

Assessing the Long-term Impacts of White-nose Syndrome on Bat Communities Using Acoustic Surveys at Fort Drum Military Installation

Tomás Nocera

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William M. Ford, Committee Chair

Alex Silvis

Laurence W. Carstensen

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Abstract

With declines in abundance and changing distribution of White-nose Syndrome (WNS)-affected bat species, increased reliance on acoustic monitoring is now the new “normal”. As such, the ability to accurately identify individual bat species with acoustic identification programs has become increasingly important. Additionally, how bat distribution and habitat associations have changed at the local to sub-landscape scale in the post WNS environment is important to understand. The significance of these changes, relative to bat activity, may be based on the species-specific susceptibility to WNS. We used data collected from Fort Drum Military Installation, New York from the summers of 2003-2017 to analyze the accuracy of acoustic software programs, and assess the changes in relative bat activity, occupancy, and distribution induced by WNS.

Our results indicate that continued acoustic monitoring of bat species, such as the little brown bat (*Myotis lucifugus*) in the Northeast, to assess ongoing temporal and spatial changes, habitat associations, and as a guide to direct future mist-netting should rely more on relative activity as the metric of choice. Furthermore, the continuous spread of WNS across North America will have strong negative effects on bat populations and communities, this study points to how individual species (both impacted and non-impacted) will respond to WNS. We believe that our results can help users choose automated software and MLE thresholds more appropriate for their needs to accurately address potential changes in communities of bat species due to impacts of WNS or other factors.

General Audience Abstract

White-nose Syndrome (WNS), was first documented in the United States in 2006. The fungus that causes WNS grows on the exposed tissues of hibernating bats and causes abnormal frequent arousal and activity through winter that consequently leads to premature loss of critical fat reserves and disruption of water balance. To date millions of cave-hibernating bats have been killed by White-nose Syndrome. With declines in abundance and changing distribution of WNS-affected bat species, the ability to accurately identify individual bat species with acoustic identification programs has become increasingly important. Additionally, how bat distribution and habitat associations have changed at the local to sub-landscape scale in the post WNS environment is important to understand. We used data collected from Fort Drum Military Installation, New York from the summers of 2003-2017 to analyze the accuracy of acoustic software programs, and assess the changes in relative bat activity, occupancy, and distribution induced by WNS.

Looking at this disease through time is important because it allows us to predict how bat communities in areas where the disease has not yet reached may change if there is an outbreak. Our results indicate that continued acoustic monitoring of bat species in the Northeast, to assess ongoing temporal and spatial changes, habitat associations, and as a guide to direct future mist-netting should rely more on relative activity as the metric of choice. This information can be directly applied with on the ground management for bats, which can buffer against the additional consequences this disease has on bat populations.

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Chapter 1: Let's Agree To Disagree: Comparing Auto-Acoustic Identification Programs

Abstract

With the declines in abundance and changing distribution of White-nose Syndrome-affected bat species, increased reliance on acoustic monitoring is now the new “normal”. As such, the ability to accurately identify individual bat species with acoustic identification program has become increasingly important. We assessed rates of disagreement between the three USFWS-approved acoustic identification software programs (Kaleidoscope Pro 4.2.0, Echoclass 3.1, and Bat Call Identification (BCID) 2.7d) and manual visual identification using acoustic data collected in the summer from 2003-2017 at Fort Drum, New York. We assessed levels of disagreement between programs through pairwise comparisons on a total nightly count level, individual file level, and grouped maximum likelihood estimate (MLE) level using pre-planned contrasts, AIC, and annual confusion matrices. Inter-program agreement on an individual file level was low, as measured by Cohen’s Kappa (0.2 - 0.6). However, site-night level pairwise comparative analysis indicated that program agreement was higher using simple occupancy metrics. In comparing analytical outcomes of our different datasets, i.e., how comparable programs and the trained biologist are regarding the relationship between environmental conditions and bat activity, we determined high levels of congruency in both the relative rankings of the model, as well as the relative level of support for each individual model. Depending on objectives, we believe our results can help users choose automated software and MLE thresholds more appropriate for their needs, and allow for the cross-comparison of studies using different automated acoustic software.

Introduction

The emergence of the fungal pathogen, *Pseudogymnoascus destructans*, causative agent of White-nose Syndrome (WNS), was first documented in the United States on February 16, 2006 at Howe's Caverns; 40 miles west of Albany, New York (Blehert et al. 2009). The pathogen has moved rapidly throughout the northeast and central regions of the United States, expanding into several provinces in Canada. By 2016, WNS had expanded into Washington State (USGS National Wildlife Health Center 2016), and as of 2018 either presence of the fungi or actual WNS has been reported in Kansas, Iowa, Mississippi and Texas (USGS National Wildlife Health Center 2018). The fungus, grows on the epithelial tissues of hibernating bats and causes abnormal frequent arousal and activity through winter, that consequently leads to premature loss of critical fat reserves and disruption of water balance (Cryan et al. 2010, Meteyer et al. 2012). To date millions of cave-hibernating bats have been killed by White-nose Syndrome (USFWS, 2018), and populations of some Myotid species have been reduced by >90% (Blehert et al. 2009, Frick et al. 2010).

As the effects of WNS increase, there is a growing need for techniques to accurately monitor these declines in bat populations generally, and document residual bat distributions specifically (Langwig et al. 2012). Furthermore, the ability to record and accurately identify individual bat species is a key tool for managers tasked with conservation of WNS-impacted species. For managers, understanding the distributions and habitat associates of threatened bat species can help guide management activities and reduce potential additive stressors. Pre-WNS, mist netting was widely used to sample distribution and abundance. However, low densities of many bat species post-WNS have led to greatly reduced capture rates, complicating documentation of true status (Coleman, 2013). Accordingly, mist-netting may not be

representative of the overall changes in population and activity trends, and may no longer be a viable technique WNS impacted areas to describe current local and regional distribution.

Both pre-WNS and post-WNS, acoustic monitoring techniques have been widely used to assess species presence and probable absence, activity patterns among different habitats, and spatial and temporal trends (Sherwin et al. 2000, Britzke et al. 2002, Weller and Zabel 2002, Ford et al. 2011, Rodhouse et al. 2011, Coleman et al. 2014*b*). Murray et al. (2001) and Britzke et al. (2002) demonstrated that acoustic sampling generally is more effective in characterizing bat community composition than mist-netting in eastern, United States. Acoustic monitoring allow managers to sample large portions of areas used by bats, and thusly can account for greater bat species richness with less effort over time than traditional mist-netting (Murray et al. 1999, Coleman et al. 2014*c*). The benefits of acoustic sampling can include 1) increased sampling nights (effort) and survey extent (sites), 2) cost-efficiency over expanded mist-netting efforts, and 3) providing a potential guide for focal mist-netting when bat capture for foraging and day-roost radio-telemetry research or tissue sample collection is needed (Britzke et al. 2002, Coleman et al. 2014*c, b*). Irrespective of WNS, the flexibility of sampling a larger area and a greater number of sites, encompassing a variety of habitats in less time, can make acoustic sampling techniques preferable to other capture methods in certain geographic areas (Britzke et al. 2013, Coleman et al. 2014*a*).

In conjunction with the advances in acoustic sampling technology, qualitative identification development of automated acoustic bat identification software has allowed for identification of voluminous numbers of bat call sequences relatively quickly (Schirmacher et al. 2007, Coleman et al. 2014*c*, Lemen et al. 2015). Advancements in acoustic sampling and identification software, combined with declining mist-net success in the post-WNS environment

led the United States Fish and Wildlife Service (USFWS) to develop acoustic guidelines to survey and/or monitor for the endangered Indiana bat (*Myotis sodalis*) (Niver et al. 2014). Despite greater acceptance and use of acoustic sampling and subsequent automated software, acoustic monitoring is not free from constraints and biases. For example, Sherwin et al. (2000) noted that acoustic sampling is unable to address abundance of an individual species beyond an index of activity, i.e., one individual recorded numerous times or numerous individuals recorded single times at a site over a night. Furthermore, the impetus for automated software programs was to identify the Indiana bat first and foremost (Britzke et al. 2013), thereby adding another source of bias from analysis of bat echolocation to assess other bat species. Constraints and biases in accurate species identification, whereby the program accuracy for a given species is in part tied to how well other species are identified can potentially lead to either constant bias (constant misidentification) or non-constant bias (increasing misclassification under changing conditions) that may provide misleading results (Samuel et al. 1992). Therefore, understanding the biases of acoustic sampling and identification of echolocation calls is vital for proper interpretation of study results, and comparison of these results among studies when different automated identification programs are used (Sherwin et al. 2000, Adams et al. 2012, Britzke et al. 2013)

Call libraries used for software algorithm training typically only incorporated high quality search phase echolocation call sequences of known species identifications rather than the full array of echolocation calls bats can emit (Britzke et al. 2013, Lemen et al. 2015). Although automated software programs acknowledge that only high quality recordings will yield accurate species identification (Wildlife Acoustics 2018, U.S. Army Corps of Engineers 2018, Bat Call Identification 2018), field recordings invariably include numerous low quality calls that may be

incongruent from software development library reference calls (Lemen et al. 2015). Structural variations in echolocation calls due to Doppler shifts and attenuation, coupled with echolocation adjustments in response to the presence of vegetation clutter, insect abundance and types, water, or other bat species, create considerable variation among echolocation recordings (Britzke et al. 2013). High inherent intra-specific variation in echolocation compounds with inter-species overlap in echolocation call characteristics, creating significant challenges in accurate species identification. In the eastern United States, high frequency Myotis and eastern red bat (*Lasiurus borealis*) have similar echolocation calls, and automated identification programs have been observed to make classification errors of omission and commission (Loeb and O’Keefe 2006, Brooks 2008, Britzke et al. 2013, Silvis et al. 2016b).

Lemen et al. (2015) observed that the level of agreement across four automated programs [BCID (Bat Call Identification, Inc., Kansas City, MO), Kaleidoscope (Wildlife Acoustic, Inc., Maynard MA), Echoclass (U.S Army Corps of Engineers, Vicksburg, MS), and Sonobat (Sonobat, Arcata, CA)] in identifying bat species was not consistent at the file level, demonstrating low levels of agreement (40%) between software packages. Janos (2013) found only a 38% level of agreement between files when comparing BCID to Echoclass. Much of this was attributable specifically to similar high frequency call structure among and between Myotis and eastern red bat (Janos, 2013). Low levels of agreements among software programs are consequential for cross-study inference and conservation planning. High rates of either false positive or false negative misidentification have conservation costs that may result in incorrect management decisions, i.e., seasonal restrictions for forest harvesting, or prescribed fire across many management ownerships, and/or use of obscurants and ordinance for military training) based on perceived, but erroneous, presence or absence of the bat species of interest. Thus, being

able to quantify the level of agreement between these programs is a needed metric for researchers or managers using a single, or combination of, automated identification programs for identifying bats with confidence relative to their stewardship needs (Lemen et al. 2015).

In 2003, prior to the arrival of WNS in the United States, an extensive long term acoustic monitoring project examining spatial and temporal bat distribution, activity, and occupancy program was initiated at Fort Drum Military Installation (Fort Drum) in northwestern New York (Ford et al. 2011). After the local discovery of summer maternity activity of the endangered Indiana bat on Fort Drum, mist netting efforts were added to the monitoring efforts in an attempt to capture and track bats to foraging and roost locations (Jachowski et al. 2016). Continuous acoustic monitoring and captures between 2003 and 2018 has documented changes in patterns of acoustical activity pre- and post- WNS and the effects WNS has had on bat community composition and structure at Fort Drum (Dobony et al. 2011, Ford et al. 2011, Coleman et al. 2014b, Jachowski et al. 2014), and provide comparative analysis among acoustic sampling techniques (Coleman et al. 2014c, a). To assess the relative agreement among three automated bat identification software programs currently widely used in eastern North America, and qualitative identification by a trained biologist, we examined 15 years of bat echolocation recording data from Fort Drum. The intent of our study was to evaluate agreements and discrepancies between Kaleidoscope Pro 4.2.0, BCID 2.7d, Echoclass 3.1 and qualitative identification to describe variation among programs, and highlight potential congruencies and discrepancies in output and performance. Because the true species identity of calls was unknown, the intent of our study was not to gauge program accuracy, but highlight potential discrepancies among programs and visual identification by a trained biologist.

Study Site

We conducted our study at Fort Drum Military Installation in Jefferson and Lewis counties in northwestern New York, USA. Situated at the junction of the St. Lawrence- Great Lakes lowlands, the base of the Adirondack Mountains, and the Tug Hill Plateau ecoregion, Fort Drum is a 43,000 ha U.S. Army installation that contains a variety of forest, wetland, and open habitat conditions. The Niagara Escarpment, which lies 10 – 15 km west of Fort Drum, contains limestone (Karst) formation caves used as winter hibernacula by bats (Ford et al. 2011). The bat fauna of Fort Drum, New York is small, with only 9 species of 3 echolocation groups: high-frequency call (minimum frequency > 40 khz) little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (MYSO), tri-colored bat (*Perimyotis subflavus*, PESU), eastern small-footed bat (*Myotis leibii*, MYLE), and eastern red bat (LABO), midrange frequency call (between 25 to 40 khz) big brown bat (*Eptesicus fuscus*, EPFU), and silver-haired bat (*Lasionycteris noctivagans*, LANO), and low frequency call (maximum frequency < 25 khz) hoary bat (*Lasiurus cinereus*, LACI) (Coleman et al. 2014a).

Methods

We examined echolocation calls recorded during summers, and in some cases early fall, of 2003-2017 at Fort Drum. We surveyed Fort Drum using 289 individual sites and 8,373 detector nights. All calls were recorded with Anabat II detectors connected to a compact flash-storage zero-crossings analysis-interface module (ZCAIM), as well as SD1 and SD2 units (Titley Electronics, Ballina, NSW, Australia). Echolocation data collected from 2003-2010, prior to the availability of automated software, was qualitatively identified by a single trained individual using an echolocation dichotomous key developed for Northeast bat species (Ford et al. 2011). Nights where the detector did not turn on or shut off within 2 hours after sunset were excluded

from the analysis. However, if a detector ran for at least 8 hours, it was included in our analysis. Calls were first identified using Anlook 4.7 and then were examined for call curvature values in Analyze 2.0 (Ford et al. 2011). We re-identified echolocation calls from all years using BCID v. 2.7d, Kaleidoscope Pro v. 4.2.0, and Echoclass v. 3.0. For each year, we visually examined two nights per site after 2010 to ensure recording accuracy and completeness, i.e., did recording occur.

We specifically selected the nine extant bat species that occur at Fort Drum for analysis by Kaleidoscope and BCID. In contrast, users are constrained to pick one of three geographically determined bat assemblages in Echoclass. Accordingly, we selected the group encompassing the Northeast region, which correctly and completely represented the bat species present at Fort Drum. Both Kaleidoscope and BCID allow users to adjust for sensitivity and specificity, however, while Kaleidoscope does this at the maximum likelihood estimate level, Echoclass does not allow the end user to adjust for any parameters. The aim of adjusting these parameters is to reduce the number of missed identifications, and extraneous identifications, respectively. The aim of increasing accuracy is to have higher proportions of correct identifications, though fewer call sequences are identified. We adjusted the signal parameters of Kaleidoscope and BCID to follow current USFWS guidelines. Currently available automated bat acoustic identification software generate species identifications for call sequences using algorithms that process and classify quantitative measures of individual calls (e.g. frequency, slope, curvature, pulse rate). Software classification algorithms are trained using reference call libraries which consist of known identity calls. These known identity calls typically are recorded using captured bats that are hand released, and more rarely from free-flying bats. Once individual acoustic files have been assigned a species identity, or classified as noise or unidentifiable, most automated

identification software generate maximum likelihood estimates (MLE) using the method of Britzke (2002). MLE values represent the probability that a species is misclassified as present when in fact it is absent, and are calculated by comparing the number of files classified as each identified species to the known misclassification rates of those species in the classification algorithm as measured using known identify calls (Britzke, 2002, Niver et al. 2014).

We used a generalized linear mixed model (GLMM) with a negative binomial distribution to examine general agreement from 2003-2010 in total nightly counts among automated identification software and qualitative identification. We used relative activity by individual species at the site-night level as our response variable blocked by year, holding site as a random effect, and having our treatment groups and the total number of files recorded at each site-night as fixed effects. When parameter significance was indicated at $\alpha \leq 0.05$ we performed *post-hoc* comparisons of treatments (programs and qualitative identification) by comparing least-square mean estimates for each treatment to determine differences. We fit our GLMM in SAS 9.4 (PROC GLIMMIX; SAS Inc., Cary NC) using a negative binomial distribution.

To examine the possibility that agreement levels would change at a finer scale, i.e., individual call file and MLE groupings, we further analyzed file by file agreement rates between two programs, Kaleidoscope Pro 4.2.0 and Echoclass 3.1 for the full range of Fort Drum data, 2003-2017. We omitted qualitative identification from these analysis as individual file identifications beyond site night totals were not completed for the later years (2011-2017). We omitted BCID from these analysis as MLE values were not fully “equivalent” in terms of site night to those of other software. We used machine learning theory (Tarca et al. 2007) to develop a set of confusion matrices that assessed the degree of misclassification between Kaleidoscope and Echoclass at the individual file level. Our comparisons included all bat species an individual

echolocation file could have been identified as from the individual program, including simply “bat” or no identification (NoID) and noise, i.e., non-bat (U.S. Fish and Wildlife Service 2017a). Although true confusion matrices compare a predicted value with a reference value (truth), we were limited in only knowing predicted identifications from classified acoustic data. Thus, we used the premise of predicted and reference values to display how one program file level identification compared to another program; and then reversing the programs’ starting position so that in turn each program was either the predicted or reference values for each comparison. This allowed us to examine the percentage of agreement of one program with the other, and assess proportion of disagreement (Type I and Type II errors) for all files identified by the reference program. We treated years (2003-2017) and the files associated with each year as independent observations. This allowed us to analyze potential shifts in a program’s ability to accurately identify species through changes in bat community structure and a species overall abundance. Although we examined each year individually, our final matrix was cumulative, encompassing all files between 2003 and 2017. We used Program R to create 11x11 confusion matrices where we assigned each program as the predictor and reference value with the function `confusionMatrix` using the `caret` package (Kuhn et al. 2017). To determine the degree of program agreement, we used Cohen’s Kappa (Allouche et al. 2006) in addition to calculations of sensitivity and specificity rates as measures of true positive and true negative performance, respectively. To visualize the confusion matrix results, we plotted the output as a heatmap in R using package `ggplot2` (Wickham et al. 2016).

Additionally, because USFWS guidelines for acoustic surveys rely on acceptance of presence or absence of target threatened or endangered species, i.e., MYSE and MYSO, we repeated these confusion matrix analysis based on recalculations of species presence on a night

level with Maximum likelihood estimates (MLE) values (confidence score) at $\alpha = 0.05$ as a threshold. Accordingly, we grouped MLE values, regardless of program into two categories, above $\alpha = 0.05$ (considered absent) or below $\alpha = 0.05$ (high confidence as present).

To assess how disagreement among software and the trained biologist classification may impact analytical outcomes, we modeled relative nightly activity of MYLU, MYSE, and MYSO for each program and the biologist using a set of candidate GLMMs with a negative binomial distribution (Fournier et al. 2012) from our 2003 – 2010 data. Because our intent was to compare analytical outcomes of our different datasets rather than model habitat associations, the candidate model set represented simple hypothesis regarding the relationship between environmental conditions and bat activity. Specific environmental conditions assessed included elevation, canopy cover, land cover type, distance to road, and distance to water. We determined the best supported model for each dataset using Akaike's Information Criterion Corrected for small sample size (AICc) (Burnham and Anderson 2002, 2004). Across datasets, we compared the relative model rankings and support for the best supported model (wAICc), as well as covariate β estimates of the best supported models. We fit GLMMs in program R (R Core Team 2018)

Results

From 2003 to 2010, we sampled 239 total detector nights; file identification, by species, assessment varied by program and qualitative identification (Table 2). From 2011-2017 we sampled an additional 8,134 total detector site nights. Over the entire study duration we recorded 1,022,188 individual files, of which > 450,000 were identified to bat species, though the individual species totals were variable by program and/or qualitative identification (Table 2; Table 3). Overall, there were numerous significant differences among nightly counts across bat species among the three programs and those echolocation passes identified visually (Table 4;

Table 5). For Myotids qualitative identification generally had the highest count estimate compared to acoustic software, often significantly different from at least one program (Table 5). No bat species had a full agreement between programs and the biologist. However, for each species, except for MYLE, there was agreement between at least two treatments (Table 5).

At the individual file level and totaled night level, agreement by species between Echoclass and Kaleidoscope varied across years measured by Cohen's Kappa, ranging from 0.25 to 0.56 depending on the year with an average Cohen's Kappa (all years and species combined) of 0.368 (Table 6). Overall agreement proportion, when either program was used as the reference, was variable among species (Figure 1). When Echoclass was the reference agreement rates for MYSE, MYSO, and LABO were $\leq 30\%$ (Figure 2; Table 7). Although the majority of disagreement between Myotids were intra-genus or NoID; LABO was misclassified frequently as MYLU (Figure 2; Table 7). When Kaleidoscope was the reference agreement rates for all Myotids always was $\leq 30\%$, with the majority of misclassification being LABO (Figure 2; Table 8). Conversely, Kaleidoscope agreed with Echoclass at most 66% of the time for one species, LANO whereas Echoclass agreed with Kaleidoscope at most 57% of the time for one species, LABO. Irrespective of year, nightly MLE comparisons between the programs (comparing two groups) had an overall agreement, measured by Cohen's Kappa, of 0.56 for MYLU, 0.60 for EPFU, 0.47 for LABO, 0.58 for LACI, 0.58 for LANO, 0.04 for MYLE, 0.25 for MYSE, 0.26 for MYSO, and 0.34 for PESU. Overall agreement proportion at 0.05 MLE or less, when either Echoclass or Kaleidoscope was the reference, was variable among species and across programs (Table 9; Table 10). Additionally, overall agreement rates were higher at the MLE grouping level than at an individual file by file level (Table 11; Table 12). Specifically, when Echoclass was the reference, we observed a 2.8-fold increase in agreement between LABO

file by file level comparison and MLE grouping (Table 11). When Kaleidoscope was the reference we observed a 4.5-fold increase in agreement between MYLU file by file level comparison and MLE grouping (Table 12).

For each program and the trained biologist the null model was outperformed by all other models across all species analyzed with regards to relative activity (Appendix Table 1,2,3). Conversely, competing models were the same between programs and the trained biologist (Appendix Table 1,2,3). The relative ranking and the relative level of support for each individual model per program and the trained biologist indicate that there is no difference between programs and the trained biologist. For MYLU, the model with the highest relative ranking and level of support for the trained biologist was the model with three parameters (Appendix Table 1). The global model and the model with six parameters for MYLU activity for each program had uniform relative ranking and level of support (Appendix Table 1). For MYSE and MYSO, the model with the highest relative ranking and level of support for the trained biologist was our global model (Appendix Table 2, 3). For MYSE, relative ranking and level of support was highest for the model with three parameters for each program (Appendix Table 2).). All three competing models for MYSO activity for each program had uniform relative ranking and level of support (Appendix Table 3). Depending on the site covariate, β estimates for site covariates among treatment models and across species were either not significantly different from zero or not significantly different from each other (Appendix Figure 1, 2, 3).

Discussion

Species recognition using acoustics has been used for many taxa (Chesmore 2004) including in insects (Chesmore and Nellenbach 2001), amphibians (Acevedo and Villanueva-Rivera 2006, Han et al. 2011, Xie et al. 2018), birds (Acevedo and Villanueva-Rivera 2006,

Tyagi et al. 2006, Venier et al. 2012), marine mammals (Parijs et al. 2002, M. Johnson et al. 2009), and bats (Britzke et al. 2013, Janos 2013, Coleman et al. 2014c). Advancements in technology and automated acoustic software programs and detectors have enhanced the ability to identify species by sound, often able to provide measures of inter- and intra-specific interactions (Chesmore 2004). Furthermore, acoustic sampling can help in monitoring, capturing, and identifying trends in population declines of once common species and/or rare species (Jaramillo-Legorreta et al. 2017, Xie et al. 2018). The constraints, however, of automated acoustic detectors and software are uniform across taxa and include: 1) the difficulty to track individuals moving in and out of acoustic range or becoming “lost” in a group of vocalizing animals (M. Johnson et al. 2009); 2) Automated software accuracy depends on a foundation of a high quality reference library that includes variation between species as well as within species (Britzke et al. 2002, Scott Brandes 2008, Xie et al. 2018). Reduction of extraneous noise is also an inherent issue when trying to record and identify species and individuals (Britzke et al. 2002, Scott Brandes 2008). Controlling for these factors are necessary to reduce high levels of false positive and false negative identification (Towsey et al. 2012). Further restrictions are applied to acoustic monitoring for bats as calls are not only ultrasonic, but can share similar patterns and considerable overlap among species, making automated acoustic identification of a bat species difficult in practice (Britzke et al. 2002, 2013).

As the effects of WNS on bats continue, causing a decline 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 to replace mist-net surveys (Coleman et al. 2014a). Consequently, managers need to clearly understand the biases associated with software programs and the limitations on inferences that can be drawn from automated bat identification, as

conservation decisions relative to bats may emanate from software use. Software packages such as Kaleidoscope Pro, Echoclass, and BCID can process acoustic data and compute a species identification for every bat call sequence, though each was specifically designed with MYSO identification as the program “driver” (Janos, 2013, Niver et al. 2014, Lemen et al. 2015). The promise of automated identification software was that internal numerical quantification and statistical analysis would produce higher rates of correct identification and offer repeatability free subjective biases associated with visual identification (Lemen et al. 2015). Although we cannot say which program is most accurate, we observed that depending on the species, overall estimates among programs, across any given site and night, is highly variable. At minimum, comparison of these estimates allowed us to determine which programs are more or less conservative in their approach to identify and count an individual bat species.

Our inclusion of the trained biologist was based on 1) allowing for a direct link to past studies and the traditional bat identification methods; 2) to understand where, when, and how systematically humans could differ from an automated acoustic program; and 3) providing a baseline to assess program discrepancies. However, our inclusion of the trained biologist is fraught with limitations, being that we do not have any idea of the overall accuracy of the human, exactly equal to the software; and we have no replication of the human. This latter issue relates to the two questions of how representative of all trained bat identifying biologists our biologist is and what level of variation, if any, our biologist had among years.

When compared to the biologist, we saw variation in program agreement with each other and with the biologist by species. This corroborates observations by Jennings (2008) comparing human identification versus automated neural networks on identifying and assessing misclassifications of bat species. We identified four areas of variation in which agreement and

disagreement can occur with bat echolocation identification: 1) programs and the trained biologist tended to agree on total bat counts by site night; 2) programs and the trained biologist tended to disagree on total bat counts by site night; 3) programs tended to disagree with the trained biologist and each other (estimating greater bat calls than the trained biologist on a site night level); and 4) programs tended to disagree with trained biologist and each other (estimating fewer bat calls than the trained biologist on a site night level). It is worth noting that for these last two sources of variation among individual programs and with the visual identification, qualitative identification acted as a baseline to assess program discrepancies.

We found high levels of agreement between two programs: agreement between BCID and Kaleidoscope relative to each other and with qualitative identification, particularly with MYLU. Conversely, Echoclass tended to identify fewer MYLU. For Echoclass, this is due to inherent software constraints and considerations to specifically find and/or minimize misclassification of MYSO (E. Britzke, U.S. Army Corps of Engineers, pers. comm, Britzke et al. 2002). BCID and Kaleidoscope, tended to agree with each other on the number of MYLU on any given site-night.

We found high levels of disagreement among all treatments for rare species in our study area. This condition typically also was associated with low numbers of identified calls of these species. As an example, the biologist estimated more MYLE than the other programs, and conversely each program disagreed between each other. At Fort Drum, MYLE are considered uncommon, even prior to the advent of WNS, and throughout our study total counts across all years were low (Ford et al. 2011). Low numbers on a nightly basis, clearly contribute to program uncertainty on correct classification (Janos 2013). In terms of distinguishing MYLE from other Myotid bats, the biologist may have been able to parse out the subtle differences in overlapping

diagnostic features, such as higher individual pulse minimum frequencies, to estimate greater MYLE presence than the programs.

For silver-haired bats each program estimated greater numbers of LANO than the trained biologist. This may be due to constraints resulting from the use of the echolocation dichotomous key for the Northeast used by the biologist (Ford et al. 2011), which did not provide sufficient differences in call characteristics between LANO and EPFU. In the qualitative identification process, suspect LANO calls were first identified using Anlook 4.7 and then were examined for call curvature values in Analyze 2.0. to differentiate from EPFU, requiring the biologist to decide whether to proceed to the second visualization software program (Betts 2009, Ford et al. 2011). However, the automated programs have the diagnostic ability to identify LANO directly (Britzke et al. 2011, Janos 2013). Moreover, at least prior to the advent of WNS, LANO were perceived to be common only during spring and fall migratory periods at Fort Drum and across New York (Whitaker and Hamilton 1998, Cryan 2003, Ford et al. 2011), which may have resulted in subjective bias against LANO identification by qualitative identification except in cases of highly diagnostic calls. Whereas automated acoustic software does not do this, this bias may be acceptable, as it helps to reduce overestimation of activity and presence of rare species.

Finally, lower estimates for MYSE by programs relative to the trained biologist constituted the fourth example of variability. We suspect that this is because of the biologist's ability to use information on temporal context, i.e., proximity of MYSE calls in file sequence. In other words, human tendency to dismiss series of calls, separated by seconds, as two different species may have resulted in greater number of counts for MYSE in Fort Drum, as observed elsewhere (Fenton 1980). Secondly, although MYSE were exceedingly abundant at Fort Drum pre-WNS, the species' low amplitude echolocation characteristics results in poor call quality

(Ford et al. 2005), and as a result are more readily dismissed as NoID or noise by automated software, whereas the biologist was comfortable assigning a species identification.

Unexpectedly, we found that the overall agreement in bat identification between Echoclass and Kaleidoscope was variable on a yearly basis. This did not conform to our original expectation that although the programs might differ overall, the rates of difference would be constant across years in terms of disagreement. It is possible that with differences in underlying use of misclassification rates set by the program's development with training data, and subsequent validation, that misclassification rates between species comparisons might be influenced differently by the proportion and/or total amount of calls analyzed (Britzke et al. 2002, Coleman et al. 2014c). File quantity and quality used in program development affect species' detection rates and classification. These programs were developed to prioritize correct classification of MYSO, as the rationale that initially precipitated software development and use (Britzke et al. 2002, Wildlife Acoustics, 2017). The subsequent listing and realization for the need to correctly identify MYSE highlights the unfortunate "Red Queen effect" between technology development and use in a highly dynamic environment, i.e., changes in management priorities among species and changing bat community structure post-WNS outpace software development (Van Valen 1977, Barnett and Hansen 1996, Voelpel et al. 2005).

Our work showed the level and direction of disagreement within these programs for detecting species of interest (MYLU, MYSE, and MYSO). For rare species in particular, analysis of only high quality calls can reduce the number of species identifications below reality. Such low identification rates can directly impact MLE value calculations, and lead to inaccurate estimates of species presence or probable absence (Britzke et al. 2002). Because programs will differ in file identifications due to classification algorithm differences and filtering, both in terms

of what files will be identified, removal of noise, and extraction of call parameters from individual calls and passes, this will also result in differences in nightly activity levels. This issue may be resolved using more accurate classification algorithms that can correctly identify species from lower quality calls, and, by use of higher quality recording equipment and optimized detector deployment and deployment sites.

When all years were combined, on an individual file level, our results indicate that there is high disagreement between species between Echoclass and Kaleidoscope. Beyond the probable, but unknown differences among programs reference library used for training and validation, the frequency and pulse rate settings within each program were not equal for the end-user, as Echoclass does not allow users to adjust the frequency and pulse count. Austin (2017) and Hyzy et al. (2018) both noted acceptable performance in both programs for identifying MYSE presence when using the MLE threshold, however in comparisons, file by file agreement generally did not exceed 40% on a site night basis. Our findings indicate relatively higher rates of agreement between Echoclass and Kaleidoscope when employing the MLE threshold either as a screen for nightly total activity or simply assessing presence for species such as MYLU, MYSE, and MYSO. Currently, use of the MLE threshold is employed by USFWS as the determinant for MYSO presence, and subsequently necessary for sampling level-of-effort (Wintle et al. 2012, Niver et al. 2014). Our findings suggest that this approach for assigning presence or absence in an occupancy analysis format (MacKenzie et al. 2006) is robust. In the context of program agreement, at the MLE group level, that Echoclass and Kaleidoscope provide similar results if used in the endangered species regulatory context to avoid or minimize take of MYSO or MYSE (USFWS 2017). In trying to develop ways to maximize consistency while minimizing uncertainties, resource management decisions necessitate that tools that are used to

make decisions be the least biased part of the process (Kareiva and Marvier 2011), yet in the case of automated acoustic software this may not yet be fully possible.

The goal of controlling the level at which presence of a species is assumed (MLE values ≤ 0.05) is to minimize the rate of type I and type II errors, whereby simultaneously maximizing both specificity and sensitivity. We observed more type II errors than type I errors, which may be a factor of higher agreement of species being absent than being present. In other words, our data had higher agreement with MLE values grouped above 0.05 than below it. Nevertheless, higher overall agreement rates among species using MLE grouping variables does indicate that these programs, at this level, provide some consistency in output. As the MLE threshold value is continued to be lowered, i.e. more conservative on determining species presence, this implies an increased rate of agreement. However, the cost of doing so is high, as the certainty of species presence or absence drops, causing the rate of false positive and false negative errors to increase. These errors are important to consider and acknowledge as they can cause issues when interpreting results that are used to guide management and regulatory actions (Taylor and Gerrodette 1993, Fielding and Bell 1997). To illustrate, if misclassifications/disagreement generate high rates of type I errors (false positive) researchers and managers may take unnecessary actions that divert attention, effort, and funds away from other stewardship activities with little impact to the target species. In the context of MYSE and MYSO, use of forest management techniques, i.e., use of prescribed fire or harvesting, potentially designed to benefit targeted bats (J. B. Johnson et al. 2009, Germain et al. 2017), but which are not actually present, may come at the cost of some other biotic factor or organism also of high conservation concern (Fisher and Wilkinson 2005, Dickinson et al. 2009, Silvis et al. 2016*b, a*). Conversely, if misclassifications/disagreements generate high rates of type II errors (false negatives)

researchers and managers may unknowingly take actions that, while beneficial to other conservation concerns, are deleterious to bats. More importantly, in terms of actions that degrade, fragment, or convert habitats, such as energy extraction and delivery, highway construction, or other forms of permanent forest conversion, the failure to account for species such as MYSE and MYSO and mitigate appropriately, could have considerable negative impacts for these species (Baerwald et al. 2009, Northrup and Wittemyer 2013).

Depending on objectives and location, we believe our results can help users choose automated software and MLE thresholds more appropriate for their needs. First, the location of a study area and the extant bat community is an important consideration in program choice, as the assemblage of bat species and community composition changes both across latitudinal and longitudinal gradients, which can lead to higher program misclassification rates. Thus, matching potential identification with known species pool becomes exceedingly important (Lemen et al. 2015). In turn, MLE values are calculated based on the species pool selected. Second, in the case of generalized bat community surveys, where the intent is to document species presence in a broad sense over a large landscape, and where a liberal approach is sufficient, any of the three programs we examined, and adjusting the MLE threshold value to allow for some variability, may suffice. However, in the case of regulatory clearance surveys, where the intent is to ascertain localized presences, i.e., MYSO or MYSE, with a high degree of certainty to minimize Type I and II errors, managers may opt to use a program that is at least equitable to qualitative identification and/or other programs, but with the ability and optionality to be conservative in identification. In this case, the MLE threshold value may need to be adjusted to be more liberal (highly probable that a species is present).

Advances in occupancy modeling (Royle and Link 2006), that incorporate false-positives have been used to estimate occurrence of bats using multiple automated identification programs (Clement et al. 2014, , Silvis et al. 2015, Austin et al. 2017). These models allow for flexibility in determining species presence or absence by adding a third category whereby both programs state that a species is present. Although false positive occupancy models using Echoclass and Kaleidoscope still revealed low levels of agreement on presence, in some instances (Austin et al. 2017), these same models had higher agreement when used for MYSE identification as found by (Hyzy et al. 2018). Though variability in agreement may be a result of the quality and amount of calls, as well as location, this modeling approach generates more precise parameter estimates than single season occupancy estimates (Silvis et al. 2015). Therefore, in this context, managers could use two programs to determine a conservative but highly accurate assessment of occupancy. Approaches such as this, for listed species such as MYSE and MYSO might be the best approach moving forward in the post-WNS environment.

When modelling relative activity between programs and the trained biologist to determine if selection of examined site covariates changed relative to the program used, the relative ranking and level of support for each individual model was the same across species and treatment. Indicating that regardless of which program is used, as well as qualitative identification, activity response resulted in similar modeled patterns of bat relative activity at Fort Drum. Specifically, among MYLU, MYSE, and MYSO there was no significant difference among the beta estimates. Not only were total counts by most species similar across site nights, program selection and qualitative identification were similar in quantifying site or habitat characteristics important for determining these species' presence on the landscape at Fort Drum. Our findings indicate that while there are inherent differences in acoustic automated software

algorithms, analytical outcomes representing the relationship between environmental conditions and bat activity is the same regardless of which program or method of bat identification is used. Our results show that studies using different programs are comparable, and that any difference in habitat assessment results are not driven by their choice or use of a program. Whereas our means comparison, individual file level, and MLE grouping level comparison potentially is contributory for both research and regulatory work (Niver et al. 2014), from a manager's perspective, knowing that any program or potential trained biologist can predict activity across the landscape similarly with large congruent results is valuable for planning and implementing acoustic monitoring work.

Conclusion

Although we do not know the true accuracy of bat echolocation data analyzed at Fort Drum, and therefore cannot assess automated software identification accuracy directly, we did determine that the level of agreement among all species, programs, and years is variable and not wholly consistent, corroborating results of Jennings et al. (2008), Janos (2013), Lemen et al. (2015). After accounting for biases at the individual file level and grouped MLE threshold levels, the total nightly counts appear to have an acceptable amount of congruence. Specifically, in comparing analytical outcomes of our different datasets, i.e., how comparable programs and a trained biologist are to each other regarding the relationship between environmental conditions and bat activity, we determined high levels of consistency in both the relative rankings of the model, as well as the relative level of support for each individual model.

Accordingly, researchers and managers need to carefully consider the purposes, and setting, for which automated bat identification software is to be used relative to their monitoring needs. Nonetheless, as WNS impacts continue to impact bats in North America, the recognition

that acoustic sampling for both research and monitoring efforts is an indispensable tool is firmly established (Jones et al. 2009, Rodhouse et al. 2012). Continuing to improve the performance of automated software through experimentation in the field and lab by 1) incorporating the widest array of training data and expanding reference call libraries; and 2) by understanding and parametrizing how programs treat wild-recordings in terms of classification errors of omission and commission, will help in addressing variation between and within species and allow for comparisons between study results when different programs were used. Finally, researchers and managers need to arrive at a consensus on what acceptable levels of accuracy are needed to meet management goals.

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Table 1. Minimum, maximum and mean number of detector nights (n=8,373) and total number of site locations (n=289) in Fort Drum Army Installation, New York 2003-2017.

Year	Minimum number of nights	Maximum number of nights	Mean number of nights	Total number of sites
2003	1	1	1.00	5
2004	1	3	1.88	17
2005	1	2	1.81	21
2006	2	2	2.00	18
2007	2	2	2.00	15
2008	1	2	1.83	12
2009	2	2	2.00	13
2010	1	6	2.63	19
2011	1	128	17.81	57
2012	1	223	38.87	55
2013	2	187	29.61	49
2014	81	131	103.60	5
2015	2	118	10.99	129
2016	8	28	14.99	81
2017	64	83	77.80	5

Table 2. Total nightly echolocation passes per species by program (BCID, Echoclass, and Kaleidoscope) and the biologist in Fort Drum Army Installation, New York 2003-2010. Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

	Program	2003	2004	2005	2006	2007	2008	2009	2010
EPFU	Kaleidoscope	6	1,060	181	578	931	455	745	900
	Biologist	10	660	318	796	767	474	663	617
	Echoclass	4	719	136	270	415	127	422	430
	BCID	3	906	206	308	997	455	508	594
LABO	Kaleidoscope	13	662	221	91	183	109	189	164
	Biologist	4	169	717	379	501	337	399	184
	Echoclass	75	1,271	1,370	781	737	328	14,88	295
	BCID	14	1068	725	464	774	221	404	149
LACI	Kaleidoscope	4	382	339	362	29	31	593	371
	Biologist	7	2532	545	857	63	53	410	179
	Echoclass	5	353	239	332	25	14	454	239
	BCID	2	289	215	260	21	20	441	172
LANO	Kaleidoscope	7	183	122	425	69	29	130	142
	Biologist	0	48	24	69	7	11	390	266
	Echoclass	4	142	81	290	67	15	161	117
	BCID	4	367	169	362	231	41	325	281
MYLE	Kaleidoscope	2	18	21	12	35	7	43	3
	Biologist	0	1150	3	17	5	0	15	34
	Echoclass	1	20	15	5	7	4	20	3
	BCID	27	51	72	63	30	5	333	17
MYLU	Kaleidoscope	135	2,580	2,315	1,795	999	533	1,464	248
	Biologist	219	650	3561	2849	794	748	837	146
	Echoclass	42	846	625	769	336	186	287	63
	BCID	74	2260	2206	1691	525	377	662	128
MYSE	Kaleidoscope	1	43	40	35	989	22	32	4
	Biologist	42	1	200	152	1556	85	88	8
	Echoclass	4	44	23	18	250	10	16	1
	BCID	3	84	82	58	1070	34	107	6
MYSO	Kaleidoscope	10	55	171	29	181	27	92	12
	Biologist	184	293	947	332	839	205	753	42
	Echoclass	44	379	1,157	290	373	141	174	37
	BCID	67	596	1293	371	490	155	1017	33
PESU	Kaleidoscope	4	89	116	296	7	18	230	70
	Biologist	0	84	9	128	4	2	267	21
	Echoclass	1	3,725	3,020	104	3	3	104	1
	BCID	4	92	205	187	20	21	143	20

Table 3. Total nightly echolocation passes per species for Echoclass and Kaleidoscope in Fort Drum Army Installation, New York 2003-2017. Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

	Program	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
EPFU	Echoclass	4	719	136	270	415	127	422	430	2,763	5582	5,247	3,375	4,505	13,927	2,355
	Kaleidoscope	6	1,060	181	578	931	455	745	900	4,451	11,274	18,884	10,760	8,130	16,017	6,188
LABO	Echoclass	75	1,271	1,370	781	737	328	14,88	295	8,239	13,772	10,273	6,467	8,452	19,477	5,920
	Kaleidoscope	13	662	221	91	183	109	189	164	2,944	10,285	4,407	2,484	2,745	6,134	2,627
LACI	Echoclass	5	353	239	332	25	14	454	239	9,061	18,143	11,129	9,030	11,856	17,979	7,351
	Kaleidoscope	4	382	339	362	29	31	593	371	16,603	37,187	23,075	11,478	19,961	3,1750	13,493
LANO	Echoclass	4	142	81	290	67	15	161	117	2,653	4,686	3,589	4,276	4,255	8,283	2,227
	Kaleidoscope	7	183	122	425	69	29	130	142	9,908	21,049	8,874	10,166	19,598	33,605	5,584
MYLE	Echoclass	1	20	15	5	7	4	20	3	192	202	308	14	46	92	27
	Kaleidoscope	2	18	21	12	35	7	43	3	168	126	105	15	59	82	31
MYLU	Echoclass	42	846	625	769	336	186	287	63	1,858	1,121	1,341	1,215	1,251	2,927	1,430
	Kaleidoscope	135	2,580	2,315	1,795	999	533	1,464	248	11,196	6317	6,418	5,939	9,048	21,191	6,738
MYSE	Echoclass	4	44	23	18	250	10	16	1	133	126	89	24	27	29	19
	Kaleidoscope	1	43	40	35	989	22	32	4	214	231	266	97	98	56	43
MYSO	Echoclass	44	379	1,157	290	373	141	174	37	997	873	1,441	796	1,171	1,277	1,759
	Kaleidoscope	10	55	171	29	181	27	92	12	779	747	701	325	708	880	766
NoID	Echoclass	390	1,978	22,261	2,840	3,155	1,202	3,354	2,108	84,015	77,218	54,428	31,357	42,916	83,653	29,088
	Kaleidoscope	96	1,625	2,329	1,260	991	327	1,614	453	17,538	30,772	19,350	7,765	15,898	3,2170	8,873
Noise	Echoclass	589	24	115	2,233	2,410	890	2,342	4,002	102,431	160,251	100,072	20,148	84,431	125,272	86,414
	Kaleidoscope	881	2,804	23,187	3,049	3,364	1,362	3,690	4,929	147,088	162,987	105,215	26,970	81,775	130,239	91,919
PESU	Echoclass	1	3,725	3,020	104	3	3	104	1	808	158	137	164	184	62	55
	Kaleidoscope	4	89	116	296	7	18	230	70	2261	1157	759	867	1074	854	383
	Total	1,159	9,501	29,042	7,932	7,778	2,920	8,822	7,296	213,150	282,132	188,054	768,66	159,094	272,978	136,645

Table 4. Type III test for fixed effect of the generalized linear mixed model testing for differences across programs (BCID, Echoclass, and Kaleidoscope) and the biologist on relative activity count by individual site night. With effect, degrees of freedom on the numerator, denominator degrees of freedom, F-statistic, and p-value ($\alpha < 0.05$). p-values $\leq \alpha = 0.05$ are significantly different. Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis* LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

	Effect	Num d.f.	Den d.f.	F Value	Pr > F
EPFU	group	3	949	3.68	0.0118
	Year	1	949	13.89	0.0002
	Total	1	949	171.36	<.0001
LABO	group	3	949	24.34	<.0001
	Year	1	949	2.77	0.0965
	Total	1	949	547.23	<.0001
LACI	group	3	949	12.05	<.0001
	Year	1	949	0.52	0.4715
	Total	1	949	63.75	<.0001
LANO	group	3	949	9.26	<.0001
	Year	1	949	10.19	0.0015
	Total	1	949	19.80	<.0001
MYLE	group	3	949	16.59	<.0001
	Year	1	949	59.75	<.0001
	Total	1	949	108.62	<.0001
MYLU	group	3	949	16.35	<.0001
	Year	1	949	173.67	<.0001
	Total	1	949	423.09	<.0001
MYSE	group	3	949	9.78	<.0001
	Year	1	949	28.52	<.0001
	Total	1	949	57.74	<.0001
MYSO	group	3	949	2.99	0.03
	Year	1	949	180.1	<.0001
	Total	1	949	209.75	<.0001
PESU	group	3	949	3.68	0.0119
	Year	1	949	8.43	0.0038
	Total	1	949	118.45	<.0001

Table 5. Mean Separation test and associated Least Square Means for each program (BCID, Echoclass, and Kaleidoscope) and the biologist across all species on Fort Drum Army Installation, New York 2003-2017. Raw mean and standard error, Least Square means and standard error for all species and programs included. Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU). * LS means with the same grouping variable (letter) are not significantly different from each other ($\alpha = 0.05$)

	Program	Mean	Standard Error	LS Mean	Grouping *	Standard Error (LS Means)
EPFU	Kaleidoscope	20.32	3.1	2.9948	A	0.1776
	Biologist	17.93	2.55	2.848	A	0.1777
	BCID	16.4	2.87	2.7083	BA	0.1778
	Echoclass	11.18	1.95	2.3957	B	0.1782
LABO	Echoclass	27.81	4.74	2.5625	A	0.1085
	BCID	15.53	3.34	2.0467	B	0.1099
	Biologist	11.2	2.09	1.9414	B	0.1103
	Kaleidoscope	5.45	0.905	1.2239	C	0.1143
LACI	Biologist	19.35	3.75	3.6804	A	0.1766
	Kaleidoscope	7.28	1.02	2.9364	B	0.1772
	Echoclass	7.81	1.14	2.8541	B	0.1773
	BCID	5.92	0.804	2.62	B	0.1776
LANO	BCID	6.94	0.773	2.4246	A	0.1662
	Kaleidoscope	4.01	0.447	2.0254	B	0.167
	Echoclass	3.84	0.424	1.924	B	0.1672
	Biologist	3.39	0.497	1.4924	C	0.1686
MYLE	Biologist	5.1	2.23	0.6696	A	0.2771
	BCID	2.46	0.996	0.03658	B	0.2844
	Kaleidoscope	0.883	0.194	-0.5523	C	0.2945
	Echoclass	0.316	0.071	-1.493	D	0.3197
MYLU	Biologist	40.85	5.51	2.6924	A	0.1395
	Kaleidoscope	35.39	5.54	2.4575	A	0.1399
	BCID	32.68	4.9	2.4236	A	0.1399
	Echoclass	13.58	1.79	1.7053	B	0.1418
MYSE	Biologist	8.88	3.92	-0.2582	A	0.3488
	BCID	5.96	3.99	-1.1324	B	0.3568
	Kaleidoscope	5.0833	3.543	-1.5846	CB	0.3635
	Echoclass	1.533	0.912	-2.2331	C	0.3773
MYSO	Biologist	14.979	3.47	1.3876	A	0.2179

	BCID	16.55	3.81	1.2349	A	0.2187
	Echoclass	10.84	2.62	1.0686	BA	0.2197
	Kaleidoscope	14.88	3.96	0.727	B	0.222
PESU	Kaleidoscope	5.29	1.04	1.6164	A	0.3034
	BCID	2.86	0.739	1.0742	BA	0.3054
	Biologist	2.14	0.6	0.8182	B	0.3068
	Echoclass	1.983	0.512	0.6035	B	0.3082

Table 5. (cont.)

** LS means with the same grouping variable (letter) are not significantly different from each other ($\alpha = 0.05$)*

Table 6. Overall agreement, measured by Cohen’s Kappa, between Echoclass and Kaleidoscope in identifying individual files on Fort Drum Army Installation, New York 2003-2017. Kappa statistic is a metric of observed accuracy versus expected accuracy, and measures the overall agreement for all files and species. Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

Year	Kappa
2003	0.25
2004	0.41
2005	0.41
2006	0.41
2007	0.38
2008	0.35
2009	0.36
2010	0.55
2011	0.31
2012	0.38
2013	0.33
2014	0.42
2015	0.45
2016	0.46
2017	0.50

Table 7: Confusion Matrix table representing percentage of time Kaleidoscope agreed with Echoclass for each species in Fort Drum Army Installation, New York 2003-2017. The diagonal of the matrix represent proportion of agreement between the two programs; anything off the diagonal represents the proportion of times Kaleidoscope disagreed with Echoclass for a given species (indicating where most of the disagreement is occurring). Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

		Echoclass										
		EPFU	LABO	LACI	LANO	MYLE	MYLU	MYSE	MYSO	NoID	Noise	PESU
Kaleidoscope	EPFU	60	11	2	7	2	3	6	2	9	1	2
	LABO	1	24	.	.	15	3	2	3	3	.	1
	LACI	3	1	69	5	1	1	1	1	13	5	4
	LANO	16	3	13	66	.	1	.	1	11	3	3
	MYLE	5	.	1
	MYLU	3	23	1	2	21	63	11	4	9	1	3
	MYSE	.	1	.	.	3	.	3
	MYSO	.	1	.	.	7	1	2	14	1	.	.
	NoID	14	26	6	14	42	13	39	22	15	5	13
	Noise	3	8	9	6	4	15	7	17	38	85	11
PESU	.	3	.	.	1	1	1	.	1	.	63	

Table 8 : Confusion Matrix table representing percentage of time Echoclass agreed with Kaleidoscope for each species in Fort Drum Army Installation, New York 2003-2017. The diagonal of the matrix represent agreement between the two programs; anything off the diagonal represents the proportion of times Kaleidoscope disagreed with Echoclass for a given species (indicating where most of the disagreement is occurring). Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

		Kaleidoscope										
		EPFU	LABO	LACI	LANO	MYLE	MYLU	MYSE	MYSO	NoID	Noise	PESU
Echoclass	EPFU	3	1	1	6	1	1	1	1	4	.	.
	LABO	11	57	1	2	19	24	2	16	14	1	24
	LACI	2	.	38	10	1	1	.	.	4	1	3
	LANO	3	.	1	19	1	1	1	1	3	.	1
	MYLE	6	.	1	1	.	.	.
	MYLU	.	1	.	.	1	12	.	3	1	.	1
	MYSE	1	.	11
	MYSO	.	1	.	.	4	6	2	27	2	.	.
	NoID	48	37	36	41	63	49	55	46	46	20	49
	Noise	6	2	23	22	4	6	7	5	26	77	5
PESU	15

Table 9: Percentage of times Kaleidoscope Agreed with Echoclass on a nightly MLE group level for both present ($\alpha \leq 0.05$) and absent ($\alpha > 0.05$) for each species in Fort Drum Army Installation, New York 2003-2017. N is the sample size (for each species) Echoclass categorized present or absent. Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

	$\alpha \leq 0.05$		$\alpha > 0.05$	
	N	% Kaleidoscope Agreed	N	% Kaleidoscope Agreed
EPFU	3,714	79.77	4,681	80.85
LABO	3,957	66.79	4,438	80.71
LACI	2,590	90.07	5,805	75.55
LANO	1,469	64.46	6,926	93.02
MYLE	16	56.25	8,379	95.65
MYLU	1,412	83.56	6,983	85.55
MYSE	112	47.32	8,283	97.23
MYSO	1,325	18.86	7,070	99.11
PESU	758	43.53	7,637	93.24

Table 10: Percentage of times Echoclass Agreed with Kaleidoscope on a nightly Maximum Likelihood Estimate (MLE) group level for both present ($\alpha \leq 0.05$) and absent ($\alpha > 0.05$) for each species in Fort Drum Army Installation, New York 2003-2017. N is the sample size (for each species) Kaleidoscope categorized present or absent. Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

	$\alpha \leq 0.05$		$\alpha > 0.05$	
	N	% Echoclass Agreed	N	% Echoclass Agreed
EPFU	3859	76.78	4536	83.44
LABO	3499	75.55	4896	73.16
LACI	3752	62.18	4643	94.44
LANO	1430	66.22	6965	92.5
MYLE	373	2.41	8022	99.91
MYLU	2189	53.9	6206	96.26
MYSE	282	18.79	8113	99.27
MYSO	313	79.87	8082	86.69
PESU	845	39	7549	94.33

Table 11: Percentage of times Kaleidoscope agreed with Echoclass on an individual file level and a nightly Maximum Likelihood Estimates (MLE) level of presence ($\alpha \leq 0.05$) for each species in Fort Drum Army Installation, New York 2003-2017. MLE values represent the probability that a species is misclassified as present when in fact it is absent on a given site night based on multiple species. Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

% Kaleidoscope agreement with Echoclass	Individual Files	Nightly MLE
EPFU	60	79.77
LABO	24	66.79
LACI	69	90.07
LANO	66	64.46
MYLE	5	56.25
MYLU	63	83.56
MYSE	30	47.32
MYSO	14	18.86
PESU	63	43.53

Table 12: Percentage of times Echoclass agreed with Kaleidoscope on an individual file level and a nightly Maximum Likelihood Estimates (MLE) level of presence ($\alpha \leq 0.05$) for each species in Fort Drum Army Installation, New York 2003-2017. MLE values represent probability that a species is misclassified as present when in fact it is absent on a given site night based on multiple species. Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

% Echoclass agreement with Kaleidoscope	Individual Files	Nightly MLE
EPFU	30	76.78
LABO	57	75.55
LACI	38	62.18
LANO	19	66.22
MYLE	6	2.41
MYLU	12	53.9
MYSE	11	18.79
MYSO	27	79.87
PESU	15	39

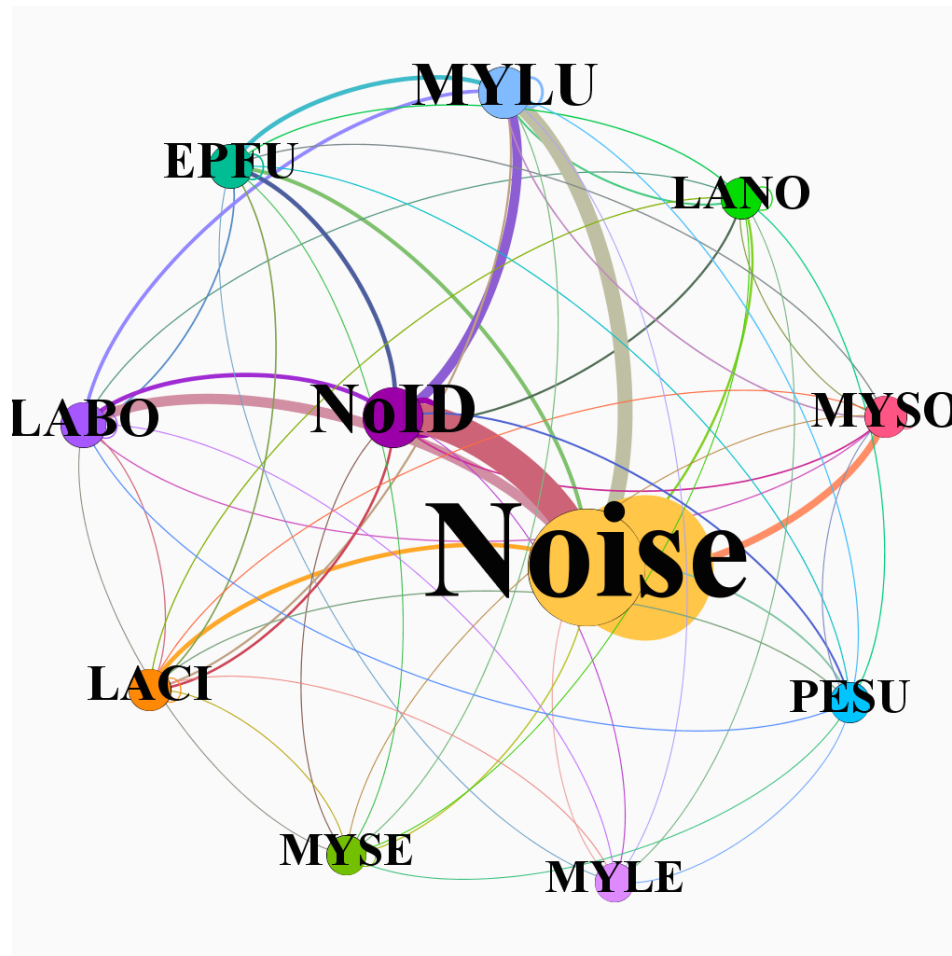


Figure 1: Network graph representing disagreement rates between Echoclass and Kaleidoscope on identifying individual species in Fort Drum Army Installation, New York 2003-2017. The thickness of the line indicates the strength of interconnectedness “misclassification” between two species. If the programs had 100% agreement all species would be disconnected and fully separated. Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

Figure 2a

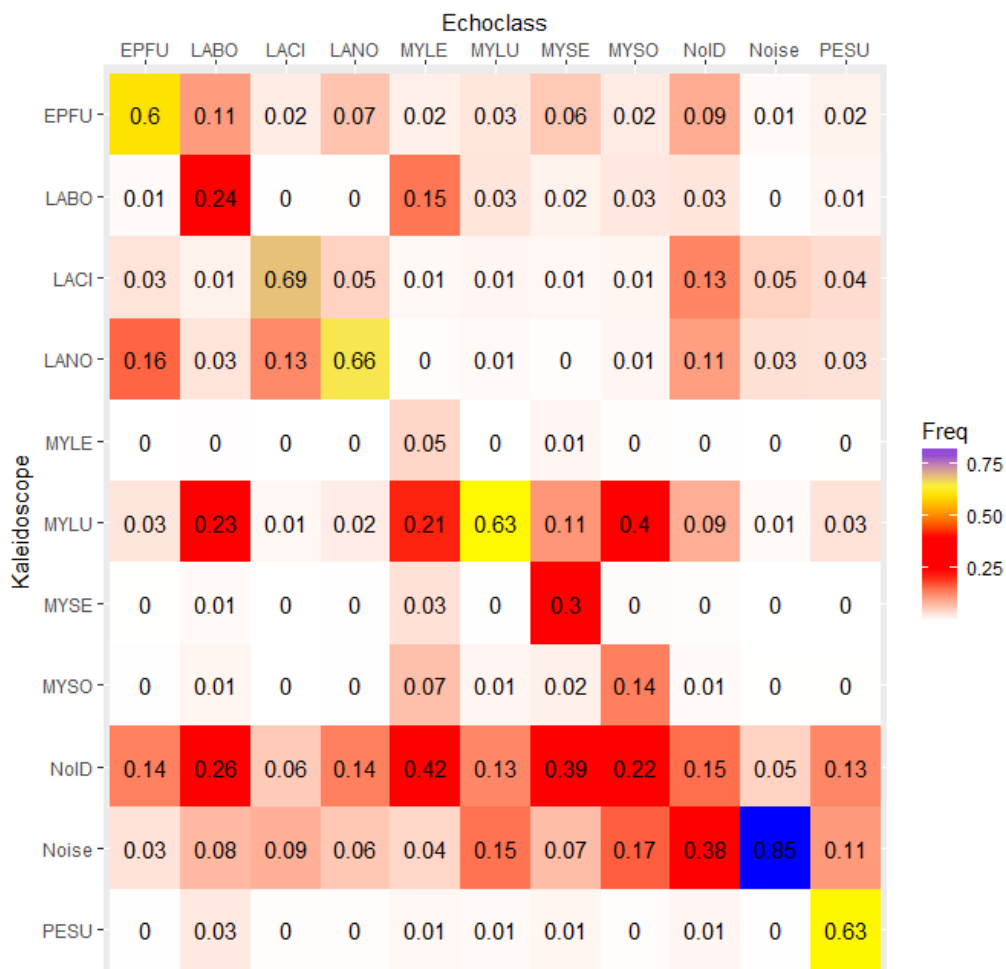


Figure 2b

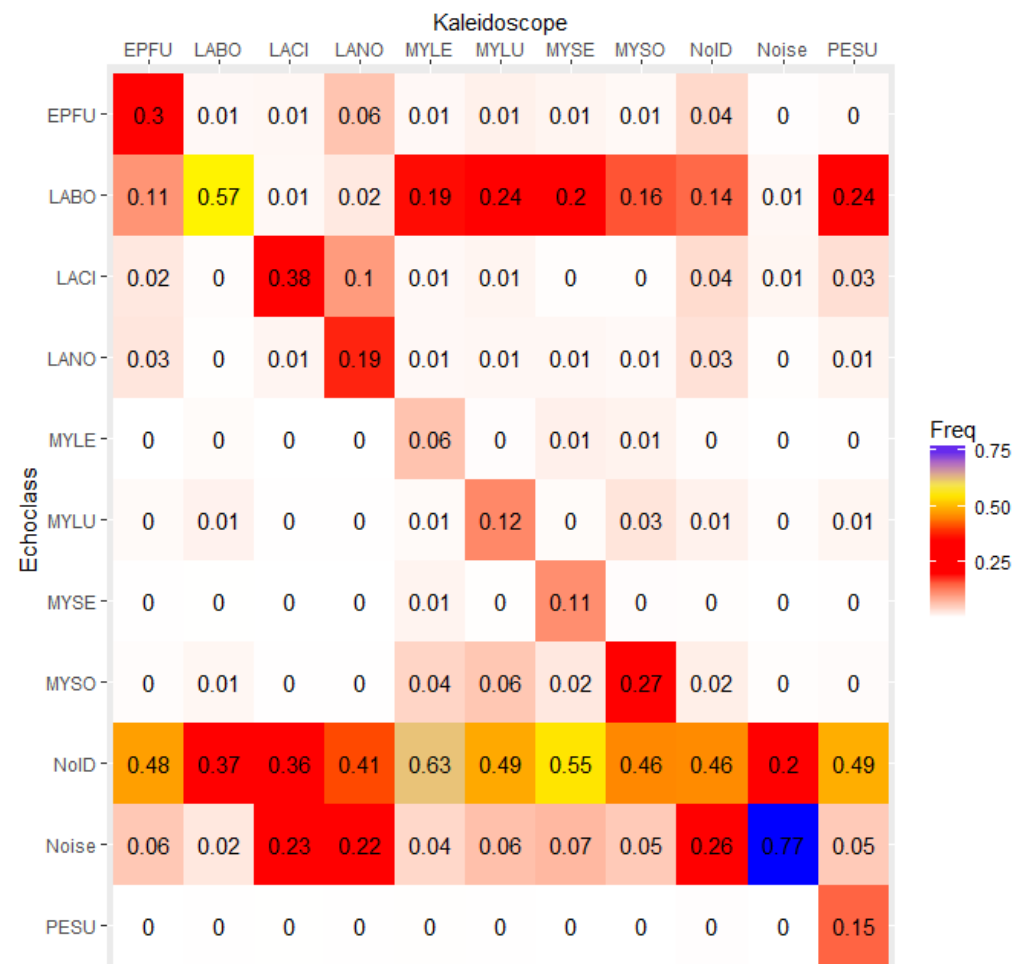


Figure 2. Heatmap depicting agreement and disagreement between Echoclass and Kaleidoscope on identifying individual files to species in Fort Drum Army Installation, New York 2003-2017. **2a.** Heat map of a confusion matrix where Echoclass is the reference and Kaleidoscope is the predictor. The diagonal of the matrix represent proportion of agreement between the two programs; anything off the diagonal represents the proportion of times Kaleidoscope disagreed with Echoclass for a given species (indicating where most of the disagreement is occurring). **2b.** Heat map of a confusion matrix where Echoclass is the reference and Kaleidoscope is the predictor. The diagonal of the matrix represent agreement between the two programs; anything off the diagonal represents the proportion of times Kaleidoscope disagreed with Echoclass for a given species (indicating where most of the disagreement is occurring). Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

Chapter 2: WNS-induced temporal and spatial changes in little brown activity

Abstract

How bat distribution and habitat associations have changed at the local to sub-landscape scale has received little attention to date despite being a critical information need for managers in the post White-nose syndrome (WNS) environment. To better understand the spatial nature of population decline, we modelled both activity patterns and occupancy from acoustic surveys for the little brown bat (*Myotis lucifugus*) on Fort Drum Army Installation in New York 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. Little brown bat 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. 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, such as the little brown bat in the Northeast, to assess ongoing temporal and spatial changes, habitat associations, and as a guide to direct future mist-netting should rely more on relative activity as the metric of choice.

Introduction

The emergence of the fungal pathogen, *Pseudogymnoascus destructans*, causative agent of White-nose Syndrome (WNS), was first documented in the United States in the winter of 2006

at Howe's Caverns, approximately 65 km west of Albany, New York (Blehert et al. 2009). Since then, the disease agent has moved rapidly throughout the Northeast and upper Southeast and central Midwest, as well as throughout much of eastern and south-central Canada (USGS National Wildlife Health Center - White-nose Syndrome (WNS) 2018). To date, WNS has been found to infect eight species of cave-dwelling bats in eastern North America: the federally endangered Indiana bat (*Myotis sodalis*, MYSE), the threatened northern long-eared bat (*Myotis septentrionalis*, MYSO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), gray bat (*Myotis grisescens*, MYGR), Southeastern bat (*Myotis austroriparius*, MYAU), big brown bat (*Eptesicus fuscus*, EPFU), and tri-colored bat (*Perimyotis subflavus*, PESU) (U.S. Fish and Wildlife Service 2017). The fungus, infects epithelial tissues of hibernating bats causing abnormally frequent arousal through winter that leads to loss of critical fat reserves and water balance disruption (Cryan et al. 2010, Frick et al. 2010, Meteyer et al. 2012).

Among impacted species, the most dramatic changes in activity patterns, abundance, and to some degree distribution have been observed for MYLU, MYSE, MYSO, and PESU (Blehert et al. 2009, Frick et al. 2010, Brooks 2011, Ford et al. 2011). Prior to the onset of WNS, populations of MYLU were either stable or increasing, making it one of the most common and abundant bats in North America; yet since the discovery of WNS populations have decline by 75-99% (Blehert et al. 2009, Frick et al. 2010, Ingersoll et al. 2016). Although individual MYLU do show healed wing membranes, post-winter survival, and reproduction after infection by WNS (Dobony et al. 2011, Dobony and Johnson 2018), significant overwintering mortality, poor female physiological condition, and energetic demands to repair dermal tissue have resulted in variable reproductive rates on the landscape, potentially limiting population recovery (Dobony et

al. 2011, Dzal et al. 2011, Ford et al. 2011, Francl et al. 2012, Langwig et al. 2012, Dobony and Johnson 2018). As a result, pre-WNS trends of activity levels increasing in mid-summer, consistent with reproduction and summer recruitment, have been greatly reduced regionally (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 (Jachowski et al. 2014a). Specifically, the reduction in MYLU has been exacerbated by the infringement of species favoring the spatial and temporal conditions MYLU inhabit (Jachowski et al. 2014a). This dramatic change in population size in a relatively short time frame makes MYLU a great model species to evaluate inter- and intraspecific interactions, and evaluate their relationship with environmental conditions.

Nonetheless, the paucity of data encompassing both pre-WNS and post-WNS years for most regions has made it difficult to compare the relative change in bat activity and occupancy between the two periods. An exception to this is the extensive long term mist-netting and acoustic monitoring of bat distribution, activity, and occupancy program initiated at Fort Drum Military Installation (Fort Drum) in northern New York (Ford et al. 2011). Much of this monitoring began in response to both known hibernacula adjacent to the base and the presence of the federally endangered MYSO on the installation during the summer (Jachowski et al. 2014b). Continuous monitoring from 2003 to present have allowed researchers to document changes in bat numbers, activity, and physiological status by pre- and post-WNS (Dobony et al. 2011, Ford et al. 2011, Coleman et al. 2014b, a, c). 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 MYSE, MYSO, and MYLU bat activity patterns decreasing the most in the years subsequent to WNS presence (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 management oriented implications for understanding the impact to threatened and endangered species, how additional species might become endangered, and how land managers need to respond to either ameliorate or adapt to WNS impacts.

Understanding the abiotic and biotic process that affect how and why species are distributed across space, i.e., 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 (Miller 2010, 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 1999, Borcard et al. 2011, Sainani 2014). Species distribution models are widely used as predictors of species presence, habitat suitability and/or range distribution. This technique often is required for natural resource research, management, and/or 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. This latter presents challenges to modeling distribution activity and occupancy, as communities and

individuals exist in complex spatial arrangements and structures; and while models may try to predict the distribution, activity or occupancy of wildlife populations onto a landscape, it assumes 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, climatic events, and dispersal), whereupon similarities between sites become ever more dependent with the increase 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 estimated or under represented, diminishing the accuracy of models (e.g. insects González-Megías et al. 2005, birds Diniz-Filho and Bini 2005, mammals Peakall et al. 2003). Complicating species modeling is the recognition that spatial structures, such as scale, size of sampling units, distance between sites, and extent of the study site influence how patterns, i.e, occupancy and distribution, relate to ecological processes (Borcard et al. 2011).

Effective conservation planning at 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 MYLU as a model species to study disease dynamics 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. Our major objectives were to 1) identify suitable site characteristics that affect MYLU 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 volant and mobile species as the model organism.

Study Site

We conducted our study at Fort Drum Military Installation in Jefferson and Lewis counties in northwestern New York, USA. Situated at the junction of the St. Lawrence- Great Lakes lowlands, the base of the Adirondack Mountains, and the Tug Hill Plateau ecoregion, Fort Drum is a 43,000 ha U.S. Army installation that contains a variety of forest, wetland, and open habitat conditions. The Niagara Escarpment, which lies 10 – 15 km west of Fort Drum, contains limestone (Karst) formation caves used as winter hibernacula by bats (Ford et al. 2011). The bat fauna of Fort Drum, New York is small, with only 9 species of 3 echolocation groups: high-frequency call (minimum frequency > 40 khz) little brown bat (MYLU), northern long-eared bat (MYSE), Indiana bat (MYSO), tri-colored bat (PESU), eastern small-footed bat (MYLE), and eastern red bat (LABO), midrange frequency call (between 25 to 40 khz) big brown bat (EPFU), and silver-haired bat (*Lasionycteris noctivagans*, LANO), and low frequency call (maximum frequency < 25 khz) hoary bat (*Lasiurus cinereus*, LACI) (Coleman et al. 2014a).

Methods

To assess MYLU presence and activity, we assembled echolocation recordings from Fort Drum during the summers of 2003-2017 that encompassed 289 individual sites over 8,373 detector nights (Figure 1). Nights where the detector did not turn on or shut off within 2 hours after sunset were excluded from the analysis. However, if a detector ran for at least 8 hours, it was included in our analysis. Anabat II detectors connected to a compact flash-storage zero-

crossings analysis-interface module (ZCAIM), and SD1 and SD2 detectors using the same transducer model (Titley Electronics, Ballina, NSW, Australia). From 2003-2011, we initially placed Anabat units in weatherproof boxes, but left the microphone exposed. We tried to only sample on dates that were projected to have no or minimal chance of inclement weather. In 2012 and onwards, we attached a PVC tube to protect the microphone from rain (to be able to leave units out for extended periods of time during variable weather), and to aid in funneling sounds into the microphone to the weatherproofing boxes. Though variability between weatherproofing methods occurred throughout the years Britzke et al (2010) found no significant difference between these two weatherproofing techniques. Additionally, this inclusion of nights with inclement weather in the later years, in conjunction with WNS, could have resulted in causing further negative bias (though not biologically meaningful relative to WNS impact). A small hole was drilled into the bottom of the PVC tube to allow water to drain out, so calls would not be reflected or distorted, and to keep water from flooding the detector (Britzke et al. 2013). Following Ford et al. (2011) and Coleman et al. (2014a, c) we placed each unit on a 1.5m tri-pod and adjusted so that sound could enter the PVC tube at an angle of 45° (Weller and Zabel 2002), this same approach was used for years without the PVC tube . Our sample sites primarily included: 1) sites along trails and forest tracks where detectors were positioned to capture sound along the trail; 2) sites with forest canopy gaps where detectors were positioned to face openings; and 3) emergent wetland sites where detectors were positioned towards water/ wetland emergent or woody vegetation. We visually scanned recorded echolocation passes for extraneous non-bat noise and 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 (USFWS)

(using 0 for the program sensitivity setting, and 3 pulse minimum) (USFWS: Indiana Bat Summer Survey Guidance 2017).

Raster Prediction

Because previous research have shown that topographic characteristics such as elevation, and land cover variables such as canopy cover, habitat, 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), percent canopy cover, landcover, distance to water and distance to road to include as variables in MYLU occupancy and relative activity models for Fort Drum. We determined environmental variables at each acoustic detector point using both ArcGIS and physical habitat measurements taken on site. 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. Furthermore, we used a 0.61m resolution Elevation data obtained from Fort Drum Army Installation to compare to the 10m. We derived percent canopy cover and land cover from the Multi-Resolution Land Characteristics Consortium (MRLC) National Land Cover Database (NLCD, 2011) at 30 meters. Because our acoustic locations varied through time, we estimated percent canopy cover for each detector for each year by extracting the values of the most recent canopy cover layer from the MRLC (2003, 2006, and 2011) to our sample locations. Additionally, for those sites where canopy cover was recorded we utilized those measurements. Additional land cover data was also obtained from Fort Drum to improve the accuracy of our derived NLC layer. We used Spatial Analyst Toolbox to reclassify our Fort Drum land cover data into 5 general categories (forest, shrub land, wetland, development, and barren).

Additionally, we acquired wetland data from the National Wetlands Inventory (USFWS 2017) along with road layers from Fort Drum Army Installation, and assigned to each acoustic detector the distance to the nearest water source and the nearest road. Previous work has collected data on the distance to water and road for each sampling point. We then calculated distance to water and distance to road for each cell value using Euclidean Distance in Spatial Analyst Toolbox in ArcGIS 10.5 (ESRI 2017), using both layers derived from Fort Drum land cover and road data and NWI. If a site did not have a record for distance to water or road, we used the Euclidean distances of water and road to assign those values to that site. We used the observed cell values for each raster layer at Fort Drum to predict relative bat activity levels. We used Program R 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. We used ArcGIS 10.5 to visualize the predicted relative activity for each year across Fort Drum at 30m resolution.

Activity

To assess MYLU activity relative to environmental characteristics on Fort Drum we fit a generalized linear mixed model (GLMM) in program R (R Development 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, distance to water, and land cover (both at a fine, 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), date, and year as fixed effects (Table 1; Table 2). 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 an *a priori* set of models representing individual hypothesis about activity patterns. We centered and scaled all continuous covariates to aid in model fitting and interpretation; notably, this puts all continuous variables on the scale, thereby permitting direct comparisons of effect sizes (Schiegg 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 for this was to ensure that if we could in fact predict MYLU relative activity across the landscape using our global model between sampled sites. In addition, we used spatial correlograms in package *pgirmess* in R (Giraudoux et al. 2018) to assess autocorrelation in MYLU relative activity per site night. We then used the same method to assess our fitted models residuals to demonstrate how spatial autocorrelation is addressed and reduced through the use of our GLMM (Dormann et al. 2007). We then used package *vegan* in R (Oksanen et al. 2018) and fit a redundancy analysis using the function *varplot* to assess the total variation that our significant positive spatial vectors explain.

Occupancy

Under USFWS MYSO survey guidelines, acceptance of presence of MYSO 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 MYLU 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 used the resulting binary data as species detection histories for each site and species to model occupancy (MacKenzie et al. 2002). We created a set of occupancy models representing *a priori* hypothesis in program PRESENCE, Version 12.10 (U.S. Geological Survey, Patuxent, MD) to estimate probabilities of occupancy (Ψ) and detection (ρ) for MYLU from 2003-2017. Due to limited sampling effort (maximum nightly sample being 2 nights) for years prior to WNS (2003-2007) we combined this data together representing pre-WNS (Table 5). 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, 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 (Figure 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 MYLU (n =76,916 passes). We found 80 significantly positive eigenvectors associated with site locations. Spatial eigenvectors only explained 0.07% of the variation in

explaining MYLU activity. The best-approximating model included date, percent canopy cover, land cover (on a broad scale level), distance to road, and year, with only three other models within 4 Δ AIC units (Table 313). In all models, date, canopy cover, and distance to road appeared to significantly affect relative activity of MYLU ($p \leq 0.05$), where MYLU activity was negatively correlated with each (Table 44). Only wetland habitats (including emergent and woody wetlands) was significantly different from zero having a positive effect on MYLU activity ($p \leq 0.05$) (Table 44). Additionally, years' post-WNS (2010-2017) were significantly different from zero, with a negative relationship with MYLU activity (Table 44). This negative trend through the years is illustrated by our predicted relative activity maps (Figures 2-15) and our fitted regression line on the mean echolocation passes for each year (Figure 16) that show an overall decreasing trend in MYLU activity across Fort Drum.

Over the years examined, MYLU presence was denoted during at least 1 sampling event, at any site, every year. 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 [$\Psi(.)$] was either competing (models within 2 Δ AIC units) or was the best supported model (Table 5). With the exception of 2013, where the best supported model included habitat as an important predictor of occurrence (Table 5), a potential artifact of targeted sampling that year for MYSE. Beyond these, other tested models that included variables such as elevation, percent canopy cover, distance to water, distance to road, and habitat had little empirical support for estimating occupancy, but were predictors for describing detection (Table 5). Occupancy estimates varied for our best supported model in each year (Table 66). Years with small number of sampling sites (5 sites for 2014 and 2017) had derived occupancy estimates, but which generated confidence intervals that ranged of all possible values from 0 to 1. Conversely, years

with large number 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 between (0.678 and 0.837) for 2011 and (0.571-0.774) for 2013 (Table 77).

Discussion

Irrespective of known habitat associations and correlates for MYLU, our findings corroborate results by (Brooks 2011, Dzal et al. 2011, Ford et al. 2011, Ingersoll et al. 2016) that relative bat activity, especially in MYLU, has significantly decreased in years proceeding WNS. Prior to WNS MYLU were one of the most abundant and common species of bats in North America, with seasonal increases in activity and abundance consistent with arrival from hibernation areas and then following 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 (Blehert 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, causing a decline 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, and describe changes in both relative activity and occupancy. Little brown bats are a good model species that are intrinsic to understand the relationship between disease dynamics, species susceptibility, and environmental conditions. We can use Fort Drum as a model to identify suitable environmental characteristics important for MYLU, understand disease dynamics as it relates to local and regional population declines, and synthesize these declines into relative activity and occupancy modeling.

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 MYLU relative activity, we observed that date (which indirectly incorporates weather influences), percent canopy cover, and distance to road were all significantly different from zero and were negatively correlated with MYLU activity. Ford et al. (2011) showed that as summer progresses in a post-WNS setting MYLU activity decreases. Moreover, variation in site placement in regards to distance to road and percent canopy cover, i.e., low to high clutter, allowed us to see how activity changes as canopy cover and distance to road increases. We found that canopy cover and distance to road had a significant negative effect on little brown bat relative activity; this is consistent with research indicating decreasing rates of bat activity and detection power as canopy cover increases, and sampling is done further away from corridors, such as roads or trails (Sherwin et al. 2000, Law and Chidel 2001, Menzel et al. 2002, Weller and Zabel 2002, Coleman et al. 2014a). Furthermore, our analysis show MYLU activity being greatest in wetland areas, as have others within the species' range (Jung et al. 1999, Zimmerman and Glanz 2000, Erickson and West 2003, Ford et al. 2005, Menzel et al. 2005).

Through our geospatial analysis of MYLU activity, we observed a time lag when MYLU 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 decrease a great deal until 2010. An artifact of the communicability and spread of WNS on the landscape, where over time, as this disease spreads among individuals 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 on Fort Drum. Although resiliency to long-term WNS exposure has been observed in some remaining MYLU, whereby some individuals continue to show relatively high reproductive effort (Dobony et al. 2011, Frick et al. 2017, Langwig et al. 2017, Dobony and Johnson 2018), since the first documented case of WNS, regional population declines are estimated to be > 90% (Blehert et al. 2009, Frick et al. 2010). Therefore, we posit that good biological performance for small segments of populations in and of itself may not necessarily be meaningful. From 2010 onwards, mean relative activity increased (Figure 16). When predicted across the landscapes this same trend was not seen, however our predictions indicate that while activity is low across Fort Drum post-WNS, our maps indicate that a stabilization of relative activity may be occurring (Figure 8-15). While we do not have the power to detect stability or an increase in MYLU populations at the scale of Fort Drum through the use of acoustic detectors, it is plausible, given our results, that there is a continuing population loss but not at the absolute scale when WNS first started to affect MYLU regionally (Frick et al. 2017, Langwig et al. 2017)., It is important to note however, that limitations in our sampling design, i.e., variations 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 illustration of MYLU at Fort Drum, specifically with pre-WNS years, is in part a sampling artifact causative of yearly differences in sampling effort and size, i.e., few sights sampled and for a limited duration (Figures 2-4). Furthermore, no sampling was done in the impact area, and minimal sampling was done in the north/northwest portion of Fort Drum. Relative activity predictions into these areas should be viewed cautiously.

Occupancy

Currently available automated bat acoustic identification software generate species identifications for call sequences using algorithms that process and classify quantitative measures of individual calls (e.g. frequency, slope, curvature, pulse rate). Software classification algorithms are trained using reference call libraries which consist of known identity calls. These known identity calls typically are recorded using captured bats that are hand released, and more rarely from free-flying bats. Once individual acoustic files have been assigned a species identity, or classified as noise or unidentifiable, most automated identification software generate maximum likelihood estimates (MLE) using the method of Britzke (2002). MLE values represent the probability that a species is misclassified as present when in fact it is absent, and are calculated by comparing the number of files classified as each identified species to the known misclassification rates of those species in the classification algorithm as measured using known identify calls (Britzke, 2002, Niver et al. 2014).

Across the landscape scale of Fort Drum, occupancy metrics suggest relatively high probability of occurrence across sampled sites regardless of year. Additionally, our yearly occupancy models suggest few of the chosen covariates are important predictors for occupancy. The fact that none of our parameters effect occupancy reflects how 1) binomial response (either present or absent) groupings in occupancy are an oversimplification of what is truly occurring on the landscape; 2) the spatial extent (Steenweg et al. 2018) 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; and 3) 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 2 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 MYLU presence for pre-WNS. Secondly, for 2014 and 2017, we had large number of sampling nights but few allocated sites (5 sites). Although we were able to generate estimates for detection and occupancy, our model lacked the ability to make broader implications across Fort Drum. Thirdly, for 2015 sampling at Fort Drum was specifically targeted for MYSE, and therefore sites were positioned in areas less suitable for MYLU, with surveys occurring in areas with a larger proportion of upland forests rather than in wetlands and more open corridors (Chris Dobony, Fort Drum Military Installation, per comm). 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 vs. 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 positive 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, changes in abundance often will have strong correlations with occupancy. Species that are highly mobile and/or with minimal habitat constraints, as occurs with avifauna and bats, the relationship between occupancy and changing abundances may not be clear (Gaston and Curnutt 1998). Being highly volant and mobile species, bats tend to have large home range sizes (Owen et al. 2003, Kniowski and Gehrt 2014, Maxell and Montana Natural Heritage Program, 2015, Nelson and Gillam 2016). At Fort Drum, MYLU, for example have core mean home ranges >143.0 ha on Fort Drum (Coleman et al. 2014b). Based on the foraging and home range characteristics of MYLU, 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 MYLU illustrate this disjunction in occupancy-abundance relationship. First, we saw minimal change in occupancy through time for MYLU. Secondly, none of our environmental variables seemed to impact occupancy, and, when they did, these differences were not significant. Conversely, our relative activity models not only identified important topographic and land cover variables important to MYLU relative activity, but had the

predictive power to see 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, knowing that current occupancy estimates are about 80% for Fort Drum may still be informative. Nevertheless, continued acoustic monitoring of bat species, such as MYLU in the Northeast, to assess ongoing temporal and spatial changes, habitat associations, and as a guide to direct future mist-netting should rely more on relative activity as the metric of choice.

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Table 1. Variables used in candidate models describing bat activity and occupancy with justification and supporting literature for each parameter. Candidate models represented bat activity on Fort Drum, New York, during the summers 2003-2017.

Parameter	Justification	Supporting Literature
Date	Bat activity varies in intensity and spatially by date	(O'Shea et al. 2003, Perry et al. 2010, Ford et al. 2011, Ford et al. 2016)
Year	WNS affect bats have lower activity post-WNS than pre-WNS	(Frick et al. 2010, Ford et al. 2011, Coleman and Reichard 2014)
Percent Canopy Cover	Bats may be attracted to openings within canopy	(Humes et al. 1999, Erickson and West 2003)
Elevation	Bat activity varies along an elevation gradient	(Wolbert et al. 2014)
Distance to Road	Bats use linear features such as roads and trails as foraging habitat	(Law and Chidel 2001, Menzel et al. 2002, Caras and Korine 2009, Hein et al. 2009)
Distance to Water	Bats utilize water bodies as drinking sources	(Brooks and Ford 2005, Ford et al. 2005, Adams and Thibault 2006, Loeb and O'Keefe 2006)
Habitat	Bats select preferential habitats associated with foraging and morphology	(Jung et al. 1999, Brooks and Ford 2005, Loeb and O'Keefe 2006, Schirmacher et al. 2007)

Table 2. Variables used in candidate models representing bat activity and occupancy on Fort Drum, New York, 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	how far a point is from a road
Distance to Water	how far a 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

Table 313. Rankings of models predicting little brown bat (*Myotis lucifugus*) activity around Fort Drum Military Installation, New York during 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 ith 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 + Distance to Road ² + Year	25	32502.4	32502.6	0	0.44214	1
Day + Day ² + Canopy Cover + Canopy Cover ² + Distance to Road + Distance to Road ² + Year	21	32503.2	32503.3	0.75105	0.30372	1.45575
Day + Day ² + Canopy Cover + Canopy Cover ² + Habitat_broadscale + Distance to Road + Distance to Road ² + Distance to Water + Distance to Water ² + Year	27	32504	32504.2	1.62737	0.19597	2.25621
Day + Day ² + Canopy Cover + Canopy Cover ² + Elevation + Elevation ² + Habitat_broadscale + Distance to Road + Distance to Road ² + Distance to Water + Distance to Water ² + Year	29	32506.4	32506.6	4.05667	0.05817	7.60144

Table 4. Parameter estimates table of our best supported model predicting little brown bat (*Myotis lucifugus*) activity around Fort Drum Military Installation, New York during summer 2003-2017. With estimate, standard error, z-score, p-value, and significance score at an ($\alpha \leq 0.05$). Significant codes represent: $p \leq 0.0001$ represented by ***; $p \leq 0.001$ **; $p \leq 0.01$ *; $p \leq 0.05$.

Parameter	Estimate	Std. Error	z	Pr(> z)	Significance ($\alpha \leq .05$)
Wetlands	3.6275	1.1672	3.11	0.00188	**
Date	0.0297	0.0276	1.08	0.28237	.
Date ²	-0.655	0.022	-29.78	< 0.0001	***
CC	-0.6882	0.1971	-3.49	0.00048	***
CC ²	-0.612	0.1947	-3.14	0.00167	**
Developed	-1.8397	0.9986	-1.84	0.06543	.
Forest	-1.2954	0.8142	-1.59	0.11161	.
Shrub	-1.198	0.8594	-1.39	0.16329	.
Open Water	-0.4611	0.8276	-0.56	0.57742	.
DR	-0.4615	0.1546	-2.98	0.00284	**
DR ²	0.0631	0.0242	2.61	0.00907	**
Year2004	2.3953	0.8881	2.7	0.007	**
Year2005	1.0047	0.8814	1.14	0.25428	.
Year2006	0.8471	0.8906	0.95	0.34153	.
Year2007	1.5712	0.9094	1.73	0.08405	.
Year2008	0.1	0.9128	0.11	0.91272	.
Year2009	0.5594	0.8387	0.67	0.50476	.
Year2010	-1.9734	0.8852	-2.23	0.0258	*
Year2011	-2.1281	0.8576	-2.48	0.01309	*
Year2012	-2.6307	0.858	-3.07	0.00217	**
Year2013	-2.4326	0.8585	-2.83	0.00461	**
Year2014	-2.0702	0.8606	-2.41	0.01615	*
Year2015	-2.1988	0.8607	-2.55	0.01063	*
Year2016	-1.5284	0.8532	-1.79	0.0732	.

Table 5. Rankings of models predicting little brown bat (*Myotis lucifugus*) occupancy around Fort Drum Military Installation, New York during summer 2003-2017. With model parameters for both occupancy (psi(.)) and detection (p(.)), Akaike's information criteria Corrected (AICc) value, , difference in AIC value between best supported model and ith model ($\Delta AICc$), and w_i (model weight). Shading highlights models where occupancy parameters were null.

Year	Model	AICc	$\Delta AICc$	w_i
Pre-WNS	psi(.),p(.)	125.63	0	0.7518
2008	psi(.),p(.)	33.07	0	0.7271
	psi(Habitat),p(DR,CC)	35.03	1.96	0.2729
2009	psi(.),p(DR,CC)	32.4	0	0.3598
	psi(Habitat),p(DR,CC)	32.4	0	0.3598
	psi(.),p(.)	34.28	1.88	0.1405
	psi(Habitat),p(.)	34.29	1.89	0.1398
2010	psi(.),p(DR,CC)	55.42	0	0.3661
	psi(Habitat),pDR,CC.)	56.31	0.89	0.2346
	psi(.),p(DR,CC,EV)	56.73	1.31	0.1902
	psi(Habitat),p(DR,CC,EV)	57.7	2.28	0.1171
2011	psi(Habitat),p(DR,CC)	1095.65	0	0.583
	psi(.),p(DR,CC)	1096.32	0.67	0.417
2012	psi(.),p(.)	1777.66	0	0.5336
	psi(Habitat),p(.)	1779.17	1.51	0.2508
	psi(Habitat),p(DR,CC)	1780.05	2.39	0.1615
2013	psi(Habitat),p(DR,CC)	1243.12	0	0.9878
2014	psi(.),p(.)	684.89	0	0.9997
2015	psi(.),p(DR,CC)	1729.32	0	0.909
2016	psi(.),p(DR,Habitat,CC)	1417.32	0	0.6833
2017	psi(.),p(cc,dr)	344.38	0	0.69
	psi(h),p(cc,dr)	345.98	1.6	0.31

Table 6. Occupancy estimates from yearly top models predicting little brown bat (*Myotis lucifugus*) occupancy around Fort Drum Military Installation, New York during summers of 2003-2017. With model parameters for both occupancy (ψ) and detection ($p(\cdot)$), N sites sampled within that given year, ψ (measure of occupancy), standard error, and 95% confidence interval.

Year	Model	N	ψ	Standard Error	95% Confidence Intervals
Pre-WNS	psi(.),p(.)	87	0.862	0.044	0.753 - 0.927
2008	psi(.),p(.)	12	0.838	0.134	0.427 - 0.972
2009	psi(.),p(DR,CC)	13	1.000	0.000	0.00 - 1.00
2010	psi(.),p(DR,CC)	19	0.785	0.135	0.431 - 0.946
2011	psi(Habitat),p(DR,CC)	57	0.505*	0.502	0.364 - 0.645
2012	psi(.),p(.)	55	0.650	0.075	0.493 - 0.779
2013	psi(Habitat),p(DR,CC)	49	0.503*	0.502	0.363 - 0.644
2014	psi(.),p(.)	5	1.000	0.000	0.00 - 1.00
2015	psi(.),p(DR,CC)	129	0.265	0.041	0.193 - 0.351
2016	psi(.),p(DR,Habitat,CC)	81	0.791	0.045	0.688 - 0.865
2017	psi(.),p(cc,dr)	5	0.800	0.179	0.308 - 0.972

Table 7. Occupancy estimates from 2011 and 2013 top models predicting little brown bat (*Myotis lucifugus*) occupancy across habitat around Fort Drum Military Installation, New York during summers of 2003-2017. With habitat condition, ψ (measure of occupancy), standard error, and 95% confidence interval.

Year	Habitat	ψ	Standard Error	95% Confidence Intervals
2011	Deciduous Forest	0.837	0.088	0.590 - 0.948
	Evergreen Forest	0.682	0.065	0.543 - 0.795
	Mixed Forest	0.678	0.064	0.542 - 0.789
	Shrub	0.678	0.064	0.542 - 0.789
	Developed	0.837	0.088	0.590 - 0.948
	Emergent Wetland	0.837	0.088	0.590 - 0.948
	Woody Wetlands	0.837	0.088	0.590 - 0.948
	Open Water	0.678	0.064	0.542 - 0.789
2013	Deciduous Forest	0.640	0.070	0.494 - 0.764
	Evergreen Forest	0.571	0.037	0.497 - 0.643
	Mixed Forest	0.643	0.072	0.494 - 0.769
	Shrub	0.637	0.069	0.495 - 0.759
	Developed	0.640	0.070	0.494 - 0.759
	Emergent Wetland	0.637	0.069	0.495 - 0.759
	Woody Wetlands	0.774	0.114	0.488 - 0.925
	Open Water	0.640	0.070	0.494 - 0.764

Figure 1. Acoustic detector locations on Fort Drum Military Installation, New York summer, 2003-2017- 289 individual sites were sampled across 15 years, with a total of 8,373 detector nights. Hash marks indicate impact zone where no sampling occurred.

Acoustic Detector Locations from 2003-2017 on Fort Drum Military Instalation, New York.

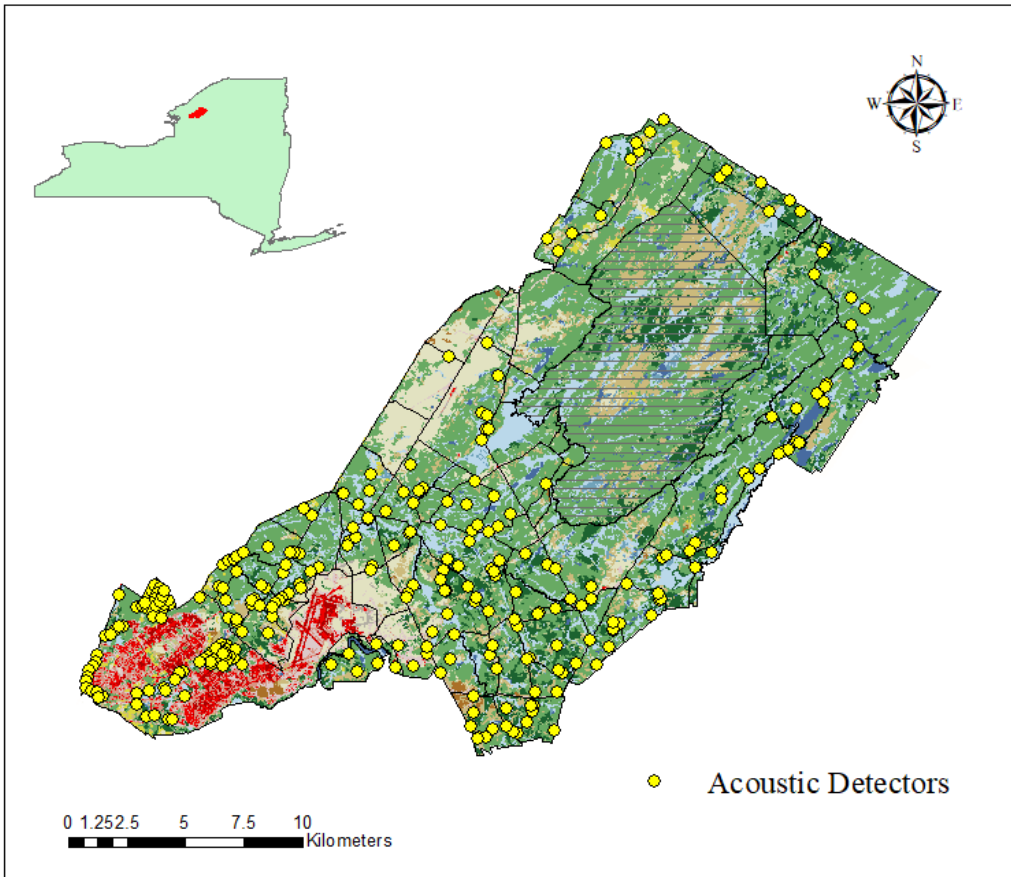


Figure 2. Predicted relative activity across Fort Drum Military Installation, New York summer, 2004. Relative activity modeled from mean echolocation passes per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity across all raster cells was calculated for the entire installation.

Predicted Relative Activity for 2004 on Fort Drum Military Instalation, New York

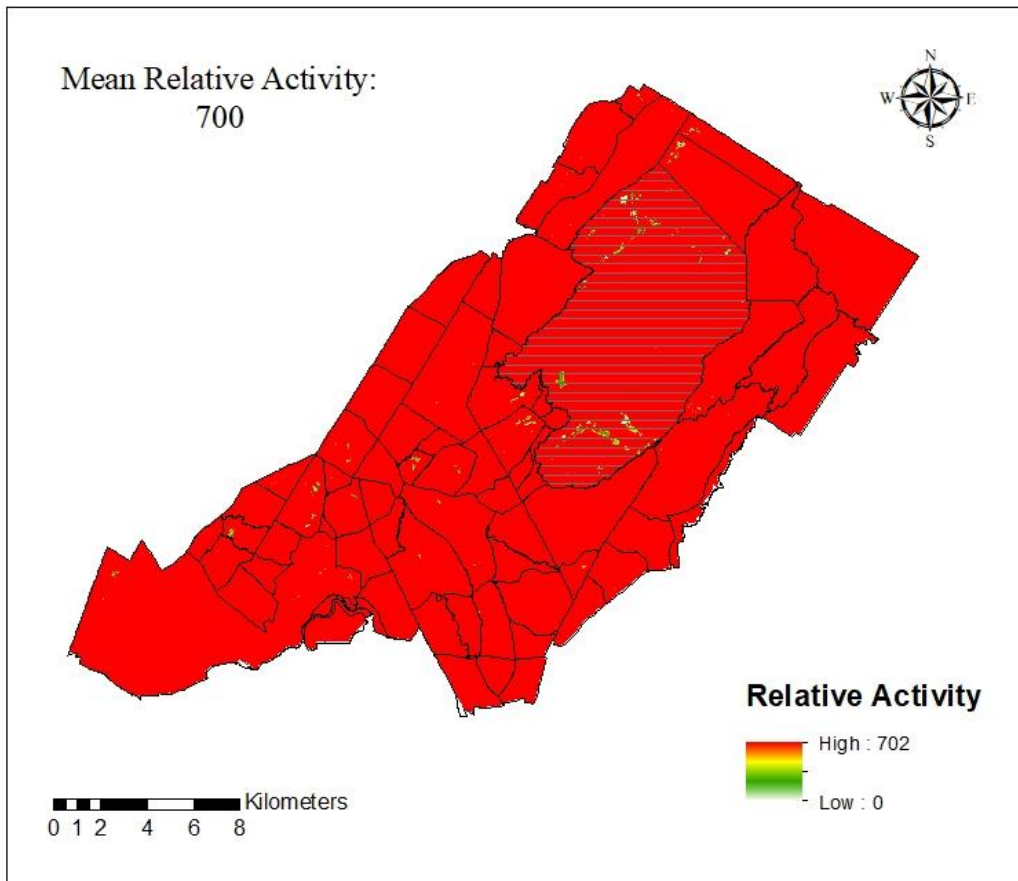


Figure 3. Predicted relative activity across Fort Drum Military Installation, New York summer, 2005. Relative activity modeled from mean echolocation passes per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity across all raster cells was calculated for the entire installation.

Predicted Relative Activity for 2005 on Fort Drum Military Instalation, New York

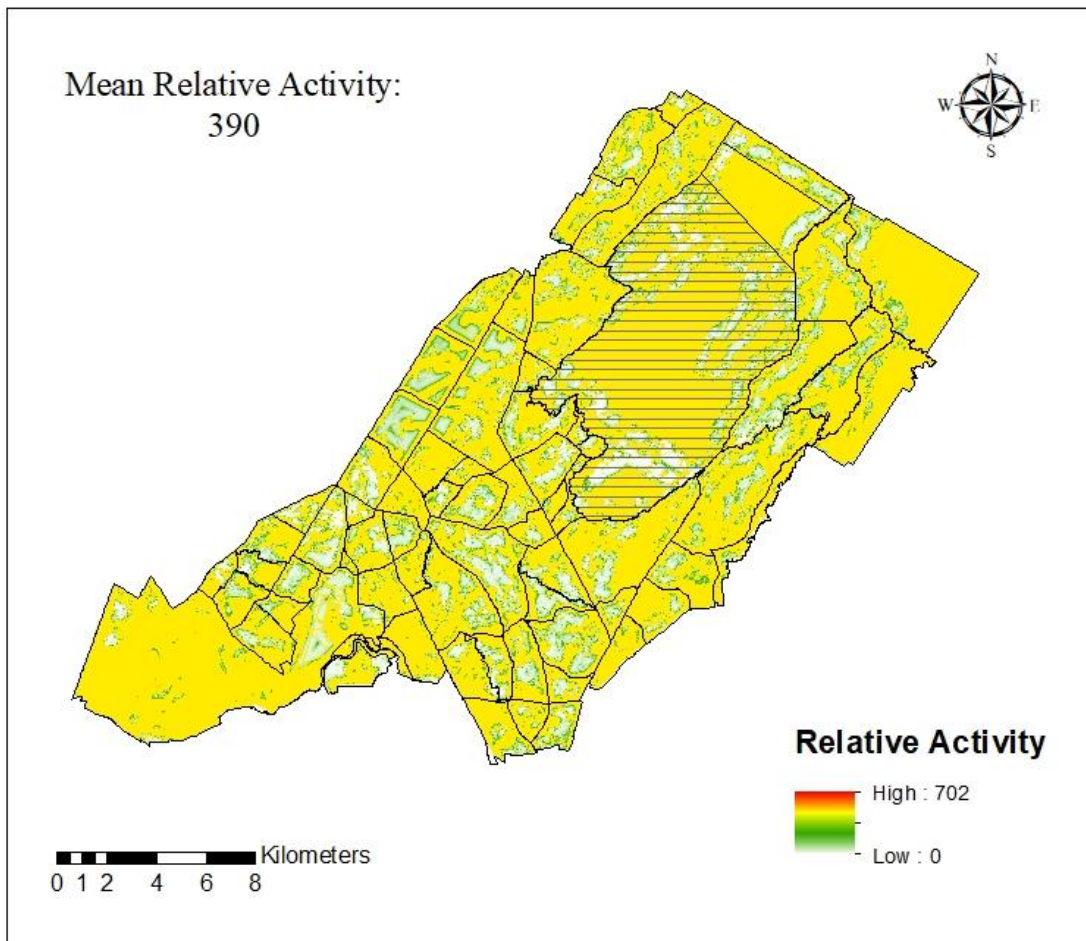


Figure 4. Predicted relative activity across Fort Drum Military Installation, New York summer, 2006. Relative activity modeled from mean echolocation passes per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity across all raster cells was calculated for the entire installation.

Predicted Relative Activity for 2006 on Fort Drum Military Instalation, New York

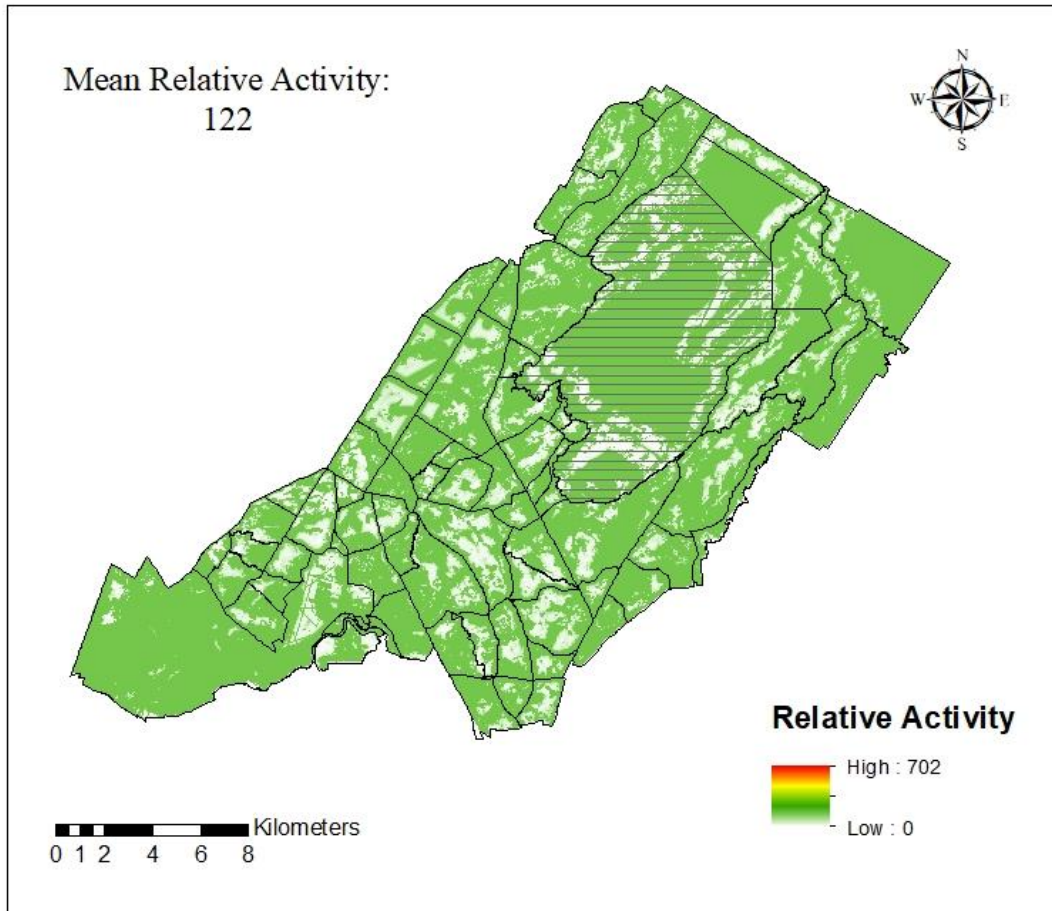


Figure 5. Predicted relative activity across Fort Drum Military Installation, New York summer, 2007. Relative activity modeled from mean echolocation passes per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity across all raster cells was calculated for the entire installation.

Predicted Relative Activity for 2007 on Fort Drum Military Instalation, New York

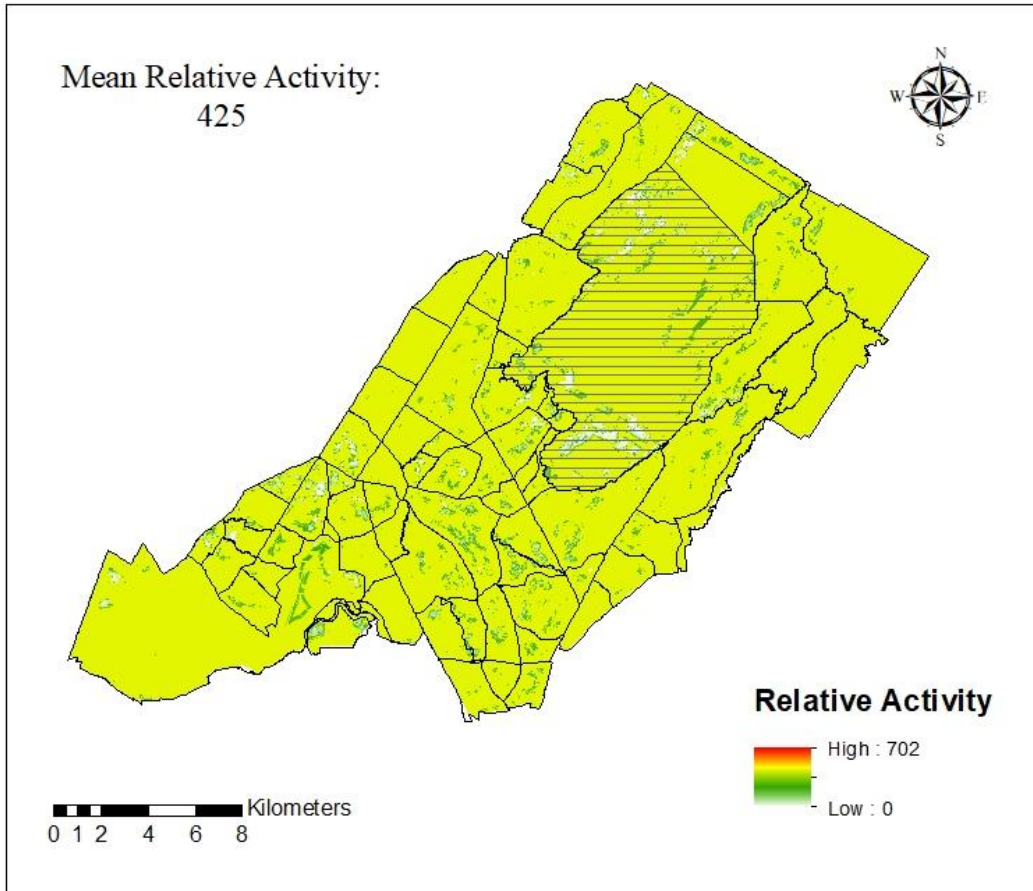


Figure 6. Predicted relative activity across Fort Drum Military Installation, New York summer, 2008. Relative activity modeled from mean echolocation passes per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity across all raster cells was calculated for the entire installation.

Predicted Relative Activity for 2008 on Fort Drum Military Instalation, New York

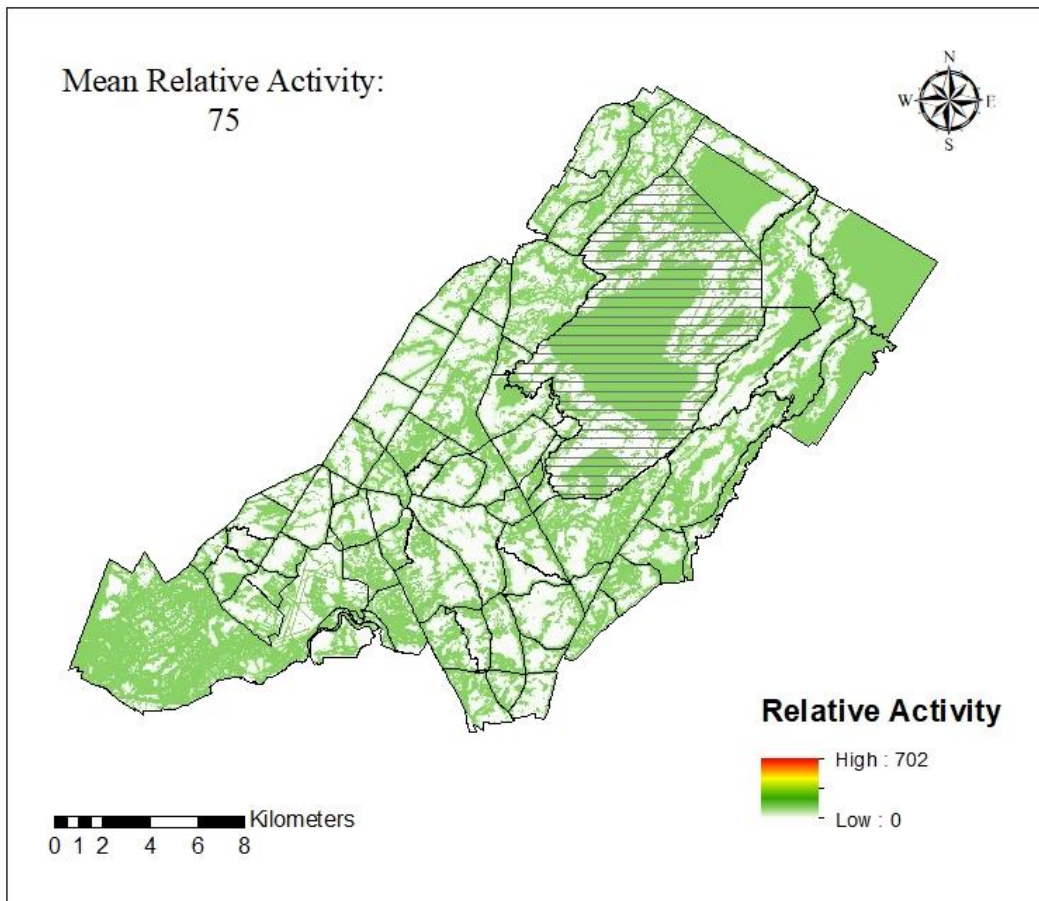


Figure 7. Predicted relative activity across Fort Drum Military Installation, New York summer, 2009. Relative activity modeled from mean echolocation passes per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity across all raster cells was calculated for the entire installation.

Predicted Relative Activity for 2009 on Fort Drum Military Instalation, New York

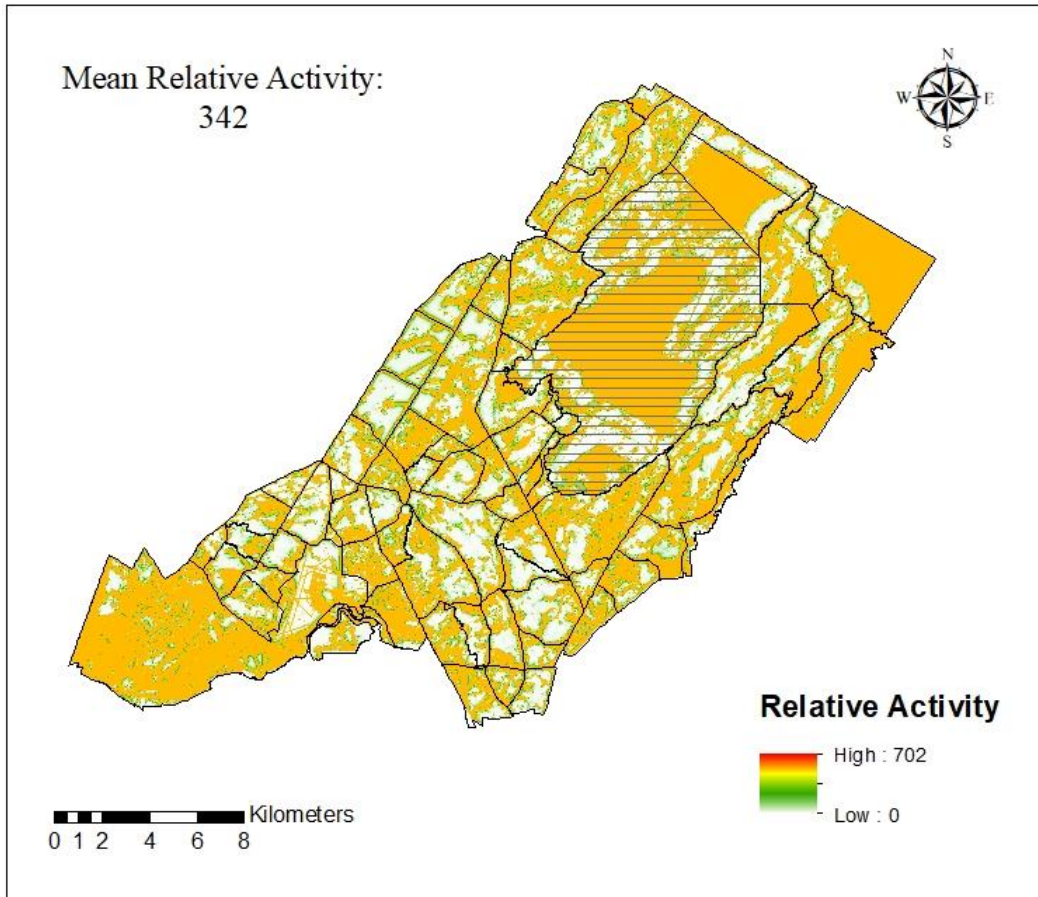


Figure 8. Predicted relative activity across Fort Drum Military Installation, New York summer, 2010. Relative activity modeled from mean echolocation passes per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity across all raster cells was calculated for the entire installation.

Predicted Relative Activity for 2010 on Fort Drum Military Instalation, New York

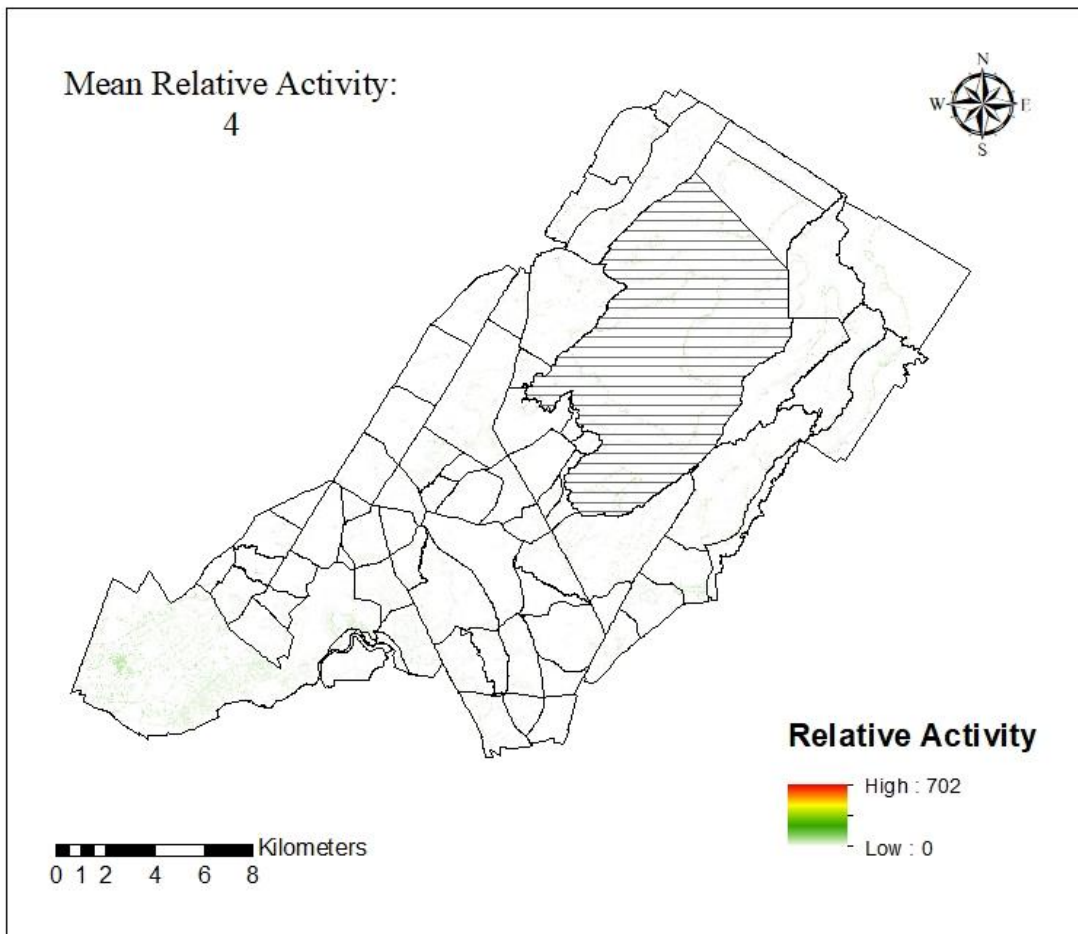


Figure 9. Predicted relative activity across Fort Drum Military Installation, New York summer, 2011. Relative activity modeled from mean echolocation passes per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity across all raster cells was calculated for the entire installation.

Predicted Relative Activity for 2011 on Fort Drum Military Instalation, New York

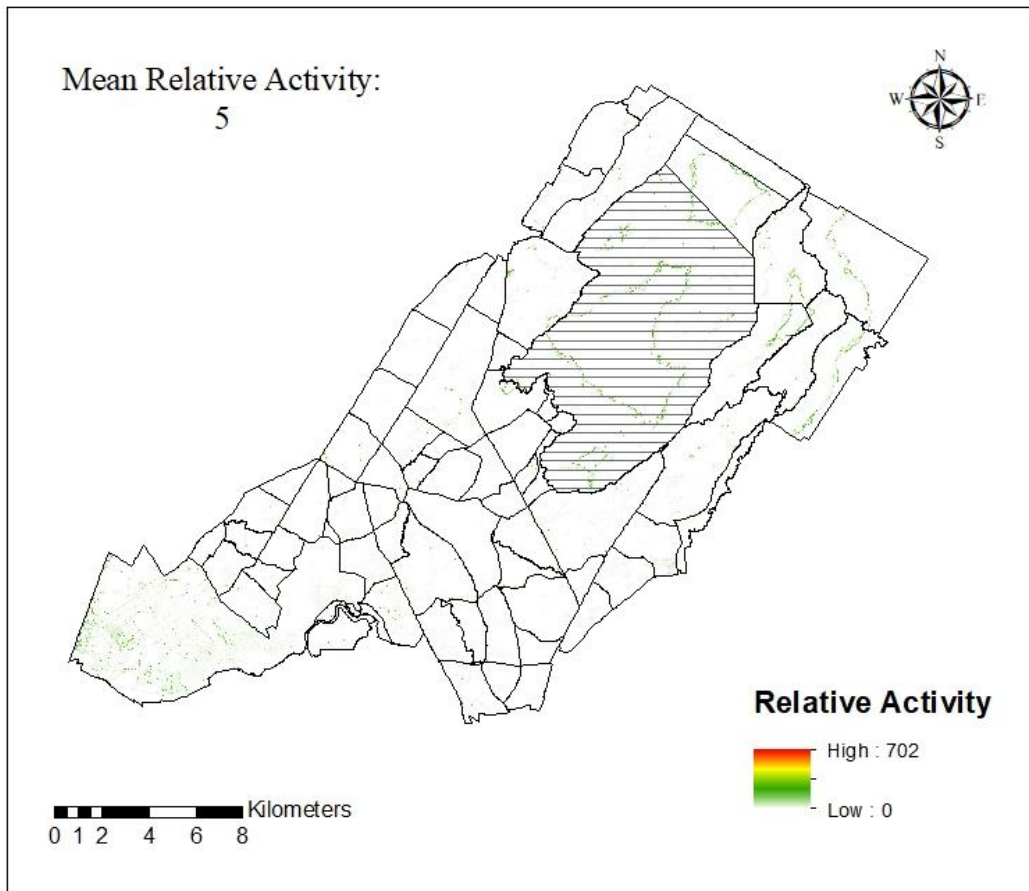


Figure 10. Predicted relative activity across Fort Drum Military Installation, New York summer, 2012. Relative activity modeled from mean echolocation passes per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity across all raster cells was calculated for the entire installation.

Predicted Relative Activity for 2012 on Fort Drum Military Instalation, New York

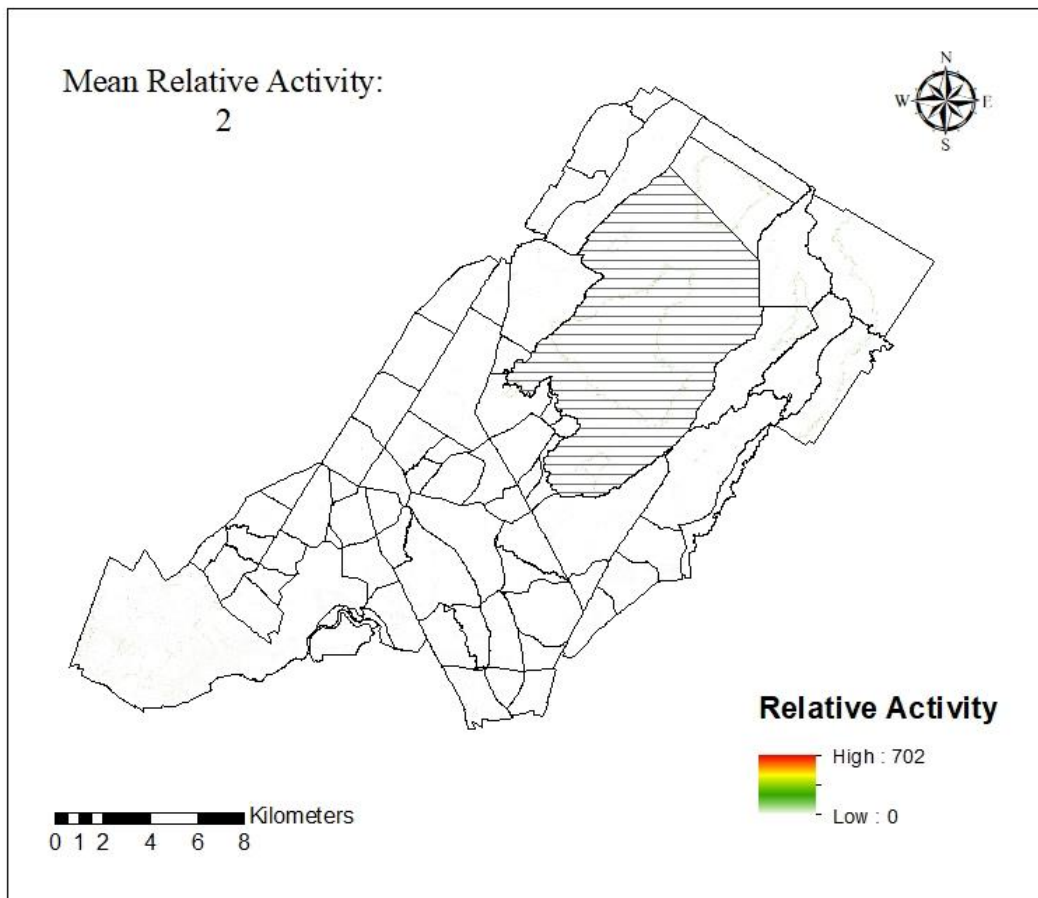


Figure 11. Predicted relative activity across Fort Drum Military Installation, New York summer, 2013. Relative activity modeled from mean echolocation passes per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity across all raster cells was calculated for the entire installation.

Predicted Relative Activity for 2013 on Fort Drum Military Instalation, New York

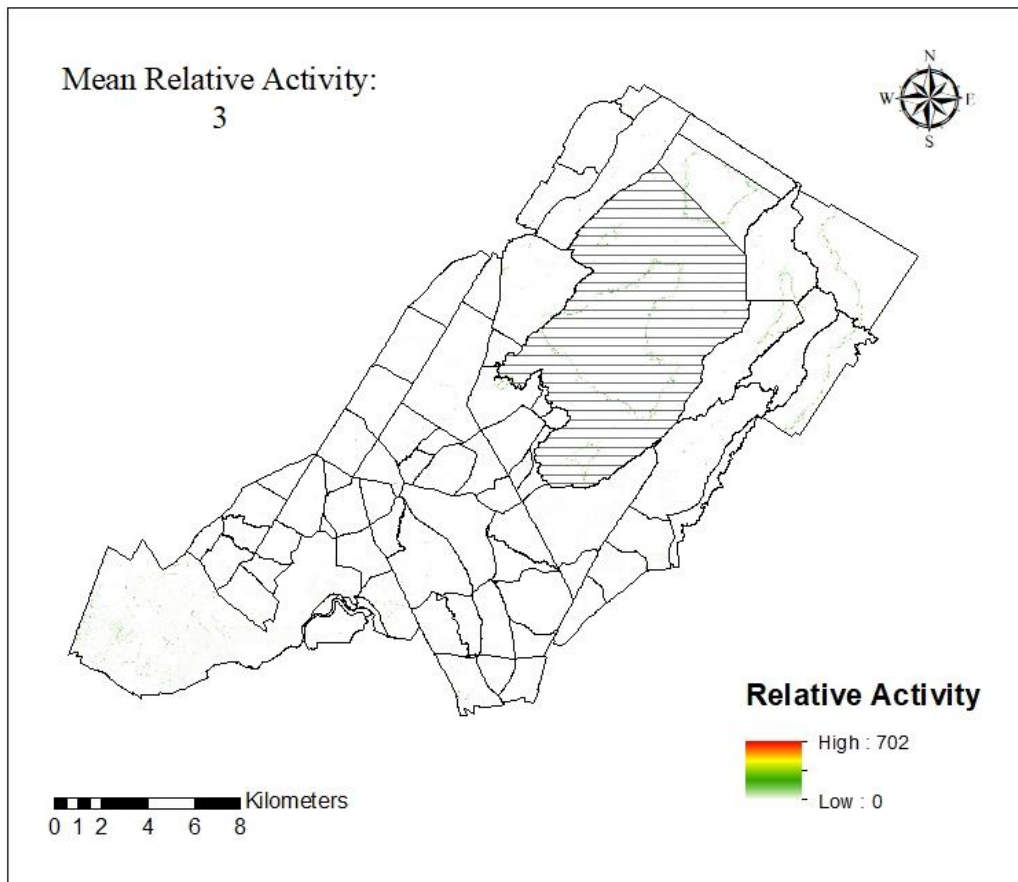


Figure 12. Predicted relative activity across Fort Drum Military Installation, New York summer, 2014. Relative activity modeled from mean echolocation passes per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity across all raster cells was calculated for the entire installation.

Predicted Relative Activity for 2014 on Fort Drum Military Instalation, New York

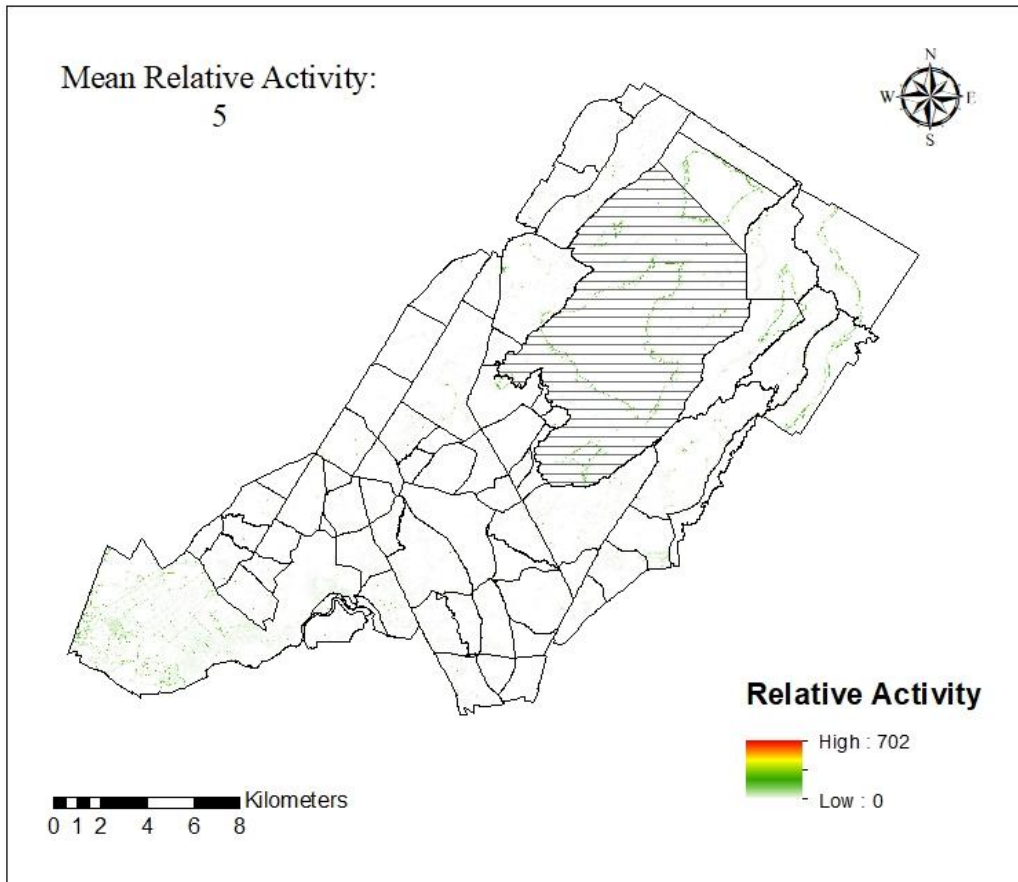


Figure 13. Predicted relative activity across Fort Drum Military Installation, New York summer, 2015. Relative activity modeled from mean echolocation passes per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity across all raster cells was calculated for the entire installation.

Predicted Relative Activity for 2015 on Fort Drum Military Instalation, New York

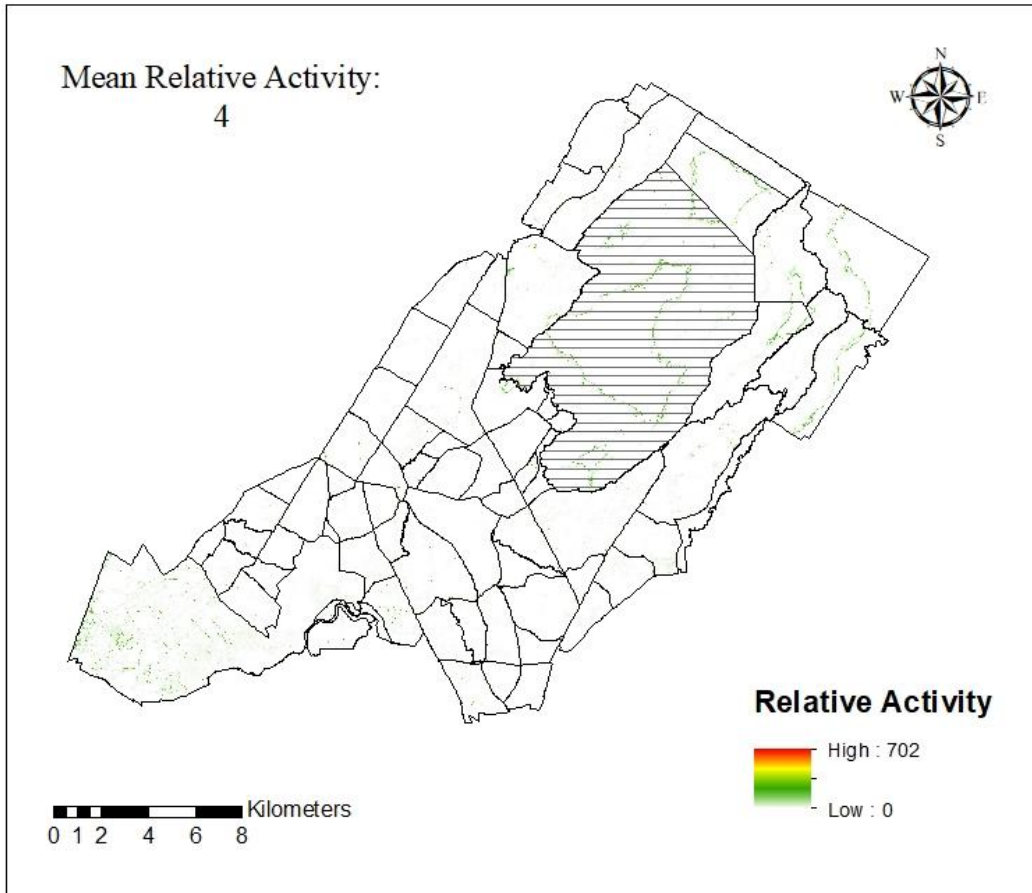


Figure 14. Predicted relative activity across Fort Drum Military Installation, New York summer, 2016. Relative activity modeled from mean echolocation passes per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity across all raster cells was calculated for the entire installation.

Predicted Relative Activity for 2016 on Fort Drum Military Instalation, New York

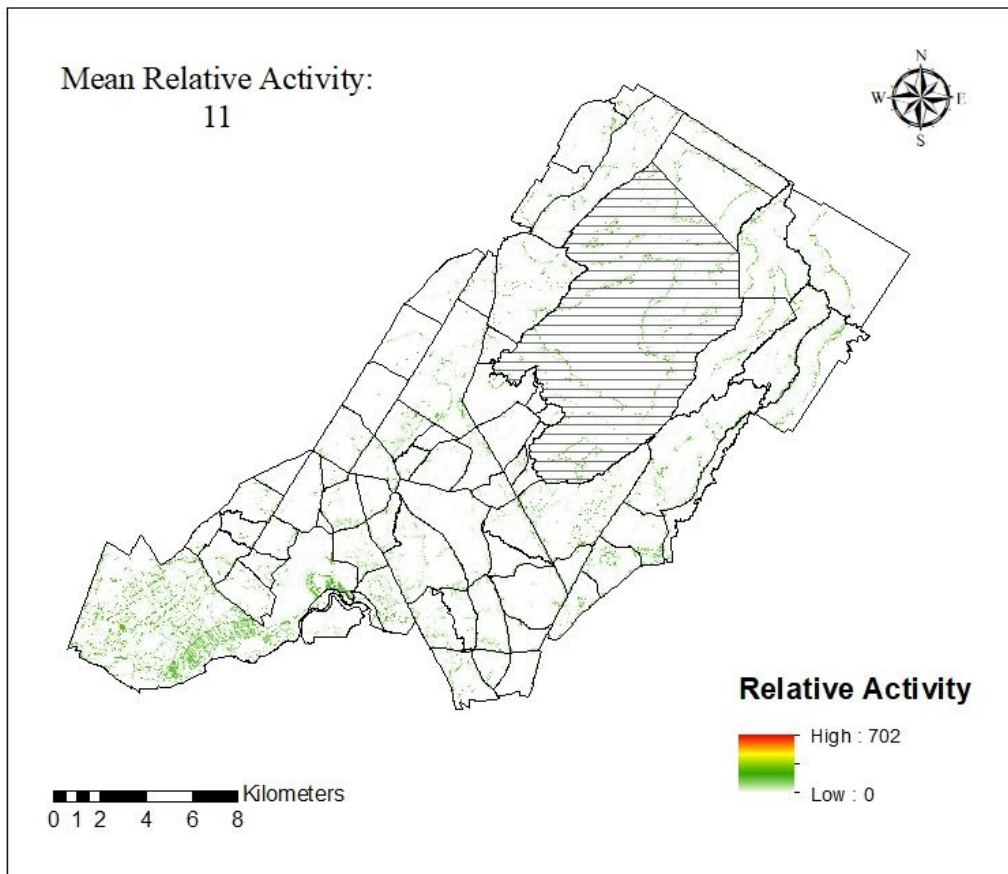


Figure 15. Predicted relative activity across Fort Drum Military Installation, New York summer, 2017. Relative activity modeled from mean echolocation p per night per site. Hash marks indicate impact zone where no sampling occurred. Mean relative activity across all raster cells was calculated for the entire installation.

Predicted Relative Activity for 2017 on Fort Drum Military Instalation, New York

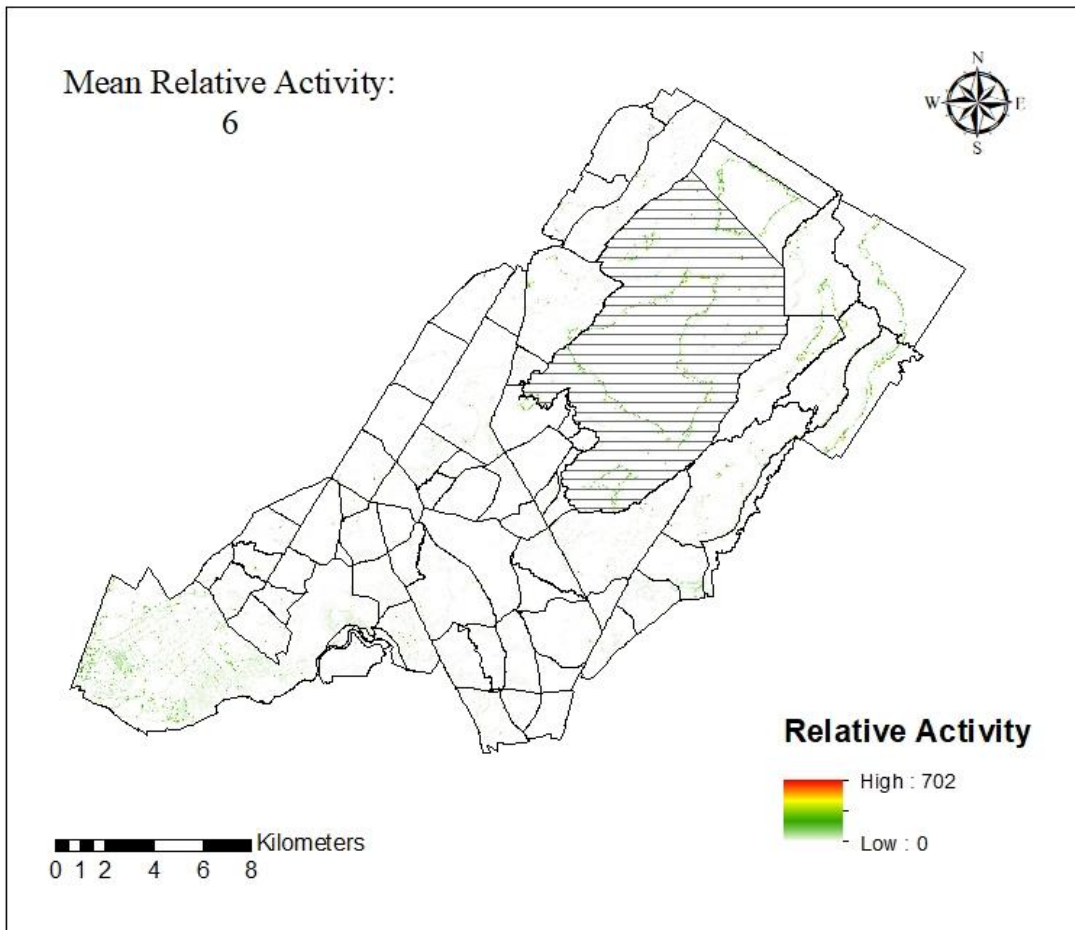
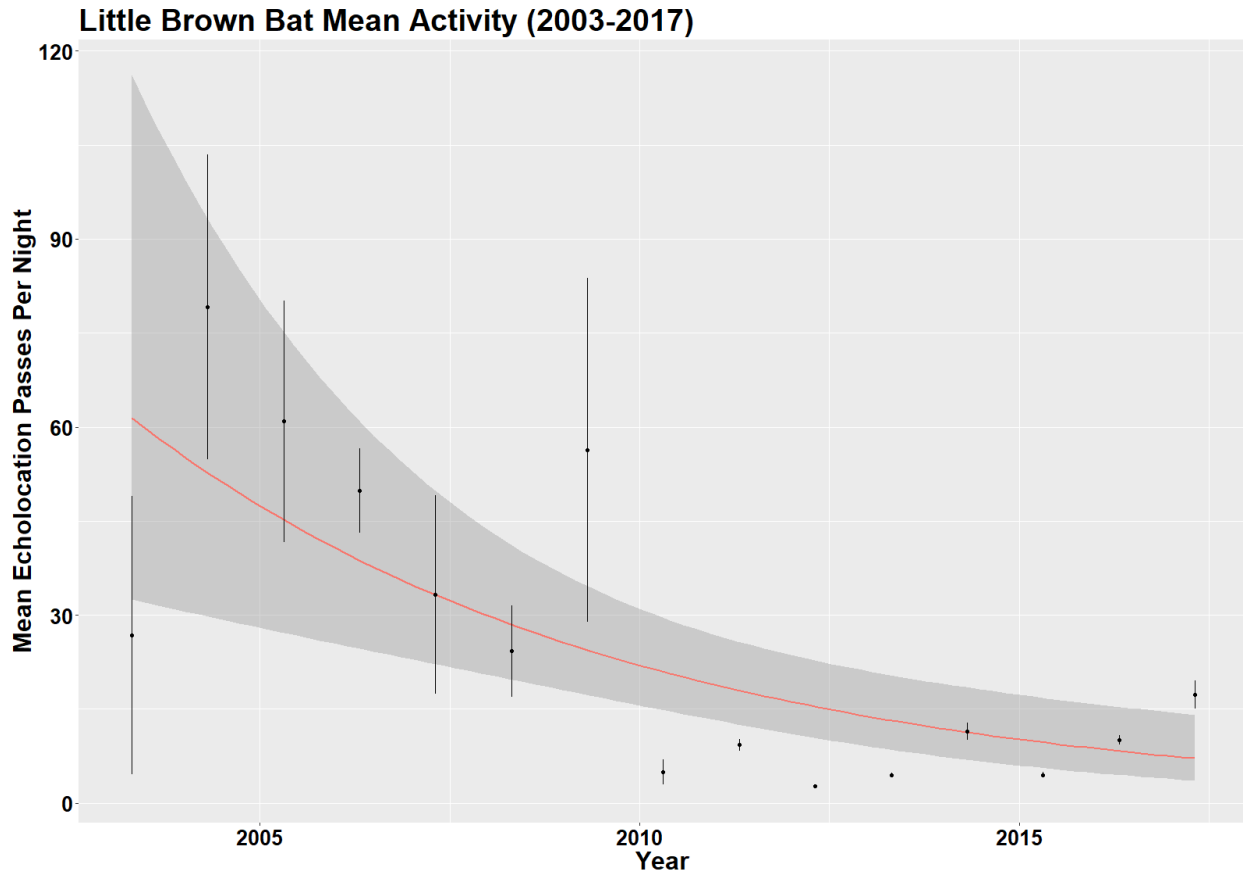


Figure 16: Long term acoustical monitoring trends during the summer 2003-2017 at Fort Drum Military Installation, New York for the little brown bat (*Myotis lucifugu*). White-nose Syndrome impacts began locally in 2008. The fitted regression line from our best-supported model indicates trend in activity.



Chapter 3: Patterns of acoustical activity of bats prior to and 10 years after WNS

Abstract

Previous acoustic surveys, netting, and count data has shown that overall activity patterns shifted among all species between pre- and post- White-nose Syndrome (WNS) years. However, the significance of these changes is based on the species-specific susceptibility to WNS. We used acoustically recorded echolocation passes obtained from Fort Drum, New York to describe changes in bat activity from 2003 through 2017. We examined seasonal and yearly changes in bat activity as it relates to the presence of WNS at Fort Drum. *A priori*, we expected 1) overall activity for Myotid bats, and other communal hibernating species would be less in the years following WNS to those preceding WNS; 2) migratory bats would show no response or positive response to WNS, due to niche relaxation; 3) minimally WNS impacted species, such as big brown bats (*Eptesicus fuscus*), would show minimal or slightly lower response to WNS; and 4) lower number of Myotid species would cause a competitive release for other non WNS affected bat species. Our results indicated an overall decrease in relative activity for Myotid bats post-WNS and within individual years thereafter WNS through early and late summer season. For WNS-susceptible species, our results reflect the high level of mortality in regional winter hibernacula, variable reproductive effort and recruitment. There was no indication that community displacement was occurring on a nightly level by any species. The continuous spread of WNS across North America will have strong negative effects on bat populations and communities, this study points to how individual species (both impacted and non-impacted) will respond to WNS.

Introduction

The emergence of the fungal pathogen, *Pseudogymnoascus destructans*, causative agent of White-nose Syndrome (WNS), was first documented in the United States in the winter of 2006 at Howe's Caverns, approximately 65km west of Albany, New York (Blehert et al. 2009). Since then, this disease agent has moved rapidly throughout the northeastern and central regions of the United States, as well as into several provinces in Canada. By 2016, WNS had expanded into Washington State (USGS National Wildlife Health Center 2016), and as of 2018 it has been reported in Kansas, Iowa, Mississippi and Texas (USGS National Wildlife Health Center 2018). To date, WNS has been found to infect eight species of cave-dwelling bats in eastern North America: the federally endangered Indiana bat (*Myotis sodalis*, MYSE), the threatened northern long-eared bat (*Myotis septentrionalis*, MYSO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), gray bat (*Myotis grisescens*, MYGR), Southeastern bat (*Myotis austroriparius*, MYAU), big brown bat (*Eptesicus fuscus*, EPFU), and tri-colored bat (*Perimyotis subflavus*, PESU) (U.S. Fish and Wildlife Service 2017). The fungus, infects epithelial tissues of hibernating bats causing abnormally frequent arousal through winter that leads to loss of critical fat reserves and water balance disruption (Cryan et al. 2010, Frick et al. 2010, Meteyer et al. 2012). Infected bats die of starvation and dehydration or exposure if they leave caves during winter months.

Among impacted species, the most dramatic changes in activity patterns, abundance, and to some degree distribution have been observed for MYLU, MYSE, MYSO, and PESU (Blehert et al. 2009, Frick et al. 2010, Brooks 2011, Ford et al. 2011). Prior to the onset of WNS, populations of specific bat species, such as MYLU were either stable or increasing, making it one of the most common and abundant bats in North America; yet since the discovery of WNS

populations have declined by 75-99%, as mirrored by acoustical sampling declines and low captures (Blehert et al. 2009, Frick et al. 2010, Dzal et al. 2011, Ingersoll et al. 2016). Although some MYLU survive winter infection and are able to reproduce (Dobony et al. 2011, Dobony and Johnson 2018), significant overwintering mortality, poor female physiological condition, and energetic demands to repair dermal tissue for most individuals have resulted in variable reproductive output and recruitment, limiting population recovery (Dobony et al. 2011, Ford et al. 2011, Francl et al. 2012, Dobony and Johnson 2018). As a result, pre-WNS trends of activity levels increasing in mid-summer, consistent with reproduction and summer recruitment of volant juveniles, did not continue after the onset of WNS in northwestern New York and elsewhere (Ford et al. 2011).

Individual bat species can become suppressed by other non-declining bat species (Haupt and Schmidt 2007, Ford et al. 2011). For example, in Europe expanding populations of pipistrelle bats (*Pipistrellus pipistrellus*) leads to suppression of the horseshoe bat (*Rhinolophus hipposideros*), that share interspecific dietary requirements (Arlettaz et al. 2000). Due to the severity of the disease, research has shown a WNS driven change in spatial and temporal niche partitioning among bat communities in the Northeast, and as a result interspecific competition has been reduced, concomitant with the reduction in MYLU (Jachowski et al. 2014a). Jachowski et al. (2014a) showed that WNS has destabilized spatial and temporal niche partitioning in Myotid bats by allowing the eastern red bat (*Lasiurus borealis*, LABO) and EPFU to increase foraging activity in areas formerly dominated by MYLU. This suggests that WNS has a cascading positive effect on behavior and interspecific interactions by species not directly impacted by WNS. Generally, it appears that sympatric species within the genus *Myotis*, i.e., MYLU, MYSE, and MYSO, appear to be increasingly restricted to smaller, isolated summer

populations due to WNS and competitive release of other non-impacted species, such as LABO (Jackowski et al. 2014b, Silvis et al. 2017).

Nonetheless, the paucity of data encompassing both pre-WNS and post-WNS years for much of North America has made it difficult to compare the relative change in bat activity between the two periods or assessing how population declines of WNS affected species allows for competitive release of non-impacted species. An exception to this is the extensive long term mist-netting and acoustic monitoring of bat distribution, activity, and occupancy program at Fort Drum Military Installation (Fort Drum) in northern New York from 2003-present. After the local discovery of summer maternity activity of MYSO on Fort Drum, mist netting efforts were added to the monitoring efforts in an attempt to capture and track bats to foraging and roost locations (Jachowski et al. 2016). Continuous acoustic monitoring and captures between 2003 and 2018 has documented changes in patterns of acoustical activity pre- and post- WNS and the effects WNS has had on bat community composition and structure at Fort Drum (Dobony et al. 2011, Ford et al. 2011, Coleman et al. 2014b, Jachowski et al. 2014), and provide comparative analysis among acoustic sampling techniques (Coleman et al. 2014c, a).

Previous acoustic surveys and netting has shown that overall activity patterns shifted among all species between pre- and post- WNS years at Fort Drum. The significance of these changes is based on the species-specific susceptibility to WNS, with MYSE, MYSO, and MYLU bat activity patterns decreasing in the years subsequent to WNS (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 the ecological dynamics of a novel, invasive disease. Secondly, these data have management-oriented implications for understanding disease impacts to threatened and endangered species, how additional species

might become imperiled, and how land managers need to respond to either ameliorate or adapt to WNS impacts. To examine these, we used acoustically recorded echolocation passes obtained from Fort Drum to describe changes in bat activity from 2003 through 2017. Accordingly, we hypothesized the following changes in bat activity after WNS at Fort Drum would be evident: 1) overall activity for Myotis bats, and other communal hibernating species would be less in the years following WNS to those preceding WNS; 2) migratory bats would show no response or positive response to WNS, due to niche relaxation; 3) minimally WNS impacted species, such as EPFU, would show minimal or lower response to WNS; and 4) Lower number of Myotis species will cause a competitive release for other non WNS affected bat species. Accordingly, we sought to compare pre-volancy and post-volancy detection rates across years to address WNS induced changes in relative activity throughout the summer, and to assess if lower activity rates of Myotis species would cause a community displacement for other bat species.

Methods

We conducted our study at the Fort Drum Military Installation in Jefferson and Lewis counties in northwestern New York, USA. Situated at the junction of the St. Lawrence- Great Lakes lowlands, the base of the Adirondack Mountains, and the Tug Hill Plateau region, Fort Drum is a 43,000 ha army installation base that contains a variety of forest, wetland, and open habitat conditions. The Niagara Escarpment, which lies 10 – 15 km west of Fort Drum, contains limestone (Karst) formation caves used as a hibernacula by bats (Ford et al. 2011). Other than the developed portions of the installation in the Cantonment and Airfield, the Fort Drum landscape is predominantly northern hardwood forest type consisting of: American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American elm (*Ulmus americana*), along with white pine (*Pinus strobus*) and Eastern hemlock

(*Tsuga canadensis*). Early successional forests, grasslands and mixed shrub habitats of quaking aspen (*Populus tremuloides*), gray birch (*Betula populifolia*), and (*Rubus spp.*) occur in the open areas maintained for training and the airfield. Aquatic and semi-aquatic habitats, which cover 20% of the installation include: lakes, beaver (*Castor canadensis*) ponds, wet meadows, and rivers.

There are 9 extant bat species at Fort Drum: MYSE, MYSO, MYLU, EPFU, LABO, PESU, MYLE, hoary bat (*Lasiurus cinereus*, LACI), and silver haired bat (*Lasionycteris noctivagans*, LANO) (Coleman et al. 2014a). Of these, the endangered MYSO, threatened MYSE, and declining MYLU were specifically targeted during acoustic surveys across the installation since 2003.

From May through early September 2003-2017, Anabat II detectors connected to a compact flash-storage zero-crossings analysis-interface module (ZCAIM), and SD1 and SD2 detectors using the same transducer model (Titley Electronics, Ballina, NSW, Australia). From 2003-2011, we initially placed Anabat units in weatherproof boxes, but left the microphone exposed. We tried to only sample on dates that were projected to have no or minimal chance of inclement weather. In 2012 and onwards, we attached a PVC tube to protect the microphone from rain (to be able to leave units out for extended periods of time during variable weather), and to aid in funneling sounds into the microphone to the weatherproofing boxes. Though variability between weatherproofing methods occurred throughout the years Britzke et al (2010) found no significant difference between these two weatherproofing techniques. Additionally, this inclusion of nights with inclement weather in the later years, in conjunction with WNS, could have resulted in causing further negative bias (though not biologically meaningful relative to WNS impact). A small hole was drilled into the bottom of the PVC tube to allow water to drain out, so

calls would not be reflected or distorted, and to keep water from flooding the detector (Britzke et al. 2013). Following Ford et al. (2011) and Coleman et al. (2014a, c) we placed each unit on a 1.5m tri-pod and adjusted so that sound could enter the PVC tube at an angle of 45° (Weller and Zabel 2002). Our sample sites primarily included: 1) sites along roads and forest tracks where detectors were positioned to capture sound along the trail; 2) sites with forest canopy gaps where detectors were positioned to face openings; and 3) emergent wetland sites where detectors were positioned towards water/ wetland emergent or woody vegetation.

We visually scanned recorded echolocation passes for extraneous non-bat noise and 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 (USFWS) (using 0 for the program sensitivity setting, and 3 pulse minimum) (USFWS: Indiana Bat Summer Survey Guidance 2017). Prior to statistical analysis, we assigned relative activity counts for each site/night and species to pre-WNS years (2003-2007) or post-WNS years (2008-2017) groups. Following, the methods outlined by Ford et al. (2011) we divided the summer into two periods, early (15 May -15 July) representing pregnancy and parturition, and late (16 July onwards), representing volancy, when juveniles bats begin to be incorporated into the population (Anthony et al. 1981).

We estimated mean nightly echolocation passes for both pre- and post-WNS summer periods for all species, and tested for differences between the two periods of summer, with respect to WNS, by performing nonparametric Mann-Whitney-Wilcoxon tests (Hollander and Wolfe 1999) to determine if mean relative activity levels through the night significantly differed between 1) early summer (pre-WNS) and early summer (post-WNS); and 2) late summer (pre-WNS) and late summer (post-WNS), for each species. We repeated these analysis to account for

the relative change among the two periods of summer for each species by testing whether relative activity levels through the night differed between 1) early summer (pre-WNS) and late summer (pre-WNS); and 2) early summer (post-WNS) and late summer (post-WNS).

We then estimated rates of change in bat relative activity across sites sampled in both pre- and post-WNS years. Out of 289 sites, 71 were sampled in both pre-WNS years and post-WNS years. We used the mean number of calls identified to a species by night for each site in both groups, to account for higher sampling effort post-WNS. We then assessed both the change in proportion and the directionality of change (either positive or negative) in activity between these same sites pre-WNS and post-WNS. For every individual site we subtracted the mean number of calls sampled during pre-WNS by the mean number of calls sampled during post-WNS, to correctly show directionality we then transformed the data with a -1 multiplication. We then used correlation coefficients and leverage plots in program R (R Core Team 2018) to assess any relationships between the change in activity between two species, using package `corrplot` (Wei and Simko 2017).

Results

From 2003 to 2017 we sampled 8373 total ‘detector’ site nights (Table 1) and recorded 472,849 bat passes from 9 bat species including MYLU (n = 76,916), EPFU (n = 80,560), LABO (n = 33,258), LACI (n = 155,658), MYSO (n = 5,483), LANO (n = 109,891), MYSE (n = 2,171), PESU (n = 8,185), and MYLE (n = 727). A total of 141,061 files were unable to be identified to a bat species. When divided into pre-WNS early summer (38 nights), pre-WNS late summer (103 nights), post-WNS early summer (4,080 nights), and post-WNS late summer (4,152 nights) activity patterns varied among species (Figure 1). Activity levels for MYLU, MYLE, MYSE, MYSO, and PESU differed significantly between pre- and post-WNS periods, with overall

activity levels declining from pre-to post-WNS (Table 2, Figure 1). However, no differences were observed for EPFU, LABO, LACI, and LANO (Table 2). Furthermore, activity levels for MYLU, MYLE, MYSE, MYSO, PESU, LANO, and LACI significantly differed between pre-WNS early summer and post-WNS early summer, with fewer number of echolocation passes post-WNS (Table 2, Figure 1). Relative activity between pre-WNS late summer and post-WNS late summer was significantly different for MYLU, MYLE, MYSE, MYSO and PESU, with reduced number of echolocation passes following WNS (Table 2; Figure 1). Although there was an increase in activity through the season for both EPFU and LABO prior to WNS, the difference was not significant. However, following the advent of WNS, relative activity throughout the summer increased with late summer having significantly higher levels of activity than in early summer (Table 2).

Prior to WNS, activity levels for MYLU, MYLE, MYSE, and MYSO increased between early summer and late summer. Following WNS this trend did not continue for MYLU and MYSE, and was significantly reduced for MYSO and MYLE (Figure 1). There was no net gain or loss in relative activity between early and late summer for MYSE, following WNS (Figure 1). However, relative activity did decrease between early and late summer following WNS for MYLU (Figure 1). Interestingly, LANO, LACI, and PESU all showed decreasing rates in activity across the summer pre-WNS, however, this difference was only significant for LACI (Table 2, Figure 1). Moreover, while there was no significant difference in relative activity between the two summer periods pre-WNS for all species, except for LANO, following WNS the difference in relative activity, either increasing or decreasing, between early and late summer was significant for all species, except for LACI (Table 2).

Of the 71 sites sampled prior to and proceeding WNS there was an overall net increase in activity for EPFU, LACI, and LANO (Table 3). We observed a net decrease in LABO, MYLU, MYLE, MYSE, MYSO, and PESU relative activity following WNS at these sites (Table 3). However, based on our correlation coefficients there were no significant relationships between the changes in relative activity between any given species (Figure 2).

Discussion

The extensive long term acoustic monitoring program on Fort Drum, spanning 15 years and encompassing both pre- and post-WNS periods, has provided a unique opportunity to assess changes and trends in bat activity and community structure on a WNS-positive landscape. Moreover, these data can provide insight into how WNS may impact bats in the upper Midwest and the West, where WNS has become evident. Although many studies have now documented the overarching effects of WNS on individual bat species through time (Frick et al. 2010, Dobony et al. 2011, Francl et al. 2012, Coleman et al. 2014a, Jachowski et al. 2014a, Reynolds and Barton 2014, Powers et al. 2015, Ingersoll et al. 2016, Silvis et al. 2016b, Langwig et al. 2017, Dobony and Johnson 2018), few have examined trends in relative activity following disease outbreak and expansion onto the landscape over a similar duration or spatial scope (Brooks 2011, Dzal et al. 2011). Our study, expanded on the initial work of Ford et al. (2011), and Jachowski et al. (2014a) that described the initial changes in relative activity both within species and among species, by looking at 10 years of acoustic data following WNS. Our results were consistent with our prediction and findings of others in the Northeast (Brooks 2011, Dzal et al. 2011) that relative bat activity, based on species susceptibility to WNS, and overwintering strategies, i.e., hibernating and/or migratory, would change between pre- and post-WNS years. In

addition to this change, our findings corroborated results of Ford et al. (2011) that relative activity would change within seasonal gradients.

Our results show that most species found at Fort Drum, with the exception of EPFU and LABO, had lower levels of activity at the beginning of the summer post-WNS as compared to pre-WNS. For WNS susceptible species, our results reflect the high level of mortality in winter hibernacula reported by Blehert et al. (2009), and Frick et al. (2010). Whereas relative activity increased between early and late summer prior to WNS for these species, following WNS activity rates between the summer ceased to increase at the same rate, a factor potentially associated with variable reproductive output and recruitment (Francl et al. 2012, Reynolds and Barton 2014). For MYLU, overall activity levels post-WNS were six times less than pre-WNS years during early summer prior to juvenile volancy, and nine times less than pre-WNS years during late summer following juvenile volancy. Additionally, MYLU relative activity decreased between early and late summer post-WNS, indicating that overwinter survivors may be less successful reproductively (Dobony et al. 2011, Francl et al. 2012). As such, the cumulative effect of poor physiological conditions and high reproductive failure is resulting in fewer young and overall less activity during the late summer period (Frick et al. 2010, Dobony et al. 2011, Ford et al. 2011, Francl et al. 2012). Similarly, both MYSE and MYSO also showed an overall decline in relative activity by at least a factor of six. Though their activity rates did not decrease through the season, the increase was marginal compared to pre-WNS years.

Interestingly, we saw a decrease in relative activity across the summer for LANO, LACI, and PESU prior to WNS. We believe this is attributed to a combination of low sampling efforts pre-WNS and their lower detection probabilities (DeGraaf and Yamasaki 2001) across Fort Drum, suggesting that though they can be present on Fort Drum they may not actively use the

landscape in a fashion analogous to Myotis species (Cryan 2003, Ford et al. 2011). Following WNS, sampling effort across Fort Drum increased to effectively and efficiently monitor for declining species, such as MYLU, MYSE and MYSO (Coleman et al. 2014a, c). Coincidentally, this increase in sampling effort could have allowed for greater detection of LANO, LACI, and PESU post-WNS, and as a result we see relative activity levels increase across the summer for LANO, LACI and PESU post-WNS. For PESU though, activity levels increased early to late summer post-WNS, opposite of pre-WNS years, activity post-WNS was still significantly lower than that of pre-WNS years. This result follows the same patterns as that of other WNS susceptible species, PESU populations have declined precipitously (Powers et al. 2015) with some areas facing a 12% decline with two years of outbreak (Pettit and O’Keefe 2017). Moreover, our results were consistent with our second hypothesis, in which we predicted that migratory bats, and those minimally impacted by WNS, would show no response or less response to WNS. For EPFU, LABO, LANO, and LACI the overall difference in activity between pre-WNS and post-WNS was not significant. Although EPFU are susceptible to WNS, this species is less impacted due to their behavior (minimal communal hibernator), and morphology (relatively large body size) (Agosta 2002, Foley et al. 2011, Frick et al. 2015, Silvis et al. 2016b). Conversely, LABO, LANO, and LACI are all migratory species and not known to be impacted by WNS. Nonetheless, in the East and locally near Fort Drum, these species have been shown to be highly susceptible to wind-energy related mortality (Arnett et al. 2008, Cryan and Barclay 2009, Arnett and Baerwald 2013), therefore monitoring for these species clearly remains warranted.

Given this differential effect of WNS on bat species, WNS impacts may indirectly effect the broader bat community structure (Jachowski et al. 2014a, Turner et al. 2015). Consequently,

the location of a study area and the extant bat community is an important consideration in the role of which WNS impacts lead to changes in community structure, as the assemblage of bat species and community composition changes both across latitudinal and longitudinal gradients. Individual bat species can become suppressed by the rapid increase of other bat species (Haupt and Schmidt 2007, Ford et al. 2011), and although our results show an overall increase in the relative activity for both EPFU and LABO, there does not seem to be any indication of community displacement between Myotid bats and non WNS impacted species, such as LABO, in regards to trends in nightly activity. Though the relative change in activity was negative for all Myotid species between sites sampled pre and post-WNS, the relative change in activity was not negatively or positively correlated to any other species. Although our results point to an increase in activity for EPFU, LACI, and LANO at sites sampled both pre- and post-WNS, the increase in activity for this species was not related to the decrease in other species. Post-WNS niche partitioning (space-use) has been shown both at Fort Drum and other areas (Frick et al. 2010, Jachowski et al. 2014a, Turner et al. 2015), we do recognize that our analysis used nightly level data rather than hourly and habitat specific data (Jachowski et al. 2014a). Although we did not detect a cause for community displacement in bat species at Fort Drum on a nightly level, further monitoring and analysis seems prudent.

Conclusion

As bat populations continue to decline and cease to exist on the landscape, becoming spatially disconnected, management will require strong efforts to record, accurately identify, and reflect the changes in bat communities over time. By comparing distribution and activity trends of bat species pre and post WNS, researchers have been able to document how once common species of bats have become functionally extirpated from the landscape due to WNS (Frick et al. 2010, Brooks 2011), with resulting changes in and impacts on bat community structure through

time (Jachowski et al. 2014*a*). Herein, we have shown that the impact of WNS on communal hibernating species has been deleterious, amounting to an overall reduction in the number of bats susceptible to WNS, including MYLU, MYSE, and MYSO at Fort Drum.

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Table 114. Minimum, maximum and mean number of detector nights and total number of site locations in Fort Drum Army Installation, New York 2003 to 2017. Total effort accounted for 8,373 detector nights over 289 individual nights 2003-2017.

Year	Minimum number of nights	Maximum number of nights	Mean number of nights	Total number of sites
2003	1	1	1.00	5
2004	1	3	1.88	17
2005	1	2	1.81	21
2006	2	2	2.00	18
2007	2	2	2.00	15
2008	1	2	1.83	12
2009	2	2	2.00	13
2010	1	6	2.63	19
2011	1	128	17.81	57
2012	1	223	38.87	55
2013	2	187	29.61	49
2014	81	131	103.60	5
2015	2	118	10.99	129
2016	8	28	14.99	81
2017	64	83	77.80	5

Table 215. Testing for differences between 1) pre White-nose Syndrome (WNS) and post-WNS; 2) early summer (pre-WNS) and early summer (post-WNS); 3) late summer (pre-WNS) and late summer (post-WNS); 4) early summer (pre-WNS) and late summer (pre-WNS); and 5) early summer (post-WNS) and late summer (post-WNS) for each species extant at Fort Drum Military Installation, New York between 2003- 2017. Pre-WNS period includes years from 2003-2007, post-WNS period include years from 2008-2017. Our two summer periods included: early (15 May-15 July) and late (16 July onwards) representing pregnancy parturition, and then volancy, when juveniles bats begin to be incorporated into the population. With (μ) mean estimate of relative activity, and $p < 0.05$ are significantly different (*). Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

Testing differences between Pre-WNS and Post-WNS			
Species	μ Pre-WNS	μ Post-WNS	p-value
EPFU	19.54	12.61	0.21
LABO	8.28	5.15	0.76
LACI	7.61	17.73	0.73
LANO	5.61	8.72	0.53
MYLE	0.59	0.07	<.0001*
MYLU	55.14	6.68	<.0001*
MYSE	7.81	0.15	<.0001*
MYSO	3.11	0.52	0.00
PESU	3.63	0.98	0.00
Testing differences between Early summer (pre-WNS) and Early summer (post-WNS)			
Species	μ Early Summer (pre-WNS)	μ Early Summer (post-WNS)	p-value
EPFU	11.55	10.75	0.28
LABO	5.63	3.47	0.34
LACI	14.66	13.68	0.003*
LANO	7.95	7.40	0.03*
MYLE	0.32	0.05	<.0001*
MYLU	43.89	7.24	<.0001*
MYSE	0.76	0.13	<.0001*
MYSO	1.13	0.43	<.0001*
PESU	5.05	0.83	<.0001*
Testing differences between Late summer (pre-WNS) and Late summer (post-WNS)			
Species	μ Late Summer (pre-WNS)	μ Late Summer (post-WNS)	p-value
EPFU	22.50	14.44	0.61
LABO	9.26	6.80	0.07
LACI	5.02	21.71	0.06
LANO	4.76	10.01	0.23
MYLE	0.70	0.08	<.0001*

Table 2.

MYLU	59.29	6.12	<.0001*
MYSE	10.42	0.18	<.0001*
MYSO	3.84	0.62	<.0001*
PESU	3.11	1.13	0.004*
Testing differences between Early summer (pre-WNS) and Late summer (pre-WNS)			
Species	μ Early Summer (pre-WNS)	μ Late Summer (pre-WNS)	p-value
EPFU	11.55	22.50	0.93
LABO	5.63	9.26	0.91
LACI	14.66	5.02	<.0001*
LANO	7.95	4.76	0.14
MYLE	0.32	0.70	0.35
MYLU	43.89	59.29	0.84
MYSE	0.76	10.42	0.15
MYSO	1.13	3.84	0.35
PESU	5.05	3.11	0.33
Testing differences between Early summer (post-WNS) and Late summer (post-WNS)			
Species	μ Early Summer (post-WNS)	μ Late Summer (post-WNS)	p-value
EPFU	10.75	14.44	<.0001*
LABO	3.47	6.80	<.0001*
LACI	13.68	21.71	0.07
LANO	7.40	10.01	<.0001*
MYLE	0.05	0.08	<.0001*
MYLU	7.24	6.12	<.0001*
MYSE	0.13	0.18	<.0001*
MYSO	0.43	0.62	<.0001*
PESU	0.83	1.13	<.0001*

Table 3. Change (Δ) in relative activity between pre-WNS and post-WNS at 71 sites sampled both in years prior to WNS (2003-2007) and years following WNS (2008-2017) at Fort Drum Military Installation, New York. Direction of change (+/-) indicate whether sites had an increase or decrease in relative activity for a given species. Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

Species	Δ Relative Activity by Site Night
EPFU	169.64
LABO	-93.47
LACI	908.3
LANO	643.28
MYLE	-19.08
MYLU	-3024.62
MYSE	-535.72
MYSO	-154.74
PESU	-164.48

Figure 1. Mean number of echolocation passes per hour, standard error for the nine extant bat species on Fort Drum Military Installation, New York in pre-White-nose Syndrome (WNS) years, 2003–2007 and post-WNS years ,2008–2017 for early summer (≤ 15 July) and late summer (> 15 July). Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

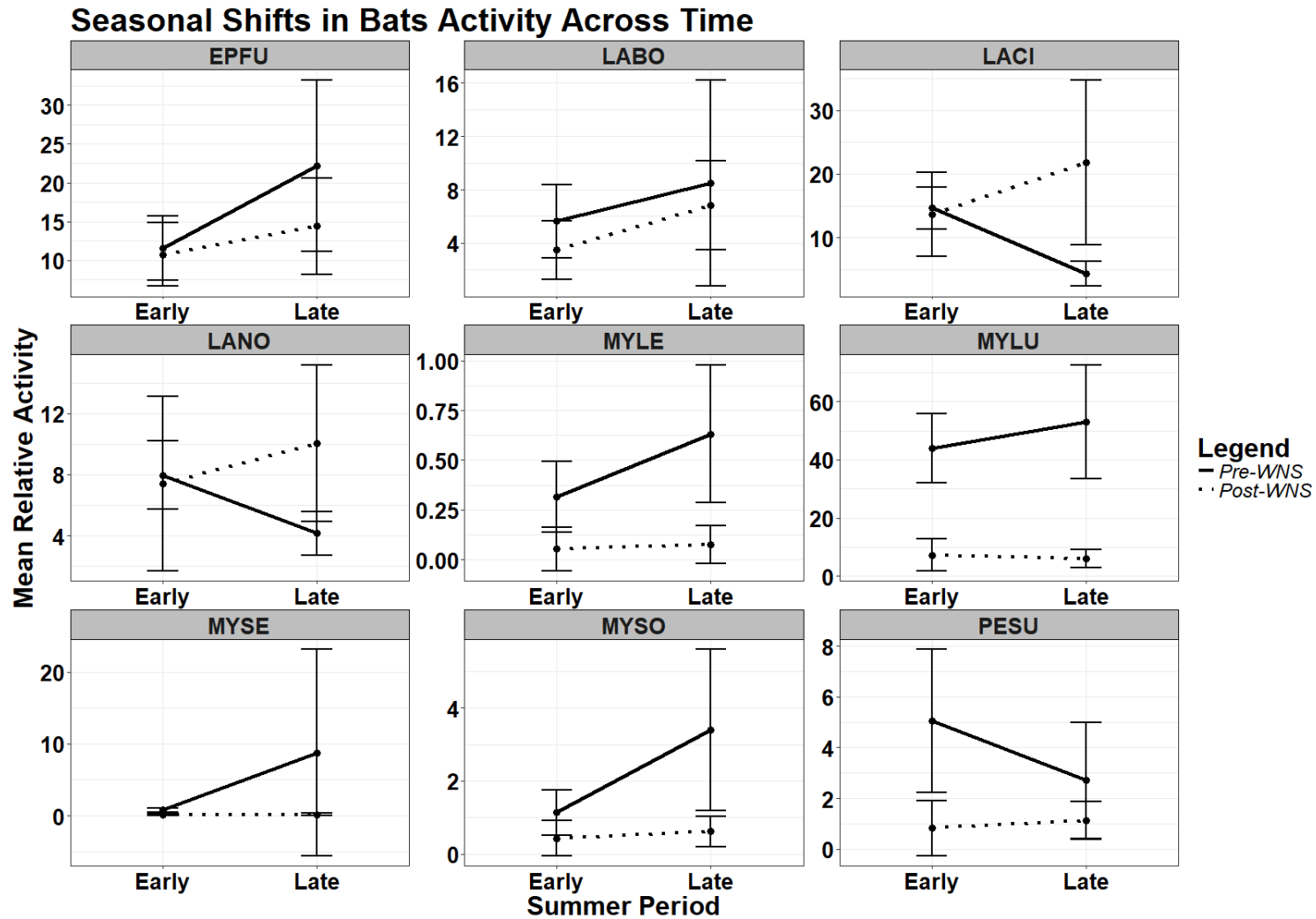


Figure 2. Correlation Matrix among the change in relative activity between pre-WNS and post-WNS at 71 sites sampled both in years prior to WNS (2003-2007) and years following WNS (2008-2017) at Fort Drum Military Installation, New York. Correlations above 0.3 or below -0.3 are significant relationships. Species include: big brown bat (*Eptesicus fuscus*, EPFU), eastern red bat (*Lasiurus borealis*, LABO), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), eastern small-footed bat (*Myotis leibii*, MYLE), little brown bat (*Myotis lucifugus*, MYLU), northern long-eared bat (*Myotis septentrionalis*, MYSE), Indiana bat (*Myotis sodalis*, MYSO), and tri-colored bat (*Perimyotis subflavus*, PESU).

	EPFU	LABO	LACI	LANO	MYLE	MYLU	MYSE	MYSO	PESU
EPFU	1.00
LABO	0.18	1.00
LACI	0.23	0.27	1.00
LANO	0.07	0.24	0.06	1.00
MYLE	.	0.06	-0.06	.	1.00
MYLU	.	0.29	-0.17	.	0.49	1.00	.	.	.
MYSE	.	.	-0.14	.	0.41	.	1.00	.	.
MYSO	0.06	.	.	.	0.66	0.53	0.30	1.00	.
PESU	.	0.13	0.14	-0.12	0.17	0.18	.	.	1.00

Appendices

Appendix 1. Rankings of models predicting little brown bat (*Myotis lucifugus*, MYLU) activity with three programs (BCID, Echoclass, and Kaleidoscope) and the biologist visual identification at Fort Drum Military Installation, New York summers 2003-2010. With relative rank and level of support for each individual model for each program w_i (model weight).

Species	Model	<i>BCID</i> w_i	<i>Echoclass</i> w_i	<i>Biologist</i> w_i	<i>Kaleidoscope</i> w_i
MYLU	Date _ Canopy Cover + Habitat + Distance to Water + Distance to Road + Year	0.55	0.68	0.11	0.36
	Date + Elevation + Canopy Cover + Habitat + Distance to Water + Distance to Road + Year	0.34	0.2	0.14	0.43
	Date + Habitat + Year	0.11	0.11	0.75	0.21
	Null	0	0	0	0

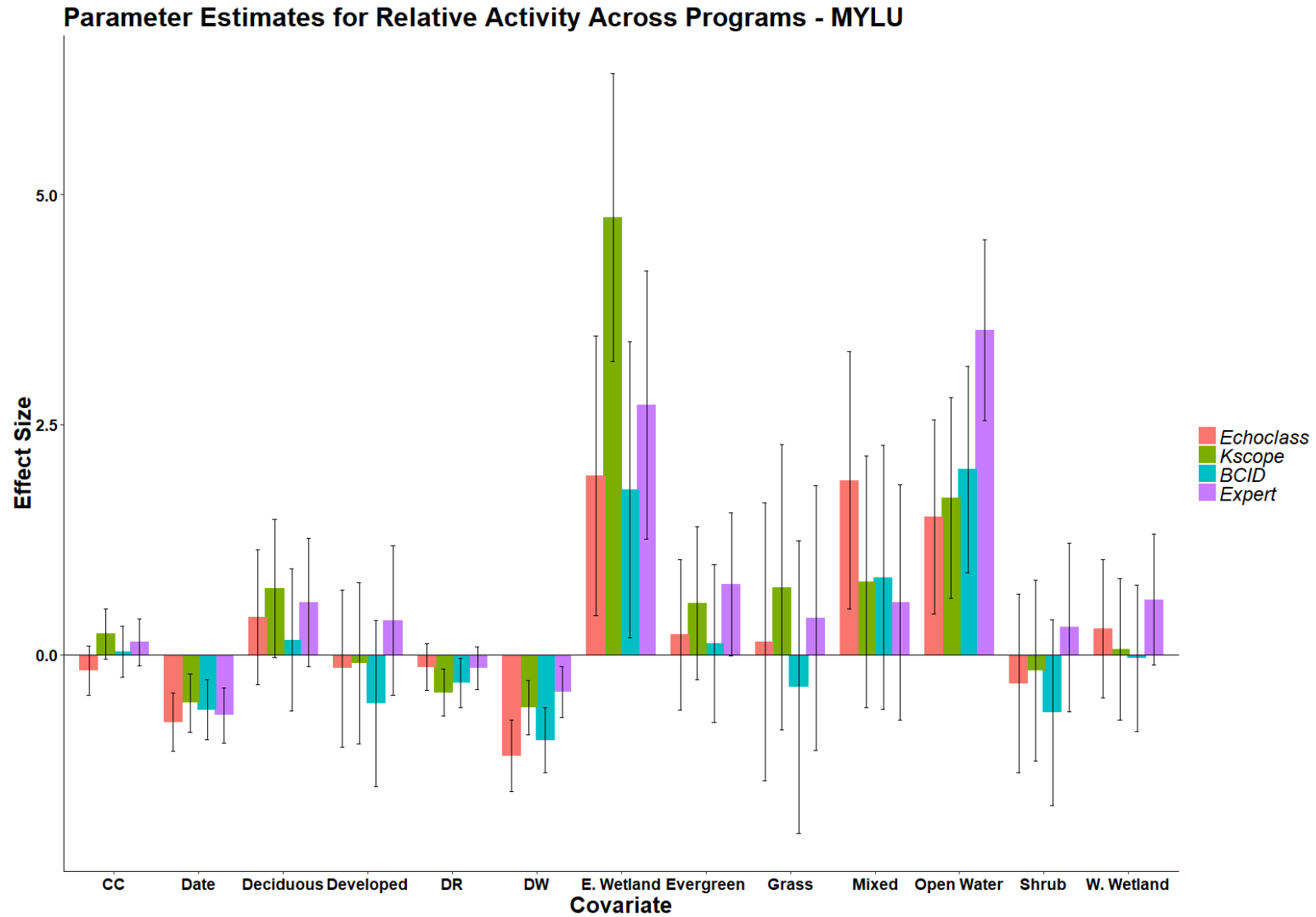
Appendix 2. Rankings of models predicting northern long-eared bat (*Myotis septentrionalis*, MYSE) activity with three programs (BCID, Echoclass, and Kaleidoscope) and the biologist visual identification at Fort Drum Military Installation, New York summers 2003-2010. With relative rank and level of support for each individual model for each program w_i (model weight).

Species	Model	<i>BCID</i> w_i	<i>Echoclass</i> w_i	<i>Biologist</i> w_i	<i>Kaleidoscope</i> w_i
MYSE	Date _ Canopy Cover + Habitat + Distance to Water + Distance to Road + Year	0.06	0.06	0.25	0.14
	Date + Elevation + Canopy Cover + Habitat + Distance to Water + Distance to Road + Year	0.1	0.05	0.58	0.23
	Date + Habitat + Year	0.84	0.89	0.17	0.64
	Null	0	0	0	0

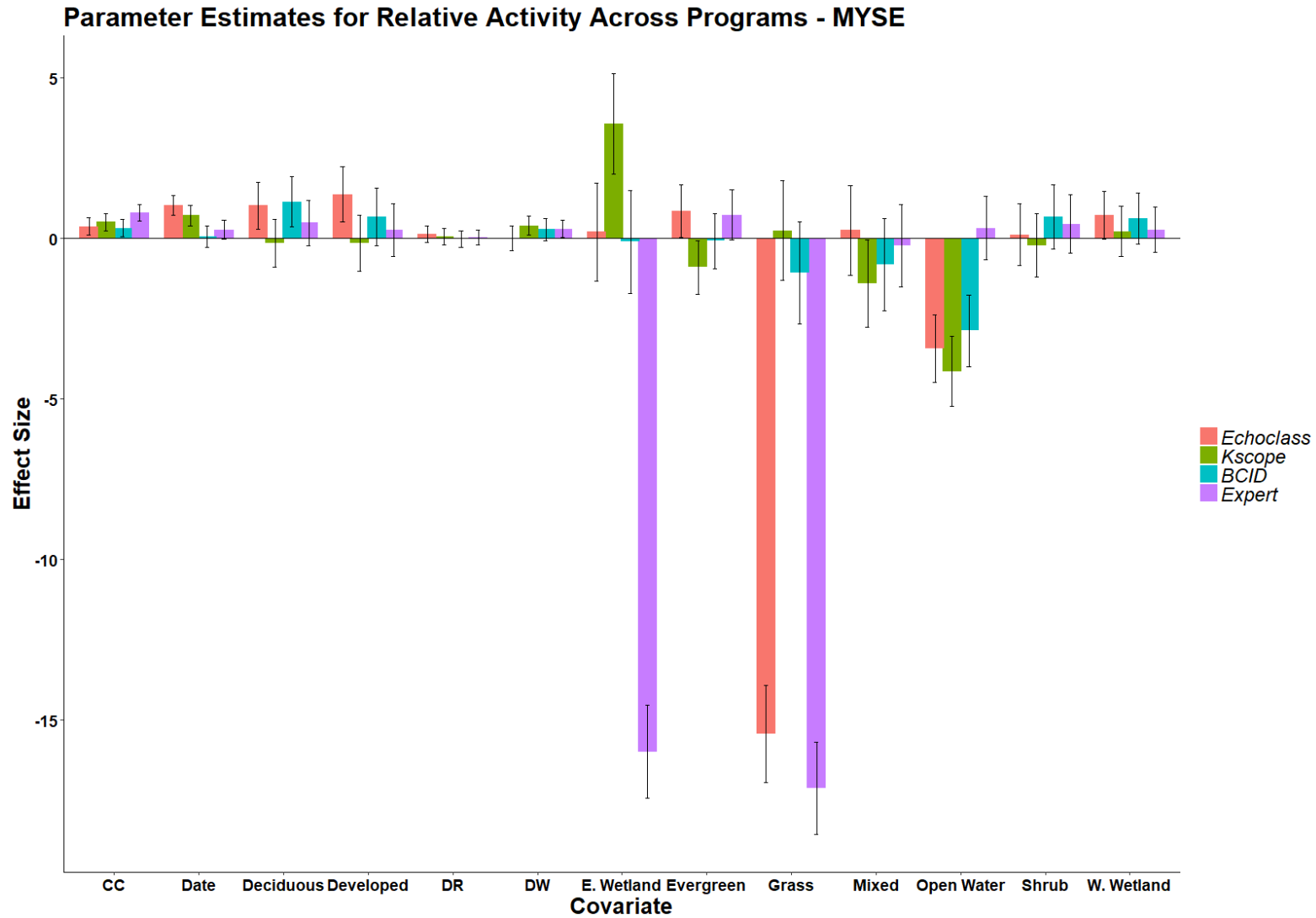
Appendix 3. Rankings of models predicting Indiana bat (*Myotis sodalis*, MYSO) activity with three programs (BCID, Echoclass, and Kaleidoscope) and the biologist visual identification at Fort Drum Military Installation, New York summers 2003-2010. With relative rank and level of support for each individual model for each program w_i (model weight).

Species	Model	<i>BCID</i> w_i	<i>Echoclass</i> w_i	<i>Biologist</i> w_i	<i>Kaleidoscope</i> w_i
MYSO	Date _ Canopy Cover + Habitat + Distance to Water + Distance to Road + Year	0.24	0.23	0.26	0.21
	Date + Elevation + Canopy Cover + Habitat + Distance to Water + Distance to Road + Year	0.43	0.35	0.73	0.15
	Date + Habitat + Year	0.33	0.43	0.01	0.64
	Null	0	0	0	0

Appendix Figure 1. Parameter estimates and standard error of our global model predicting little brown bat (*Myotis lucifugus*, MYLU) activity around Fort Drum Military Installation, New York during summer 2003-2010. Parameters include: Canopy Cover (CC), date, deciduous forest, developed areas, distance to road (DR), distance to water (DW), emergent wetlands, evergreen forests, grass, date, mixed forest, open water, shrub, and woody wetland.



Appendix Figure 2. Parameter estimates and standard error of our global model predicting *Myotis septentrionalis* (northern long-eared bat, MYSE) activity around Fort Drum Military Installation, New York during summer 2003-2010. Parameters include: Canopy Cover (CC), date, deciduous forest, developed areas, distance to road (DR), distance to water (DW), emergent wetlands, evergreen forests, grass, date, mixed forest, open water, shrub, and woody wetland.



Appendix Figure 3. Parameter estimates and standard error of our global model predicting *Myotis sodalis* (Indiana bat, MYSO) activity around Fort Drum Military Installation, New York during summer 2003-2010. Parameters include: Canopy Cover (CC), date, deciduous forest, developed areas, distance to road (DR), distance to water (DW), emergent wetlands, evergreen forests, grass, date, mixed forest, open water, shrub, and woody wetland.

