centered and scaled all continuous covariates to aid in model fitting and interpretation. Notably, this puts all continuous variables on the same scale, thereby permitting direct comparisons of effect sizes (Schielzeth, 2010). To assess potential curvilinear effects of certain variables and explore nonlinear relationships between our environmental variables and bat activity, we assessed post hoc models that fit 2nd order polynomials on continuous variables (Royston and Altman, 1994). We then compared models using Akaike's Information Criterion Corrected for small sample size (AICc) (Burnham and Anderson, 2002, 2004).

Accounting for Spatial Autocorrelation

We assessed spatial autocorrelation among acoustic detector sites using Moran's I and neighborhood matrices (Dray *et al.*, 2006). Our goal was to ensure that we could predict *M. lucifugus* relative activity across the landscape using our global model between sampled sites. In addition, we used spatial correlograms in package pgirmess (ver. 1.6.9) in R (Giraudoux *et al.*, 2017) to assess autocorrelation in *M. lucifugus* relative activity per site night. We then used the same method to assess our fitted models' residuals to demonstrate how spatial autocorrelation is

TABLE 2. Variables included in candidate models describing bat activity and occupancy with justification and supporting literature for each parameter. Candidate models represented bat activity on Fort Drum during the summer, 2003–2017

Parameter	Justification	Supporting literature
Date	Bat activity varies in intensity and spatially by date	O'Shea <i>et al.</i> , 2003; Perry <i>et al.</i> , 2010; Ford <i>et al.</i> , 2011
Year	WNS affect bats have lower activity post-WNS than pre-WNS	Frick <i>et al.</i> , 2010; Ford <i>et al.</i> , 2011; Coleman and Reichard, 2014
Percent canopy cover	Bats may be attracted to openings within canopy	Humes <i>et al.</i> , 1999; Erickson and West, 2003
Elevation	Bat activity varies along an elevation gradient	Wolbert <i>et al.</i> , 2014
Distance to road/trail	Bats use linear features such as roads and trails as foraging habitat	Law and Chidel, 2001; Menzel <i>et al.</i> , 2002; Caras and Korine, 2009; Hein <i>et al.</i> , 2009
Distance to water	Bats utilize water bodies as drinking sources	Brooks and Ford, 2005; Ford <i>et al.</i> , 2005; Adams and Thibault, 2006; Loeb and O'Keefe, 2006
Habitat	Bats select preferential habitats associated with foraging and morphology	Jung <i>et al.</i> , 1999; Brooks and Ford, 2005; Loeb and O'Keefe, 2006; Schirmacher <i>et al.</i> , 2007

TABLE 3. Variables included in candidate models representing bat activity and occupancy on Fort Drum during the summer, 2003–2017. Variables were used in different combinations, and highly correlated variables were not included within a single candidate model

Variable name	Variable Explanation
Date	Day of year
Year	Years expanding our study (2003–2017)
Canopy cover	Percent canopy cover
Elevation	Elevation gradient across Fort Drum
Distance to road/trail	Distance of sampling point from road/trail
Distance to water	How far sampling point is from a water source
Habitat—Fine scale	Included all landcover types associated with NLCD
Habitat—Broad scale	Included general habitats: forest, wetlands, shrub, open water, development, and barren

addressed and reduced through the use of our GLMM (Dormann *et al.*, 2007). We then used package *vegan* (ver. 2.5-5) in R (Oksanen *et al.*, 2018) to fit a redundancy analysis using the function *varplot* to assess the total variation explained by our significant positive spatial vectors.

Occupancy Analysis

Under USFWS *M. sodalis* survey guidelines, acceptance of presence of *M. sodalis* must have a maximum likelihood estimate (MLE), the probability that a species is misclassified as present when in fact it is absent, $\alpha \leq 0.05$ threshold (U.S. Fish and Wildlife Service, 2017a). Accordingly, we applied this same filter to *M. lucifugus* and grouped automated identification nightly MLE values into two categories for each individual year. We considered MLE values ≤ 0.05 to indicate species nightly presence, values above that were considered to indicate absence. We then used the resulting binary data as species detection histories for each site to model occupancy for *M. lucifugus* (MacKenzie *et al.*, 2002). We created a set of occupancy models representing a priori hypotheses in program PRESENCE, Version 12.10 (U.S. Geological Survey, Patuxent, MD) to estimate probabilities of occupancy (Ψ) and detection (ρ) for *M. lucifugus* from 2003–2017. Due to limited sampling effort (maximum nightly sample being two nights) for years prior to WNS (2003–2007), we combined this data together representing pre-WNS, under the assumption that site wide occupancy did not change across pre-WNS years. For each year, we fit all possible subsets incorporating the same covariates used in our relative activity models, including: percent canopy cover, elevation, distance to road/trail, distance to water, and land cover (both at fine and broad scale) as covariates that may affect probabilities of occupancy and detection. We used AICc to rank models and compare weights of evidence among models in the candidate set (Burnham and Anderson, 2002, 2004).

RESULTS

From 2003 to 2017, we sampled 8,373 total detector nights, encompassing 289 individual sites across Fort Drum (Fig. 1). Over the entire study duration, this accounted for 1,022,188 individual files, of which 472,849 were identified by the software as bat passes from the nine bat species, including *M. lucifugus* ($n = 76,916$ passes). We found 80

significantly positive eigenvectors associated with site locations. Spatial eigenvectors only explained 0.07% of the variation in *M. lucifugus* activity. The best-approximating model included date, percent canopy cover, land cover (on a broad scale level), distance to road/trail, and year, with only three other models within four Δ AIC units (Table 4). In all models, date, canopy cover, and distance to road/trail appeared to significantly affect relative activity of *M. lucifugus* ($P \leq 0.05$), where *M. lucifugus* activity was negatively correlated with each (Table 5). Only wetland habitat (including emergent and woody wetlands) was significantly different from zero having a positive effect on *M. lucifugus* activity ($P \leq 0.05$) (Table 5). Additionally, the years' post-WNS (2010–2017) were significantly different from zero, with a negative relationship with *M. lucifugus* activity (Table 5). This overall negative trend through the years is illustrated by the *M. lucifugus* predicted relative activity maps prior to WNS, 2004–2007, during the initial WNS onset, 2008–2009, full WNS impact, 2010–2015 and post-WNS localized stability (Fig. 2) and the fitted regression line on the mean echolocation passes for each year (Fig. 3).

Myotis lucifugus presence was denoted during at least 1 sampling event, at any site, for all years examined. Of our predictive models tested, the best supported model varied by year, however, the model where occupancy estimates were constant with regard to environmental factors [$\Psi(\cdot)$] was either competing (models within two Δ AIC units) or was the best supported model (Table 6). The exception was 2013 where the best supported model included habitat as an important predictor of occurrence (Table 6). Beyond these, other tested models that included variables such as elevation, percent canopy cover, distance to water, distance to road/trail, and habitat had little empirical support for estimating occupancy, but were predictors for describing detection (Table 6). Occupancy estimates varied for our best supported

TABLE 4. Rankings of models predicting *M. lucifugus* activity at Fort Drum during the summer 2003–2017, with k (number of parameters), Akaike's information criteria (AIC) value, Akaike's information criteria Corrected (AIC_c) value corrected for small sample size, difference in AIC_c value between best supported model and i^{th} model (ΔAIC_c), w_i (model weight), and ER_i (evidence ratio)

Model	k	AIC	AIC _c	ΔAIC_c	w_i	ER_i
Day + Day ² + Canopy cover + Canopy cover ² + Habitat_broadscale + Distance to road/trail + Distance to road/trail ² + Year	25	32502.4	32502.6	0	0.44	1.00
Day + Day ² + Canopy cover + Canopy cover ² + Distance to road/trail + Distance to road/trail ² + Year	21	32503.2	32503.3	0.75	0.30	1.45
Day + Day ² + Canopy cover + Canopy cover ² + Habitat_broadscale + Distance to road/trail + Distance to road/trail ² + Distance to water + Distance to water ² + Year	27	32504.0	32504.2	1.63	0.20	2.26
Day + Day ² + Canopy cover + Canopy cover ² + Elevation + Elevation ² + Habitat_broadscale + Distance to road/trail + Distance to road/trail ² + Distance to water + Distance to water ² + Year	29	32506.4	32506.6	4.06	0.06	7.60

model in each year (Table 7). Years with small number of sampling sites (five sites for 2014 and 2017) had derived occupancy estimates but confidence intervals that ranged from 0 to 1. Conversely, years with large numbers of sampling sites (129 sites for 2015) had occupancy estimates much lower than other years (0.265 versus 0.505, the next lowest metric). For 2011 and 2013, where fine scale habitat metrics were in our best supported model,

occupancy estimates per habitat varied 0.678 to 0.837 for 2011 and 0.571 to 0.774 for 2013 (Table 8).

DISCUSSION

Irrespective of known habitat associations and correlates for *M. lucifugus*, our findings corroborate results by (Brooks, 2011; Dzal *et al.*, 2011; Ford *et al.*, 2011; Ingersoll *et al.*, 2016) that relative *M. lucifugus* activity has significantly decreased in years following WNS. Prior to WNS, *M. lucifugus* was one of the most abundant and common species of bats in North America, with seasonal increases in activity and abundance consistent with spring arrival from hibernation areas and juvenile volancy in mid-summer (Frick *et al.*, 2010; Ford *et al.*, 2011). Collapse of such a prominent species in a short time period, > 90% in a single year (Bleher *et al.*, 2009; Frick *et al.*, 2010), has had both inter and intraspecific consequences for the bat community at Fort Drum and presumably elsewhere in the Northeast (Jachowski *et al.*, 2014a). As the effects of WNS on bats continue to cause declines in the distribution and abundance of affected bat species (Frick *et al.*, 2010; Langwig *et al.*, 2012), there is an increased need to employ acoustic sampling in addition to (or in place of) mist-netting to adequately describe changes in both relative activity and occupancy. *M. lucifugus* is a good model species intrinsic to understanding the relationship between disease dynamics, species susceptibility, and environmental conditions. Fort Drum can be used as a model to identify suitable environmental characteristics important for *M. lucifugus*, to understand disease dynamics as it relates to local and regional population declines, and to synthesize these declines into relative activity and occupancy modeling.

TABLE 5. Parameter estimates of best supported model predicting *M. lucifugus* activity at Fort Drum during the summer, 2003–2017

Parameter	Estimate	SE	z	$P(> z)$
Wetlands	3.63	1.17	3.11	0.002
Date	0.03	0.03	1.08	0.282
Date ² , a	-0.66	0.02	-29.78	< 0.001
Canopy cover	-0.69	0.20	-3.49	< 0.001
Canopy cover ² , a	-0.61	0.19	-3.14	0.002
Developed	-1.84	1.00	-1.84	0.065
Forest	-1.29	0.81	-1.59	0.112
Shrub	-1.20	0.86	-1.39	0.163
Open Water	-0.46	0.82	-0.56	0.577
Distance to road/trail	-0.46	0.15	-2.98	0.003
Distance to road/trail ² , a	0.06	0.02	2.61	0.009
Year2004	2.40	0.89	2.70	0.007
Year2005	1.00	0.88	1.14	0.254
Year2006	0.85	0.89	0.95	0.341
Year2007	1.57	0.91	1.73	0.084
Year2008	0.10	0.91	0.11	0.912
Year2009	0.56	0.84	0.67	0.505
Year2010	-1.97	0.88	-2.23	0.026
Year2011	-2.13	0.86	-2.48	0.013
Year2012	-2.63	0.86	-3.07	0.002
Year2013	-2.43	0.86	-2.83	0.005
Year2014	-2.07	0.86	-2.41	0.016
Year2015	-2.20	0.86	-2.55	0.011
Year2016	-1.53	0.85	-1.79	0.073
Year2017	-1.86	0.86	-2.16	0.031

^a — Quadratic term

Relative Activity

The use of models incorporating relative activity to describe changes in bat communities is widely used (Law and Chidel, 2001; Brooks and Ford, 2005; Brooks, 2011; Dzal *et al.*, 2011; Ford *et al.*, 2011; Ingersoll *et al.*, 2016). For our models of *M. lucifugus* relative activity, date (which indirectly incorporates weather influences), percent canopy cover, and distance to road/trail were all significantly different from zero and were negatively correlated with *M. lucifugus* activity. Further, it is important to note that the inclusion of nights with inclement weather and during full moon periods in the later years (2012–2017) in conjunction with WNS, could have caused further negative bias in recording echolocation passes. Ford *et al.* (2011)

showed that as summer progresses in a post-WNS setting, *M. lucifugus* activity decreased, suggesting limited recruitment. However, our reexamination of presumed volancy dates for juveniles may suggest the temporal decrease reported in Ford *et al.* (2011) may have overestimated the extent of decreased reproduction and recruitment (Nocera *et al.*, 2019). Our sample variation in site placement in regards to distance to road/trail and percent canopy cover, i.e., low to high clutter, allowed us to better assess activity changes relative to these habitat features. Canopy cover and distance to road/trail had significant negative effects on *M. lucifugus* relative activity. This is consistent with research indicating decreasing rates of bat activity and detection power as canopy cover increases, and increased distance of sampling sites from more open corridors as this species is adapted

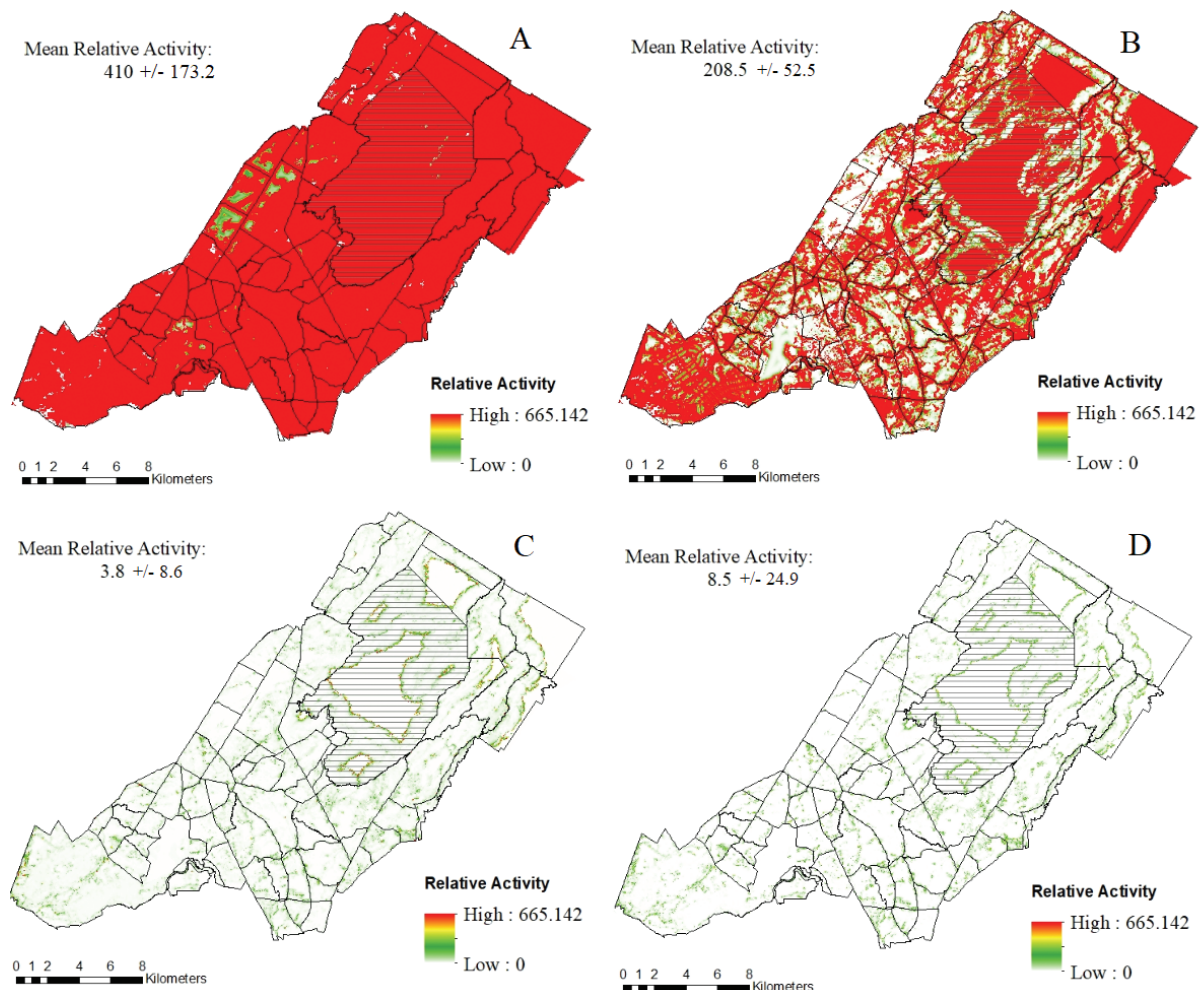


FIG. 2. Predicted relative activity for *M. lucifugus* across Fort Drum during the summer, 2004–2007: A — prior to white-nose syndrome onset, 2008–2009; B — with the initial onset of white-nose syndrome, 2010–2015; C — following full impact of white-nose syndrome, and, 2016–2017; D — as bats display localized stability following white-nose syndrome. Relative activity modeled from mean echolocation passes per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity + SE across all raster cells was calculated for the entire installation

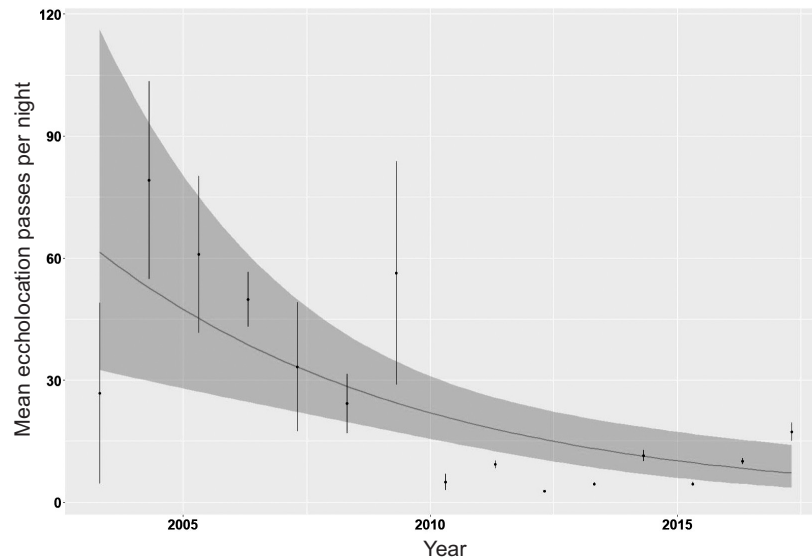


FIG. 3. Long-term acoustical monitoring trends for *M. lucifugus* during the summers, 2003–2017 at Fort Drum. Mean echolocation passes with Standard Error for each year are indicated by points. White-nose syndrome impacts began locally in 2008. The fitted regression line from our best-supported model indicates trend in activity with 95% confidence interval

to foraging in low-clutter environments (Sherwin *et al.*, 2000; Law and Chidel, 2001; Menzel *et al.*, 2002; Weller and Zabel, 2002; Coleman *et al.*,

TABLE 6. Rankings of models predicting *M. lucifugus* occupancy at Fort Drum during the summer, 2003–2017. With model parameters for both occupancy ($\psi(\cdot)$) and detection ($p(\cdot)$), Akaike's information criteria Corrected (AIC_c) value, difference in AIC value between best supported model and i -th model (ΔAIC_c), and w_i (model weight). Model abbreviations are as follows: CC = Canopy cover, DRT = Distance to road/trail, and EV = Elevation

Year	Model	AIC_c	ΔAIC_c	w_i
Pre-WNS	$\psi(\cdot), p(\cdot)$	125.63	0	0.75
2008	$\psi(\cdot), p(\cdot)$	33.07	0	0.73
	$\psi(\text{Habitat}), p(\text{DRT}, \text{CC})$	35.03	1.96	0.27
2009	$\psi(\cdot), p(\text{DRT}, \text{CC})$	32.4	0	0.36
	$\psi(\text{Habitat}), p(\text{DRT}, \text{CC})$	32.4	0	0.36
	$\psi(\cdot), p(\cdot)$	34.28	1.88	0.14
	$\psi(\text{Habitat}), p(\cdot)$	34.29	1.89	0.14
2010	$\psi(\cdot), p(\text{DRT}, \text{CC})$	55.42	0	0.37
	$\psi(\text{Habitat}), p(\text{DRT}, \text{CC})$	56.31	0.89	0.23
	$\psi(\cdot), p(\text{DRT}, \text{CC}, \text{EV})$	56.73	1.31	0.19
	$\psi(\text{Habitat}), p(\text{DRT}, \text{CC}, \text{EV})$	57.7	2.28	0.12
2011	$\psi(\text{Habitat}), p(\text{DRT}, \text{CC})$	1095.65	0	0.58
	$\psi(\cdot), p(\text{DRT}, \text{CC})$	1096.32	0.67	0.42
2012	$\psi(\cdot), p(\cdot)$	1777.66	0	0.53
	$\psi(\text{Habitat}), p(\cdot)$	1779.17	1.51	0.25
	$\psi(\text{Habitat}), p(\text{DRT}, \text{CC})$	1780.05	2.39	0.16
2013	$\psi(\text{Habitat}), p(\text{DRT}, \text{CC})$	1243.12	0	0.99
2014	$\psi(\cdot), p(\cdot)$	684.89	0	0.99
2015	$\psi(\cdot), p(\text{DRT}, \text{CC})$	1729.32	0	0.91
2016	$\psi(\cdot), p(\text{DRT}, \text{Habitat}, \text{CC})$	1417.32	0	0.68
2017	$\psi(\cdot), p(\text{CC}, \text{DRT})$	344.38	0	0.69
	$\psi(\text{h}), p(\text{CC}, \text{DRT})$	345.98	1.60	0.31

2014b). Furthermore, our analysis showed *M. lucifugus* activity was greatest in wetland areas, as did other studies (Zimmerman and Glanz, 2000; Ford *et al.*, 2005; Menzel *et al.*, 2005). Nonetheless, our expansive inclusion of road/trail conditions as one variable type and the close proximity of many wetland survey sites limits somewhat our inference regarding *M. lucifugus* response in other areas of the Northeast where roads are associated with more urbanized environments, experience greater vehicular traffic, or occur in primarily upland conditions.

Through our geospatial analysis of *M. lucifugus* activity, we observed a time lag when *M. lucifugus* began to show significant changes in relative activity due to WNS. Though the disease was first documented at Fort Drum in 2008 (Dobony *et al.*, 2011), our analysis suggests that activity did not greatly decrease until 2010. An artifact of the communicability and spread of WNS on the landscape, where, as this disease spreads among individuals over time and across the region fewer areas offer less protection (Wilder *et al.*, 2011). Unfortunately, our temporal and spatial analysis point to no clear signs of wide scale recovery across the entire landscape, as measured through the surrogate of relative activity, over the 10 years that WNS has affected bats at Fort Drum. Since the first documented case of WNS, regional population declines in the Northeast are estimated to be $> 90\%$ (Blehert *et al.*, 2009; Frick *et al.*, 2010; Dzal *et al.*, 2011). Still, resiliency to long-term WNS exposure has been observed in some remaining *M. lucifugus* locally, whereby some

TABLE 7. Occupancy estimates from yearly top models predicting *M. lucifugus* occupancy at Fort Drum during the summer, 2003–2017. With model parameters for both occupancy (ψ (.)) and detection (p (.)), N sites sampled within that given year, ψ (measure of occupancy), SE (standard error), and 95% CI (confidence interval). Model abbreviations are as follows: CC = Canopy cover, DRT = Distance to road/trail, and EV = Elevation

Year	Model	N	ψ	SE	95% CI
Pre-WNS, 2003–2007	ψ (.), p (.)	87	0.86	0.04	0.75–0.93
2008	ψ (.), p (.)	12	0.84	0.13	0.43–0.97
2009	ψ (.), p (DRT,CC)	13	1.00	0.00	0.00–1.00
2010	ψ (.), p (DRT,CC)	19	0.79	0.14	0.43–0.95
2011	ψ (Habitat), p (DRT,CC)	57	0.51	0.50	0.36–0.65
2012	ψ (.), p (.)	55	0.65	0.08	0.49–0.78
2013	ψ (Habitat), p (DRT,CC)	49	0.50	0.50	0.36–0.64
2014	ψ (.), p (.)	5	1.00	0.00	0.00–1.00
2015	ψ (.), p (DRT,CC)	129	0.26	0.04	0.19–0.35
2016	ψ (.), p (DRT,Habitat,CC)	81	0.79	0.05	0.69–0.87
2017	ψ (.), p (CC,DRT)	5	0.80	0.18	0.31–0.97

individuals continue to show relatively high reproductive effort (Dobony *et al.*, 2011; Frick *et al.*, 2017; Langwig *et al.*, 2017; Dobony and Johnson, 2018). Whether good biological performance for small segments of populations is meaningful for the wider landscape in the near-term is unknown. Still, from 2010 onwards, mean relative activity did increase at Fort Drum, though activity is still low relative to pre-WNS years (Fig. 2). Our work shows that a stabilization of *M. lucifugus* relative activity may be occurring. If more localized colony increases are realized, hopefully, widespread relative activity increases may become measurable in the Northeast in the future. However, because colonies remain small and activity remains primarily concentrated around maternity sites, any individual

colony's spatial distribution may not encompass sampling locations across broader landscapes. Therefore, positive changes in relative activity may be difficult to document on the wider landscape. Additionally, *M. lucifugus* on Fort Drum may be associated with multiple hibernation sites where there could be wide variability in survivorship in these wintering populations. Therefore, additional time may be needed to fully understand accurate population level changes expressed on this summer landscape. It is plausible, given our results, that there is either a continuing population loss but not at the absolute scale when WNS first started to affect *M. lucifugus* regionally (Frick *et al.*, 2017; Langwig *et al.*, 2017) or stable population, in which increases are beyond our power to detect broadly. It is important to note however, that limitations in our sampling design including variation in sampling effort and number of sampling sites between years, did affect our ability to predict activity across Fort Drum temporally over the years surveyed. Although we can accurately predict relative activity across Fort Drum by combining all sites and years into a single model, the variability from the spatial illustrations of *M. lucifugus* at Fort Drum, specifically with pre-WNS years, is in part a sampling artifact causative of yearly differences in sampling effort and size (Figs. 2 and 3). Furthermore, minimal sampling was done in the western portion of Fort Drum and no sampling was done in the Impact Area. Though it is likely that bats utilize these areas, relative activity predictions into these areas should be viewed cautiously.

Occupancy

Across the landscape scale of Fort Drum, occupancy metrics suggest relatively high probability of

TABLE 8. Occupancy estimates from 2011 and 2013 top models predicting *M. lucifugus* occupancy across habitat types at Fort Drum during the summer, 2003–2017. With habitat condition, ψ (measure of occupancy), SE (Standard Error), and 95% CI (Confidence Interval)

Year	Habitat	ψ	SE	95% CI
2011	Deciduous forest	0.84	0.09	0.59–0.95
	Evergreen forest	0.68	0.06	0.54–0.79
	Mixed forest	0.68	0.06	0.54–0.79
	Shrub	0.68	0.06	0.54–0.79
	Developed	0.84	0.09	0.59–0.95
	Emergent wetland	0.84	0.09	0.59–0.95
	Woody wetlands	0.84	0.09	0.59–0.95
	Open water	0.68	0.06	0.54–0.79
2013	Deciduous forest	0.64	0.07	0.49–0.76
	Evergreen forest	0.57	0.04	0.49–0.64
	Mixed forest	0.64	0.07	0.49–0.77
	Shrub	0.64	0.07	0.49–0.76
	Developed	0.64	0.07	0.49–0.76
	Emergent wetland	0.64	0.07	0.49–0.76
	Woody wetlands	0.77	0.11	0.49–0.93
	Open water	0.64	0.07	0.49–0.76

occurrence across sampled sites regardless of year. Additionally, our yearly occupancy models suggest few of the chosen covariates are important predictors for occupancy. There are four probable reasons to why none of the included covariates effected *M. lucifugus* occupancy. First, the variables we measured might not be highly important factors in predicting occupancy for bats on Fort Drum. Potential unmeasured variables (i.e. fine scale landscape features) in this analysis might be important predictors for occupancy. Second, the binary response (either present or absent) groupings in occupancy are an oversimplification of what is occurring on the landscape. Third, the spatial extent of Fort Drum, and the degree to which our sites are spatially autocorrelated, may limit the ability to address the importance of environmental variables on occupancy as bats are highly vagile (Steenweg *et al.*, 2018). Lastly, the sampling effort and size, influences occupancy estimates. As such, understanding the underlying limitations of occupancy metrics with regards to changing abundances, spatial scale, and autocorrelation is critical for researchers and managers looking to effectively and efficiently monitor for threatened and endangered species (MacKenzie *et al.*, 2002). In our analysis, occupancy estimates were influenced by the balance of sampling effort and sample size. First, due to low sampling effort (maximum two nights) and few sites surveyed each individual year pre-WNS, we could not develop robust occupancy models for each individual year from 2003–2007. Therefore, we had to combine these years to be able to develop an accurate model to determine *M. lucifugus* presence for pre-WNS. Second, for 2014 and 2017, we had a large number of sampling nights but few allocated sites (five sites). Although we were able to generate estimates for detection and occupancy, our model lacked the ability to draw strong inference across Fort Drum. Finally, for 2015 sampling at Fort Drum was specifically targeted for *M. septentrionalis*, and therefore sites were positioned in areas less suitable for *M. lucifugus*, with surveys occurring in areas with a larger proportion of upland forests rather than in wetlands and more open corridors. Accordingly, our analysis for 2015 had a lower occupancy estimate than any other year that was both accurate and precise in terms of estimating occupancy across Fort Drum. However, this is caveated by the fact that increased sampling effort may have allowed for sites to record presence if the survey duration had been longer that year at these sites.

Relative Activity versus Occupancy

The patterns associated with occupancy and population dynamics, such as abundance, relative activity, and distribution of a species are affected by different spatial and temporal scales (Hecnar and M'Closkey, 1997; Donovan and Flather, 2002; Steenweg *et al.*, 2018). Specifically, research on amphibians, reptiles, and birds has shown these relationships relative to environmental conditions (Wiens *et al.*, 1987; Hecnar and M'Closkey, 1997; Hurlbert and Jetz, 2007; Steenweg *et al.*, 2018). Although there are clear examples of how decreasing abundance does not indicate a negative trend in occupancy (Hecnar and M'Closkey, 1997; Blackburn *et al.*, 1998; Boeken and Shachak, 1998; Donald and Fuller, 1998; Gaston and Curnutt, 1998; Gaston *et al.*, 2000; Latham *et al.*, 2014), the premise that wildlife populations occupy the same locations both prior to and following a reduction in size has garnered little attention in the literature, especially in bats. The vagility of a species and associated habitat constraints does influence the relationships between occurrence and abundance (Gaston and Curnutt, 1998; Gaston *et al.*, 2000; Frick *et al.*, 2008). For example, species that are restricted to a suite of local environmental conditions and with low or short dispersal rates, such as herpetofauna, a change in abundance will often have strong correlations with occupancy. Species that are highly mobile or have minimal habitat constraints, such as avifauna and bats, the relationship between occupancy and changing abundances may not be clear (Gaston and Curnutt, 1998). Being highly mobile, bats tend to have large home range sizes (Owen *et al.*, 2003; Kniewski and Gehrt, 2014; Maxell, 2015; Nelson and Gillam, 2016). At Fort Drum, *M. lucifugus* have core mean home ranges > 140 ha (Coleman *et al.*, 2014c). Based on the foraging and home range characteristics of *M. lucifugus*, a reduction in overall abundance could have no effect on occupancy as even a reduced population still, in theory, could be present anywhere at Fort Drum over the summer season.

Nonetheless, our analysis of *M. lucifugus* illustrate this dichotomy in the occupancy-abundance relationship. We saw minimal change in occupancy through time for *M. lucifugus*. Similarly, none of our environmental variables seemed to impact occupancy, and when they did, these differences were not significant. This might be attributed to the fact that occupancy analysis requires more site-level and landscape variability as well as more instances of

complete absences than encountered at Fort Drum. Conversely, our relative activity models not only identified important topographic and land cover variables important to *M. lucifugus* relative activity, but had the predictive power to document changes in relative activity induced by WNS across Fort Drum over 15 years. When compared to occupancy, relative activity reflected both the change in activity we predicted and the contraction of populations resulting from WNS; whereas occupancy modeling, with the oversimplification of data as simply present or absent, represented a loss of resolution even at the large landscape scale of Fort Drum. However, realizing that there is an 80% chance of *M. lucifugus* occupancy at any site at Fort Drum may still be informative. Regardless, continued acoustic monitoring of bat species, such as *M. lucifugus* in the Northeast to assess ongoing temporal, spatial, and habitat association changes, and as a guide to efficiently direct mist-netting should rely more on relative activity as the metric of choice rather than occupancy estimates.

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