

Articles

Deriving Habitat Models for Northern Long-Eared Bats from Historical Detection Data: A Case Study Using the Fernow Experimental Forest

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Abstract

The listing of the northern long-eared bat (*Myotis septentrionalis*) as federally threatened under the Endangered Species Act following severe population declines from white-nose syndrome presents considerable challenges to natural resource managers. Because the northern long-eared bat is a forest habitat generalist, development of effective conservation measures will depend on appropriate understanding of its habitat relationships at individual locations. However, severely reduced population sizes make gathering data for such models difficult. As a result, historical data may be essential in development of habitat models. To date, there has been little evaluation of how effective historical bat presence data, such as data derived from mist-net captures, acoustic detection, and day-roost locations, may be in developing habitat models, nor is it clear how models created using different data sources may differ. We explored this issue by creating presence probability models for the northern long-eared bat on the Fernow Experimental Forest in the central Appalachian Mountains of West Virginia using a historical, presence-only data set. Each presence data type produced outputs that were dissimilar but that still corresponded with known traits of the northern long-eared bat or are easily explained in the context of the particular data collection protocol. However, our results also highlight potential limitations of individual data types. For example, models from mist-net capture data only showed high probability of presence along the dendritic network of riparian areas, an obvious artifact of sampling methodology. Development of ecological niche and presence models for northern long-eared bat populations could be highly valuable for resource managers going forward with this species. We caution, however, that efforts to create such models should consider the substantial limitations of models derived from historical data, and address model assumptions.

Keywords: acoustical sampling; day roosts; distribution model; habitat model; landscape distribution; maximum-likelihood modeling; mist-net sampling; *Myotis septentrionalis*; northern long-eared bat

Received: January 9, 2015; Accepted February 1, 2016; Published Online Early: February 2016; Published: June 2016

Citation: Ford WM, Silvis A, Rodrigue JL, Kniewski AB, Johnson JB. 2016. Deriving habitat models for northern long-eared bats from historical detection data: A case study using the Fernow Experimental Forest. *Journal of Fish and Wildlife Management* 7(1):86-98; e1944-687X. doi: 10.3996/012015-JFWM-004

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Introduction

Conservation interest has been increasing for the northern long-eared bat (*Myotis septentrionalis*) as a result of severe population declines from white-nose syndrome (WNS) mortality and reduced recruitment of surviving bats (Turner et al. 2011; Francl et al. 2012). Because of these factors, the species has been listed as federally threatened under the U.S. Endangered Species Act (ESA 1973, as amended; U.S. Office of the Federal Register 2015). Because of this, understanding of the distribution and ecological niche characteristics of the northern long-eared bat is a high priority for resource managers in eastern North America. Activities such as forest management, forest clearing, highway construction, and surface mining may directly affect bats by removing or modifying day roosts and foraging habitat. In these affected areas, models of day-roost habitats and their distribution on the landscape are particularly needed. Unfortunately, the once-common northern long-eared bat has received relatively little study beyond being linked to forested habitats, and in the core of its range, most habitat relationships of the species are unknown (Menzel et al. 2002; Owen et al. 2003; Ford et al. 2006a, 2006b; Johnson et al. 2009; Silvis et al. 2012).

Although northern long-eared bats appear to still be present across much of their range, reduced population densities and the low amplitude of their echolocation calls greatly decrease their probability of detection in both mist-net and acoustic surveys (Coleman et al. 2014). Occupancy modeling using data from repeated site visits is a standard method to assess wildlife distribution and habitat relationships (MacKenzie et al. 2002); however, collecting new data for development of occupancy models likely will be difficult in areas affected by WNS. Historical capture and detection data that may be useful in modeling are available in many areas, but several considerations remain. For example, although there are many historical bat data sets maintained by federal and state agencies, universities, and natural-history museums, many contain presence-only data that are unsuitable for standard occupancy modeling because of the lack of repeated site visits and absence data (MacKenzie et al. 2002). Fortunately, models for and analysis of presence-only data for ecological niche modeling using tools such as maximum entropy or maximum likelihood has become routine over the past decade (Baldwin 2009; Royle et al. 2012; Merow et al. 2013). For cryptic species that are difficult to document, such as bats, these approaches have enabled researchers to extrapolate from limited capture data or historical records to potential, predicted distributions over wide landscapes for basic biodiversity assessments (Hughes et al. 2010;

Moratelli et al. 2011; de Moraes et al. 2012; Pinto et al. 2013; Buckman-Sewald et al. 2014) or assess vulnerability to climate change (Rebelo et al. 2010; Lee et al. 2012) and WNS (Flory et al. 2012).

Historical bat presence data may be grouped into three general categories: physical capture, acoustic detection, and known day-roost locations. Given the varied life history and behavior of most species of bats, data type may have a substantial impact on the output and interpretation of distribution and niche models. To date, there has been little discussion of the limitations of individual data types, differences in bat distribution and niche model outputs, or the impacts of combining different data types (but see Barnhart and Gillam 2014), although models combining multiple data types have been created for some bat species (e.g., Weber and Sparks 2013). Our objective in this study is to explore the potential impacts of presence data type on development of northern long-eared bat distribution and ecological niche models at local to small landscape scales using historical data sets similar to what many forest managers may already possess. Our goal is not to generate detailed habitat association and selection models for the northern long-eared bat. For our case-study, we used a historical data set from the Fernow Experimental Forest (FEF), mostly collected as part of inventory and monitoring work and observational study. The FEF is a small area for which a relatively large and complete data set of acoustic survey data, mist-net capture data, and both maternity-colony and male day-roost data exist for the northern long-eared bat (Ford et al. 2006b; Johnson et al. 2009, 2010, 2013). Herein, we compare presence-only model results generated from physical capture, acoustic detection, and day-roost locations in a topographically complex, forested landscape. On the basis of known levels of intensity of collection for each data type, we expected *a priori* that roost location and acoustic data would provide more precise model estimates and relationships consistent with habitat preferences noted in other areas compared with capture data (Owen et al. 2003; Ford et al. 2005). Further, on the basis of capture protocols, we expected that netting data would show a bias toward streams.

Methods

We modeled the presence probability of northern long-eared bats on the FEF, Tucker County, West Virginia using a historical monitoring data set containing three presence record data types: acoustic detection locations, capture locations, and known roost locations (Table S1). Between April 15 and November 15, 1999–2013, northern long-eared bat presence on the FEF was



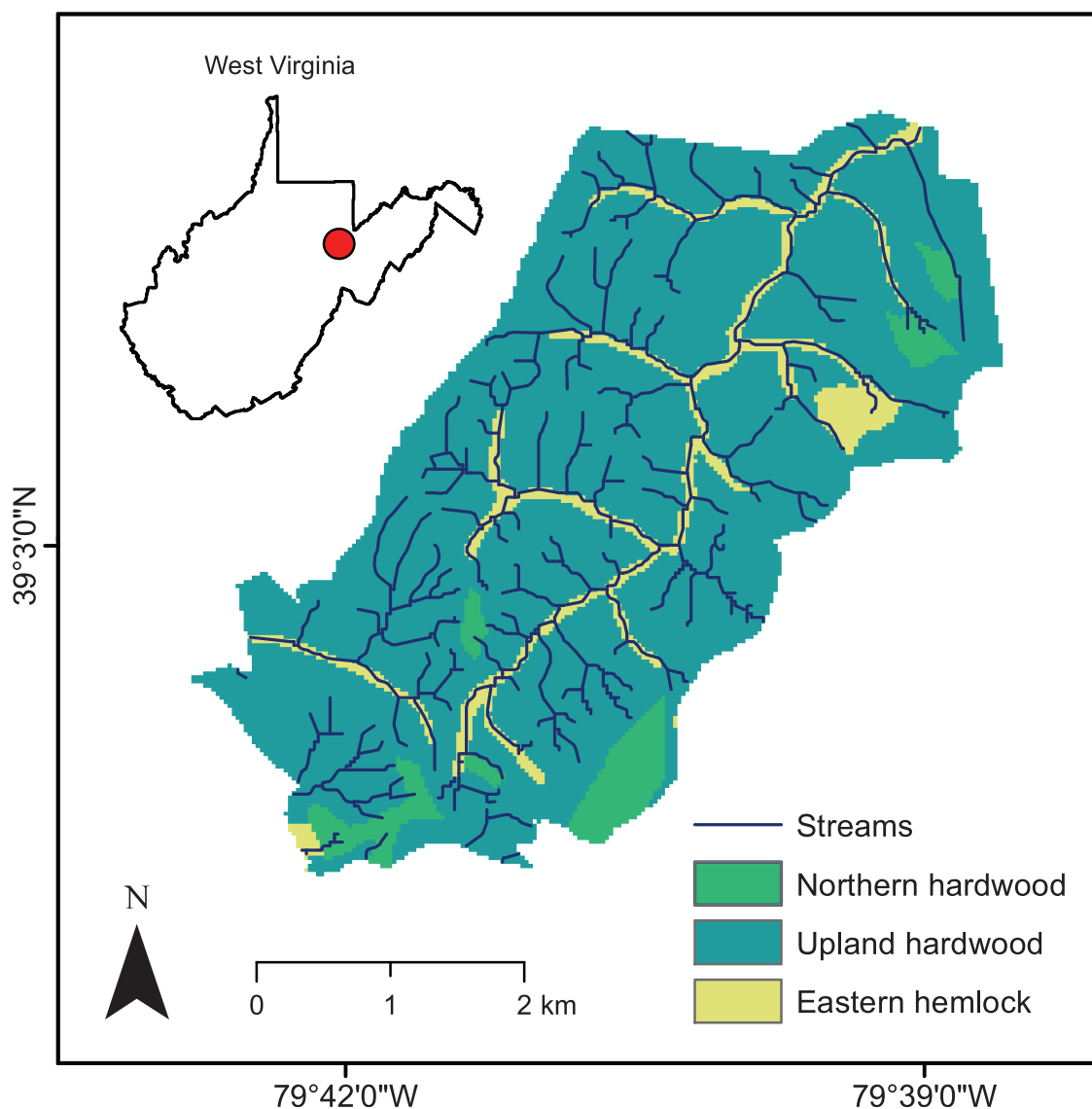


Figure 1. Forest habitat distribution and stream network on the Fernow Experimental Forest, West Virginia for deriving habitat models for northern long-eared bats (*Myotis septentrionalis*). Inset shows location of Fernow Experimental Forest.

recorded at 11 mist-net capture locations and 32 acoustic detector locations. Capture locations represent multiple individual mist nets, but because of proximity (nets within 30 m of one another), these data were collapsed into a single value for each location. Similarly, we collapsed all presence records across years at individual acoustic sites into a single record for that site. One hundred thirty-one day roosts were located by tracking radiotagged bats (see Ford et al. 2005, 2006b; Johnson et al. 2009, 2012 for specific capture, radio-tracking, and acoustic detection details). These data were collected by the U.S. Forest Service, Northern Research Station, U.S. Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit, Virginia Tech Department of Fish and Wildlife Conservation, and West Virginia University Division of Forestry personnel in support of active research, land management, and biodiversity monitoring on the FEF.

The FEF is a 1,900-ha experimental forest maintained by the U.S. Forest Service Northern Research Station for long-term silvicultural and forest ecology research. Located within the Unglaciated Allegheny Mountains subsection of the Appalachian Plateau Physiographic Province, the topography at the FEF is characterized by steep slopes, broad ridge tops, narrow valleys, and high-gradient streams. Elevations range from approximately 500 m to 1,200 m. The climate is cool and moist with mean summer daily maximum temperature of 26.8°C and mean annual precipitation of 130 cm (Madarish et al. 2002). Upland forest cover primarily is a mixed mesophytic type consisting of sugar maple (*Acer saccharum*), red maple (*A. rubrum*), northern red oak (*Quercus rubra*), chestnut oak (*Q. prinus*), yellow poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), sweet birch (*Betula lenta*), black cherry (*Prunus serotina*), and basswood (*Tilia americana*; Figure 1). Overstories of

eastern hemlock (*Tsuga canadensis*) and dense shrub layers of rosebay rhododendron (*Rhododendron maximum*) dominate riparian areas. Higher elevations on the eastern portion of the FEF contain northern hardwood forest consisting of American beech, sugar maple, and yellow birch (*B. alleghaniensis*; Madarish et al. 2002). Most forests are mature, second growth (>80 y old); however, numerous forest stands on the FEF are in younger age classes or stands with lower stocking as a result of ongoing or previous silvicultural research. Approximately 275 ha of the FEF have been subjected to prescribed burning over the past decade. Underlain by the Greenbrier Limestone formation, the FEF contains several small and one large cave system. The large system, Big Springs Cave, was a winter hibernacula for northern long-eared bats, little brown bats (*M. lucifugus*), and the endangered Indiana bat (*M. sodalis*) before the advent of WNS (Ford et al. 2006b) in the winter of 2010–2011 (Johnson et al. 2013).

We fit presence probability models for each presence data type and the combination of all data using the presence-only maximum-likelihood method of Royle et al. (2012) using R (R Development Core Team 2014) with package maxlike (Royle et al. 2012). We created *a priori* models using combinations of physiographic and forest type predictor variables on the basis of the existing literature and previous research on or in proximity to the FEF (Ford et al. 2005; Johnson et al. 2010, 2013; Table S2). Physiographic predictors we selected were elevation (m), topographic exposure index (TEI; Odom and McNab 2000), slope degree, distance to stream (m), and aspect (northeast, northwest, southeast, southwest; Figure S1); these variables were indicated by Schirmacher et al. (2007) and Johnson et al. (2010) to be important determinants of bat activity in Appalachian landscapes, and by Menzel et al. (2002) and Johnson et al. (2009) as important determinants of roost locations. All terrain variables were derived from U.S. Geological Survey 1 arc-second (30-m resolution) digital elevation models (Gesch et al. 2002; Gesch 2007) using the spatial analyst toolbox within ArcGIS (Version 10.2.2, Environmental Systems Research Institute, Redlands, CA). Topographic exposure was derived by subtracting the average elevation of the area within a 1-km radius surrounding a pixel from the elevation of the pixel. Relatively high TEI values indicate that sites were exposed peaks or ridges, whereas low or negative values indicate that sites were sheltered landforms such as coves, lower slopes, and stream corridors (Evans et al. 2014; Ford et al. 2015). Ford et al. (2005) and Owen et al. (2003) indicated that divisions among riparian and upland forests locally on the FEF were important predictors of bat occurrence and bat foraging habitat selection. Distance from streams often is considered important in studies of the sympatric Indiana bat, and previously has been found to have an influence on roosting, distribution, and activity of northern long-eared bats (Owen et al. 2003, Ford et al. 2005, Schirmacher et al. 2007, Johnson et al. 2013).

Because predictors of roosting and foraging habitats often are similar (Menzel et al. 2002; Owen et al. 2003; Ford et al. 2005; Johnson et al. 2009, 2013), we created a

single candidate model set to assess acoustic and roost location data. Our candidate model set for capture data consisted of only single variables because of the limited sample size. Variable combinations that we explored tested hypotheses that occurrence was driven only by forest type, only by physiographic variables, distance to water features (streams) while accounting for related physiographic variables, and the combination of physiographic and forest type. We specifically included an interaction between elevation and TEI to account for the differential effects of sheltering, exposure, and cold air drainage over elevational gradients. Because we had a forest type that was relatively unique to this study area in comparison with other studies (i.e., hemlock forest), we made some specific models around this forest type. Although hemlock distribution is somewhat correlated with streams, actual presence is limited, and hemlock occurs in absence of streams under some relatively common conditions at the site. Therefore, we regarded the potential correlation between stream presence and hemlock as discontinuous and negligible in this study.

For ease of model fitting and interpretation, we centered and scaled our continuous physiographic predictors. Forest type was divided into three categories: upland hardwood (uplhw), northern hardwood (norhw), and eastern hemlock (hemlock). We extracted predictor variables from raster data with 30-m cell resolution. Specific variables relative to the FEF such as forest type and stream network were provided by U.S. Forest Service, Northern Research Station databases (Schuler et al. 2006; Adams et al. 2010). We compared models using Akaike's information criterion corrected for small sample size (AIC_c), the difference between the model with the lowest AIC_c and the AIC_c of the i th model (Δ_i), and Akaike's weights (w_i ; Burnham and Anderson 2002). We dropped models that did not converge from the candidate set. Because our goal was to show limitations and implications of data type rather than provide detailed models of habitat association and selection, we did not model average or evaluate model predictive accuracy. Additionally, we note that model averaging is not recommended in all cases (Cade 2015).

Results

Our best supported model predicting presence from acoustic detection data contained TEI, slope, distance from stream, and aspect (Table 1). Imprecise parameter estimates indicate that although this was the best supported model, it has poor fit and therefore little explanatory power (Table 2; Figure 2). The best supported model predicting presence from capture locations contained distance from stream and indicated that probability of presence decreases with distance from stream (Tables 3 and 4; Figure 3). The best supported model predicting presence from roost locations included forest type, elevation, TEI, slope, distance from stream, and the interaction of TEI with elevation. This model indicates that roost presence probability increases with distance from stream and is greater in upland hardwood and eastern hemlock forest than in

Table 1. Ranking of models used to predict northern long-eared bat (*Myotis septentrionalis*) presence from acoustic detection data on the Fernow Experimental Forest, West Virginia. Data were collected from 1999 through 2013. Model parameters are given as well as number of parameters (K), Akaike's information criteria corrected for small sample size (AIC_c), difference in AIC_c value between top model and i th model (Δ_i), and model support (w_i). Model parameters included topographic exposure index (TEI), slope degree (slope), distance from stream in meters (dist. from stream), aspect (northeast, northwest, southeast, southwest), elevation in meters (elevation), and forest type (eastern hemlock = hemlock, upland hardwood = uplhw).

Model	K	Likelihood	AIC_c	Δ_i	w_i
TEI + slope + dist. from stream + northeast + southeast + southwest	7	-307.255	633.18	0.00	0.90
Elevation \times TEI + slope	5	-313.427	639.16	5.98	0.04
Hemlock	2	-317.589	639.59	6.41	0.04
Uplhw + hemlock	3	-317.145	641.15	7.97	0.02
Uplhw + hemlock + elevation \times TEI + slope	7	-312.729	644.13	10.95	0.00
Elevation \times TEI + slope + dist. from stream + northeast + southeast + southwest	9	-310.086	646.35	13.18	0.00
Uplhw + hemlock + elevation \times TEI + slope + dist. from stream + southeast + southwest	10	-308.163	646.80	13.62	0.00
Uplhw + hemlock + elevation \times TEI + slope + dist. from stream	8	-312.8	647.86	14.68	0.00
Global model	11	-311.015	657.23	24.05	0.00
Null model	1	-338.095	678.32	45.15	0.00

northern hardwood forest types, and decreases with TEI, slope, and the interaction of TEI and elevation (Tables 5 and 6; Figure 4). The best supported model predicting presence for the combined data contained elevation, TEI, slope, and the interaction of TEI and elevation, with presence probability increasing with elevation (Tables 7 and 8; Figure 5).

Discussion

The number of locations that we used to create our acoustic and capture models would be unacceptably small to construct habitat models over a broader landscape. However, the amount of data available in our case study far exceeds the per-area density that could be expected in most historical presence data sets from general bat fauna survey work. In many cases, historical data are collected for site-specific regulatory clearance purposes and their use in distribution and habitat selection models may not be robust because of sample distribution (e.g., netting near streams) and intensity. Most historical data sets containing monitoring data also likely do not contain all three presence data types that we used. Nonetheless, we suspect that many forest land managers will be interested in attempting to

create distribution models using local site data to address state and federal regulatory concerns resulting from the recent listing of this species as federally threatened. Managers may be tempted to combine data types, but this should be carefully considered. Theoretically, combining data will provide maximal information about where northern long-eared bats occur. However, models created using pooled data may mask trends relative to specific aspects of northern long-eared bat foraging and day-roosting ecology, and undoubtedly may violate modeling assumptions. In our study, we found that combining all of our data types yielded results similar to those produced using roost data exclusively. This is unsurprising given the preponderance of roost locations in the data set, but it highlights the importance of evaluating data attributes when combining data types relative to the specific desired output and desired management application. Combining data types in this study violated several important assumptions of the method that we used (such as point independence

Table 2. Parameter summary for best supported model predicting northern long-eared bat (*Myotis septentrionalis*) presence from acoustic detection data on the Fernow Experimental Forest, West Virginia. Data were collected from 1999 through 2013. Model parameters are topographic exposure index (TEI), slope degree (slope), distance from stream in meters (dist. from stream), and aspect (northeast, southeast, southwest).

Parameter	Estimate	SE	Z	P-value
(Intercept)	295	400	0.737	0.46
TEI	-324	475	-0.683	0.49
Slope	-327	495	-0.66	0.51
Dist. from stream	513	779	0.658	0.51
Northeast	879	1,370	0.641	0.52
Southeast	159	286	0.556	0.58
Southwest	-395	567	-0.696	0.49

Table 3. Ranking of models used to predict northern long-eared bat (*Myotis septentrionalis*) presence from capture data on the Fernow Experimental Forest, West Virginia. Data were collected from 1999 through 2013. Model parameters are given as well as number of parameters (K), Akaike's information criteria corrected for small sample size (AIC_c), difference in AIC_c value between top model and i th model (Δ_i), and model support (w_i). Model parameters included topographic exposure index (TEI), slope degree (slope), distance from stream in meters (dist. from stream), elevation in meters (elevation), and forest type (eastern hemlock = hemlock, upland hardwood = uplhw).

Parameter	K	Likelihood	AIC_c	Δ_i	w_i
Dist. from stream	2	-106.208	216.83	0.00	0.53
Hemlock	2	-107.502	219.42	2.59	0.14
TEI	2	-107.571	219.56	2.73	0.13
Elevation	2	-107.874	220.16	3.33	0.10
Uplhw	2	-108.49	221.39	4.57	0.05
Slope	2	-108.796	222.01	5.18	0.04
Null	1	-116.22	234.57	17.75	0.00
Global	11	-99.9721	235.14	18.32	0.00



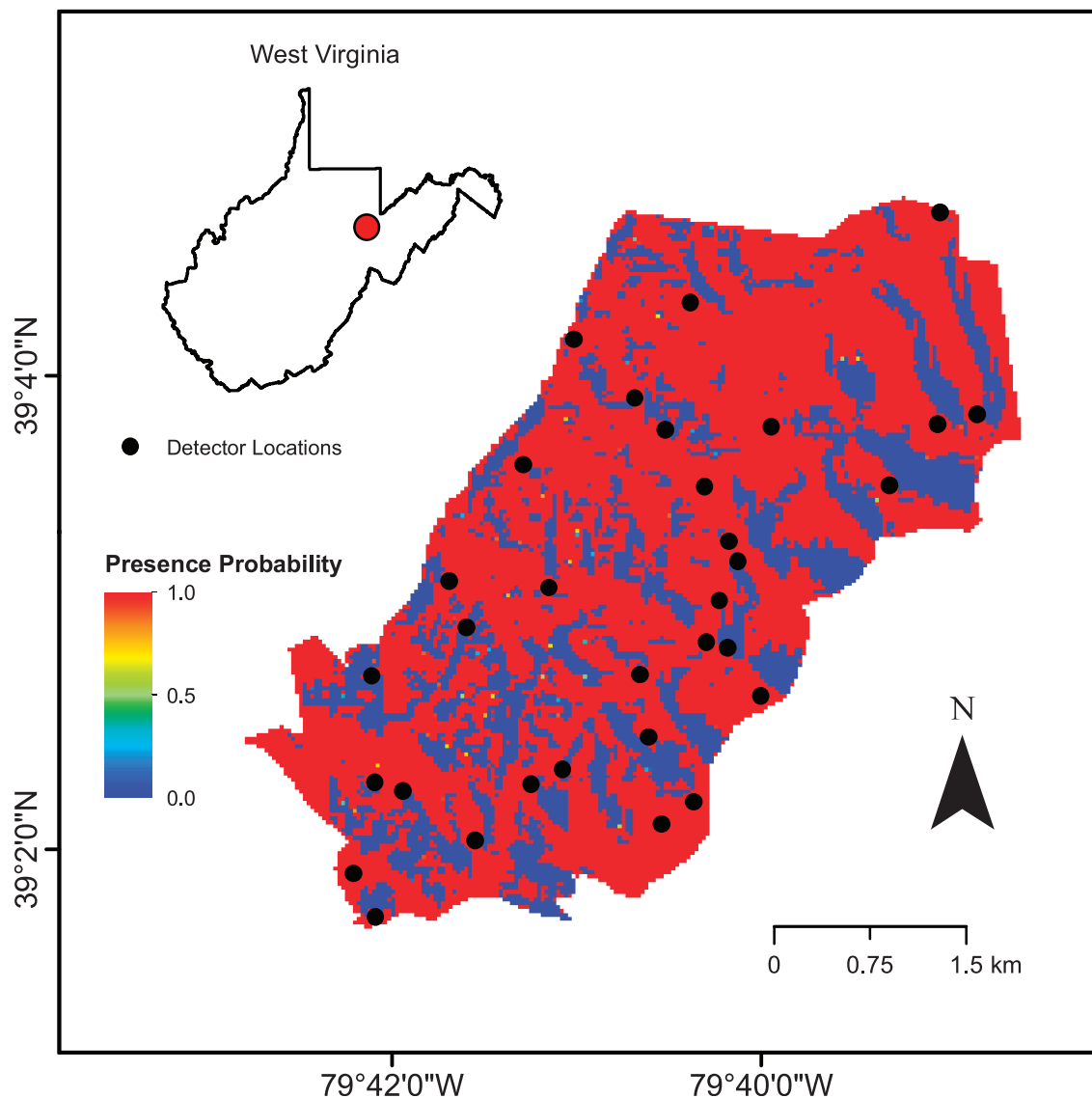


Figure 2. The best supported model of predicted probability of presence of northern long-eared bats (*Myotis septentrionalis*) on the Fernow Experimental Forest, West Virginia, derived from presence-only acoustic detection locations. Data were collected from 1999 through 2013. Inset shows location of Fernow Experimental Forest.

and equal and constant detection probability), as it also would have with other widely used modeling methods such as maximum entropy. Therefore, it is crucial to clearly define the desired objective of any predictive model early in the development process, whether that would be a landscape suitability metric for roosting or a

Table 4. Parameter summary for best supported model predicting northern long-eared bat (*Myotis septentrionalis*) presence from capture locations on the Fernow Experimental Forest, West Virginia. Data were collected from 1999 through 2013. Model parameter is distance from stream in meters (dist. from stream).

Parameter	Estimate	SE	z	P-value
Intercept	-11.44	202.30	-0.06	0.95
Dist. from stream	-1.22	0.61	-1.98	0.05

small-scale model of likely foraging habitats in a project area slated for active management. Models created using pooled data types should be regarded at the outset as exploratory (although still potentially informative at the local scale) unless the chosen modeling method deals with violations of assumptions and differences in data type directly. However, historical data may be used in conjunction with post-WNS presence records to guide current and future sampling efforts and validate models created from post-WNS survey records.

Our best supported models predicting northern long-eared bat presence differed substantially among our presence data types. As a result, our predicted presence maps for the FEF differed with little overall consensus in patterns of where northern long-eared bats likely occur. On the basis of research conducted at the FEF and published literature, all of our best supported models

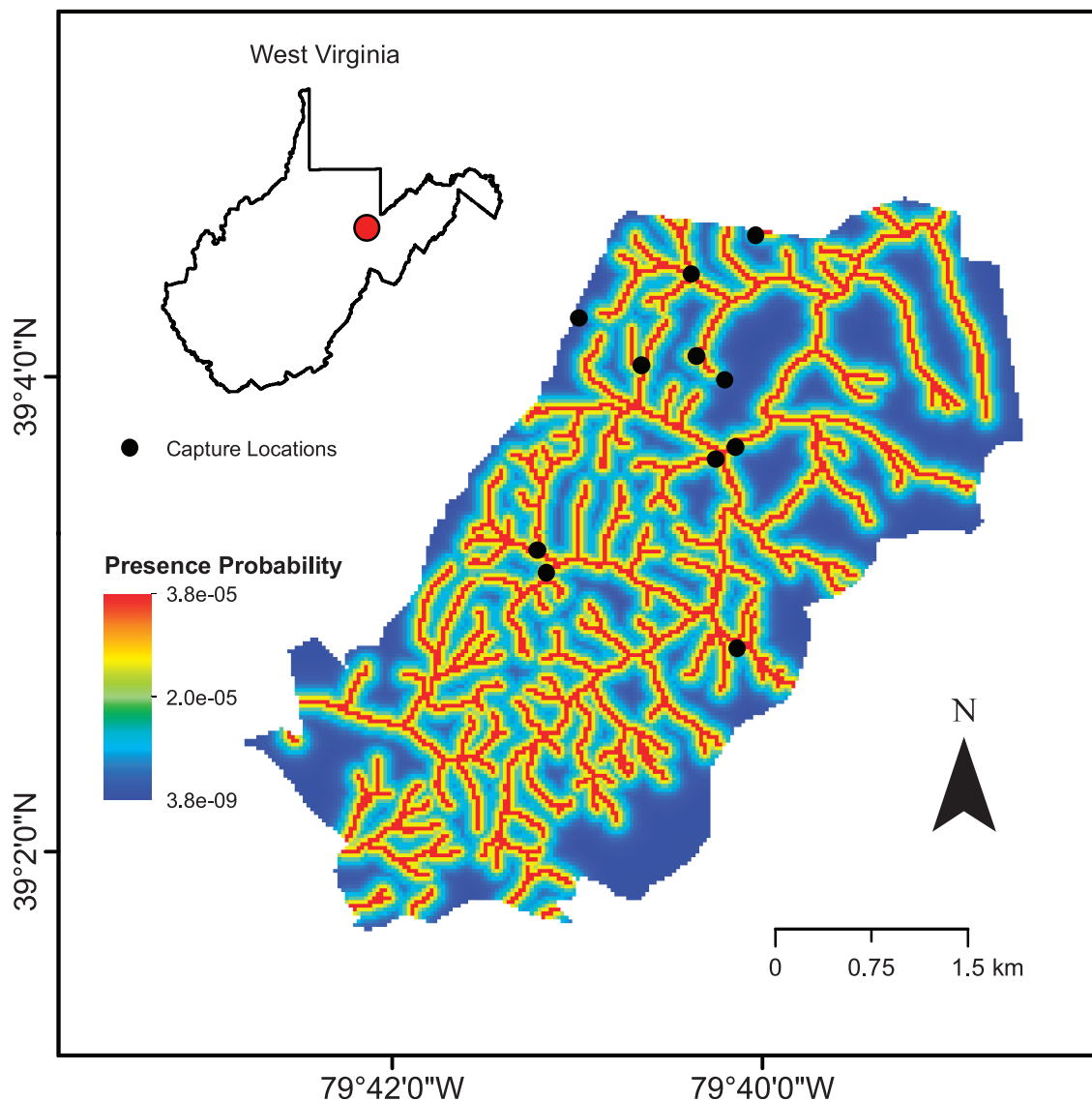


Figure 3. The best supported model of predicted probability of presence of northern long-eared bats (*Myotis septentrionalis*) on the Fernow Experimental Forest, West Virginia derived from presence-only capture locations. Data were collected from 1999 through 2013. Inset shows location of Fernow Experimental Forest.

correspond with known traits of the northern long-eared bat or are easily explained in the context of the particular data collection protocol involved. The predicted overall high likelihood of northern long-eared bat presence generated from the acoustic data corresponds with the generally widespread detection of the species; however, the model fit poorly and therefore offers little insight into habitat associations. Nonetheless, the best supported acoustic location model differed from the best supported roost location model. Differences in the best supported model set for these two data sets highlights the effect that different types of presence data could have on habitat management. The importance of distance from stream in our capture-based model clearly is an artifact of capture methodology associated with mist netting. At the FEF, capture efforts occurred to support research involving radiotracking northern long-

eared bats and Indiana bats. As a result, capture locations were biased toward known congregation points or where deployment of mist nets was effective, in this case, small ponds and first- to second-order streams.

The presence model created using roost locations probably is the most useful model relative to habitats that could be affected or modified by management activities on the FEF. In part, this is due to the larger number of sample locations relative to our other data sources, but also because these data are less biased relative to sampling protocol (e.g., intentional sampling near easy access areas). It is important to note, however, that bias induced by the roost selection preferences of tracked bats reduces generalizability of this model and others created using similar data. For example, social roost selection, whereby bats select roosts within

Table 5. Ranking of models used to predict northern long-eared bat (*Myotis septentrionalis*) presence from roost location data on the Fernow Experimental Forest, West Virginia. Data were collected from 1999 through 2013. Model parameters are given as well as number of parameters (K), Akaike's information criteria corrected for small sample size (AIC_c), difference in AIC_c value between top model and i th model (Δ_i), and model support (w_i). Model parameters included topographic exposure index (TEI), slope degree (slope), distance from stream in meters (dist. from stream), aspect (northeast, southeast, southwest), elevation in meters (elevation), and forest type (eastern hemlock = hemlock, upland hardwood = uplhw).

Parameter	Estimate	SE	z	P-value
(Intercept)	-4.20	2.43	-1.72	0.08
Uplhw	2.24	1.47	1.52	0.13
Hemlock	0.73	1.62	0.45	0.65
Elevation	0.77	0.47	1.63	0.10
TEI	-1.08	0.44	-2.47	0.01
Slope	-0.30	0.14	-2.11	0.04
Dist. from stream	0.25	0.14	1.82	0.07
Elevation \times TEI	-1.24	0.27	-4.67	0.00

individual colony areas (Johnson et al. 2012, Silvis et al. 2014), could introduce a substantial amount of bias into this model. Although the presence model created from roosting locations produces a map that corresponds accurately to our observed data, it predicted low overall likelihood of northern long-eared bat presence across the FEF.

We observed low precision for some of our model parameters (i.e., large standard errors relative to parameter estimates) across our models and data types due to the small sample sizes of the data sets we used. This likely also contributed to differences in our model predictions, and highlights potential issues in creation of local landscape distribution models using data from historical records. In many cases, historical data are collected for monitoring purposes and their use in distribution and habitat selection models may not be robust because of sample distribution (e.g., netting near streams) and intensity. When parameter precision is low, it is difficult to assign certainty even to parameter sign; for individual parameters, this may result in improper assessment effects such that a believed positive effect may in fact be a negative effect. Poor parameter precision within models also can reduce the interpretability of entire models, as effects may be synergistic.

Because our primary objective was to explore the potential impacts of presence data type on development of northern long-eared bat distribution and ecological niche models at local to small landscape scales using historical data sets rather than to objectively compare performances of individual data types, we did not compare the relative performances of the different data types under equal sampling conditions using rarefaction or other resampling methods. We believe that the proportion of data in each class in our data set generally is representative of the historical records kept by many state and federal agencies. Thus, our approach provides a reasonable summary of what results may be expected.

Table 6. Parameter summary for best supported model predicting northern long-eared bat (*Myotis septentrionalis*) presence from roost locations on the Fernow Experimental Forest, West Virginia. Data were collected from 1999 through 2013. Model parameters are topographic exposure index (TEI), slope degree (slope), distance from stream in meters (dist. from stream), elevation in meters (elevation), and forest type (eastern hemlock = hemlock, upland hardwood = uplhw).

Parameter	Estimate	SE	z	P-value
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Elevation \times TEI	-1.24	0.27	-4.67	0.00

Applied conservation-directed uses of ecological niche and distribution modeling have been limited relative to bats, but these approaches have been shown to have great utility in bat conservation. For example, Roscioni et al. (2013) and Santos et al. (2013) assessed potential mortality risks to bats from current and planned wind-energy developments. Weber and Sparks (2013) delineated potential summer habitat through maximum entropy modeling for the endangered Indiana bat across eight states in the eastern United States using a combination of mist-net records, acoustic recordings, and documented day roosts. The work of Weber and Sparks (2013) was highly beneficial for showing regions of low predicted probability of Indiana bat presence over large areas within the species' distribution. For example, despite limitations relative to understanding the importance of topographic complexity and forestry type, they found low probability of presence where forests are highly fragmented in parts of the agricultural Midwest or where the climate is too cold and wet, such as in much of the northern Appalachians and Adirondack mountains. Barnhart and Gillam (2014) compared model results derived separately from acoustic recordings and physical capture for several species throughout North Dakota and found highly discordant results for the northern long-eared bat. This was attributed to the clumpy nature of the distribution of the forest-obligate northern long-eared bat in a largely nonforested state and differential detection probability between acoustics and mist netting. At more local scales using a maximum-likelihood approach on state forests in Indiana, Pauli (2014) also showed that presence maps developed from acoustic sampling and those developed from day-roost locations also were dissimilar for the northern long-eared bat. However, at local scales, presence data types could be combined to produce plausible simulations of the impact of forest management activities on overall northern long-eared bat habitat suitability.

Conclusion

Northern long-eared bat numbers are continuing to decline across WNS-affected areas. For many local



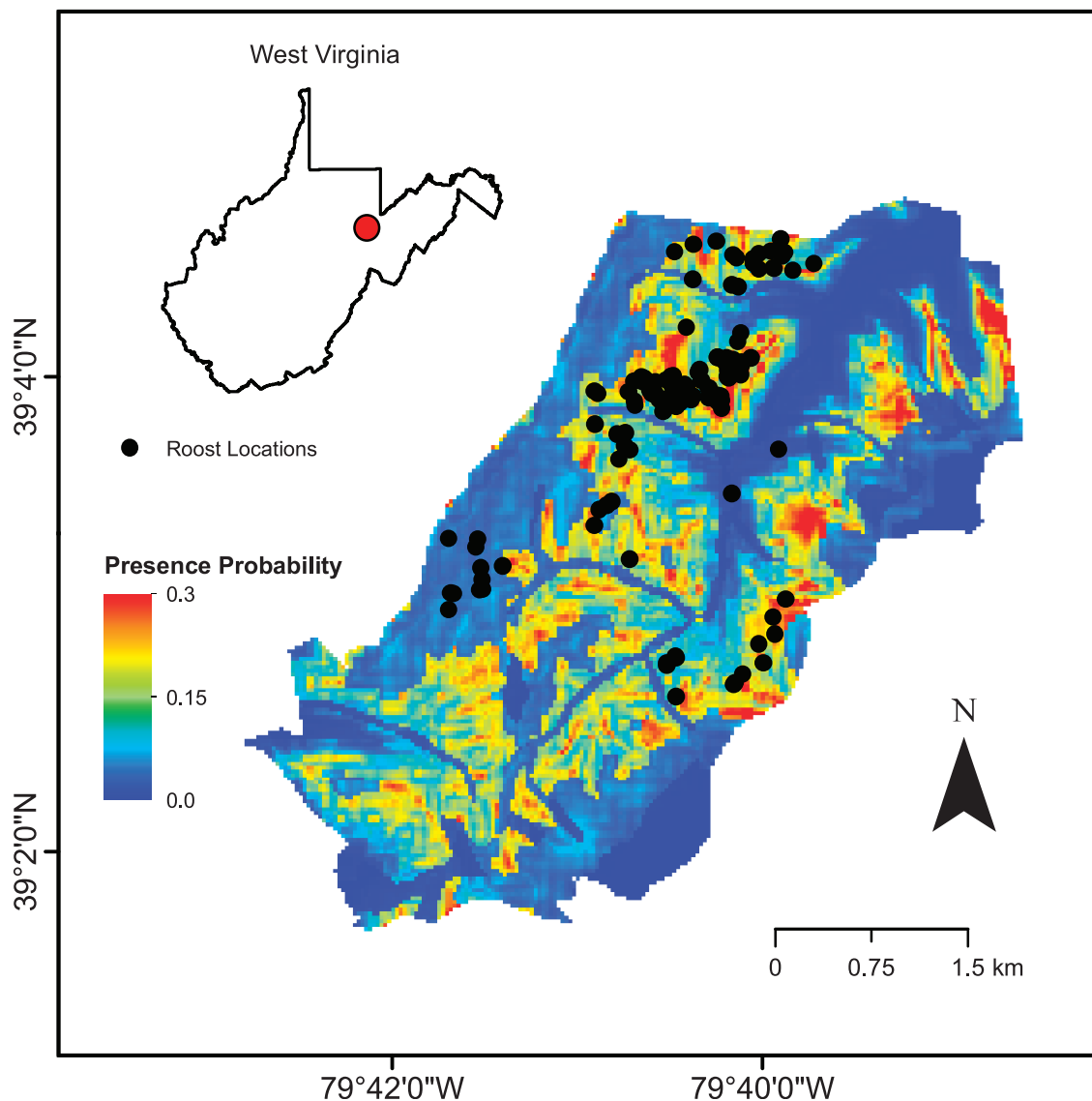


Figure 4. The best supported model of predicted probability of presence of northern long-eared bats (*Myotis septentrionalis*) on the Fernow Experimental Forest, West Virginia, derived from presence-only roost locations. Data were collected from 1999 through 2013. Inset shows location of Fernow Experimental Forest.

Table 7. Ranking of models used to predict northern long-eared bat (*Myotis septentrionalis*) presence from the combined acoustic, capture, and roost location data on the Fernow Experimental Forest, West Virginia. Data were collected from 1999 through 2013. Model parameters are given as well as number of parameters (K), Akaike's information criteria corrected for small sample size (AIC_c), difference in AIC_c value between top model and i th model (Δ_i), and model support (w_i). Model parameters included topographic exposure index (TEI), slope degree (slope), distance from stream in meters (dist. from stream), aspect (northeast, southeast, southwest), elevation in meters (elevation), and forest type (eastern hemlock = hemlock, upland hardwood = uplhw).

Model	K	Likelihood	AIC_c	Δ_i	w_i
Elevation \times TEI + slope	5	-1,536.45	3,083.25	0.00	0.37
Uplhw + hemlock + elevation \times TEI + slope + dist. from stream	8	-1,533.4	3,083.66	0.41	0.30
Uplhw + hemlock + elevation \times TEI + slope	7	-1,534.56	3,083.79	0.54	0.28
Elevation \times land form index + slope + dist. from stream + northeast + southeast + southwest	9	-1,534.19	3,087.48	4.23	0.04
Uplhw + hemlock + elevation \times TEI + slope + dist. from stream + southeast + southwest	10	-1,535.37	3,092.09	8.84	0.00
Global model	11	-1,534.43	3,092.49	9.24	0.00
TEI + slope + dist. from stream + northeast + southeast + southwest	7	-1,549.33	3,113.33	30.07	0.00
Uplhw + hemlock	3	-1,554.34	3,114.82	31.57	0.00
Hemlock	2	-1,556.95	3,117.96	34.71	0.00
Null model	1	-1,658.78	3,319.58	236.33	0.00

Table 8. Parameter summary for best supported model predicting northern long-eared bat (*Myotis septentrionalis*) presence from combined acoustic, capture, and roost location data on the Fernow Experimental Forest, West Virginia. Data were collected from 1999 through 2013. Model parameters are topographic exposure index (TEI), slope degree (slope), and elevation in meters (elevation).

Parameter	Estimate	SE	z	P-value
(Intercept)	-4.09	6.17	-0.66	0.51
Elevation	0.34	0.32	1.06	0.29
TEI	-0.60	0.29	-2.08	0.04
Slope	-0.30	0.09	-3.12	0.00
Elevation \times TEI	-0.53	0.12	-4.45	0.00

landscapes and even some regions, little is known about the specific habitat or distribution of this species. Currently, developing ecological niche models to inform managers and regulators about northern long-eared bat foraging and day-roosting habitat suitability is a priority. Similarly, for conservation-oriented landscapes such as state and federal property, documentation of known habitat will be critical for balancing the conservation needs of multiple competing objectives and even competing endangered species (e.g., northern long-eared bat vs. Indiana bat habitat management). If historical data are used to model presence, it will be imperative to use data appropriately through consideration of spatial scale and the aspect of bat ecology represented by the historical data, determination of whether project objectives are amenable to combining presence data types, and whether this violates assumptions of the selected modeling approach. Because of

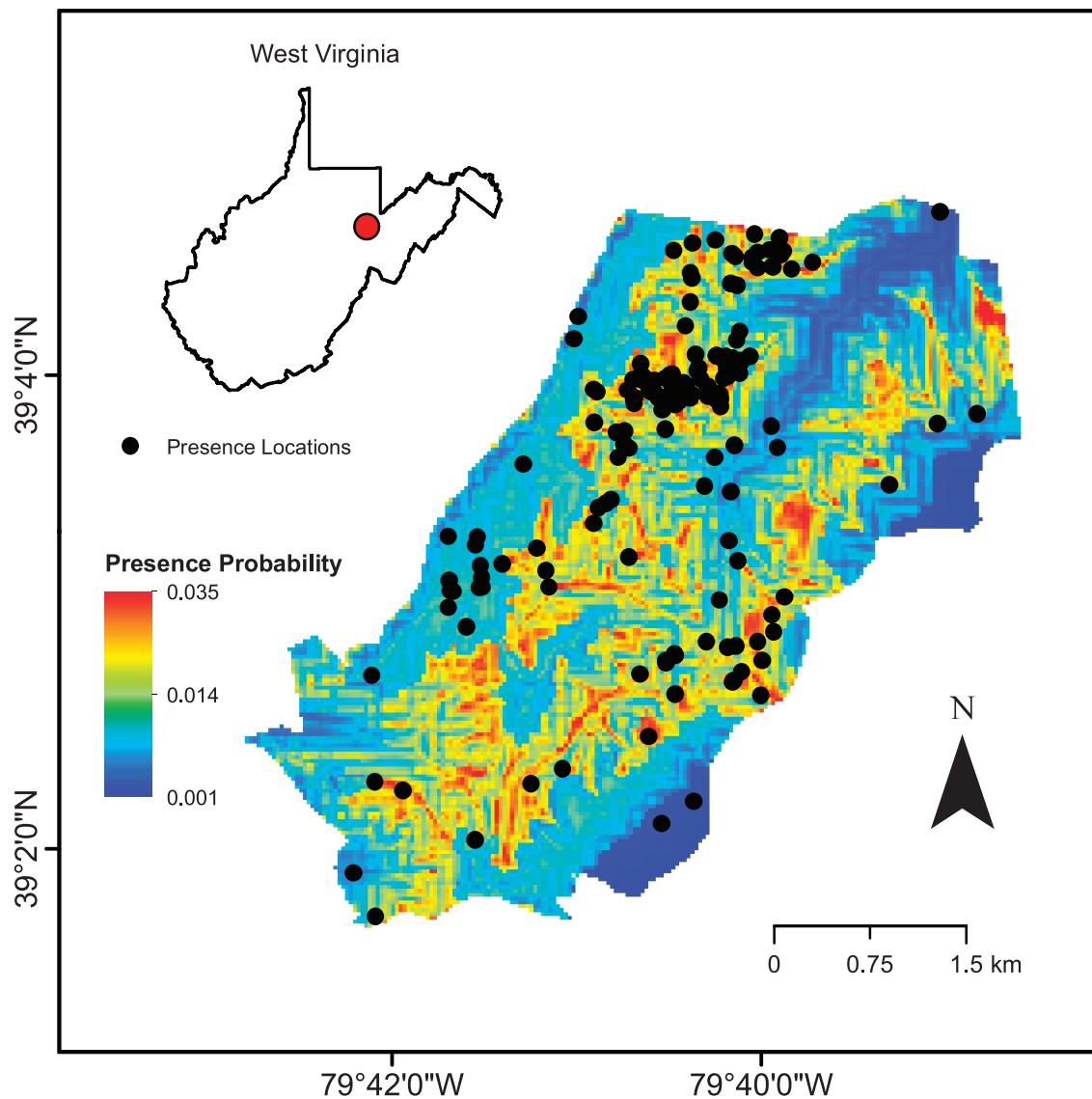


Figure 5. The best supported model of predicted probability of presence of northern bats (*Myotis septentrionalis*) on the Fernow Experimental Forest, West Virginia, derived from a combined data set including acoustic detection, capture, and roost locations. Data were collected from 1999 through 2013. Inset shows location of Fernow Experimental Forest.

declines in northern long-eared bats as a result of WNS, the ability to gather presence data in post-WNS environments will likely remain limited for the foreseeable future. As such, our results provide valuable understanding of the limitations of historical data, as well as how presence data type may yield substantially different models of northern long-eared bat presence within an individual landscape. Finally, recent advances have been made in modeling occupancy with imperfect detection from single site visits (Lele et al. 2012); we encourage the application and exploration of these models for historical bat presence-absence data sets.

Supplemental Material

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

Table S1. Roost, acoustic, and capture record locations for northern long-eared bats (*Myotis septentrionalis*) on the Fernow Experimental Forest, West Virginia. Locations are provided by type, in Universal Transverse Mercator coordinates, NAD1983, zone 17N. Data were collected from 1999 through 2013.

Found at DOI: <http://dx.doi.org/10.3996/012015-JFWM-00451> (5.35 KB CSV).

Table S2. *A priori* model set used to predict occurrence of northern long-eared bats (*Myotis septentrionalis*) on the Fernow Experimental Forest, West Virginia. Data were collected from 1999 through 2013.

Found at DOI: <http://dx.doi.org/10.3996/012015-JFWM-00452> (906 BYTE CSV).

Figure S1. Geospatial data used to build models of northern long-eared bat (*Myotis septentrionalis*) occurrence on the Fernow Experimental Forest, West Virginia. Layer foresttype.tif provides forest type classification at 30-m resolution. (304 KB TIF). Forest types are as follows: 1 = red maple– red oak, 2 = red maple–basswood, 3 = hemlock, 4 = chestnut oak–red oak, 5 = beech, 6 = sugar maple beech. Layer elevation.tif provides elevation values in meters above sea level, 30-m resolution. (1.92 MB TIF). Layer TEI.tif provides topographic exposure index (TEI) values derived from 30-m resolution elevation data. (304 KB TIF). Topographic exposure was derived by subtracting the average elevation of the area within a 1,000-m radius surrounding a pixel from the elevation of the pixel. Layer slope.tif provides slope in degrees derived from 30-m resolution elevation data. (304 KB TIF). Layer streamdist.tif provides linear distance from streams in meters. (304 KB TIF). Layer aspect.tif provides aspect derived from 30-m resolution elevation data. (304 KB TIF). Aspect is divided categorically into four categories: 1 = northeast, 2 = southeast, 3 = southwest, 4 = northwest.

Found at DOI: <http://dx.doi.org/10.3996/012015-JFWM-00453>.

Reference S1. Adams MB, Edwards P, Rodrigue JL, Schuler TM, Thomas-Van Gundy M, Wood F. Final environmental impact statement, Fernow Experimental Forest, Tucker County, West Virginia. 2010. Prepared by U.S. Department of Agriculture (USDA) Forest Service, Northern Research Station. On file with the U.S. Environmental Protection Agency. Copies are available from the USDA Forest Service, Northern Research Station, Parsons, West Virginia.

Found at DOI: <http://dx.doi.org/10.3996/012015-JFWM-00454> (3.08 MB PDF).

Reference S2. Johnson JB, Rodrigue JL, Ford WM. 2013. Nightly and yearly bat activity before and after white-nose syndrome on the Fernow Experimental Forest in Tucker County, West Virginia. U.S. Department of Agriculture Forest Service Northern Research Station Research Paper NRS-Research Paper 24.

Found at DOI: <http://dx.doi.org/10.3996/012015-JFWM-00455> (1.26 MB PDF).

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Reference S4. Odom RH, McNab WH. 2000. Using digital terrain modeling to predict ecological types in the Balsam Mountains of western North Carolina. U.S. Department of Agriculture Forest Service Research Note SE-8, Southern Research Station, Asheville, North Carolina.

Found at DOI: <http://dx.doi.org/10.3996/012015-JFWM-00457> (2.18 MB PDF).

Acknowledgments

U.S. Forest Service Northern Research Station, U.S. Geological Survey, Cooperative Research Unit Program, and Virginia Tech Department of Fish and Wildlife Conservation provided financial support for this project. Field assistance was provided by D. Lowther and R. Hovatter. We thank C. Johnson for numerous discussions about northern long-eared bat ecology that ultimately led to this research endeavor. We thank the three anonymous reviewers for their helpful comments.

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

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