**Use of Forested Habitat Adjacent to Highways by Northern Long-Eared Bats**

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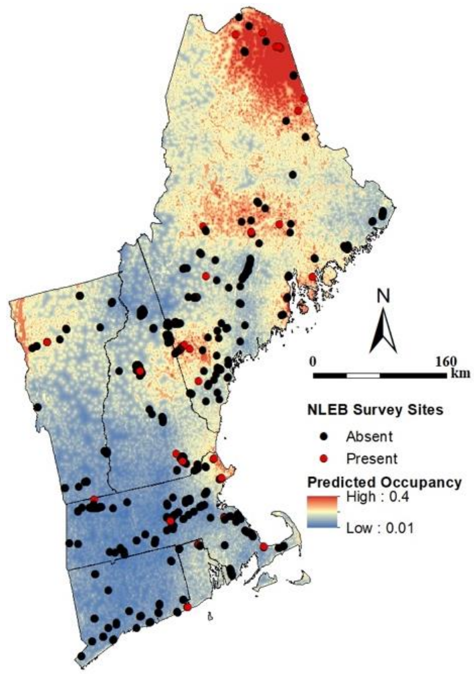


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16. Abstract
Bat populations throughout the Northeast have undergone precipitous declines in less than a decade due to the fungal disease white-nose syndrome, with *Myotis septentrionalis* (Northern long-eared bat, hereafter NLEB) suffering the most severe declines of any species. The overarching objective of the proposed research was to address several major gaps in the knowledge of NLEB distributions and activity as they relate to the use of habitat along or adjacent to highways in New England. We compiled all available survey data to assist with determining habitat use and the effects of roads on NLEB, with a focus on habitats of the New England region. Using cutting-edge presence-absence occupancy models, we determined that NLEB distributions change spatially across New England but did not find a strong relationship between their distribution and highway or other landscape features.

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# SI* (MODERN METRIC) CONVERSION FACTORS

## APPROXIMATE CONVERSIONS TO SI UNITS

| SYMBOL | WHEN YOU KNOW | MULTIPLY BY | TO FIND | SYMBOL |
|---|---|---|---|---|
| | | **LENGTH** | | |
| in | inches | 25.4 | millimeters | mm |
| ft | feet | 0.305 | meters | m |
| yd | yards | 0.914 | meters | m |
| mi | miles | 1.61 | kilometers | km |
| | | **AREA** | | |
| $in^2$ | square inches | 645.2 | square millimeters | $mm^2$ |
| $ft^2$ | square feet | 0.093 | square meters | $m^2$ |
| $yd^2$ | square yard | 0.836 | square meters | $m^2$ |
| ac | acres | 0.405 | hectares | ha |
| $mi^2$ | square miles | 2.59 | square kilometers | $km^2$ |
| | | **VOLUME** | | |
| fl oz | fluid ounces | 29.57 | milliliters | mL |
| gal | gallons | 3.785 | liters | L |
| $ft^3$ | cubic feet | 0.028 | cubic meters | $m^3$ |
| $yd^3$ | cubic yards | 0.765 | cubic meters | $m^3$ |
| | | NOTE: volumes greater than 1000 L shall be shown in $m^3$ | | |
| | | **MASS** | | |
| oz | ounces | 28.35 | grams | g |
| lb | pounds | 0.454 | kilograms | kg |
| T | short tons (2000 lb) | 0.907 | megagrams (or "metric ton") | Mg (or "t") |
| | | **TEMPERATURE (exact degrees)** | | |
| °F | Fahrenheit | 5 (F-32)/9<br>or (F-32)/1.8 | Celsius | °C |
| | | **ILLUMINATION** | | |
| fc | foot-candles | 10.76 | lux | lx |
| fl | foot-Lamberts | 3.426 | candela/$m^2$ | cd/$m^2$ |
| | | **FORCE and PRESSURE or STRESS** | | |
| lbf | poundforce | 4.45 | newtons | N |
| lbf/$in^2$ | poundforce per square inch | 6.89 | kilopascals | kPa |

## APPROXIMATE CONVERSIONS FROM SI UNITS

| SYMBOL | WHEN YOU KNOW | MULTIPLY BY | TO FIND | SYMBOL |
|---|---|---|---|---|
| | | **LENGTH** | | |
| mm | millimeters | 0.039 | inches | in |
| m | meters | 3.28 | feet | ft |
| m | meters | 1.09 | yards | yd |
| km | kilometers | 0.621 | miles | mi |
| | | **AREA** | | |
| $mm^2$ | square millimeters | 0.0016 | square inches | $in^2$ |
| $m^2$ | square meters | 10.764 | square feet | $ft^2$ |
| $m^2$ | square meters | 1.195 | square yards | $yd^2$ |
| ha | hectares | 2.47 | acres | ac |
| $km^2$ | square kilometers | 0.386 | square miles | $mi^2$ |
| | | **VOLUME** | | |
| mL | milliliters | 0.034 | fluid ounces | fl oz |
| L | liters | 0.264 | gallons | gal |
| $m^3$ | cubic meters | 35.314 | cubic feet | $ft^3$ |
| $m^3$ | cubic meters | 1.307 | cubic yards | $yd^3$ |
| | | **MASS** | | |
| g | grams | 0.035 | ounces | oz |
| kg | kilograms | 2.202 | pounds | lb |
| Mg (or "t") | megagrams (or "metric ton") | 1.103 | short tons (2000 lb) | T |
| | | **TEMPERATURE (exact degrees)** | | |
| °C | Celsius | 1.8C+32 | Fahrenheit | °F |
| | | **ILLUMINATION** | | |
| lx | lux | 0.0929 | foot-candles | fc |
| cd/$m^2$ | candela/$m^2$ | 0.2919 | foot-Lamberts | fl |
| | | **FORCE and PRESSURE or STRESS** | | |
| N | newtons | 0.225 | poundforce | lbf |
| kPa | kilopascals | 0.145 | poundforce per square inch | lbf/$in^2$ |

*SI is the symbol for the International System of Units. Appropriate rounding should be made to comply with Section 4 of ASTM E380.

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# Introduction

## Project Context

Bat populations throughout the Northeast have undergone precipitous declines in less than a decade due to the fungal disease white-nose syndrome (Blehert et al. 2009). Several bat species are at risk of local extirpation (Frick et al. 2010, Langwig et al. 2012), with *Myotis septentrionalis* (Northern long-eared bat, hereafter NLEB) suffering the most severe declines of any species. Indeed, much of the research that has documented the cause and outcomes of these declines has been done by our lab group (e.g. Frick et al. 2015, Janicki et al. 2015, Langwig et al. 2015a, Langwig et al. 2015b, Hoyt et al. 2016). As a result of rapid population loss, the US Fish & Wildlife Service (USFWS) listed *M. septentrionalis* as threatened under the Endangered Species Act (ESA) on April 2, 2015. USFWS subsequently issued a 4(d) rule, a subsection of the ESA, that allows for flexible implementation of the Act but nonetheless requires that various regulations must be followed on projects that may affect NLEB. Federally funded or Federally Licensed projects, including road projects by the Departments of Transportation of New England states in the NETC, require Section 7 consultation under ESA to minimize the effects of activities on listed species. NLEB roost under the bark of various tree species, so activities potentially affecting these roosts must be carefully evaluated. NLEB also may use open areas such as highways in which to fly and forage. Attributes of highways such as noise, canopy opening, and other physical features may influence bat use of roadside habitat by species such as NLEB (and other rare bat species). Roads have been shown to influence bat behavior in a variety of environments (Berthinussen and Altringham 2012, Bennett and Zurcher 2013, van der Ree et al. 2015). Thus, it is essential that these potential effects of highways be assessed.

## Project Objectives and Overview

The overarching objective of the proposed research was to address several major gaps in the knowledge of NLEB distributions and activity as they relate to the use of habitat along or adjacent to highways in New England. Although we proposed also including other rare bats in the region such as Eastern small-footed bat (*M. leibii*) and tri-colored bat (*Perimyotis subflavus*), insufficient datasets did not allow for the inclusion of these other species. However, if sufficient data can be found or generated with new surveys to supplement the existing data, our modeling approach can be readily applied to these species as well if other researchers want to delve further.

Our first completed objective was comprehensive literature review of peer-reviewed journal articles on the habitat use, distribution, roosting locations, and effects of noise on NLEB throughout the United States and Canada (Task 1). Combined with the literature review, we also compiled all available survey data to assist with determining habitat use and the effects of roads on NLEB, with a focus on habitats of the New England region. The primary use of these data was to develop a screening tool in GIS that DOT personnel in NETC can use to determine the effects of highways on NLEB and how that can be mitigated/addressed when assessing future highway construction projects. However, this goal shifted as data analyses showed that we did not have enough NLEB data to effectively parametrize such a tool. While we collated over a thousand survey points, once we excluded problematic data (e.g. uncertain species ID), only 65 of 711 survey points had a verified NLEB presence. Using cutting-edge presence-absence occupancy models we were able to assess that NLEB distribution does change spatially over New England but did not find a strong relationship between their distribution and highway or other landscape features. A lack of significant effects of highway and landscape features prohibited us from building the GIS screening tool. However, we do include NLEB distribution maps and a R Statistical Environment tool that can be used to assess occupancy in other species.

## Task 1: Literature Review

Relevant literature on the distribution, ecology, and status of the northern long-eared bat (*Myotis septentrionalis*; NLEB) were reviewed. We also reviewed known relationships between bats and roads, regardless of species or geographic location, but we highlight information pertaining to NLEB in particular. As noted in later tasks, NLEB habitat requirements and the effects of anthropogenic disturbance specific to roadways and adjacent habitat are poorly studied.

### Distribution of NLEB

NLEB are distributed in the eastern United States and Canada (Figure 1). NLEB are present in all six New England states (Caceres and Barclay 2000). The species ranges from northern Canada to Florida and westward into Wyoming but is uncommon in the western parts of its range.

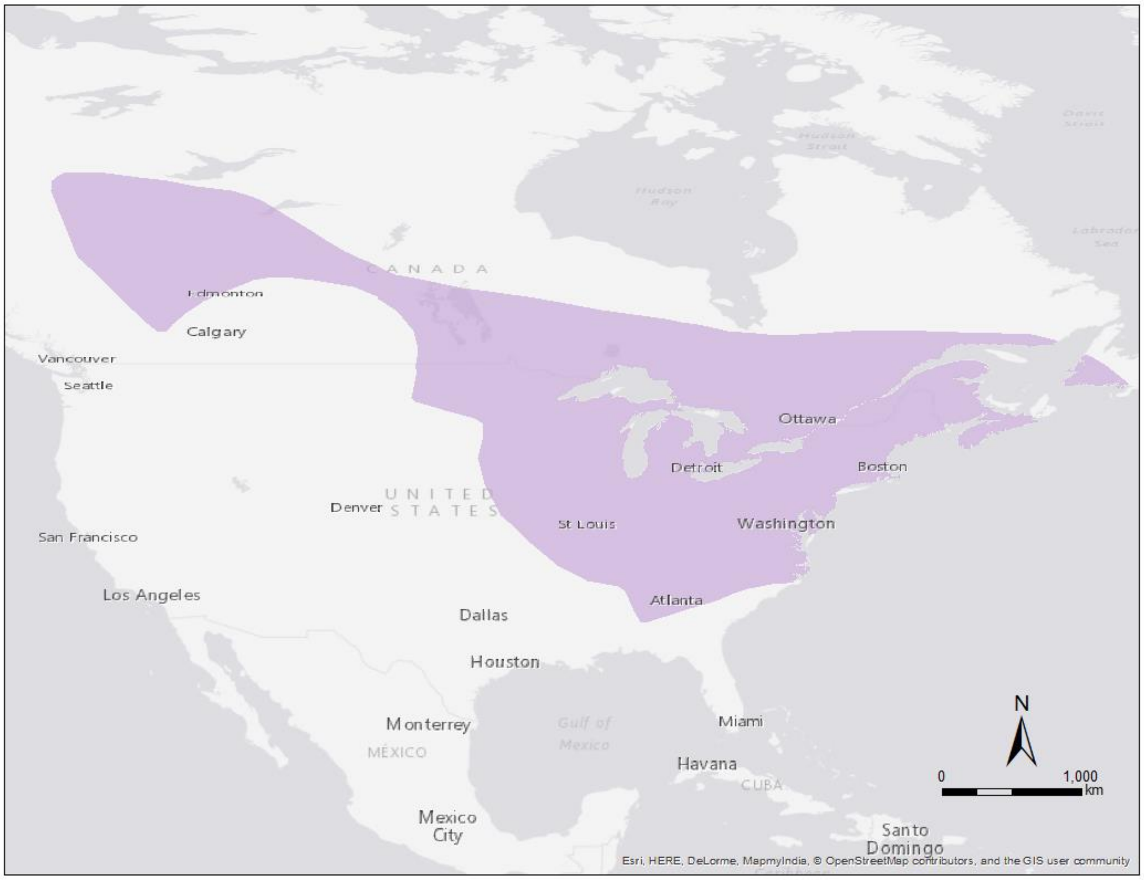



**Figure 1.** Range Map for NLEB, data from IUCN Red List 2017.

**Roosting Ecology**

Roost sites are critical for survival and reproductive success (Vonhof and Barclay 1996), thus species distributions are often driven by preferred roost availability within a landscape. NLEB hibernate in caves during winter months and use trees for summer day roosts and for rearing pups (Caire et al. 1979, Kunz et al. 2003).

*Summer Roosts*

NLEB roost in trees in North American forests during the summer. Tree roosts primarily consist of loose bark on dead trees or cavities in living or dead trees (Foster and Kurta 1999, Lacki et al. 2009), although they have occasionally been found in bat boxes (Ritzi et al. 2005, Whitaker et al. 2006) and under bridges (Civjan et al. 2016). Females tend to roost in groups of <100 (Caceres and Barclay 2000), while males are solitary roosters (Lacki and Schwierjohann 2001). The characteristics of summer roosts and the surrounding landscape have been extensively studied. Roost trees have an average diameter of 30.0 cm (Lacki et al. 2009), an average height of 23.3 m in Michigan (Foster and Kurta 1999) and 15.8 m in Illinois (Carter and Feldhome 2005), and roosts are an average of 6.95 m above the ground (Lacki et al. 2009). NLEB exhibit plasticity in selection of tree species for roosts, occurring both in coniferous and deciduous trees, although studies have shown that within a given study area NLEB can show preferences for different tree species (Foster and Kurta 1999, Lacki and Schwierjohann, Menzel et al. 2002, Broders and Forbes 2004, Perry and Thill 2007). In the only New England study, NLEB showed a preference for hardwood snags with American Beech (*Fagus grandifolia*), Silver Maple (*Acer saccharum*), Yellow Birch (*Betula alleghaniensis*), and Red maple (*Acer rubrum*) being the most frequently selected tree species (Sasse and Pekins 1996). NLEB roost trees tend to occur in mature, intact forests either in or below the forest canopy (Foster and Kurta 1999, Menzel et al. 2002, Carter and Feldhome 2005, Broders et al. 2006, Pauli et al. 2015). NLEB exhibit a high rate of roost switching, with most bats switching roosts every two days and with an average distance of 333 m between roosts (Foster and Kurta 1999). Males and females show differences in preferred roost tree characteristics (Perry and Thill 2007) and in maximum roosting area with roosting area being almost six times larger for females than males (Broders et al. 2006). Reproductive status can also affect roost selection in female NLEB. Compared to pregnant bats, lactating bats choose trees in areas with a more open canopy and lower tree density (Garroway and Broders 2008).

*Hibernacula*

NLEB hibernate in caves and abandoned mines during the winter (Caceres and Barclay 2000). Hibernation may start as early as September and end as late as May, depending on latitude and other environmental factors (Caire et al. 1979, Fenton 1969, Nagorsen and Brigham 1993, Whitaker and Rissler 1992a, 1992b). NLEB share hibernacula sites with other bat species but NLEB individuals most frequently hibernate solitarily within the hibernacula (Brack 2007). NLEB are most frequently found in the deepest part of the cave or mine (most thermally stable and humid portion) and are usually squeezed into tight crevices (Brack 2007). Hibernacula temperatures for NLEB range from 0.6–13.9˚C (Raesly and Gates 1987, Webb et al. 1996, Brack 2007) and mean humidity is 65.2% (Raesly and Gates 1987). Finally, NLEB have been documented migrating an average of 100 km between hibernacula and summer roosts (Caceres and Barclay 2000, Fleming and Eby 2003). Copulation in NLEB occurs at hibernacula (Fenton 1969, Caire et al. 1979).

**Foraging Ecology**

NLEB are traditionally believed to be a gleaning species, detecting, locating, and capturing insects on surfaces (Foster and Kurta 1999), although laboratory studies have shown that NLEB are able to capture airborne prey (Ratcliffe and Dawson 2003). The echolocation characteristics of NLEB are similar to most gleaning bats, with high peak frequencies (mean = 97 kHz), short durations (mean = 1.01 ms), and loud intensities (mean dB at 10 cm = 78) (Faure et al. 1993), which allow for highly maneuverable flight even in cluttered flying environments. NLEB are also morphologically adapted to foraging in complex environments due to shorter, broader wings and small body sizes (Norberg and Rayner 1987). The diet of NLEB consists mostly of moths (Lepidoptera) though Coleoptera, Trichoptera, Araneae, Diptera, and Hymenoptera have also been identified from fecal pellets (Thomas et al. 2012; O'Rourke & Foster unpubl. data). The presence of non-flying prey (e.g. spiders and larvae) in the NLEB diet highlights its gleaning abilities (Brack and Whitaker 2001, Thomas et al. 2012). NLEB forage and commute in cluttered forested areas and show a preference of foraging near and above water sources (Patriquin and

Barclay 2003, Broders et al. 2006, Henderson and Broders 2008, Badin 2014). In agricultural landscapes, NLEB may follow linear forested areas to foraging areas and water sources and even if a NLEB is recorded in an open area, it is usually within 78 m of forest features (Henderson and Broders 2008). Logging also negatively affects NLEB as this species apparently does not forage in nor flies across clear-cuts, and instead mostly forages within intact commutes forest (Patriquin and Barclay 2003). NLEB also prefer to forage in mature forests rather than young forests (Krusic et al. 1996, Jung et al. 1999, Loeb and O'Keefe 2006). Similar to roosting area, foraging area for female NLEB is larger than that of males (Broders et al. 2006), with females having a mean home range of 65 ha (Owen et al. 2003).

**Conservation Status**

The most recent International Union for Conservation of Nature (IUCN) Red List assessment listed NLEB as a species of least concern as it has a wide distribution and had a large population (Arroyo-Cabrales and Álvarez-Castañeda 2008). Threats at that time were listed as timber harvest, insecticides, and cave disturbance. However, since that review, NLEB have been listed as a threatened species by the US Fish & Wildlife Service because of drastic population declines due to White-Nose Syndrome (WNS). WNS is a disease caused by a fungal pathogen (*Pseudogymnoascus destructans*) that first emerged in North America in bats at a New York state cave in 2006 (Blehert et al. 2009). *Pseudogymnoascus destructans* causes skin infections during hibernation that disrupts hibernation cycles and causes morbidity and mortality (Meteyer et al. 2009, Warnecke et al. 2012, Langwig et al. 2015). While WNS has caused massive population declines in many bat populations, NLEB is one of the most heavily affected species and is predicted to face extinction due to the disease (Frick et al. 2010, Langwig et al. 2012, Frick et al. 2015).

**Effects of Roads**

Bat abundance and diversity has been documented to be lower around roads, with the effect extending at least 1.6 km from the road (Berthinussen and Altringham 2012b). Bats are affected by roads through direct mortality, movement barriers, and various pollutants (e.g. light, noise) (Berthinussen and Altringham 2012b, Altringham and Kerth 2016). The influence of roads is mediated by age, sex, reproductive status, and ecology (Fensome and Mathews 2016). Habitat occupancy for NLEB was low near roads (< 2 km) (Pauli et al. 2015). NLEB have been shown to use small, forest roads for foraging and commuting (Owen et al. 2003), but larger roads most likely act as a movement barrier and deterrent for NLEB (Zurcher et al. 2010). Road effects on NLEB have never been directly tested but they are ecologically similar (gleaning foragers) to bats that are negatively affected (Kerth and Melber 2009).

*Negative Effects of Roads*

<u>Direct Mortality</u>

Bats have been found dead along roads in numerous studies (reviewed in Fensome and Mathew 2016). Bats are vulnerable to vehicle collisions because most bat species fly at low speeds (<20 km/h) and fly close to the ground (0–4 m) (Russell et al. 2009, Berthinussen and Altringham

2012b). Bat casualties at a small two-lane road ranged from 0.3 bats/km/year in urban/suburban areas to 6.8 bats/km/year at roads surrounded by trees (Lesinski 2007)—although road mortality research may underestimate road kills by 12–16 fold, as scavengers remove most small carcasses within 30 min (Slater 2002). While no studies have been conducted in New England, low-flying gleaning bat species that are similar to NLEB have higher mortality rates than high-flying aerial hawking species (Lesinski 2007). Higher causalities occur when roads cross preexisting bat flyways (often linear landscape features) or are near high quality bat habitat or roost sites (Medinas et al. 2013). Mortality is also high when roads are near water bodies or cross between forests and water (Gaisler et al. 2009). Mortality also changes over life history, with higher casualties around birthing times for females and when juveniles start to fly (Lesinski 2007, Medinas et al. 2013).

*Movement Barrier*

Roads may reduce access to foraging and roosting sites if bats are unwilling or unlikely to cross roads (Schaub et al. 2008, Kerth and Melber 2009, Fensome and Mathew 2016). Some bat species will avoid gaps in commuting routes that are greater than 2 m (Bennett and Zurcher 2012). Gleaning bats are less likely to cross roads than bats that forage in open spaces and gleaners have smaller foraging areas near roads (Kerth and Melber 2009). Indiana bats (*Myotis sodalis*) reversed flight direction 60% of the time if vehicles were present, compared to only 32% when vehicles were not present on road, which may indicate that bats are exhibiting “predator” avoidance behavior in response to road traffic (Zurcher et al., 2010). Road avoidance by bats is also influenced by landscape structure surrounding the road. More bats in Indiana (possibly some NLEB) reversed flight direction when the road was surrounded by trees (84%) compared to when it was bordered by an agricultural field (50%) (Bennett and Zurcher 2012). Bennett et al. (2013) simulated the effects of roads on Indiana bats and reviewed how changes in road characteristics (e.g. traffic volume, number of lanes) changed these effects; they found that the barrier effect increased with higher traffic volumes. County roads with fewer than 10 cars per 5 min period had no effect on bats but roads with more than 10 cars per 5 mins acted as movement filters and roads with >200 vehicles per 5 min acted as complete foraging barriers. However, quality, quantity, and spatial configuration of foraging habitat heavily influenced road effects. If Indiana bats had at least 5 $km^2$ of foraging habitat, it was simulated that they did not need to cross roads and thus were less affected by the presence of roads (Bennett et al. 2013).

*Noise*

In laboratory settings, the foraging success and flight time of gleaning bats such as the greater mouse-eared bat (*Myotis myotis*) was decreased in the presence of traffic noise (Schaub et al. 2008). Traffic noise may have a greater negative effect on gleaning bats, such as NLEB, because they often detect prey by listening for prey-produced sounds, thus excessive noise may mask prey sounds and decrease foraging efficiency. Bennett and Zurcher (2012), found that bats in Indiana (possibly including NLEB) reversed flight direction if traffic noise was above 88 dB. Traffic noise was also 20 dB higher if roads were exposed and not bordered by trees thus bats more frequently avoided exposed roads although it is not clear if this is truly a noise effect or due to a habitat factor such as lack of trees being barrier as mentioned previously in the Movement Barrier section. No studies have assessed the effect of road noise on bat breeding success, species diversity, or abundance/occupancy.

*Light*

Artificial light can affect roosting and foraging behavior. Bats will delay leaving roosts that are near lights (Downs et al. 2003), which reduces foraging opportunities (Jones and Rydell 1994). Light near roosts also leads to lighter and smaller juvenile bats due to delayed parturition and slower growth rates (Boldogh et al. 2007). Road lighting deters slow-flying, forested-adapted species such as NLEB (Rydell 1992, Blake et al. 1994, Stone et al. 2009). Older sodium lights and new LED lights deter forest species even at low light intensities (>3.6 lux) (Stone et al. 2012). Bats will reverse flight direction when they perceive low intensity light sources (0.6–3.2 lux) (Kuijper et al. 2008). Street lights are usually between 10–60 lux (Gaston et al. 2012), thus dimming lights to acceptable levels for bats may not be feasible. Open space foraging bats can benefit from lights with improved foraging efficiency, as insects exhibit positive phototaxis resulting in higher insect abundances around light sources (Rydell 1992, Blake et al. 1994). However, this concentrating effect on insects reduces insect prey in dark foraging areas thus decreasing prey abundance and foraging success for light phobic genera such as *Myotis* spp. (Eisenbeis 2006, Evens 2012). While the effects of lights on NLEB have not been directly assessed, NLEB is a forest-dependent species (light adverse) whose primary prey, moths, are highly phototaxic, thus it stands to reason that NLEB foraging success may be greatly reduced in lighted landscapes.

*Chemical Pollution*

Roads exude a myriad of chemicals (e.g. heavy metals, salt, and ozone), which can alter the surrounding environment (Trombulak and Frissell 2001). Bats are negatively affected by chemical runoff when they drink contaminated water or feed on contaminated insects (Korine et al. 2016). Vehicle exhaust is associated with declining arthropod diversity and abundance near roads (Przybylski 1979), with a significant effect up to 30 m from roads (Motto et al. 1970, Muskett and Jones 1980). However, no studies have assessed the effects of chemical road pollution on bats.

*Positive Effects of Roads*

Roads overwhelmingly have a negative effect on bats; however, there are some benefits. Road bridges serve as roosts for bats, including NLEB (Keeley and Tuttle 1999, Civjan et al. 2016). Road bridges were more frequently used by bats if they were over water, in forests, or over infrequently used roads (Bennett et al. 2008, Altringham and Kerth 2016). As previously mentioned, street lights can improve foraging success of open-space bats (e.g. *Pipistrellus* and *Nyctalus* sp.), but as a deterrent to forest-dependent species, such as NLEB (Rydell 1992, Blake et al. 1994, Stone et al. 2009, 2012). Roads also serve as a linear landscape element that many bat species use for commuting and foraging (Hein et al. 2009). NLEB have been found commuting along small forest roads (Owen et al. 2003). Use of roads as a foraging or commuting route is dependent on surrounding vegetation structure, road size, and level of traffic. Large, open roads with "heavy" traffic are rarely used by various bat species (Waters et al. 2009, Zurcher et al. 2010, Bellamy et al. 2013, Altringham and Kerth 2016), although we note that there is inconsistent quantification of measures such a traffic volume

*Mitigation Techniques*

Both bridge and underpass mitigation structures have been built in attempts to mitigate the negative effects of roads on bats. However, none of these mitigation techniques show great efficacy, as very few bats commonly use these structures (Altringham and Kerth 2016). Occasionally some of these structures are heavily used by bats but only those built over pre-existing commuting routes (Berthinussen and Altringham 2012a). Both bridges and underpasses are more frequently used by bats if they are directly adjacent to vegetation or water (Limpens et al. 2005, Boonman 2011, Abbott 2012).

Lights may be used to deter bats from dangerous road crossing points if species are light phobic, however, this may exacerbate barrier effects (Altringham and Kerth 2016). Modifying light structures or temporal lighting patterns may reduce barrier effects or insect phototaxis (Altringham and Kerth 2016), but these effects will be species specific, thus strategies would need to be tailored to region, species, and conservation purpose.

Maintaining and improving flyways and the habitat surrounding roads shows the greatest promise for mitigating negative effects on forest-dependent bats, such as NLEB (Berthinussen and Altringham 2012a, Altringham and Kerth 2016). Russell et al. (2009) estimated that >20 m high trees adjacent to roads would improve over-road commuting for bats. If existing flyways are bisected by roads, vegetation gaps should be minimized by interlinking the tree canopies on either side of the road (Bennett and Zurcher 2012). Linear vegetation features along roads should also be planted or improved to increase landscape permeability for bats that follow linear features (e.g. NLEB). Promoting vegetation around roads not only improves bat mobility but can also reduce casualties and traffic noise. Bats will fly at or above canopy height over roads if cars are present, thus if a high tree canopy is maintained it would increase bat-to-vehicle distance consequently reducing causalities and noise (Bennett and Zurcher 2012).

## Task 2. Develop a "Zone of Influence" matrix for highway induced stressors

As identified in the literature review for Task 1, there are several potential highway-induced stressors on bats, including traffic or roadway noise (Bennett and Zurcher 2012), light (Altringham and Kerth 2016), air and water quality (Li and Kalcounis-Rueppell 2018), and wind and physical disturbance. A factor that makes these stressors difficult to include in models of NLEB distributions is that they are highly correlated with urbanization (Kalcounis-Rueppell et al. 2007) and that urbanization can have a strong effect on bat populations (Russo and Ancillotto 2015). Thus, identifying which specific factors are acting as highway-induced stressors and disentangling the effects of urbanization is problematic. As we conclude in our Summary section at the end of this report, there are extremely limited data on bat habitat use and stressor tolerance as they relate to roads. A small-scale study within two state forests of Indiana showed that NLEB occupancy was only significant associated (positively) with forest proportion within 1 km of roost site (Pauli et al. 2015). The presence-only models within that study estimated that NLEB roost occupancy is greatest at intermediate distances (~4 km) from major road (average traffic rates exceeding 2 cars/min) and that within 2 km of major roads NLEB occupancy is reduced. It can be difficult for regional studies such as ours to estimate similar effects. Nonetheless, our models developed in Task 5 include some features of highways such as roadway width that may correlate potential stressors such as roadway noise. For this task, we (and perhaps the NETC Technical Committee) initially envisioned a spatial raster data set where each cell would indicate how "negatively influenced" bats would be by a particular road, with the assumption that bats would be more affected closer to roads. For the regional data we worked with in our analyses, it is not possible to build such a raster, since there no significant factors for any of the variables we measured nor any way to measure the effects of distance from the roadway. In our Summary section, we suggest additional survey approaches to address the lack of data on these potential stressors—data that are essential for developing a zone of influence matrix.

## Task 3. Compile existing data on NLEB and other rare bat species distributions

## Task 4. Request presence/absence data from State DOTs and other sources.

These two tasks were combined in this final report due to their overlapping aims of compiling NLEB data.

### Locality Data

NLEB locality data were compiled from government, academic, and nonprofit sources (Table 1) Data with missing or erroneous date, geographic, or species identification information were excluded from analysis, which yielded 866 independent survey locations from 2015–2017. Of these 867 locations, 155 lacked absence data so these surveys were excluded from the final analysis. The final dataset consisted of 711 surveys with 65 locations having verified NLEB presence (Figure 2). Within those 65 locations, NLEB were occasional detected more than once thus the total number of detections for the three years was 93.

**Table 1.** NLEB data sources and contacts.

| Data Source | Contact |
|---|---|
| USFWS New England Office | Susi von Oettingen |
| MA Department of Conservation and Recreation | Ken MacKenzie |
| MA Department of Transportation | Tim Dexter |
| NH Audubon | Vanessa Johnson |
| CT Department of Energy & Environmental Protection | Kate Moran |
| VT Fish and Wildlife Department | Alyssa Bennett |
| Vermont Agency of Transportation | Glenn Gingras |
| Maine Department of Transportation | Sarah Boyden |
| White Mountain National Forest | Keith VanGorden |
| New Hampshire Bureau of Environment | Rebecca Martin |

## Task 5. Determine land cover (habitat) being used or not used by NLEB

### Landscape and Highway Data

In preliminary analysis, we assessed the effects of 20 highway and landscape variables on NLEB presence (Table 2). Initially, all landscape characteristics were proportions within a 1 km buffer (based on a minimum foraging distance of 0.5 km for female NLEB). However, the final analysis used the 1 km grid square value that encompassed the survey location. We have included maps of landscapes characteristics (Figures 3–5). Highway density was calculated by summing the length of all roads within the buffers and grid squares. The final set of landscape and highway characteristics used for the NLEB occupancy model were total forest, distance to water, and road density.

**Table 2.** Landscape and Highway Characteristics with Sources.

| Landscape Characteristic | Source |
|---|---|
| Total Forest | USGS National Land Cover Database |
| Deciduous forest | USGS National Land Cover Database |
| Evergreen forest | USGS National Land Cover Database |
| Grass/scrub | USGS National Land Cover Database |
| Wetland | USGS National Land Cover Database |
| Water | USGS Hydrography Dataset |
| Agriculture | USGS National Land Cover Database |
| Developed (cities) | USGS National Land Cover Database |
| Distance to water (closest to survey point) | USGS Hydrography Dataset |
| Tree height | LANDFIRE fuel dataset |
| Tree canopy cover | LANDFIRE fuel dataset |
| Highway density | U.S. Department of Transportation |
| AADT (traffic level) | U.S. Department of Transportation |

| | |
|---|---|
| Highway width | U.S. Department of Transportation |
| Speed limit | U.S. Department of Transportation |

**Figure 2.** Map of compiled NLEB data.

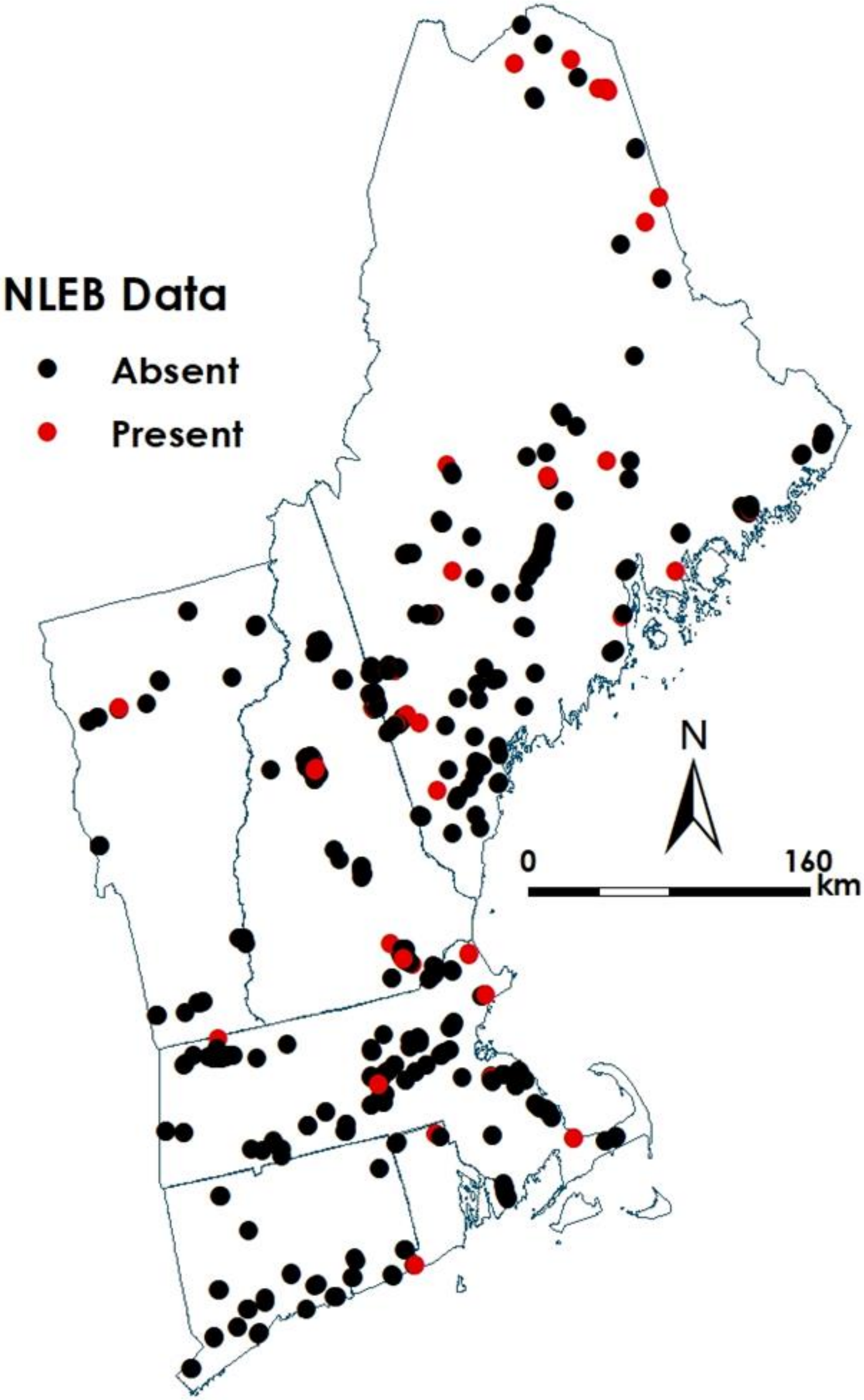



**Figure 3.** New England Land Cover used for NLEB Occupancy Models.

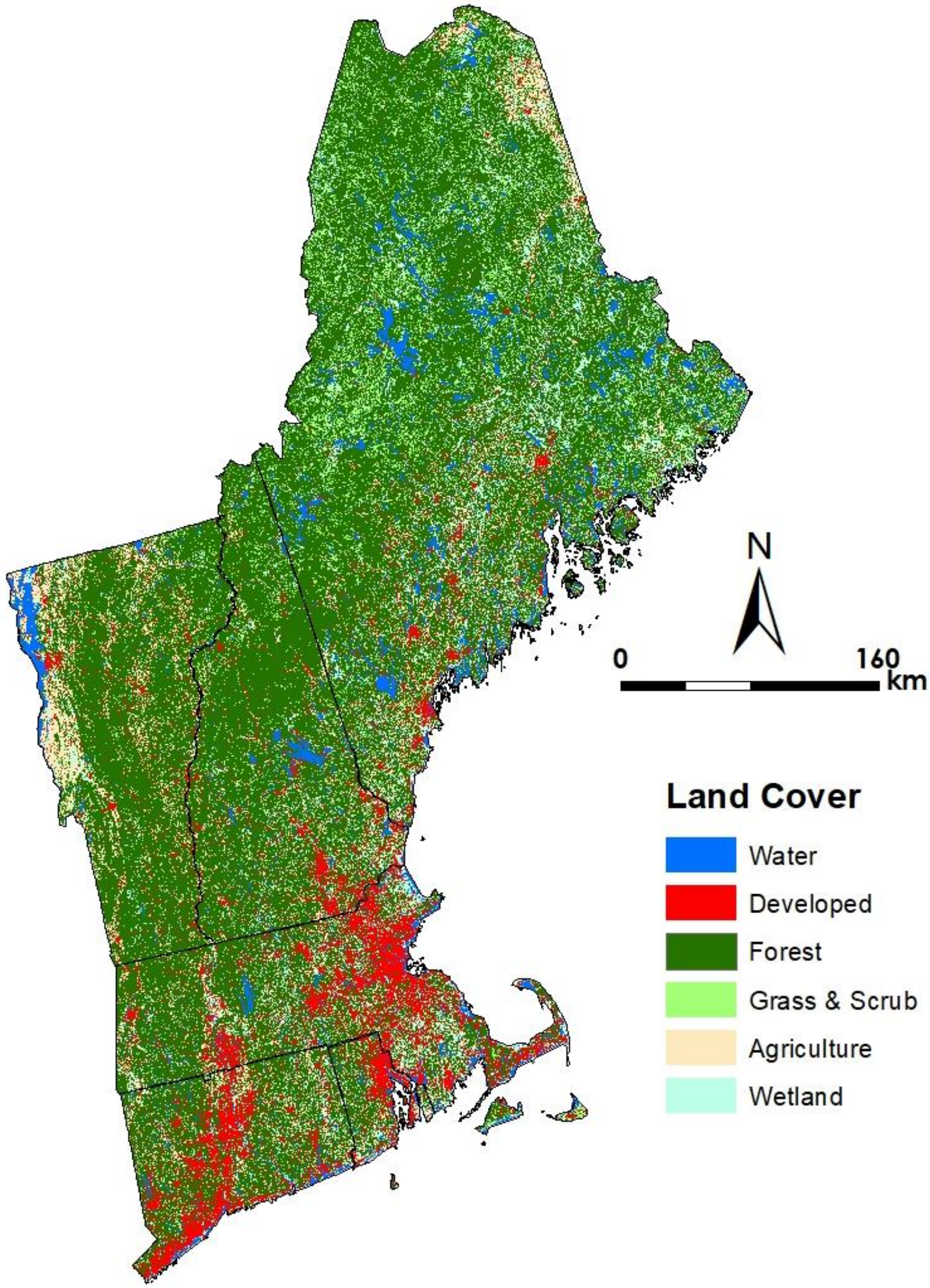



**Figure 4.** New England Water Distances used for NLEB Occupancy Models.

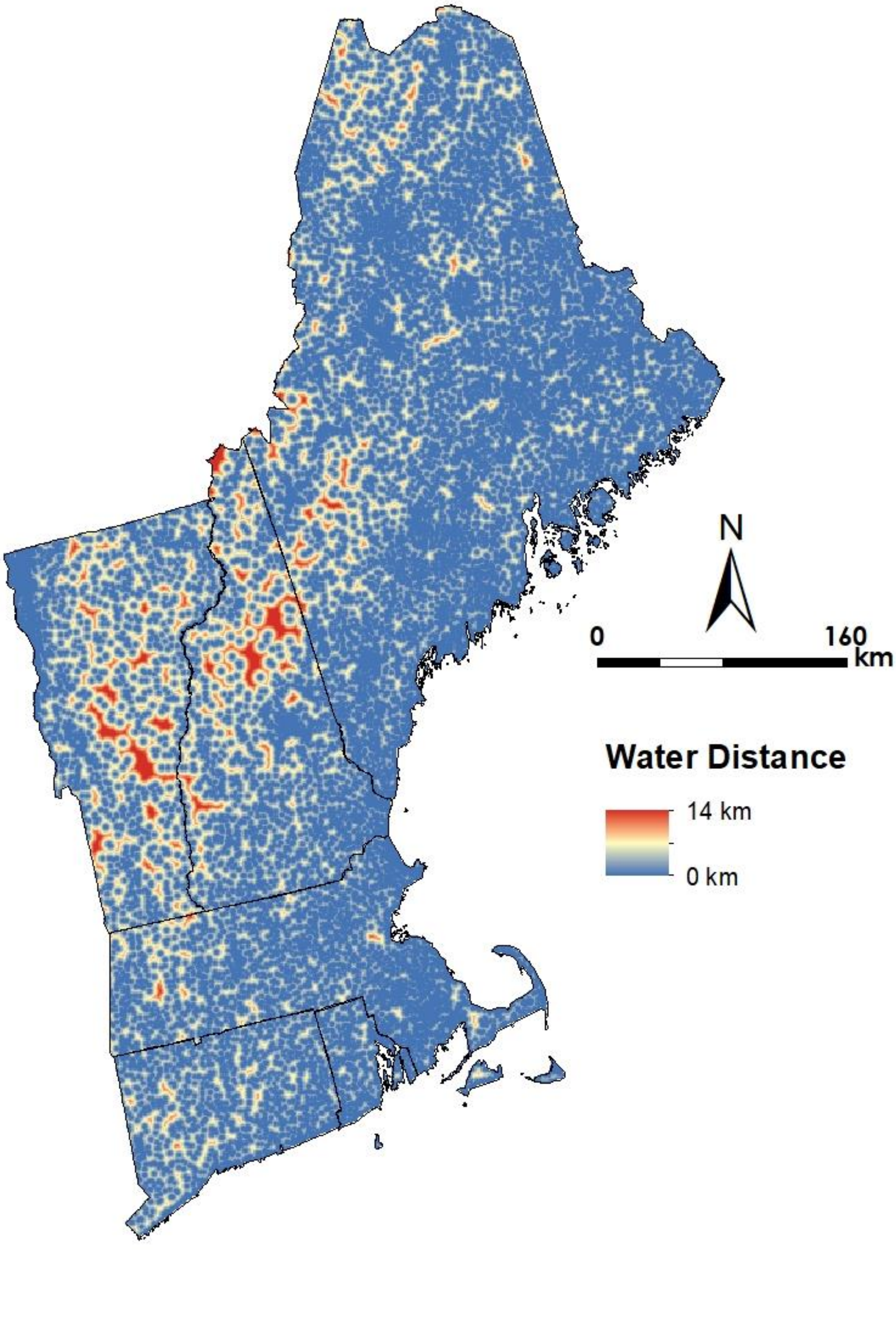
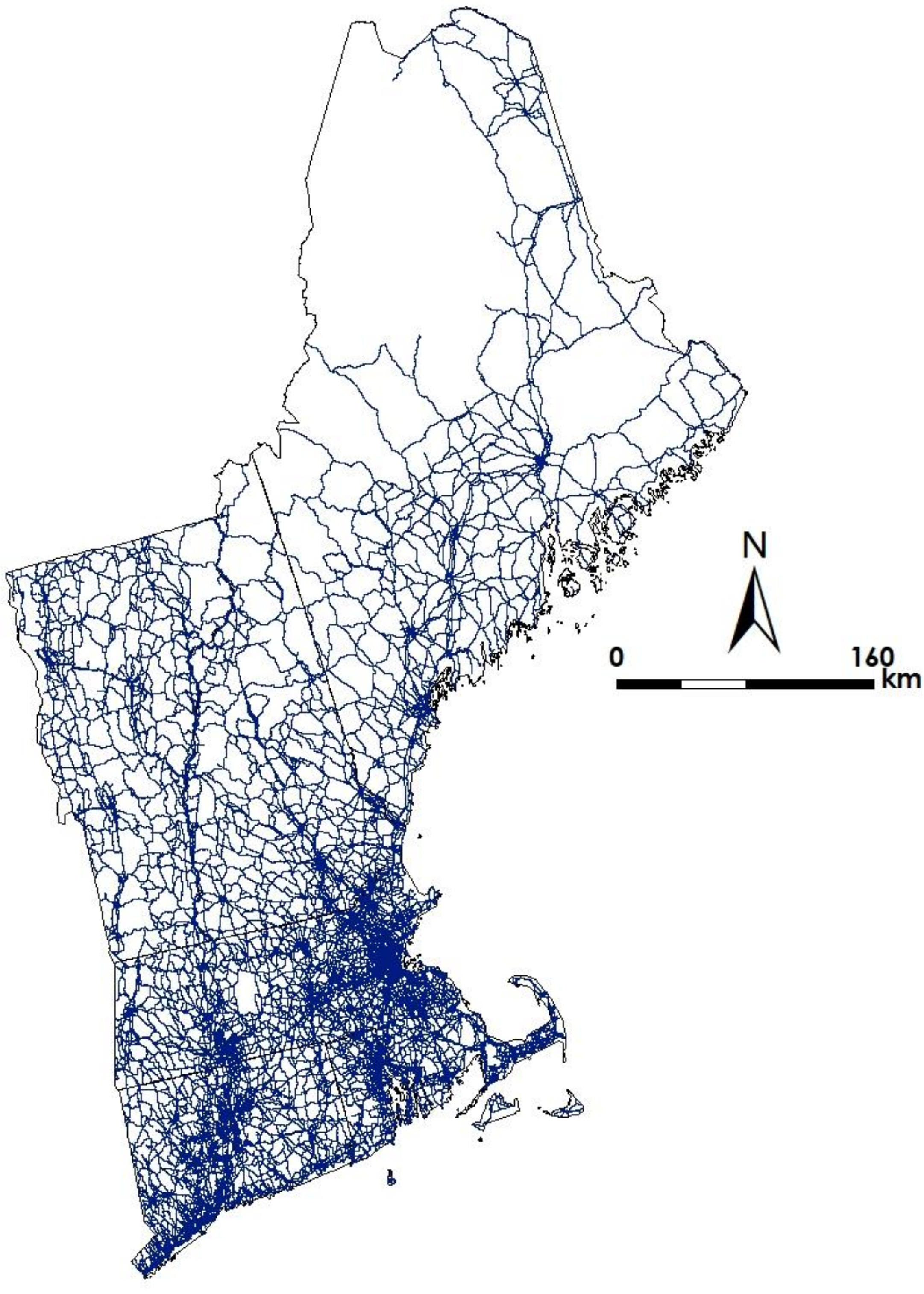



**Figure 5.** New England Highways used for NLEB Occupancy Models. Highway data were downloaded from the U.S. Department of Transportation. Of the National Highway GIS

dataset, the roads included in analysis (per USDOT descriptors) were interstates, principal arterials (freeways and other), minor arterials, major collectors, and minor collectors.



**Modeling process**

We fit an occupancy model to the NLEB detection-non-detection data to estimate probability of occurrence while accounting for imperfect detection (MacKenzie et al. 2002) and incorporated a spatial predictive process (PP) for unexplained spatial variation (Finley et al. 2009, Viana et al. 2013). The hierarchical structure of an occupancy model includes both an ecological sub-model (here, the occurrence of NLEB at a survey site) and an observation sub-model (detection of NLEB, given occurrence at a survey site), with generalized linear models for each probability allowing variation to be explained by covariates. As such, we modeled the probability of detecting NLEB as a Bernoulli random variable:

$$\Pr(y_{ij} = 1) = \text{Bernoulli}(p_{ij} \times z_i)$$

where $p_{ij}$ is the probability of detecting NLEB at site $i$ during survey $j$, and $z_i$ is the true latent occurrence state for NLEB at site $i$. We modeled variation in detection probability using the following logit-linear model:

$$\text{logit}(p_{ij}) = \alpha_0 + \alpha_1\text{forest}_i + \alpha_2\text{date}_j + \alpha_3\text{date}_j^2 + \alpha_4\text{year}_j$$

Here, $p_{ij}$ varied as a function of both site and survey covariates, with the $\boldsymbol{\alpha}$ regression coefficients describing the average detection probability and linear and quadratic effects on the logit scale. Site covariates included the proportion of forest surrounding the site while survey covariates included the date and year of the survey.

The true latent occurrence state (i.e., presence/absence of NLEB) was also a Bernoulli random variable such that:

$$\Pr(z_i = 1) = \text{Bernoulli}(\psi_i)$$

where $\psi_i$ is the probability that NLEB occur at a given site. The occupancy probability was a logit-linear function of landscape covariates and a spatial random effect governed by a predictive process:

$$\text{logit}(\psi_i|\boldsymbol{s}) = \beta_0 + \beta_1\text{forest}_i + \beta_2\text{roads}_i + \beta_3\text{water}_i + \omega(\boldsymbol{s}) + \varepsilon_i$$

Here, the $\boldsymbol{\beta}$ coefficients describe the average occupancy probability and linear effects of site covariates including the proportion of forest, road density, and distance to water. In addition, residual variation was modeled by: $\omega(\boldsymbol{s})$, a mean zero spatial PP that depends on the XY location, $\boldsymbol{s}$, of the site; and $\varepsilon_i$, a non-spatial error term such that $\varepsilon_i \sim N(0, \sigma^2)$. While the occupancy model framework is well-known and widely used, the spatial PP is a relatively uncommon approach with statistical notation that requires more explanation.

Following Viana et al. (2013), we defined a set of spatial knots across the landscape to capture the unexplained spatial variation in the response variable (here, occupancy probability). We defined $K = 107$ knots spaced on a 50 km grid spanning the full extent of the study area (Figure 6), each with XY location defined by $\boldsymbol{s}^*$. We specified a Gaussian process on the spatial knots with a covariance that was a function of distance. First, following the notation of Viana et al. 2013, we can define a generic covariance function between 2 locations:

$$C(\boldsymbol{s}_a, \boldsymbol{s}_b \mid \phi) = \sigma_s^2\rho(\boldsymbol{s}_a, \boldsymbol{s}_b \mid \phi)$$

where $\rho(\boldsymbol{s}_a, \boldsymbol{s}_b \mid \phi) = \exp[-|d_{a,b}|/\phi]$ is the correlation between locations $\boldsymbol{s}_a$ and $\boldsymbol{s}_b$ and $d_{a,b}$ is the distance between the locations; $\sigma_s^2$ is the spatial random effect variance; and $\phi$ is a scale parameter controlling the rate of decay in correlation between points as distance increases. By using coarse-scale spatial knots on which to define the Gaussian process, the computational burden of the modeling procedure is greatly reduced. We therefore defined the process as follows:

$$\tilde{\omega}(\boldsymbol{s}^*) \sim GP(0, \sigma_s^2 \rho(\boldsymbol{s}^*, \boldsymbol{s} \mid \phi))$$

where the covariance function is simply calculated between the locations of the spatial knots, $\boldsymbol{s}^*$, and the survey sites, $\boldsymbol{s}$. Translating the Gaussian process on the knots back to the spatial PP for sites requires a more complex correction (Finley et al. 2009), as noted in Viana et al. 2013:

$$\omega(\boldsymbol{s}) = C(\boldsymbol{s}^*, \boldsymbol{s} \mid \phi) C(\boldsymbol{s}^*, \boldsymbol{s}^* \mid \phi)^{-1} \tilde{\omega}(\boldsymbol{s}^*) + \varepsilon_s$$
$$\varepsilon_s \sim N(0, diag(C(\boldsymbol{s}, \boldsymbol{s} \mid \phi) - C(\boldsymbol{s}, \boldsymbol{s}^* \mid \phi) C(\boldsymbol{s}^*, \boldsymbol{s}^* \mid \phi)^{-1} C(\boldsymbol{s}^*, \boldsymbol{s} \mid \phi))$$

Here, the covariance functions are calculated for the relevant sets of locations (sites, knots), and *diag* refers to a matrix with off-diagonal elements set to 0. This correction prevents the spatial PP from over-smoothing.

We fit the model using a Bayesian approach and estimated the posterior distributions of parameters via Markov chain Monte Carlo methods with JAGS (Plummer 2003) and R (R Core Team 2018). We used vague priors for most parameters, with slightly-informative priors for the scale parameter, $\phi \sim Ga(1, 0.1)$, and the inverse of the spatial random variance, $1/\sigma_s^2 \sim Ga(2, 1)$. The model was run for 50,000 iterations over 3 chains after an adaption phase of 50,000. Convergence was achieved by examining trace plots and ensuring that the potential scale reduction factor was <1.1 for all parameters (Gelman and Rubin 1992). After model fitting, predictions were created using the posterior distributions of $\boldsymbol{\beta}$ and $\tilde{\omega}(\boldsymbol{s}^*)$ combined with the knots and raster maps of landscape covariates across the study area.

## Task 6. Determine data gathering needs to improve model inference

NLEB occupancy varied spatially across New England, with highest occupancy in Northern Maine (Figure 7). Predictions of NLEB occupancy at sites across New England were low, only ranging from 0.01–0.4 chance of occupancy (Figure 7). Regional occupancy was based on the average predicted occupancy for the spatial knots, which also spatially varied (Figure 8) and had large 95% confidence intervals (Figure 9). None of the landscape or highway characteristics significantly influenced occupancy, although there was a trend of NLEB occupancy being higher closer to water (Table 3). Detection probability was significantly negatively affected by total forest cover (Table 3).

A substantial challenge of our analyses was the limited number of detections of NLEBs. Thus, increased sampling, both spatially and across more years, would unquestionably help with future modeling efforts. Due to some overlap between Tasks 6 and 7, future data gathering needs are more fully detailed in the following Task that seeks to identify data gaps in sampling of NLEB in specific habitats that may require additional data collection on presence/absence. Yet, we emphasize that unless NLEB populations in New England make a significant rebound after the enormous losses from white-nose syndrome, the limited number of detections will severely hinder future modeling efforts. At the same time, detections of NLEBs wintering in coastal Massachusetts and New York, particularly Martha's Vineyard, Nantucket and Long Island (S. Hoff and L. Johnson, pers. comm.), indicate that NLEB are persisting in some areas, especially within human structures such as attics. Summering locations for these coastal bats are not known however, nor are the reasons for persistence despite the detection of *P. destructans* on bats during hibernation (S. Hoff and J. Foster, unpubl. data).

**Figure 6.** Map Showing Placement Spatial Knots in Purple Circles.

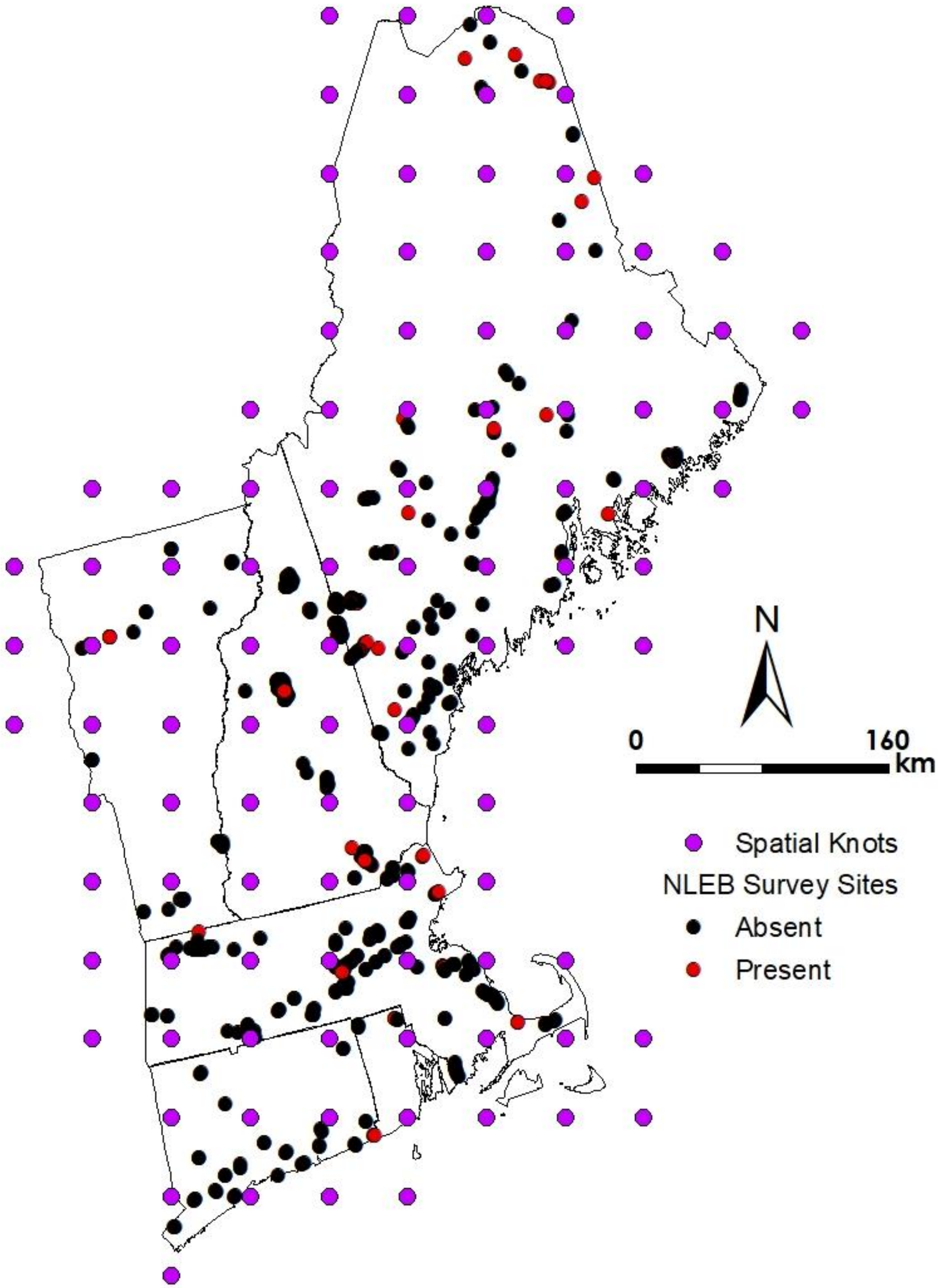


**Figure 7.** NLEB Occupancy in New England

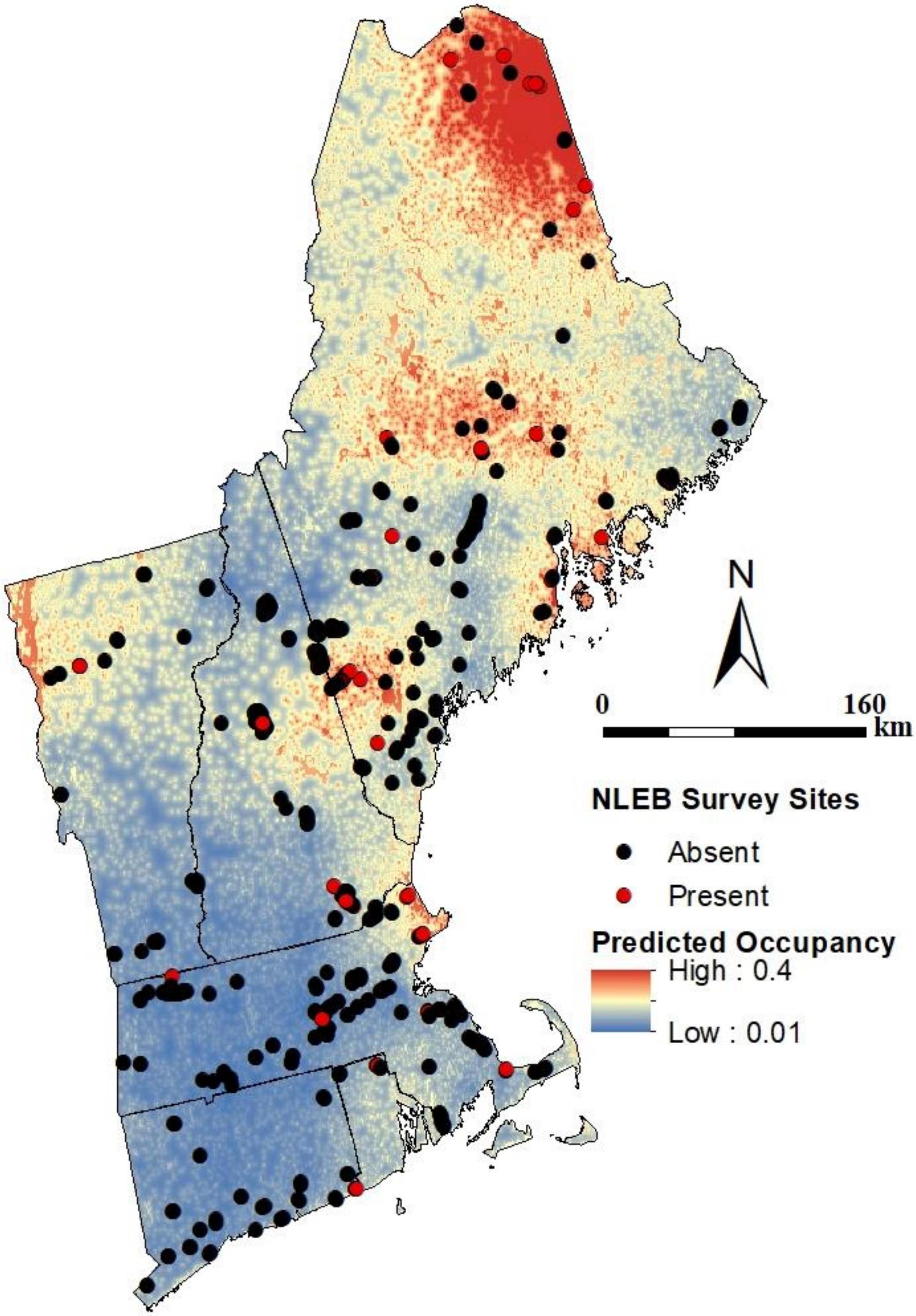


**Figure 8.** Map of variation in average occupancy probability across spatial knots. Knots were placed outside the study area (e.g. in the Atlantic Ocean and Canada) to avoid edge effects in the model.

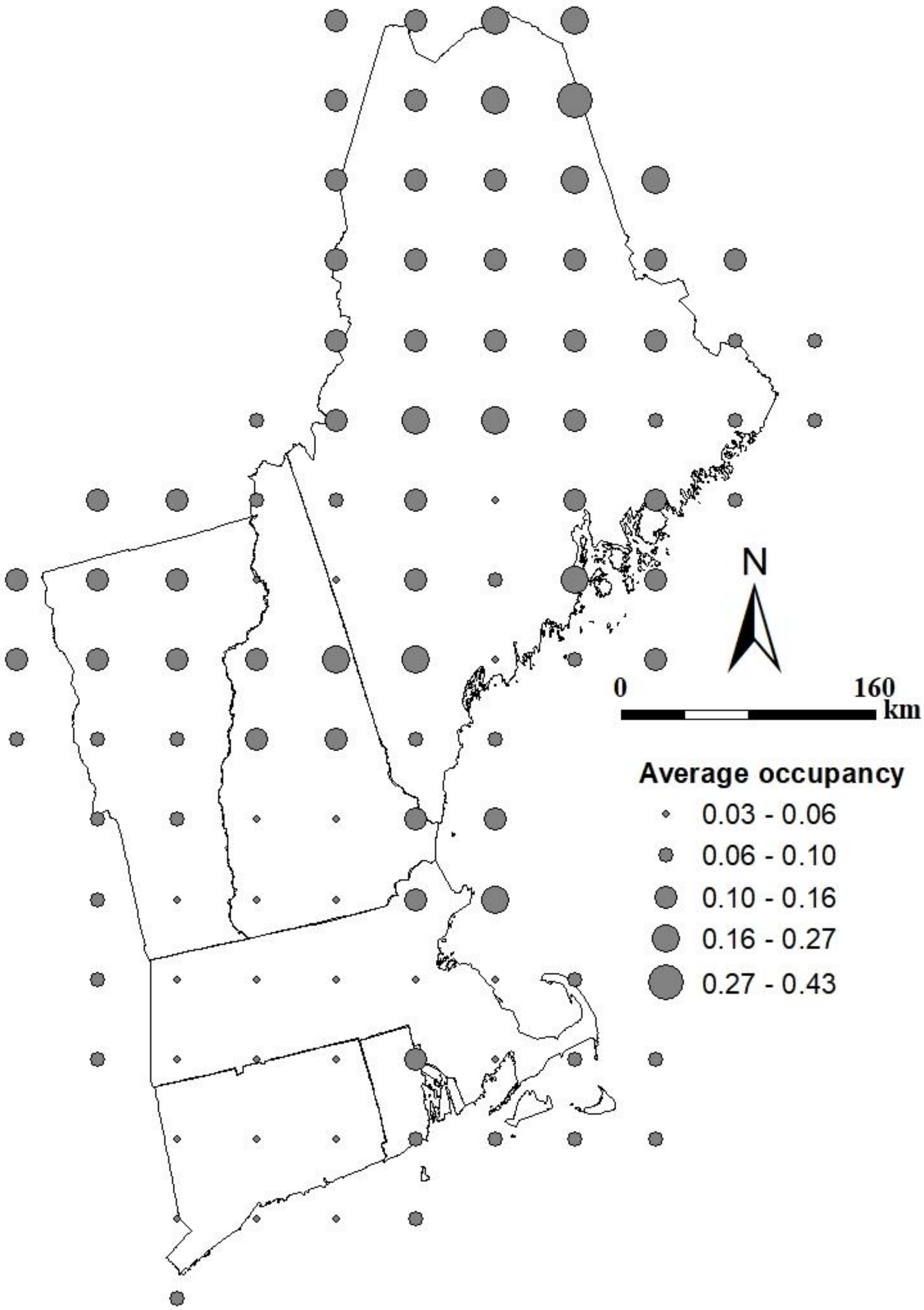


**Figure 9.** Variation in average occupancy probability across spatial knots with 95% CI.

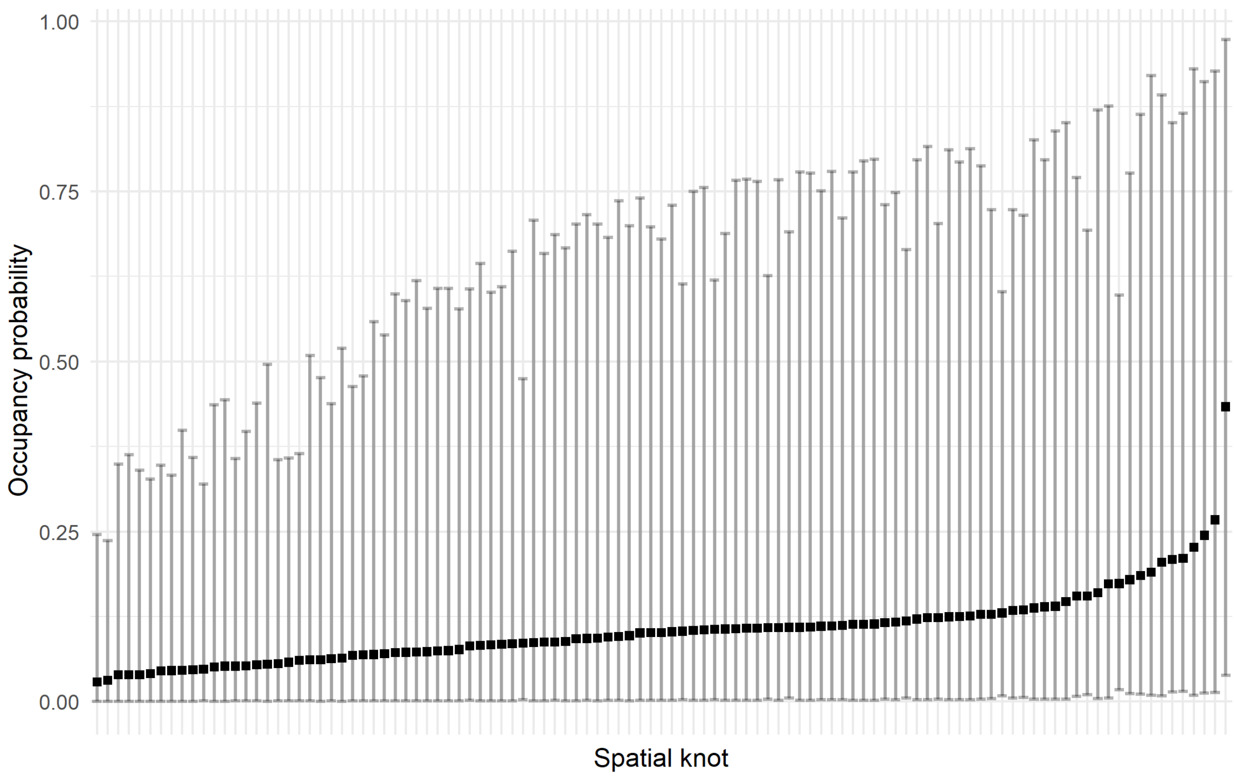



**Table 3.** Model parameter estimates (mean, standard deviation, and 95% credible intervals)

| Parameter | covariate | mean | SD | 2.5% | 50% | 97.5% |
|---|---|---|---|---|---|---|
| $\alpha_0$ | | 0.20 | 1.82 | -3.40 | 0.15 | 3.96 |
| $\alpha_1$ | forest | -0.51 | 0.20 | -0.91 | -0.51 | -0.11 |
| $\alpha_2$ | date | 0.21 | 0.25 | -0.28 | 0.21 | 0.69 |
| $\alpha_3$ | date$^2$ | 0.05 | 0.17 | -0.29 | 0.05 | 0.38 |
| $\alpha_4$ | year | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| $\beta_0$ | | -2.30 | 0.87 | -4.24 | -2.22 | -0.84 |
| $\beta_1$ | forest | -0.11 | 0.32 | -0.74 | -0.11 | 0.52 |
| $\beta_2$ | roads | -1.56 | 3.64 | -8.81 | -1.53 | 5.47 |
| $\beta_3$ | water | -4.18 | 3.28 | -10.77 | -4.15 | 2.12 |
| $\phi$ | | 36.44 | 14.28 | 17.33 | 33.55 | 71.98 |
| $\sigma_s^2$ | | 2.67 | 3.15 | 0.32 | 1.71 | 11.05 |
| $\sigma^2$ | | 1.44 | 2.39 | 0.04 | 0.59 | 8.31 |

## Task 7. Identify data gaps in sampling of NLEB in specific habitats that may require additional data collection on presence/absence

From a spatial sampling standpoint, adding acoustic surveys in central Vermont, southwestern New Hampshire, north central Connecticut, much of Rhode Island, and northwestern and parts of eastern Maine will fill substantial gaps in coverage (see Figure 7). We recognize that limited access may preclude adding some of these survey points (e.g. much of the unsurveyed sections of Maine are remote and have few roads). Relatively few of the survey points were distant from roads, which makes sense because conducting acoustic surveys along roads is standard practice and allows for coverage of large survey areas. Moreover, many of these surveys are conducted by state Departments of Transportation so having survey data from along or adjacent to roadways is an important consideration. Additional surveys more distant from roads, such as our points in the White Mountain National Forest, can help evaluate NLEB occupancy in habitat less affected by human activities, although we did find that detection probability was significantly negatively affected by total forest cover. Our modeling also indicated a trend of higher NLEB occupancy at sites closer to freshwater. Getting access to NLEB detection data from other surveyors such as environmental consultants conducting bat surveys at wind turbine sites, pipelines, transmission lines, and other areas where potential environmental impacts on bats need to be assessed with surveys. In practice, getting permission to use these data has proven to be very difficult. Finally, to rigorously evaluate potential stressors of roads on bats, such as noise creating a zone of influence at specific distances from the roadway, surveys should be established at increasing distances perpendicular to the road using an appropriate experimental design. In practice, the extensive roadways throughout much of New England make survey design quite challenging.

## Task 8. Develop screening tool and GIS model that would show zones of influence around highways

Task 8 was not an achievable goal given the existing data and the results of our spatial analyses. For example, the effects of roadway noise and specific decibel thresholds have not been quantified for NLEBs or other similar bats. As indicated in Task 2, a spatial raster data set showing zones of influence around highways could not be built with our dataset. We thus utilized cutting-edge modeling techniques in Task 5 that maximized the available NLEB detection data. In our analyses, we did not detect an effect of highways on NLEB occupancy. Thus, there was no screening tool or GIS model that could be built. We are writing a manuscript describing our modeling approach and documenting the NLEB distributions and occupancy across the region. We also provide in the Tech Transfer Toolbox an annotated guide to our modeling process, the code we used for our final analyses, our datasets (where possible, Memoranda of Understanding with some data providers may limit this distribution), and a spatial layer of the NLEB occupancy predictions for use in ArcGIS.

## Summary and Conclusions

Bat populations throughout the Northeast have undergone precipitous declines in less than a decade due to the fungal disease white-nose syndrome. Several bat species are at risk of local extirpation, with the Northern long-eared bat suffering the most severe declines of any species. NLEB may use open areas such as highways in which to fly and forage. Attributes of highways such as noise, canopy opening, and other physical features may influence bat use of roadside habitat by NLEB (and other rare bat species). Roads have been shown to influence bat behavior in a variety of environments. Thus, it is essential that these potential effects of highways be assessed. The overarching objective of the proposed research was to address several major gaps in the knowledge of NLEB distributions and activity as they relate to the use of highway habitat in New England.

Our extensive literature review in Task 1 encapsulated NLEB ecology and the influence highways have on bat distributions and diversity. While the effects of highways on NLEB have never been directly tested, our review demonstrates that bats with similar ecology (gleaning foragers) can be negatively affected by highways. Bats are vulnerable to direct mortality through vehicle collisions and highways can be a movement barrier for commuting or foraging routes. Noise and light pollution can reduce foraging efficiency, while chemical pollution can reduce arthropod prey diversity and abundance. Mitigation of the negative effects on bats may be possible with bridge and underpass structures, but bats are rarely found to use these structures unless they are placed over existing commuting routes. On the other hand, roads may be beneficial to bats, providing habitat heterogeneity and may serve as linear landscape elements that bats, including NLEB, use for commuting. Maintaining and improving habitat around highways shows the greatest promise for mitigating negative effects on forest-dependent bats, such as NLEB. Linear vegetation planted around roads increases landscape permeability for bats and may reduce direct mortality and traffic noise. However, we emphasize that without detailed studies on NLEBs specifically, it is exceedingly difficult to make conclusions about the direct or indirect effects of roads on their distributions. Our work sought to help start to address that gap in knowledge.

Based on this initial review, we hypothesized that NLEB occupancy would be negatively affected by highway attributes such as road width, traffic level, speed limit, and highway density. However, significant effects of these factors were not seen in our occupancy models. Total detections of NLEB for surveys from 2015–2017 were very low across New England, with NLEB detected at 65 locations during 711 surveys. Multiple detections at some sites raised the total number of detections to 93, although this total number of detections remains exceedingly low relative to the survey effort. These detections were used to estimate probability of presence with occupancy modeling, indicating a range of 0.01–0.4 chance of occupancy across the region. We assessed the effect of a range of landscape and highway attributes on the presence of NLEB and none significantly affected occupancy. There was a trend of NLEB occupancy being higher at sites closer to water but this was not significant, indicating that either sample sizes were too low or the relationship is weak at best. Highest occupancy rates occurred in northeastern Maine, with regions of moderate occupancy in central and southwestern Maine, central New Hampshire along the Maine border, northwestern Vermont, and the northeastern coast of Massachusetts. Occupancy was low across the remainder of Massachusetts, as well as throughout Connecticut and Rhode Island.

Most importantly for this project, we found no strong relationship between NLEB occupancy and any of our measures of highways and road characteristics. We cannot rule out that this lack of a relationship was due to few detections of NLEB across the region, that is, low occupancy does not allow for robust estimation of the relationships between NLEB presence and highway characteristics. As a consequence of this finding, current NLEB data do not allow for parametrization of a GIS selection tool as a project deliverable although we do provide a spatial layer of NLEB occupancy from our modeling.

**Recommendations**

- More systematic surveys across New England, with a focus on gaps in coverage seen in Figure 7 (and listed above in the text)
- Additional surveys occurring distant from roads (i.e. not conducted along roads)
- Get access to additional existing survey data from other sources
- Surveys experimentally designed to explicitly test stressor tolerance related to distance from the roadway
- Experimental or observational studies of NLEB behavior near roads
- Additional NLEB surveys that focus on northern Maine, the region containing the highest NLEB occupancy

Unfortunately, population trend data, where they exist, suggest declining NLEB populations throughout much of their range. White-Nose Syndrome has been the leading source of these declines, with NLEB among the species hardest hit by this disease. Thus, even with more extensive sampling, sufficient detections of NLEB may not be achievable for more robust estimates of occupancy and to assess potential landscape and road effects. An alternative would be to model detections of other *Myotis* spp. detected during these same surveys and we encourage this in future work, particularly as additional bat species potentially become threatened. However, the relatively unusual foraging strategy of NLEBs and their specific habitat usage may limit the inferences made by using data from other bat species.

## References

Abbott, I. M. (2012). *Assessment of the effectiveness of mitigation measures employed on Irish national road schemes for the conservation of bats*. Doctoral dissertation. University College Cork, Ireland.

Altringham, J. D., & Kerth, G. (2016). Bats and roads. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 1–606). Springer, International Publishing. https://doi.org/10.1007/978-3-319-25220-9

Arroyo-Cabrales, J. & Álvarez-Castañeda, S.T. (2008). *Myotis septentrionalis*. The IUCN Red List of Threatened Species 2008: e.T14201A4420750. Downloaded on 15 September 2017. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T14201A4420750.en.

Badin, H. (2014). *Habitat selection and roosting ranges of northern long-eared bats (Myotis septentrionalis) in an experimental hardwood forest system*. Doctoral Dissertation. Retrieved from: http://cardinalscholar.bsu.edu/bitstream/123456789/198110/1/BadinH_2014-2_BODY.pdf

Bellamy, C., Scott, C., & Altringham, J. (2013). Multiscale, presence-only habitat suitability models: fine-resolution maps for eight bat species. *Journal of Applied Ecology*, *50*(4), 892-901.

Bennett, F. M., Loeb, S. C., Bunch, M. S., & Bowerman, W. W. (2008). Use and selection of bridges as day roosts by Rafinesque's big-eared bats. *The American Midland Naturalist*, *160*(2), 386-399.

Bennett, V. J., Sparks, D. W., & Zollner, P. A. (2013). Modeling the indirect effects of road networks on the foraging activities of bats. *Landscape Ecology*, *28*(5), 979–991. https://doi.org/10.1007/s10980-013-9874-0

Bennett, V. J., & Zurcher, A. A. (2012). When corridors collide: Road-related disturbance in commuting bats. *Journal of Wildlife Management*, *77*(1), 93–101. https://doi.org/10.1002/jwmg.467

Berthinussen, A., & Altringham, J. (2012a). Do bat gantries and underpasses help bats cross roads safely? *PLoS ONE*, *7*(6). https://doi.org/10.1371/journal.pone.0038775

Berthinussen, A., & Altringham, J. (2012b). The effect of a major road on bat activity and diversity. *Journal of Applied Ecology*, *49*(1), 82–89. https://doi.org/10.1111/j.1365-2664.2011.02068.x

Blake, D., Hutson, A. M., Racey, P. A., Rydell, J., & Speakman, J. R. (1994). Use of lamplit roads by foraging bats in southern England. *Journal of Zoology*, *234*(3), 453-462.

Blehert, D.S., Hicks, A.C., Behr, M., Meteyer, C.U., Berlowski-Zier, B.M., Buckles, E.L., Coleman, J.T., Darling, S.R., Gargas, A., Niver, R. and Okoniewski, J.C. (2009). Bat white-nose syndrome: an emerging fungal pathogen?. *Science*, *323*(5911), 227-227.

Boldogh, S., Dobrosi, D., & Samu, P. (2007). The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica*, *9*(2), 527-534.

Boonman, M. (2011). Factors determining the use of culverts underneath highways and railway tracks by bats in lowland areas. *Lutra*, *54*(1), 3-16.

Brack, V. (2007). Temperatures and locations used by hibernating bats, including *Myotis sodalis* (Indiana bat), in a limestone mine: implications for conservation and management. *Environmental Management*, *40*(5), 739-746.

Brack, V. J., & Whitaker, J. O. J. (2001). Foods of the northern myotis, *Myotis septentrionalis*, from Missouri and Indiana, with notes on foraging. *Acta Chiropterologica*, *3*(January 2001), 203–210.

Broders, H. G., & Forbes, G. J. (2004). Interspecific and intersexual variation in roost-site selection of northern long-eared and little brown bats in the Greater Fundy national park ecosystem. *The Journal of Wildlife Management*, *68*(3), 602–610.

Broders, H. G., Forbes, G. J., Woodley, S., & Thompson, I. D. (2006). Range extent and stand selection for roosting and foraging in forest-dwelling northern long-eared bats and little brown bats in the Greater Fundy ecosystem, New Brunswick. *Journal of Wildlife Management*, *70*(5), 1174–1184. https://doi.org/http://dx.doi.org/10.2193/0022-541X(2006)70[1174:REASSF]2.0.CO;2

Caceres, M. C., & Barclay, R. M. R. (2000). *Myotis septentrionalis*. *Mammalian Species*, (634), 1–4.

Caire, W., LaVal, R. K., LaVal, M. L., & Clawson, R. (1979). Notes on the ecology of *Myotis keenii* (Chiroptera, Vespertilionidae) in eastern Missouri. *American Midland Naturalist*, 404-407. Prepared for The New England Transportation Consortium.

Carter, T. C., & Feldhamer, G. A. (2005). Roost tree use by maternity colonies of Indiana bats and northern long-eared bats in southern Illinois. *Forest Ecology and Management*, *219*(2–3), 259–268. https://doi.org/10.1016/j.foreco.2005.08.049

Civjan, S., Dumont, E., & Bennett, A. (2016). Investigation of northern long-eared bat roosting sites on bridges. Prepared for New England Transportation Consortium.

Downs, N. C., Beaton, V., Guest, J., Polanski, J., Robinson, S. L., & Racey, P. A. (2003). The effects of illuminating the roost entrance on the emergence behaviour of *Pipistrellus pygmaeus*. *Biological Conservation*, *111*(2), 247–252. https://doi.org/10.1016/S0006-3207(02)00298-7

Eisenbeis, G. 2006. Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. In Rich, C. and Longcore, T. eds *Ecological consequences of artificial night lighting*: 345–364. Washington, Island Press.

Evens, N. 2012. Shedding light on bat activity: artificial lighting has species-specific effects on British bats. Doctoral dissertation.

Faure, P. A., Fullard, J. H., & Dawson, J. W. (1993). The gleaning attacks of the northern long-eared bat, *Myotis septentrionalis*, are relatively inaudible to moths. *Journal of Experimental Biology*, *189*, 173–189.

Fensome, A. G., & Mathews, F. (2016). Roads and bats: a meta-analysis and review of the evidence on vehicle collisions and barrier effects. *Mammal Review*, *46*(4), 311–323. https://doi.org/10.1111/mam.12072

Fenton, M. B. (1969). Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. *Canadian Journal of Zoology*, *47*(4), 597-602.

Finley, A. O., Sang, H., Banerjee, S., & Gelfand, A. E. (2009). Improving the performance of predictive process modeling for large datasets. Computational statistics & data analysis, 53(8), 2873-2884.

Foster, R. W., & Kurta, A. (1999). Roosting ecology of the northern bat (*Myotis septentrionalis*) and comparisons with the endangered Indiana bat (*Myotis sodalis*). *Journal of Mammalogy*, *80*(2), 659–672.

Frick, W.F., Pollock, J.F., Hicks, A.C., Langwig, K.E., Reynolds, D.S., Turner, G.G., Butchkoski, C.M. and Kunz, T.H., 2010. An emerging disease causes regional population collapse of a common North American bat species. *Science*, *329*(5992), pp.679-682.

Frick, W.F., Puechmaille, S.J., Hoyt, J.R., Nickel, B.A., Langwig, K.E., Foster, J.T., Barlow, K.E., Bartonička, T., Feller, D., Haarsma, A.J. and Herzog, C. (2015). Disease alters macroecological patterns of North American bats. *Global Ecology and Biogeography*, *24*(7), 741-749.

Gaisler, J., Řehák, Z., & Bartonička, T. (2009). Bat casualties by road traffic (Brno-Vienna). *Acta Theriologica*, *54*(2), 147–155. https://doi.org/10.1007/BF03193170

Garroway, C. J., & Broders, H. G. (2007). Nonrandom association patterns at northern long-eared bat maternity roosts. *Canadian Journal of Zoology*, *85*(9), 956–964. https://doi.org/10.1139/Z07-079

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical science*, *7*(4), 457-472

Gaston, K. J., Davies, T. W., Bennie, J., & Hopkins, J. (2012). Reducing the ecological consequences of night-time light pollution: options and developments. *Journal of Applied Ecology*, *49*(6), 1256-1266.

Hein, C. D., Castleberry, S. B., & Miller, K. V. (2009). Site-occupancy of bats in relation to forested corridors. *Forest Ecology and Management*, *257*(4), 1200–1207. https://doi.org/10.1016/j.foreco.2008.09.054

Henderson, L. E., Farrow, L. J., & Broders, H. G. (2009). Summer distribution and status of the bats of Prince Edward Island, Canada. *Northeastern Naturalist*, *16*(1), 131–140.

Hoyt, J.R., Sun, K., Parise, K.L., Lu, G., Langwig, K.E., Jiang, T., Yang, S., Frick, W.F., Kilpatrick, A.M., Foster, J.T. & Feng, J. (2016) Widespread bat white-nose syndrome fungus, northeastern China. *Emerging infectious diseases*, *22*(1), p.140.

Jones, G., & Rydell, J. (1994). Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *346*(1318), 445-455.

Jung, T. S., Thompson, I. D., Titman, R. D., & Applejohn, A. P. (1999). Habitat selection by forest bats in relation to mixed-wood stand types and structure in central Ontario. *The Journal of Wildlife Management*, 1306-1319.

Kalcounis-Rueppell, M. C., Payne, V. H., Huff, S. R. & Boyko, A. L. (2007). Effects of wastewater treatment plant effluent on bat foraging ecology in an urban stream system. *Biological Conservation* 138:120-130.

Keeley, B. W., & Tuttle, M. D. (1999). *Bats in American bridges*. Bat Conservation International Incorporated.

Kerth, G., & Melber, M. (2009). Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. *Biological Conservation*, *142*(2), 270–279. https://doi.org/10.1016/j.biocon.2008.10.022

Korine, C., Adams, R., Russo, D., Fisher-Phelps, M., & Jacobs, D. (2016). Bats and water: anthropogenic alterations threaten global bat populations. In *Bats in the Anthropocene: conservation of bats in a changing world* (pp. 215-241). Springer International Publishing. https://doi.org/10.1007/978-3-319-25220-9_8

Krusic, R. A., Yamasaki, M., Neefus, C. D., & Perkins, P. J. (1996). Bat habitat use in White Mountain National Forest. *The Journal of Wildlife Management*, *60*(3), 625–631.

Kuijper, D. P., Schut, J., van Dullemen, D., Toorman, H., Goossens, N., Ouwehand, J., & Limpens, H. J. G. A. (2008). Experimental evidence of light disturbance along the commuting routes of pond bats (*Myotis dasycneme*). *Lutra*, *51*(1), 37.

Kunz, T. H., Lumsden, L. F., & Fenton, M. B. (2003). Ecology of cavity and foliage roosting bats. *Bat ecology*, *1*, 3-89.

Lacki, M. J., Cox, D. R., & Dickinson, M. B. (2009). Meta-analysis of summer roosting characteristics of two species of myotis bats. *The American Midland Naturalist*, *162*(2), 318–326. https://doi.org/10.1674/0003-0031-162.2.318

Lacki, M. J., & Schwierjohann, J. H. (2001). Day-roost characteristics of northern bats in mixed mesophytic forest. *The Journal of Wildlife Management*, *65*(3), 482–488.

Langwig, K. E., Frick, W. F., Bried, J. T., Hicks, A. C., Kunz, T. H., & Marm Kilpatrick, A. (2012). Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. *Ecology letters*, *15*(9), 1050-1057.

Langwig, K.E., Frick, W.F., Reynolds, R., Parise, K.L., Drees, K.P., Hoyt, J.R., Cheng, T.L., Kunz, T.H., Foster, J.T. and Kilpatrick, A.M. (2015). Host and pathogen ecology drive the seasonal dynamics of a fungal disease, white-nose syndrome. *Proceedings of the Royal Society of London B: Biological Sciences*, *282*(1799), p.20142335.

Lesinski, G. (2007). Bat road casualties and factors determining their number. *Mammalia*, *71*(3), 138–142. https://doi.org/10.1515/MAMM.2007.020

Li, H., and Kalcounis-Rueppell, M. (2018). Separating the effects of water quality and urbanization on temperate insectivorous bats at the landscape scale. *Ecology and Evolution* 8:667-678.

Limpens HJGA, Twisk P, Veenbaas G. (2005) Bats and road construction. Dutch Ministry of Transport, Public Works and Water Management Directorate-General for Public Works and Water Management, Road and Hydraulic Engineering Institute, Delft, the Netherlands and the Association for the Study and Conservation of Mammals, Arnhem, the Netherlands

Loeb, S. C., & O'Keefe, J. M. (2006). Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics. *Journal of Wildlife Management*, *70*(5), 1210-1218.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Andrew Royle, J., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*(8), 2248-2255.

Medinas, D., Marques, J. T., & Mira, A. (2013). Assessing road effects on bats: The role of landscape, road features, and bat activity on road-kills. *Ecological Research*, *28*(2), 227–237. https://doi.org/10.1007/s11284-012-1009-6

Menzel, M. A., Owen, S. F., Ford, W. M., Edwards, J. W., Wood, P. B., Chapman, B. R., & Miller, K. V. (2002). Roost tree selection by northern long-eared bat (*Myotis septentrionalis*) maternity colonies in an industrial forest of the central Appalachian mountains. *Forest Ecology and Management*, *155*(1–3), 107–114. https://doi.org/10.1016/S0378-1127(01)00551-5

Meteyer, C. U., Buckles, E. L., Blehert, D. S., Hicks, A. C., Green, D. E., Shearn-Bochsler, V., ... & Behr, M. J. (2009). Histopathologic criteria to confirm white-nose syndrome in bats. *Journal of Veterinary Diagnostic Investigation*, *21*(4), 411-414.

Motto, H. L., Daines, R. H., Chilko, D. M., & Motto, C. K. (1970). Lead in soils and plants: its relation to traffic volume and proximity to highways. *Environmental Science & Technology*, *4*(3), 231-237.

Muskett, C. J., & Jones, M. P. (1980). The dispersal of lead, cadmium and nickel from motor vehicles and effects on roadside invertebrate macrofauna. *Environmental Pollution Series A, Ecological and Biological*, *23*(3), 231-242.

Nagorsen, D. W., & Brigham, R. M. (1993). *Bats of British Columbia* (Vol. 1). UBC press.

Norberg, U. M., & Rayner, J. M. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *316*(1179), 335-427.

Pauli, B. P., Badin, H. A., Haulton, G. S., Zollner, P. A., & Carter, T. C. (2015). Landscape features associated with the roosting habitat of Indiana bats and northern long-eared bats. *Landscape Ecology*, *30*(10), 2015–2029. https://doi.org/10.1007/s10980-015-0228-y

Patriquin, K. J., & Barclay, R. M. R. (2003). Foraging by bats in cleared, thinned and unharvested boreal forest. *Journal of Applied Ecology*, *40*(4), 646–657. https://doi.org/10.1046/j.1365-2664.2003.00831.x

Perry, R. W., & Thill, R. E. (2007). Roost selection by male and female northern long-eared bats in a pine-dominated landscape. *Forest Ecology and Management*, *247*(1–3), 220–226. https://doi.org/10.1016/j.foreco.2007.04.041

Plummer, M. (2003, March). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In Proceedings of the 3rd international workshop on distributed statistical computing (Vol. 124, No. 125.10).

Przybylski, Z. (1979). The effects of automobile exhaust gases on the arthropods of cultivated plants, meadows and orchards. *Environmental Pollution*, *19*(2), 157-161.

Owen, S. F., Menzel, M. A., Ford, W. M., Chapman, B. R., Miller, K. V., Edwards, J. W., & Wood, P. B. (2003). Home-range size and habitat used by the northern myotis (*Myotis septentrionalis*). *The American Midland Naturalist*, *150*(2), 352-359.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Raesly, R. L., & Gates, J. E. (1987). Winter habitat selection by north temperate cave bats. *American Midland Naturalist*, 15-31.

Ratcliffe, J. M., & Dawson, J. W. (2003). Behavioural flexibility: the little brown bat, *Myotis lucifugus*, and the northern long-eared bat, *M. septentrionalis*, both glean and hawk prey. *Animal Behaviour*, *66*(5), 847–856. https://doi.org/10.1006/anbe.2003.2297

Ritzi, C. M., Everson, B. L., & Whitaker, J. O. (2005). Use of bat boxes by a maternity colony of Indiana myotis (*Myotis sodalis*). *Northeastern Naturalist*, *12*(2), 217–220. https://doi.org/10.1656/1092-6194(2005)012[0217:UOBBBA]2.0.CO;2

Russell, A. L., Butchkoski, C. M., Saidak, L., & McCracken, G. F. (2009). Road-killed bats, highway design, and the commuting ecology of bats. *Endangered Species Research*, *8*(1–2), 49–60. https://doi.org/10.3354/esr00121

Russo, D., & Ancillotto, L. (2015). Sensitivity of bats to urbanization: a review. *Mammalian Biology* 80:205-212.

Rydell, J. (1992). Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology*, 744-750.

Sasse, D. B., & Pekins, P. J. (1996). Summer roosting ecology of northern long-eared bats (*Myotis septentrionalis*) in the White Mountain National Forest. *Bats and Forests Symposium*, 91–101.

Schaub, A., Ostwald, J., & Siemers, B. M. (2008). Foraging bats avoid noise. *The Journal of Experimental Biology*, *211*(Pt 19), 3174–80. https://doi.org/10.1242/jeb.037283

Slater, F. M. (2002). An assessment of wildlife road casualties –the potential discrepancy between numbers counted and numbers killed. *Web Ecology*, *3*(1), 33-42.

Stone, E. L., Jones, G., & Harris, S. (2009). Street lighting disturbs commuting bats. *Current Biology*, *19*(13), 1123–1127. https://doi.org/10.1016/j.cub.2009.05.058

Stone, E. L., Jones, G., & Harris, S. (2012). Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. *Global Change Biology*, *18*(8), 2458–2465. https://doi.org/10.1111/j.1365-2486.2012.02705.x

Thomas, H. H., Moosman, P. R., Veilleux, J. P., & Holt, J. (2012). Foods of bats (Family Vespertilionidae) at five locations in New Hampshire and Massachusetts. *Canadian Field-Naturalist*, *126*(2), 117–124. https://doi.org/10.22621/cfn.v126i2.1326

Trombulak, S. C., & Frissell, C. a. (2001). Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, *14*(1), 18–30. https://doi.org/10.1046/j.1523-1739.2000.99084.x

Viana, M., Jackson, A. L., Graham, N., & Parnell, A. C. (2013). Disentangling spatio-temporal processes in a hierarchical system: a case study in fisheries discards. *Ecography*, *36*(5), 569-578.

Vonhof, M. J., & Barclay, R. M. (1996). Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. *Canadian Journal of Zoology*, *74*(10), 1797-1805.

Warnecke, L., Turner, J. M., Bollinger, T. K., Lorch, J. M., Misra, V., Cryan, P. M., ... & Willis, C. K. (2012). Inoculation of bats with European *Geomyces destructans* supports the novel pathogen hypothesis for the origin of white-nose syndrome. *Proceedings of the National Academy of Sciences*, *109*(18), 6999-7003.

Waters, D., Jones, G., & Furlong, M. (1999). Foraging ecology of Leisler's bat (*Nyctalus leisleri*) at two sites in southern Britain. *Journal of Zoology*, *249*(2), 173-180.

Webb, P. I., Speakman, J. R., & Racey, P. A. (1996). How hot is a hibernaculum? A review of the temperatures at which bats hibernate. *Canadian Journal of Zoology*, *74*(4), 761-765.

Whitaker Jr, J. O., & L. J. Rissler. (1992a). Seasonal activity of bats at Copperhead Cave. *Proceedings of the Indiana Academy of Science*, *101*,127-134.

Whitaker Jr, J. O., & Rissler, L. J. (1992b). Winter activity of bats at a mine entrance in Vermillion County, Indiana. *American Midland Naturalist*, 52-59.

Whitaker, J. O., Sparks, D. W., & Brack, V. (2006). Use of artificial roost structures by bats at the Indianapolis International Airport. *Environmental Management*, *38*(1), 28–36. https://doi.org/10.1007/s00267-005-0117-2

Zurcher, A. A., Sparks, D. W., & Bennett, V. J. (2010). Why the bat did not cross the road? *Acta Chiropterologica*, *12*(2), 337–340. https://doi.org/10.3161/150811010X537918