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Bat species distribution and habitat associations in northern Ontario, Canada

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Bats are facing threats from disease, wind power development, and climate change, which are causing populations of many species to decline. The northern range limits of many temperate species are not well characterized, but the true distribution of threatened bat species is critical information for their conservation. We used passive acoustic monitoring and false-positive occupancy models to estimate the distributions of six species of bats in northern Ontario (north of ca. 50.5°N). We confirmed the presence of big brown bats (*Eptesicus fuscus*), hoary bats (*Lasiurus cinereus*), eastern red bats (*Lasiurus borealis*), silver-haired bats (*Lasionycteris noctivagans*), little brown myotis (*Myotis lucifugus*), northern long-eared myotis (*Myotis septentrionalis*), and tri-colored bats (*Perimyotis subflavus*) in our study area. We found that big brown bats, hoary bats, and little brown myotis likely are more widespread and common in northern Ontario than previously thought. Our models also provided evidence of associations between temperature and habitat types and bat occupancy probabilities. Our occupancy probability maps for each species support bat conservation by providing much finer-scale distribution information than previously available. These results provide a much-needed baseline for future studies of the distribution of these bat species in northern Ontario against which to measure the effects of white-nose syndrome, resource development, and climate change.

Key words: Chiroptera, distribution, false positive, habitat associations, northern Ontario, occupancy modeling, passive acoustic monitoring

Knowledge of the distribution and biology of bats in northern Ontario has become critical to managing bat populations due to the emergence and spread of white-nose syndrome (WNS) in southern Ontario since 2009 (White-nose Syndrome Response Team 2018). WNS is a disease caused by the cryophilic fungus *Pseudogymnoascus destructans* (Minnis and Lindner 2013). The bat species most vulnerable to WNS are those that hibernate, such as little brown myotis (*Myotis lucifugus*), northern long-eared myotis (*Myotis septentrionalis*), eastern small-footed myotis (*Myotis leibii*), tri-colored bats (*Perimyotis subflavus*), and to a lesser extent, the big brown bat (*Eptesicus fuscus*—Frick et al. 2015; Ingersoll et al. 2016). WNS can cause significant mortality among hibernating bats and is thought to be the leading cause of decline of bat species in Ontario (COSEWIC 2012a, 2012b). In addition to WNS, climate change and anthropogenic disturbances such as bat mortality from wind turbines also are having negative impacts on bat populations (Zimmerling and Francis 2016). Climate influences food availability, timing of hibernation, reproduction, development rates of juveniles, and rates of energy expenditure (Sherwin et al. 2013). Climate change is expected to have the greatest impact on bats at their most northern extent

(Burns et al. 2015); therefore, it is crucial that we increase our understanding of the distribution of bats in these northern areas to better evaluate the impacts of disease, climate change, and anthropogenic disturbance over time to these sensitive species.

There are eight species of bats documented in Ontario: big brown bats, hoary bats (*Lasiurus cinereus*), eastern red bats (*Lasiurus borealis*), silver-haired bats (*Lasionycteris noctivagans*), little brown myotis, northern long-eared myotis, tri-colored bats, and eastern small-footed myotis (van Zyll de Jong 1985; Naughton 2012). Of these species, the little brown myotis, northern long-eared myotis, tri-colored bat, and eastern small-footed myotis are listed provincially as endangered (Ontario Regulation 230/08), and as a result are afforded protection under Ontario's Endangered Species Act (ESA), S.O. 2007, c.6. Apart from the eastern small-footed myotis, these species also are listed federally as endangered under the Species at Risk Act (SARA), S.C. 2002, c.29, and are afforded similar protections across Canada.

The distribution of bats is well documented in southern Ontario, but their distribution in northern Ontario is uncertain. Naughton (2012) indicated that little brown myotis, silver-haired bats, eastern red bats, hoary bats, and northern long-eared myotis were found throughout most of Ontario except for north of the boreal forest. Mills et al. (2013) detected big brown bats at a site near Timmins, Ontario (48.4761°N, 81.3283°W), approximately 200 km north of the range limit described by van Zyll de Jong (1985). Other reports of big brown bats at more northern latitudes in Alaska and Saskatchewan suggested they can tolerate the climate of northern Ontario (Parker et al. 1997; Kalcounis et al. 1999). Trapping data suggested that tri-colored bats and eastern small-footed myotis were found only in southern and eastern Ontario (Naughton 2012). However, stable isotope analyses revealed that tri-colored bats may occur at more northern latitudes than previously thought, including the southern tip of James Bay (Fraser et al. 2012). While tri-colored bats may be found in more northern areas, it is likely that the availability of open areas for foraging and roost sites are limiting factors in the northern range of this species (Ethier and Fahrig 2011; Mills et al. 2013). Eastern small-footed myotis were a rare species in Ontario, but their abundance may be under-estimated because traditional capture methods are less effective for detecting this species than others (Huth et al. 2015). However, eastern small-footed myotis were detected as far north as Agawa Bay on the eastern shore of Lake Superior (Best and Jennings 1997).

Silver-haired bats, eastern red bats, and hoary bats are long-distance migrants. They typically start migration between mid-August and October and range in distances traveled (Fleming and Eby 2003). Eastern red bats and hoary bats migrate to milder climates, with eastern red bats hibernating south of 40°N and hoary bats over-wintering in the southern United States and Mexico (van Zyll de Jong 1985). Silver-haired bats hibernate in more northern locations with above-freezing average winter temperatures (≥ 2°C), but can tolerate cooler locations (McGuire et al. 2012). Females of all migratory species give birth upon returning to the northern parts of their ranges in late May–July (van Zyll de Jong 1985). Northern long-eared myotis, little brown myotis, eastern small-footed myotis, tri-colored bats, and big brown bats hibernate in cool, humid caves or abandoned mines, and big brown bats also hibernate in buildings (Hitchcock 1965; Naughton 2012). Females of hibernating species give birth in June or July (van Zyll de Jong 1985).

We examined relationships between bat occupancy probabilities and variables representing habitat types, temperature, and primary productivity that are known to influence bat habitat use and distribution. Foraging habitat and roost availability are crucial to bats and may be key factors limiting their distribution, but the needs of each species vary (Fenton 1997). Forest-roosting bats, such as eastern red bats, hoary bats, silver-haired bats, and little brown myotis, typically prefer tall, large-diameter trees in stands with open canopies near water (Kalcounis-Rüppel et al. 2005; McGowan and Houge 2016). All of Ontario's bat species are insectivores; therefore, edge habitats are needed by bats because they provide higher abundances of insects as well as protection from predators (Fenton 1997; Gruebler et al. 2008). Many of the bat species in Ontario forage in edge and riparian habitats but can be opportunistic in their choice of foraging habitat (Ethier and Fahrig 2011; Mills et al. 2013). Although there are general trends, there is wide variation in habitat usage. Vegetative structure and plant species diversity may be correlated with prey availability (Burford et al. 1999) and thus could influence the distribution of bats. Temperature and primary productivity also may influence distribution of bats because these factors influence the types of prey and habitat available (Rodhouse et al. 2012; Michaelsen 2016). Resources often are separated by large distances, so bats may commute over several kilometers between foraging and roosting sites each night (Broders et al. 2006). Riparian areas provide unobstructed commuting corridors that allow bats to travel the long distances necessary to access all resources needed (Burns et al. 2015). Bats also travel long distances to and among their swarming sites, areas near the hibernacula where bats display intense flight activity that may be related to mating (Norquay et al. 2013; van Schaik et al. 2015).

We conducted an extensive survey of the distribution of bat species in northern Ontario by use of passive acoustic monitoring and false-positive occupancy models. Previous efforts to define the northern range limits of bats in our study area were limited to extrapolating from sparse location records (van Zyll de Jong 1985; Naughton 2012; Mills et al. 2013). Our objectives were to estimate the probability of summer occupancy and habitat associations of all bat species detected (2010–2015) across northern Ontario. We evaluated the relationships of occupancy probability to temperature, primary productivity, and landscape-level habitat variables. We also evaluated whether type of detector used, number of recording nights, and local-level habitat variables influenced detection probability.

MATERIALS AND METHODS

Study area.—The Ontario Ministry of Natural Resources and Forestry conducted passive acoustic monitoring as part of the Far North Biodiversity Project. The overall purpose of the Far North Biodiversity Project was to provide a foundation of information on the terrestrial living resources of the Far North of Ontario in support of local First Nations' (Indigenous) community-based land use planning activities. These results may help inform land use planning and conservation discussions and serve as a basis for assessing future change. Sampling occurred over a 5-year period (2010–2014) across the Hudson Bay Lowlands and Ontario Shield ecozones within the geographic boundaries of the Far North of Ontario, as defined by Ontario's Far North Act, 2010, S.O. 2010, c.18 s.2 (Fig. 1). In general, the Far North of Ontario is the area of Ontario north of the limits of commercial forestry operations, where abiotic factors limit tree growth rates. Additional recording data for one location near the Neskantaga First Nation were collected in 2015.

The Hudson Bay Lowlands ecozone is a region of northern Ontario characterized by flat topography of underlying limestone and poor drainage (Crins et al. 2009), resulting in a landscape dominated by saturated peatlands (bogs and fens—Riley 2003). Open boreal forest dominated by black spruce (*Picea mariana*) and tamarack (*Larix laricina*) occurs throughout, with upland coniferous forests occurring on well-drained sites (Riley 2003). Numerous ponds and connecting waters were present across the ecozone. However, lakes were rare and generally shallow, and lakes and rivers account for less than 3% of the region's surface area (Marshall and Jones 2011). Mean annual temperatures range from −5.1°C to 0.5°C and mean annual precipitation values from 490 to 833 mm (Mackey et al. 1996a, 1996b).

The Far North of Ontario also encompasses the northern portion of the Ontario Shield ecozone (Ecoregions 2W and 3S). This region varies in its topography and drainage and is characterized by its underlying Precambrian bedrock. Coniferous forests represented by black spruce and jack pine (*Pinus banksiana*) dominate the landscape: wetlands (predominately peatlands) and open water more abundant to the west in Ecoregion 2W (Crins et al. 2009). Lakes were widespread and varied in size, depth, and shoreline complexity (Marshall and Jones 2011). Mean annual temperatures ranged from −4.1°C to 1.0°C and mean annual precipitation from 550 to 787 mm (Mackey et al. 1996a, 1996b).

We centered annual data collection areas on First Nation communities that we selected based on their land use planning status, existing information gaps, and community near-term interest in land use planning (Fig. 1). We used AS-350 B2 and Eurocopter EC130 B4 helicopters (Airbus Helicopters Canada, Fort Erie, Ontario) to transport field staff and equipment to plots. The operational range of the helicopters required us to select study areas within 150 km of each community.

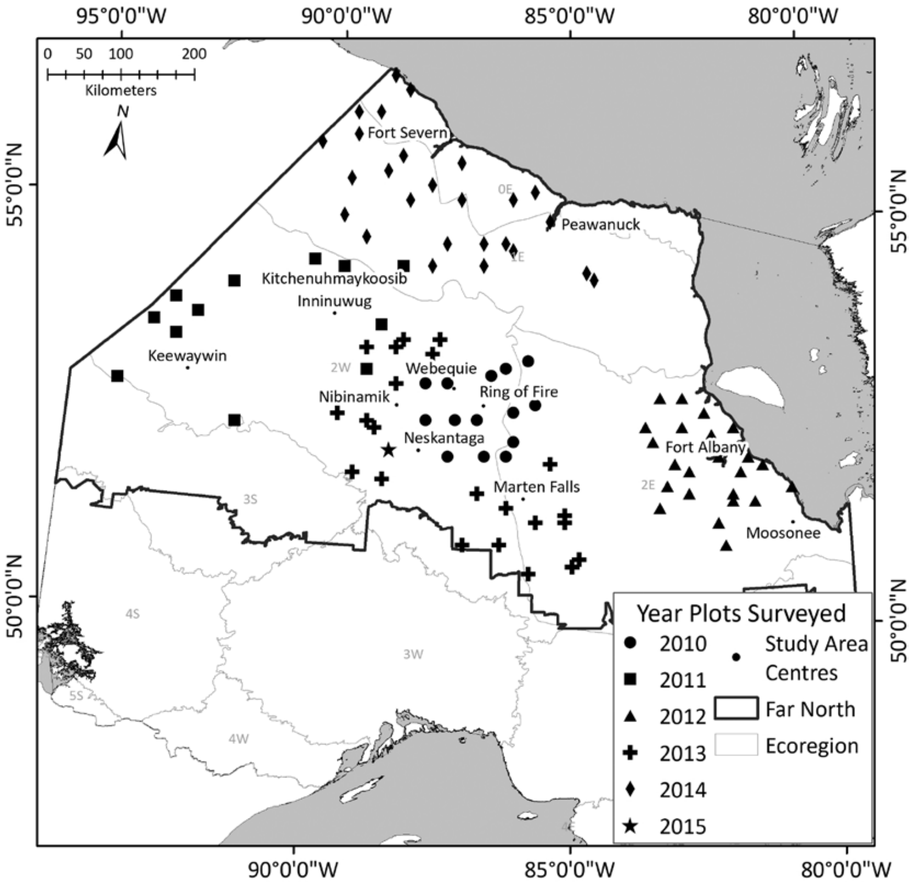

Fig. 1.—Map of northern Ontario, Canada, illustrating area where acoustic sampling of bats was conducted from 2010 to 2015. Symbols reflect distribution of plots across years.

Site selection and acoustic sampling.—We randomly selected plot locations within each annual data collection area from the National Forest Inventory 20 × 20 km sampling grid (Gillis et al. 2005). We categorized plots as either electronic recorder plots or comprehensive plots. Electronic recorder plots, included in the survey protocol from 2012 to 2014, were established early in the field season, left to record until their batteries or memory capacity was exhausted, and were retrieved at the end of the field season. Comprehensive plots were established for much shorter periods (typically 6 to 7 days) and were designed to have field crews remain on site to complete a range of biological surveys, including bat acoustic surveys. Because of random plot selection, some plots were inaccessible due to site conditions (e.g., unsuitable for helicopter landing or too wet for camping). In such instances, plots were relocated to the nearest location in similar habitat with suitable landing or camping conditions.

Electronic recorder plots had one bat recorder station, whereas comprehensive plots had three to five bat recorder stations, where multiple stations served as spatial replicates (Loeb et al. 2015). Song Meter SM2BAT recorders with SMX-US Ultrasonic Microphones (Wildlife Acoustics, Inc., Concord, Massachusetts) were deployed at a single station on each electronic recorder plot. Electronic recorder plots had four predetermined stations, but the field crew made an on-the-ground determination and placed the recorder at or near (within 30 m of) the station with the best perceived bat habitat, specifically ecological edges (i.e., between habitat types). On comprehensive plots, a minimum of two batcorder 2.0 (ecoObs, Nuremberg, Germany) and one SM2BAT recorders were strategically located along ecological edges greater than 200 m from each other to maximize the detection of most bats. SM2BAT recorders were deployed on electronic recorder plots because of their relatively longer battery life in comparison to the batcorder 2.0 and because the SM2BAT recorders were also used for acoustical bird surveys on these plots.

We conducted acoustic sampling for bat echolocation calls using batcorder 2.0 (2010–2014) and SM2BAT (2012–2014) recorders throughout June and July of each year. Some additional, opportunistic sampling occurred at eight electronic recorder plots in August of 2014 for 7 days and at three additional electronic recorder plots in July of 2015 for 4 days. This study conforms to published ASM guidelines for the use of wild mammals in research (Sikes et al. 2016). Each unit was affixed securely using bungie cords, at approximately 1.5 m above ground level, to a tree, snag, or where there were no trees of sufficient size, to a tripod fabricated of material available on the plot. We positioned recorders with the microphone oriented parallel to the ground (or angled slightly downward for batcorder 2.0 units to avoid water accumulation and interference). We removed vegetation within 1 m of each recorder to minimize acoustic interference.

We programmed batcorder 2.0 units to record daily, in all years, from 2300 to 0500 h in auto-detection mode. We set the units to record calls higher than 16 kHz and louder than −27 dB, with a sampling rate of 500 kHz, and used a post-trigger interval of 400 ms. We used the default "quality" setting of 20 (ecoObs 2010). From 2013 to 2014, SM2BAT recorders were programmed at a sampling rate of 192 kHz using Wildlife Acoustics' Configuration Utility software (Wildlife Acoustics, Inc.) to conduct through-the-night recording beginning at 2300 h and ending at 0500 h to be consistent with the recording schedule of the batcorder 2.0 units. In 2012, the SM2BAT recorders were programmed to record twelve 10-min recordings at 192 kHz between 2330 and 0430 h. The sampling rate used with the SM2BAT recorders is not ideal for distinguishing *Myotis* species, specifically northern long-eared myotis; however, at the time of data collection, there were technological limitations that prevented another sampling rate from being used. This design resulted in 660 h of recordings over 110 nights in both 2010 and 2011, 1,576 h over 552 nights in 2012, 2,082 h over 347 nights in 2013, 1,722 h over 287 nights in 2014, and 72 h over 12 nights in 2015. Early deployment (i.e., early June) of SM2BAT units at electronic recorder plots necessitated that the recording schedule accommodates limited battery capacity. These units began recording on 27 June to be better aligned with demonstrated periods of higher local bat activity to maximize the probability of detection. Comprehensive plot data from 2010 to 2012 indicated bat activity was minimal in these far north locations prior to late June.

Species identification.—We identified acoustic recordings to species-level when possible using two methods: quadratic discriminant function analysis (qDFA) and a proprietary acoustic classifier, Kaleidoscope Pro (Wildlife Acoustics, Inc.; www.wildlifeacoustics.com). We recorded in full-spectrum in either RAW (batcorder) or WAC (SM2BAT) format. We converted RAW files to WAV files with a custom MATLAB script and converted WAC files to WAV files with Kaleidoscope Pro. We excluded recordings from further analysis if they contained < 3 calls as per the North American Bat Monitoring Program (NABat—Loeb et al. 2015). A call was defined as a single pulse of sound produced by an echolocating bat navigating through its environment (Loeb et al. 2015).

We extracted 11 call parameters for each call in all recordings using the automated detection feature of callViewer18, a custom echolocation sound analysis program written in MATLAB. The 11 call parameters were duration, maximum frequency, minimum frequency, frequency with most energy, 10th, 60th, and 90th percentiles of energy, median energy slope, median frequency slope, median energy smoothness, and median frequency smoothness. The qDFA classified each call to species based on a reference library, including known calls from seven species of bats present in Ontario, provided by Western University (following Mills et al. 2013), using the qda() function in the "MASS" package (Venables and Ripley 2002) in R (version 3.4.1—R Development Core Team 2017) and RStudio (version 1.0.153—RStudio Team 2016). This training set of calls did not include the eastern small-footed myotis because its echolocation calls are difficult to distinguish from little brown myotis (Mukhida et al. 2004). The calls in the classifier were from various locations over a number of years and were search phase calls from free flying bats. No classifier data came from hand-released individuals. We only included the fundamental harmonic in analyses, to eliminate the possibility of pseudoreplication. We filtered data to eliminate noise and weak fragmented calls (removed calls < 0.99 and > 30 ms duration, and with a minimum frequency < 14 kHz).

We also used Kaleidoscope Pro 4.3.0 to classify recordings to species with the North American 4.3.0 classifier. We also excluded eastern small-footed myotis from the North American 4.3.0 classifier for the reason previously described. For Kaleidoscope Pro to attempt an identification of a call sequence of interest, the calls must have been between 15 and 120 kHz, 1.5 and 50 ms in duration, with a maximum intersyllable gap of 500 ms, and containing ≥ 3 calls (Loeb et al. 2015). The sensitivity level was set to 0 (balanced). We compared the two classification methods with a confusion matrix to determine the consistency of the classifiers.

Detectability and occupancy covariates.—We used a suite of individual land cover types to assess the influence of different types of habitat on bat species detectability and occupancy. We acquired spatial data for the habitat variables from the Far North Land Cover v.1.2 layer of the Ontario Land Cover Compilation v.2.0 (Ontario Ministry of Natural Resources 2014). This layer included nine habitat types: water, marsh, swamp, bog, fen, treed peatland, forest, nontreed (i.e., heath and bedrock), and disturbance. We collapsed these habitat types to examine characteristics ecologically significant to bats. We defined six variables pertaining to habitat: 1) water (water and marsh), 2) swamp, 3) bog-fen (bog and fen), 4) forest (treed peatland and forest), 5) open (nontreed), and 6) disturbance (natural disturbances). Water and marsh habitats were grouped because marshes make up a small fraction of the Far North (marshes averaged cover of 0.2% of the study area) and are almost always associated with open water. Swamp was kept separate from the bog-fen category because swamps are characterized by the presence of woody plants and trees although they made up a smaller fraction of the Far North (swamps cover 9.7% and bog-fen covers 51.5% of the study area). Inclusion of these six variables as potential predictors allowed us to estimate and examine the influence of habitat on bat species detectability and occupancy. The Far North Land Cover v.1.2 layer is a raster with a spatial resolution of 30 m. In addition to land cover as landscape-scale explanatory variables of occupancy, we also examined the influence of average temperature in the warmest quarter (ATWQ—McKenney et al. 2013), and the normalized difference vegetation index (NDVI) computed from MODIS remote sensing data (Tucker et al. 2004, 2005; Pinzon et al. 2005) as a measure of primary productivity.

We examined covariates at two spatial scales: local (30-m radius around stations) and landscape (10-km radius around stations). We used local-level habitat data as explanatory variables for detection because the habitat directly around a detector is one of many factors that influences the ability to detect and record a bat call (McGowan and Hogue 2016). A 30-m radius was chosen because it roughly coincides with the detection range of the SM2BAT (SMX-US; Wildlife Acoustics, Inc.; www.wildlifeacoustics.com) and batcorder 2.0 microphones (Adams et al. 2012). We used landscape-level habitat data as explanatory variables for occupancy. Previous studies found landscape-level environmental characteristics aggregated to coarse-scale units of analysis to be meaningful predictors of bat distributions (e.g., a 10 × 10 km scale—Rodhouse et al. 2012; Clement et al. 2014). A 10-km radius around the plot center also minimizes overlap between plots because the average nearest neighbor distance is 35 km (minimum nearest neighbor distance is 10.6 km). Each station within a plot had similar, if not identical, values of the environmental covariates, allowing the stations to serve as spatial replicates for each plot (Loeb et al. 2015). For both local- and landscape-level data, we used buffers (with radii of 30 m and 10 km, respectively) and calculated the proportion of land cover type, and mean values for NDVI and ATWQ within the buffers for each station.

Detectability and occupancy modeling.—We modeled bat species distribution using the false-positive occupancy model developed by Royle and Link (2006) and modified by Miller et al. (2011), with the observation confirmation extension described by Chambert et al. (2015). Acoustic detection surveys using automated identification methods can generate false positives, defined as signs from a nonfocal species that are present, found, and erroneously assigned to the focal species (Preatoni et al. 2005). The estimated false positive parameter describes the probability that in a hypothetical 10 × 10 km sampling unit not occupied by the species, the acoustic survey method will produce one or more false species detections during each recording night (Clement et al. 2014). Different identification methods may also provide different results. The observation confirmation design subjects acoustic records to further identification, typically by human interpretation of the recordings (Chambert et al. 2015).

We generated detection histories for each species based on nightly observations at each station. Observation states for the detection history were: 1) certain detection, 2) uncertain detection, and 3) nondetection. At a given station on a given night, detection was defined as at least one recorded and identified bat call (Loeb et al. 2015). We considered detections that were identified to the same species by both methods to be "certain" detections of a focal species. We applied a confusion matrix approach to examine the agreements and disagreements among all species, to account for potential issues with the use of agreement to gain insight to accuracy (Lemen et al. 2015; Russo and Voigt 2016). There was high disagreement between the two automated classification methods for hoary bats and silver-haired bats. We performed a round of blind manual identification for a random 10% subset of those disagreement files. Of those manually identified files, 77.6% of them agreed with the classification from the DFA, so we used the original classification from that method for all of the hoary–silver-haired disagreement files. For the remaining disagreements between methods, we followed the NABat Monitoring Protocol recommendation to consider both species possible and classified them as "uncertain detections" (Loeb et al. 2015). Detection histories then were used to estimate probability of occupancy, probability of detection, and probability of false positives.

We performed all occupancy modeling using the "OccuFP" function in the "unmarked" package in R, version 3.4.3 (Fiske and Chandler 2011; R Development Core Team 2017). Occupancy models assume that plots represent closed populations during surveys (i.e., no changes in occupancy). We conducted all surveys between 1 June and 12 August, so seasonal migration had minimal effects on the occupancy state of each plot (Rodhouse et al. 2012). Recordings were collected over 6 years (2010–2015). There were likely no changes in the occupancy of each plot within each year and bat demographics suggested that populations were relatively stable across years in the absence of disease outbreaks such as WNS (Barclay et al. 2004; Rodhouse et al. 2012).

Models for each species, except tri-colored bats, were estimated in a multistep process (Clement et al. 2014; Niedballa et al. 2015; Glisson et al. 2017). Analysis could not be done for tri-colored bats because there were only five identifications of this species and there was no agreement between the classifiers; we manually identified the five files for this species. The first step in the model development process was to examine the influence of covariates on detection probability (ρ), while holding occupancy probability (Ψ) constant (Glisson et al. 2017). All detection covariates were station-specific. We considered eight variables that we hypothesized would influence detection probability: type of detector used to record bat calls (detector), number of recording nights (recording nights), and the six local-level habitat variables (water, swamp, bog-fen, forest, open, and disturbance). First, we developed models to examine the influence of detector and recording nights individually and together. All models were ranked according to their Akaike's information criterion (AICc) values. We incorporated the top-ranked model into a second set of detection probability models that included the six local-level habitat variables individually and in all possible additive combinations. These models were again ranked using AICc and the top-ranked detection model was then used in all subsequent occupancy modeling.

We considered eight variables that we hypothesized would influence occupancy probability of bat species: temperature (ATWQ), an index of net primary productivity (NDVI from LandSat data), and the six landscape-level habitat variables (water, swamp, bog-fen, forest, open, and disturbance). Occupancy models were evaluated in a manner similar to that used for selection of the detection models by first evaluating temperature and NDVI, and then evaluating the top-ranked temperature and NDVI model with all combinations of the six landscape-level habitat variables. Therefore, the top-ranked occupancy model for each species contained the covariates from the top-ranked detection model and all top-ranked occupancy covariates. The continuous detection and occupancy covariates were *z*-transformed prior to analysis to standardize their coefficients and improve the performance of the model comparison (Clement et al. 2014). We used principal component analysis (PCA) to examine correlations among independent variables. It was determined that NDVI and temperature were highly correlated, as were bog-fen and forest; therefore, these variables were never included in the same model.

To create distribution maps for each species, we created a raster of 10 × 10 km grid cells across the study area and each cell was assigned values for all covariates included in the analysis. We computed covariates for the center point of each grid cell in the same way they were computed for each station. Conditional occupancy probabilities were generated for each grid cell using the top-ranked occupancy model for each species and the predict() function in R (R Development Core Team 2017). We made conditional occupancy probabilities at the scale of 10 × 10 km grid cells distributed across the study area rather than at the scale of stations, because stations within plots were unlikely to represent closed populations between recording nights (Clement et al. 2014). We generated maps of the conditional occupancy probabilities to indicate species distribution.

RESULTS

Across all years, there were 7,118 files recorded; however, we excluded 817 files because they contained < 3 calls. We identified the remaining 6,301 files to species or as noise using the two

Table 1.—Confusion matrix between discriminant function analysis (DFA) and Kaleidoscope Pro identifications of 6,301 recordings of bat echolocations in the Far North of Ontario, 2010–2015. Rows indicate identifications according to DFA, columns indicate identifications according to Kaleidoscope Pro. Bold font indicates the numbers of identifications agreed upon by both methods.

		Kaleidoscope Pro									
		Big brown bat	Eastern red bat	Hoary bat	Silver-haired bat	Little brown myotis	Northern long-eared myotis	No ID	Noise	Tri-colored bat	Grand total
DFA	Big brown bat	**3**	2	6	6			18			35
	Eastern red bat		**335**			117	3	160		2	617
	Hoary bat	29		**294**	863	3		139	14		1,342
	Silver-haired bat				**4**			2			6
	Little brown myotis	1	20		4	**2,082**	73	840	6	1	3,031
	Myotis					32	2	27			61
	Northern long-eared myotis					15	**22**	50			87
	Noise	3	4	3	1	30	1	29	**1,013**		1,084
	Tri-colored bat		2								2
	Multiple species		2	3	5	16	2	8			36
	Grand total	36	364	306	883	2,295	103	1,273	1,033	3	6,301

classification methods (Table 1; Supplementary Data SD1–SD7). Both methods identified 16% of the files as noise; thus, these were excluded from further analysis. We detected seven of the eight species known to be present in Ontario: big brown bats, eastern red bats, hoary bats, little brown myotis, northern long-eared myotis, silver-haired bats, and tri-colored bats. Hoary bats were identified by both methods at 32.3% of plots and by at least one of the methods at 38.4% of plots. Silver-haired bats were identified by both methods at only 5.1% of plots and by at least one of the methods at 10.1% of plots. Tri-colored bats were only identified by one method at 5.1% of plots. We only had five recordings that were identified as tri-colored bats by our methods, but a manual check confirmed that one of these files (recorded at 51.317, −85.746) was a tri-colored bat (see Supplementary Data SD7). All other species were identified at an intermediate percentage of plots (Table 2).

The top models for all species indicated that detection probability always varied with number of recording nights (Table 3). Temperature was a consistent occupancy covariate in all the species' top models. Detection probabilities varied among species; little brown myotis had the highest probability of being detected (0.49) and northern long-eared myotis had the lowest probability of being detected (3.35×10^{-7}). Occupancy probabilities indicated the proportion of plots estimated as occupied during our study (Glisson et al. 2017). For example, little brown myotis had an occupancy probability of 0.84, which means they likely occurred in 84% of the plots during our study although we only detected them in 30% of the plots (Table 3).

Table 2.—Percentage of plots (n = 99) at which each species was identified by each method individually, both methods, and by at least one method

Species	Percentage of plots where species identified by			
	qDFA	Kaleidoscope	Both methods	At least one method
Big brown bat	15.2	10.1	3.0	20.2
Hoary bat	25.3	8.1	32.3	38.4
Little brown myotis	26.3	19.2	30.3	32.3
Silver-haired bat	2.0	6.1	5.1	10.1
Eastern red bat	18.2	11.1	15.2	23.2
Northern long-eared myotis	11.1	8.1	9.1	13.1
Tri-colored bat	2.0	3.0	0.0	5.1

We produced predicted distribution maps for the six bat species analyzed in our study, showing the probability of occupancy across the Far North of Ontario. These maps indicated that big brown bats (Fig. 2A), hoary bats (Fig. 2B), and little brown myotis (Fig. 2C) are likely more widespread and common in the Far North of Ontario than previously thought. The maps also indicated that the presence of any bat species near the northern border of Ontario is unlikely. All species had predicted occupancy probabilities ranging from 0 to 1.0 except for silver-haired bats, which only had occupancy probabilities up to 0.7 (Fig. 2D). The predicted distribution maps for eastern red bats (Fig. 2E), hoary bats, little brown myotis, and northern long-eared (Fig. 2F) bats showed a similar trend of higher occupancy probabilities at more northern latitudes in the west compared to the east. This follows a similar trend of forest cover ranging farther north in the west than in the east. Big brown bats and silver-haired bats had lower occupancy probabilities and were more patchily distributed than the other species.

All species analyzed had significantly higher occupancy probabilities with a higher temperature within a 10-km buffer around the plot center (Table 3). We found that hoary bats had a significant negative correlation with the proportion of open habitat ($r = -0.48$). Eastern red bats ($r = -0.50$), big brown bats ($r = -1.24$), and silver-haired bats ($r = -0.98$) also showed a negative correlation with swamp or water habitats. An unexpected finding was that occupancy probabilities of the northern long-eared myotis were positively correlated with proportion of water, even though this species typically is highly associated with forest habitats. Little brown myotis was the only species that showed a positive correlation with the amount of forest habitat in their top model.

Discussion

We documented all five bat species thought to occur in the Far North of Ontario (hoary bat, eastern red bat, silver-haired bat,

Table 3.—Top models for each bat species in the Far North of Ontario, 2010–2015. For each model, the standardized regression coefficient(s) and parameter estimates with 95% confidence intervals in parentheses for occupancy probability (Ψ), detection rate of bat detectors (ρ), and false positive rate for detectors (f) are shown. Variables are defined in "Materials and Methods."

Species	Top model	Ψ	ρ	f
Big brown bat	Ψ([3.48]·temperature + [−1.24] water) ρ([−0.80]·recording night)	0.32 (0.06–0.77)	0.18 (0.12–0.27)	1.54×10^{-4} (0–1.00)
Hoary bat	Ψ([3.00]·temperature + [−0.48]·open) ρ([−1.43]·recording night + [0.14]·forest)	0.74 (0.58–0.90)	0.41 (0.35–0.47)	0.01 (0.01–0.03)
Little brown myotis	Ψ([3.44]·temperature + [0.38]·forest) ρ([−1.17]·recording night)	0.84 (0.67–0.93)	0.49 (0.42–0.56)	0.01 (0–0.02)
Silver-haired bat	Ψ([4.00]·temperature + [−0.98]·water) ρ([−0.96]·recording night + [−16.35]·swamp)	0.16 (0.01–0.85)	4.97×10^{-4} (0–1.00)	2.28×10^{-3} (5.80×10^{-4}–0.01)
Eastern red bat	Ψ([5.69]·temperature + [−0.50]·swamp) ρ([0.03]·detector + [0.85]·recording night +[0.29]·forest)	0.86 (0.66–0.95)	0.37 (0.27–0.47)	2.43×10^{-6} (0–1.00)
Northern long-eared myotis	Ψ([9.14]·temperature + [0.91]·water) ρ([−2.06]·recording night + [−36.48]·swamp)	0.97 (0.66–1.00)	3.35×10^{-7} (0–1.00)	9.13×10^{-4} (0–0.01)

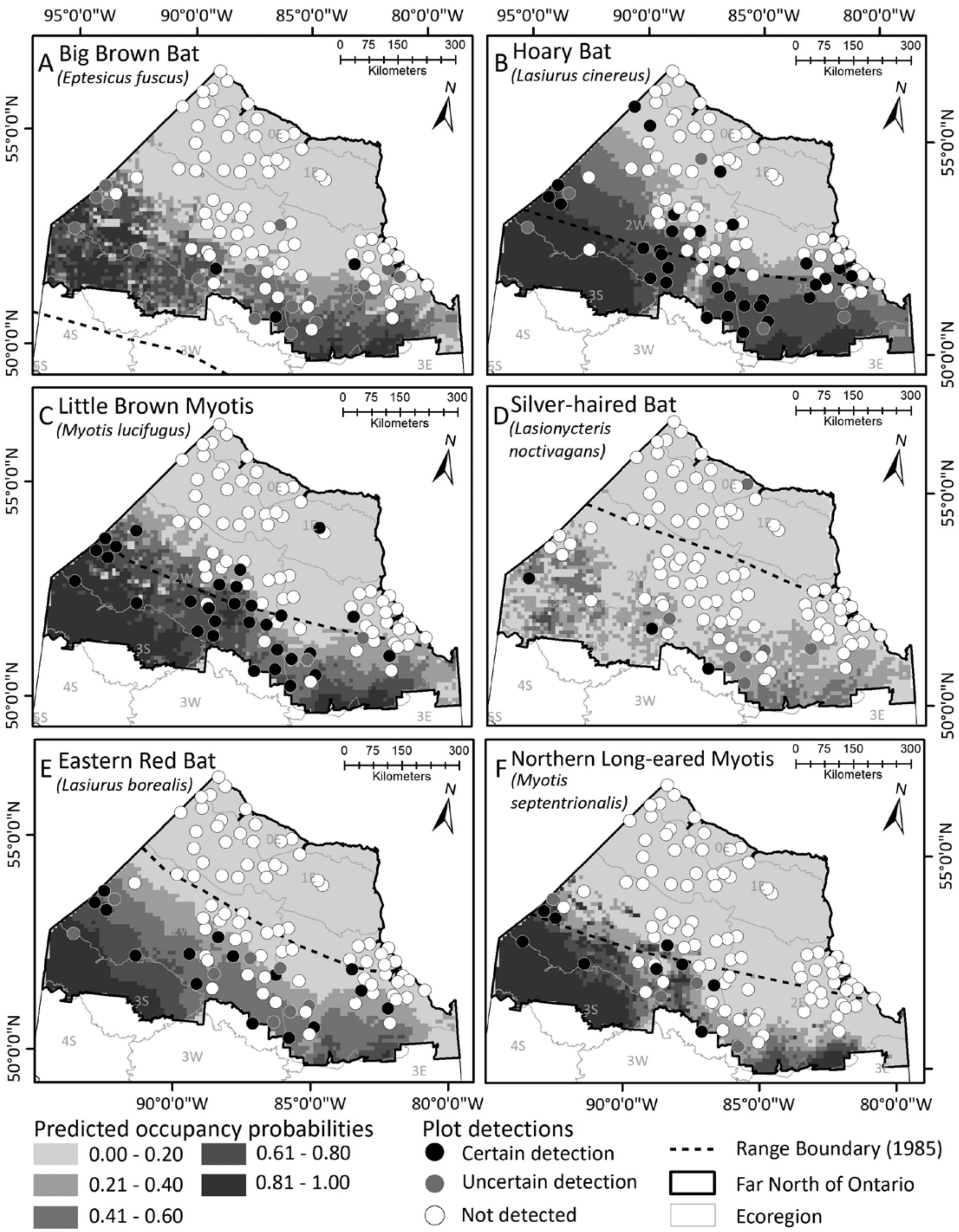

Fig. 2.—Predicted distribution maps showing probability of occurrence of six bat species throughout the Far North of Ontario. Probabilities were derived from false-positive occupancy models. The 1985 range boundaries are from the *Handbook of Canadian Mammals* (van Zyll de Jong 1985).

little brown myotis, and northern long-eared myotis) as well as the big brown bat and the tri-colored bat. Our methods could not differentiate between little brown and eastern small-footed myotis, so we cannot rule out the possibility that all eight species range into the Far North. Our false-positive occupancy models identified variables representing ecological and biological factors associated with roosting and foraging habitats of each species. We found that the distribution of all species identified in this study had a significant association with temperature. Knowledge of bat distribution in this area previously was based on only a few isolated records (van Zyll de Jong 1985; Naughton 2012). Our study demonstrates that large-scale acoustic monitoring can greatly expand and refine the known distributions of bat species in previously little-studied areas.

Our results extend the known northern range limits of the tri-colored bat. A lack of suitable roost sites is thought to limit the distribution of tri-colored bats because they most commonly roost in deciduous trees; however, they can be flexible when this roost type is not available (Carter and Menzel 2007; Poissant et al. 2010). Fraser et al. (2012) found tri-colored bats may engage in annual latitudinal migrations and may migrate as far north as the southern tip of James Bay in summer. While we could not produce an accurate distribution map for the tri-colored bat because of the small number of confirmed records, our finding supports the idea that they may be found at more northern latitudes than previously thought. Further research will be needed to confirm the northern extent of the tri-colored bat's range.

We found that the distribution of all species identified in this study had a significant positive association with temperature (average temperature in the warmest quarter). Temperature was a predominant variable in all of the top models selected in this study, and therefore had a large effect on the predicted distributions. This is evident in the higher occupancy probabilities in the southwestern portion of our study area where temperatures in the warmest quarter are highest. An average temperature in the warmest quarter of 14°C appears to be a minimum threshold constraining the northern extent of bat species in northern Ontario. The number of days with warm temperatures (degree-days) can affect prey availability, as well as suitable roosting and foraging habitats, which constrain the ranges of many species across Ontario (Jung et al. 1999; Dubois and Monson 2007). Climate change is likely to increase temperatures in the Far North of Ontario. This may lead to positive impacts such as further northward range expansions of these bat species (Sherwin et al. 2013), or negative impacts such as reductions in reproductive output (Adams 2010). There still are many uncertainties about what the impacts of climate change and increasing temperatures will be on bats.

Hoary bats were the most commonly detected species in our study and accounted for the greatest proportion of detected bat activity. However, acoustic bat activity cannot be converted accurately to bat abundance because differences in echolocation call characteristics can influence detection probabilities (Corcoran and Weller 2018). Hoary bats generally prefer open areas because of their morphology and echolocation call characteristics (van Zyll de Jong 1985; McGowan and Hogue 2016), but also have a close association with forest cover (Brigham 2007; Mills et al. 2013). The top model for this species did not support a positive association with open areas. Corcoran and Weller (2018) suggested that hoary bats sometimes fly without echolocation, and in open habitats they use a different type of call that has less sound energy than typical calls, making them difficult to record with detectors. They may not forage within forest habitat; however, they roost among tree foliage (van Zyll de Jong 1985) and forage over water and riparian areas in forest-edge habitats (Brigham 2007). Because of this association with forest habitats, the range of hoary bats is limited in the Far North of Ontario largely by the northern extent of the boreal forest (Fig. 2B). Our predicted distribution map for the hoary bat illustrates they may occur at more northern latitudes than the previous range description by van Zyll de Jong (1985).

Little brown myotis and eastern red bats had similar predicted distribution maps, though they were not predicted to occur as far north as the hoary bat (Figs. 2C and 2E). Our predicted distributions for these species are similar to those of van Zyll de Jong (1985). Little brown myotis and eastern red bats were the next most frequently detected species in our study. Eastern red bats, like hoary bats, are long-distance migratory species and roost almost exclusively in trees (McGowan and Hogue 2016). Little brown myotis had a close association with forest habitat in this study (Table 3), but are generalists in roost selection (Frick et al. 2010). However, they do forage over riparian areas along forest edges (Belwood and Fenton 1976; Mills et al. 2013). Northern long-eared myotis also had a predicted distribution map similar to those of the previous species, but were not predicted to occur as far north (Fig. 2F). These three species likely are limited by available foraging habitat, as they are typically highly associated with forests (Jung et al. 1999).

Silver-haired bats also are a long-distance migratory species and only spend the summer months in the Far North of Ontario. We detected this species at only 5% of our plots, and the predicted occupancy probability for this species indicated that it may have been present at 16% of our plots. Silver-haired bats typically roost in tree trunks or behind loose bark and most commonly use large, mature trees (Jung et al. 1999). The low occupancy probabilities and patchy distribution map of this species (Fig. 2D) may be due to a lack of suitable roosting habitat. Another explanation may be our inability to accurately detect and identify silver-haired bat echolocation calls. There were many files identified as silver-haired bats by one method and hoary bats by the other. The calls of these species are similar, but usually can be distinguished by the search phase calls, which differ because they employ different foraging strategies (Barclay 1986). However, in the presence of environmental clutter, both species can adjust their calls and the distinguishing features become less clear (Broders et al. 2004). Manual identification to solve this disagreement classified many of these files as hoary bats; three of the four files identified by both methods as silver-haired bats were correctly identified (Table 1).

Our records extended the previously documented northern range limit of big brown bats (van Zyll de Jong 1985; Fig. 2A). We confidently detected big brown bats at only 3% of our plots, but our model predicted that this species may have occurred at 32% of our plots. There were only three files that had agreement between the classification methods, so to ensure that this species was present in our study area we manually identified a random 50% subset of the files identified as big brown bats by at least one of the classification methods. Of these files, seven (18%) were confirmed to be big brown bats. Mills et al. (2013) also detected this species near the southern edge of our study area, but other studies did not detect big brown bats at the northern border of their previously known range in Ontario (Jung et al. 1999). Big brown bats are foraging habitat generalists (Kurta and Baker 1990), but have a strong preference for roosting in buildings and rock crevices (van Zyll de Jong 1985). Big brown bats also are likely limited by available roosting habitats at northern latitudes.

We estimated the distribution of six species of bats in the Far North of Ontario using a finer scale and larger sample size than previous studies, resulting in a greatly improved understanding of their habitat associations, distributions, and northern range limits. Sharing our findings with the First Nations communities of the Far North of Ontario may serve to support community-based land use planning activities. Our research, in combination with other studies (e.g., Kalcounis et al. 1999; Lacki et al. 2007), illustrates the relationships between forest habitat and temperature and the northern limits of the ranges of many bat species. We found that temperature generally had the greatest effect on occupancy at these northern limits. Climate change is predicted to cause greater temperature increases in northern areas, implying an uncertain future for the future ranges of these northern bat populations (Rodhouse et al. 2012; Michaelsen 2016). Our study took place in 2010–2015, before WNS was detected in our study area; however, WNS may have entered the study area during the study period (Canadian Wildlife Health Cooperative 2014; White-nose Syndrome Response Team 2018). Our predicted distribution maps provide valuable information on the northern ranges of bat species to assess potential effects of WNS, anthropogenic disturbance, and climate change in the Far North of Ontario.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Map of proportion of total identifications classified by each method (qDFA or Kaleidoscope) at plots as big brown bats (*Eptesicus fuscus*).

Supplementary Data SD2.—Map of proportion of total identifications classified by each method (qDFA or Kaleidoscope) at plots as hoary bats (*Lasiurus cinereus*).

Supplementary Data SD3.—Map of proportion of total identifications classified by each method (qDFA or Kaleidoscope) at plots as little brown myotis (*Myotis lucifugus*).

Supplementary Data SD4.—Map of proportion of total identifications classified by each method (qDFA or Kaleidoscope) at plots as silver-haired bats (*Lasionycteris noctivagans*).

Supplementary Data SD5.—Map of proportion of total identifications classified by each method (qDFA or Kaleidoscope) at plots as eastern red bat (*Lasiurus borealis*).

Supplementary Data SD6.—Map of proportion of total identifications classified by each method (qDFA or Kaleidoscope) at plots as northern long-eared myotis (*Myotis septentrionalis*).

Supplementary Data SD7.—Map of proportion of total identifications classified by each method (qDFA or Kaleidoscope) at plots as tri-colored bats (*Perimyotis subflavus*).

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