



Applying mobile acoustic surveys to model bat habitat use across sinuous routes

Vanessa G. Rojas¹  | Susan C. Loeb²  | Joy M. O'Keefe¹ 

¹Center for Bat Research, Outreach, and Conservation, Indiana State University, 600 Chestnut Street, Terre Haute, IN 47809, USA

²United States Department of Agriculture Forest Service, Southern Research Station, 233 Lehotsky Hall, Clemson University, Clemson, SC 29634, USA

Correspondence

Vanessa G. Rojas, State University of New York, College of Environmental, Science and Forestry, The Ranger School, 257 Ranger School Rd., Wanakena, NY 13695, USA.
Email: vanessaxrojas@gmail.com

Present address

Vanessa G. Rojas, State University of New York, College of Environmental Science and Forestry, The Ranger School, 257 Ranger School Road, Wanakena, NY 13695, USA.
Joy M. O'Keefe, University of Illinois at Urbana-Champaign, 1102 South Goodwin Avenue, Urbana, IL 61801, USA.

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Abstract

Mobile acoustic surveys allow estimates of overall bat activity, relative abundance, and species richness across large areas. Protocols for estimating relative abundance recommend using non-sinuous routes to ensure individual bats are only recorded once. We conducted mobile acoustic surveys along 12 sinuous routes in the mountainous terrain of northeastern Tennessee. Our objectives were to 1) determine if more calls were recorded in sinuous segments of mobile survey routes, thus violating assumptions of mobile surveys, and 2) analyze mobile transect data to assess bat habitat use. To test for effects of road sinuosity, we divided transects into ~1.6-km segments, calculated a sinuosity value, and summed the number of identified call files recorded for each segment. Using generalized linear models, we determined sinuosity did not affect the number of identified acoustic files. We assessed habitat use for 3 bat phonic groups (Low, Mid, *Myotis*), comparing 10 models with temporal detection and spatial occupancy covariates. Date were informative for all phonic groups. Low and mid-frequency bats were more likely to be detected on later survey dates within the summer, whereas *Myotis* bats had a higher probability of detection earlier within the season. As proportion of agriculture around the transect segment increased, probability of use by low-frequency bats decreased. The proportion of forest surrounding the transect segment had a positive effect on use by *Myotis* bats. No environmental covariates were informative regarding mid-frequency bats.

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We conclude that mobile acoustic surveys are an efficient method for gathering data on habitat use by bats. We recommend following guidelines set forth by the North American Bat Monitoring Program for mobile acoustic surveys but note that sinuosity of the route did not affect the number of calls recorded in our study; thus, we suggest that sinuous roads in mountainous terrain are appropriate for mobile acoustic transects.

KEYWORDS

bats, land cover, *Myotis*, occupancy modeling, sinuosity, Southern Appalachians

Bat populations in North America are declining due to multiple factors. White-nose syndrome, a disease that afflicts cave-hibernating bats, continues to spread across the continent, with confirmed presence in more than half of U.S. states and Canadian provinces (Frick et al. 2017, White-nose Syndrome Response Team 2018). In addition, bats experience direct fatalities due to wind turbines (Arnett and Baerwald 2013), and direct or indirect impacts from habitat loss and other anthropogenic factors (O'Shea et al. 2016). To assess population trends and bat-habitat relationships, it is important for resource managers to be able to efficiently monitor bats across large areas (e.g., national parks and forests). The North American Bat Monitoring Program (NABat) was developed to facilitate and organize large-scale, long-term monitoring of bats across the continent (Loeb et al. 2015). The NABat program provides guidelines for monitoring species with acoustic survey methods and includes factors to be considered when choosing the appropriate survey method.

Acoustic monitoring is a non-invasive approach recommended by NABat that requires less labor per survey site than mist netting. With acoustics, biologists can survey sites that are impractical for capture surveys (e.g., open areas or well-traveled roads). Stationary acoustic surveys require minimal time and effort in the field, as acoustic equipment can be deployed and left to record automatically. Yet, stationary acoustic surveys only record at one specific location and do not provide specific data on population size (Weller 2007; but see Kloepper et al. 2016 for using acoustic data to estimate population size for cave-dwelling colonies). In addition, assessing bat habitat preferences across a large, heterogenous landscape with stationary detectors requires ample time, effort, and equipment.

As an alternative to stationary methods, some researchers have applied mobile acoustic surveys (e.g., cycling, driving), which can cover large areas and yield an estimate of population size (Roche et al. 2011, Tonos et al. 2014). With mobile acoustic transects for which the vehicle is moving at 32 km/h, a speed faster than most bats typically fly (Patterson and Hardin 1969, Studier and Howell 1969, de la Cueva Salcedo et al. 1995), we assume that one call file represents one individual bat (Tonos et al. 2014, Loeb et al. 2015). However, we suspect on a sinuous route it might be possible to pick up the same bat twice if it cuts across the route and intersects other parts of the route. Mobile acoustic surveys facilitate sampling in residential (D'Acunto et al. 2018) and urban areas (Li and Wilkins 2014) and provide a more accurate measure of bat activity than stationary acoustic surveys in semi-arid, open landscapes (Fisher-Phelps et al. 2017). When compared to stationary acoustic surveys, mobile surveys may be more cost effective (Whitby et al. 2014), allowing researchers to sample a wider variety of habitat types within one night, while also obtaining an overall index of activity, density, and richness (Roche et al. 2005). With mobile acoustic data, activity and habitat use can be compared across time and space.

As with other acoustic survey methods, mobile acoustic transects have limitations, such as concerns about unequal detectability as some species are more likely to be detected along roads (e.g., *Tadarida brasiliensis* in Texas,

USA; Fisher-Phelps et al. 2017) and others are less likely to be detected (e.g., *Myotis* spp. in South Carolina, USA; Neece et al. 2019). Some bats may avoid roads while others are attracted to them, particularly forest roads (Zurcher et al. 2010, Loeb and O'Keefe 2011, Bennett and Zurcher 2013). In addition, high-frequency echolocation calls attenuate more rapidly than low- or mid-frequency calls and, thus, high-frequency bats foraging along road sides may not be detected from a vehicle (Tonos et al. 2014). Braun de Torrez et al. (2017) noted that stationary surveys may be more effective for assessing composition of the local bat assemblage in places where road access is limited. Wind and other noise associated with surveys from a moving vehicle could yield poor quality call files identifiable only to guild, but in some environments mobile surveys yield more identifiable calls (Tonos et al. 2014, Whitby et al. 2014). Even if call files are not identifiable to species, they can be classified to phonic group (Kaiser and O'Keefe 2015a) and are still useful for identifying important conservation areas (Luck et al. 2013) and population trends (Roche et al. 2011).

When the aim is to estimate relative abundance, Britzke and Herzog (2009) recommend conducting mobile acoustic surveys in a straight line and in one direction. However, in mountainous terrain, roads are often curved. When the road is not a straight line, the assumption that one call file equals one individual bat could be invalid. North American Bat Monitoring Program guidelines suggest that if a route is curved, points along opposite sides of these curved sections should be >100 m apart (Loeb et al. 2015). Ensuring survey points are >100 m apart is not always feasible in mountainous terrain. If we exclude sinuous roads, we may be unable to adequately assess trends, occupancy, and habitat relationships for bats using mobile transects.

We applied data from mobile acoustic transect surveys in the northern districts of the Cherokee National Forest in northeastern Tennessee to assess the relative effects of land-cover types on the habitat use of 3 phonic groups of bats. Many of the mobile transects were conducted on roads that climbed steep grades on the sides of mountains and contained many vertical curves. Thus, we tested the effects of road sinuosity on the number of call files recorded within transect segments during a mobile transect survey to determine if sinuous roads should be used in NABat monitoring. We predicted that road sinuosity within a segment would inflate the number of call files recorded. In northeastern Tennessee, there was a regular juxtaposition of agriculture, forest, and developed areas and there are few data on habitat associations for bats. Northeastern Tennessee hosts at least 12 species of bats (Appendix A), including several *Myotis* species, and low- and mid-frequency bats (Bernard et al. 2020). Although *Myotis* bats may be detected less frequently than other phonic groups overall, we predicted that these forest-adapted, high-frequency echolocators would most often use forested areas (Loeb and O'Keefe 2011, Altringham and Kerth 2016). In contrast, we predicted that bats in the low-frequency phonic group would be found more often in open areas (agriculture/pasture land; Lee and McCracken 2002, Loeb and O'Keefe 2011) and in developed regions because big brown bats (*Eptesicus fuscus*) and Mexican free-tailed bats (*Tadarida brasiliensis*) often use anthropogenic roosts (e.g., buildings, bridges; Brigham and Fenton 1986, McCracken et al. 2018). Mid-frequency bats, most likely to be eastern red bats (*Lasiurus borealis*) in our study area (Rojas et al. 2019), are adept at navigating in both cluttered and open areas (Furlonger et al. 1987, Elmore et al. 2005, Loeb and O'Keefe 2011); thus, we predicted we would find them using both forested and agricultural landscapes. We recorded a low number of calls per phonic group in each transect segment, so we modeled occupancy rather than abundance.

STUDY AREA

Our study was conducted in a 7-county region that encompasses the northern ranger districts of the Cherokee National Forest (NCNF) in northeast Tennessee (Figure 1). The 140,350 hectares of the NCNF are within the southern Appalachian Mountains. Mobile transect routes ranged in elevation from 241 to 1482 m (\bar{x} = 679 m) above sea level and were composed of approximately 37% hardwood forest (no conifer component), 11% forest with conifer, 36% agriculture, and 11% development. The major forest type was chestnut oak (*Quercus montana*), with oak (*Quercus*)-yellow pine (*Pinus* subgenus *Diploxylon*) and poplar (*Liriodendron*)-oak components (Southeast Gap

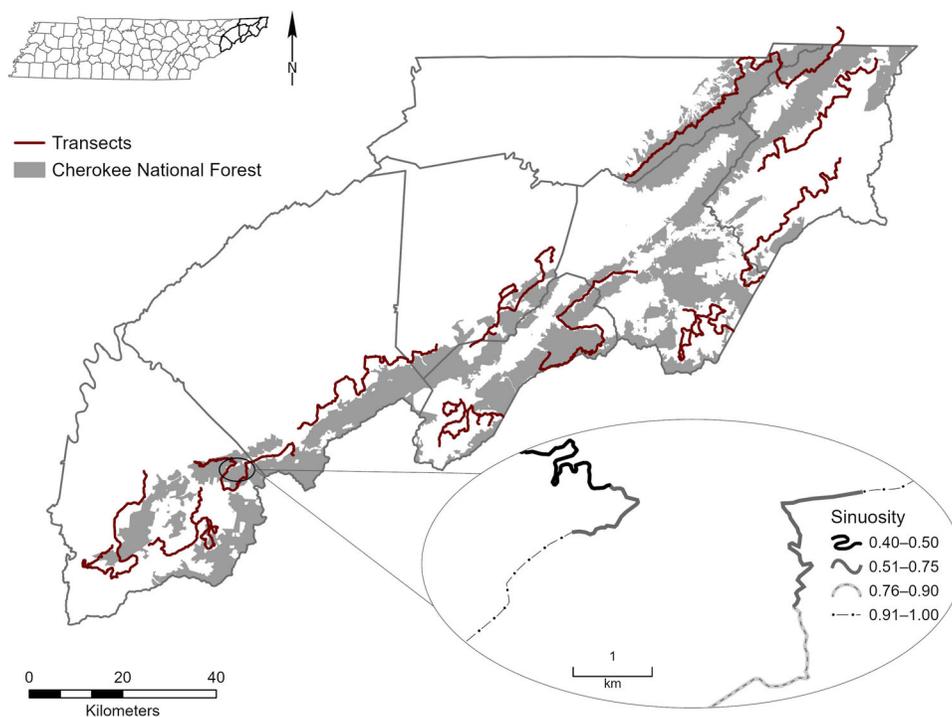


FIGURE 1 Twelve mobile acoustic transects in a 7-county region in northeastern Tennessee, USA, were surveyed during June and July 2014–2015. One transect ended in Virginia. Each transect was surveyed twice each year, for a total of 4 surveys per transect. The inset map shows segment sinuosity along one transect; lower values are more sinuous and higher values are more linear.

Analysis Project 2014; Appendix B). Agricultural land surrounding the forest was mainly hay pasture. Anthropogenic development was more prominent in the northern region, but most was low- to moderate-intensity development (Southeast Gap Analysis Project 2014); the population in most towns was <5,000, but the largest city, Johnson City, was just over 66,000 (U.S. Census 2011).

METHODS

We established 12 mobile driving transects (T1–T12), each an average of 49 km in length (37–56 km; Figure 1). Five transects were in the southern portion (Unaka Ranger District) of the study area and 7 were in the northern portion (Watauga Ranger District). Transects were generally ≥ 6.5 km apart and did not intersect, excluding one transect that overlapped the end of another; we excluded the overlapping portion (11 km) from 1 of those 2 transects.

To create driving routes, we used ArcMap (v10.3.1; ESRI 2015), topographic maps, Garmin Basecamp™ software (v4.3.5, Garmin 2014), and Google Maps (Google 2014). We used U.S. Forest Service data to confirm roads were paved and accessible with low-clearance vehicles; we avoided sections of gravel longer than 1 km. We positioned routes to sample multiple land-cover types (2011 National Land Cover Data, 30-m resolution, USGS 2014). Use of Google Maps enabled us to cross-check routes before testing in the field, as sometimes these maps were the most up to date and highest image resolution of digital road views. After generating potential routes, we conducted trials during the day to assess the suitability, accessibility, safety, and length of the routes. Once we

confirmed transect suitability, we uploaded the route onto a GPS (Garmin nüvi 2555LMT) using Garmin Basecamp™ software to aid in navigation when conducting the survey.

To assess summer bat populations, transects were surveyed twice each year for 2 consecutive years (2014–2015) during June and July for a total of 4 surveys per transect. Surveys included pre- (June) and post-volancy (July) stages for juvenile bats born during the maternity season (Jones 2000). For all transects, we followed guidelines set forth by Britzke and Herzog (2009), who suggested the routes be driven at approximately 32 km/h and begin 30 minutes after sunset (start time ~21:15 EDT) on evenings suitable for bat activity (no rain or fog, wind ≤ 24 km/h, temperature $\geq 12^\circ\text{C}$). Transects were driven in the same direction each time (Britzke and Herzog 2009). Start and end points varied in terms of site characteristics but starting point characteristics were not the same for every transect. The second survey of each transect occurred approximately 3–4 weeks after the initial survey each year. We discarded data recorded when we pulled to the side to allow another vehicle to pass, or if we were off the transect due to a missed turn.

To record bat calls we used a Titley Anabat SD2 ultrasonic recording device (Titley Scientific, Columbia, MO, USA) with an Anabat Hi microphone mounted on the roof (oriented 0° from vertical and with the surface of the microphone 23 cm above the vehicle's surface). We connected and synced a GPS receiver (BR-35554; USGlobalSat, Inc., Chino, CA, USA) to the Anabat to record location coordinates every second.

Acoustic analyses

We used Bat Call Identification software (v2.7c, Bat Call Identification BCID 2016) followed by manual vetting to identify recorded call files to phonic group. Preliminary examination of the data using BCID indicated we recorded few calls identifiable to species and, therefore, we used the phonic group designations produced by the software. The software classifies call files mainly using 4 parameters: average minimum frequency (F_{\min}), slope, average frequency at the knee of the call (F_k), and duration (C. R. Allen, BCID, personal communication). For bats in the low-frequency group F_c (characteristic frequency of the pulse, typically equal to F_k , Gannon et al. 2004) was < 30 kHz, for mid-frequency F_c was 30–60 kHz, and *Myotis* were usually $F_c \geq 40$ kHz (Appendix A) with higher F_{\min} , steeper slope, and shorter duration than other phonic groups. To identify calls to phonic group, we required a 3-pulse minimum within 15 s, a 70% group confidence level, and minimum discriminant probability of 0.35 (Romeling et al. 2012, Kaiser and O'Keefe 2015a); otherwise, files were marked as unknown. Following BCID automated identifications, we manually vetted *Myotis* calls to confirm phonic group identification. To verify *Myotis* identifications, both V. Rojas and J. O'Keefe independently assessed all files marked as *Myotis* by BCID (Romeling et al. 2012, Braun de Torrez et al. 2017). We kept the *Myotis* designation for files which we agreed upon and marked all others as unknown. We excluded files that BCID could not clearly assign to phonic group from all analyses.

Environmental data

We recorded temperature ($^\circ\text{C}$) and the Beaufort wind scale value (Barua 2005) at the start and end of each transect. We averaged start and end temperatures for the temperature detection covariate used in our occupancy analysis. We used ArcMap (v10.3.1; ESRI 2015) to reclassify National Land Cover Data into 3 dominant land-cover types (agriculture, development, forest; Appendix B). Road transect points were often classified as developed non-concrete open space, but this designation ignored land cover adjacent to the road; hence, we excluded the developed non-concrete land-cover type from our analysis.

We divided each transect into 30 segments using the Split tool in ArcMap. Segments averaged 1.6 km, ranging from 1.2 to 1.9 km. All segments were used in our sinuosity analysis; however, to limit the influence of spatial autocorrelation in our occupancy analysis we systematically selected alternating segments for each transect

(Russ et al. 2003). We added a 250-m buffer to each side of the segment and calculated the proportion of forest and agriculture within the buffer area (Appendix B). If alternating segment buffers overlapped due to a curve along the transect, we randomly selected one segment to exclude from the analysis, with a final count of 162 segments in our occupancy analysis. For each segment, we measured the distance from the center point of the segment to the nearest city or town boundary (m; Tennessee Department of Finance and Administration 2017) and nearest lake or river (m; hereafter, water; U.S. Geological Survey Hydrography 2013). All transect segments were relatively close to streams (average of 200 m away); therefore, we only included navigable lakes and river water bodies for the water covariate. We calculated the mean elevation (m) for each segment using GPS data points collected during the survey.

Statistical analyses

Sinuosity

Using the Calculate Sinuosity Python code add-on tool (ESRI 2011), we calculated the sinuosity value of every segment on every transect. We used generalized linear mixed models (lme4 package; Bates et al. 2015) in R (v3.3.2; R Core Team 2015) to test the effects of sinuosity on the number of acoustic files identified to phonic group. Due to inadequate call file numbers per segment (Low \bar{x} = 2.6 call files per segment, Mid \bar{x} = 2.1, *Myotis* \bar{x} = 0.3), we did not analyze separate models for each phonic group and instead grouped all files for the sinuosity analysis. We compared 3 models for which the response variable was the number of acoustic files per segment (count); each model included transect as a random effect (intercept). In Models 1 and 2, the slope was set equal to 1. The simplest model, Model 1, had no fixed effects [count ~ (1 | transect)]. In Model 2, sinuosity was a fixed effect [count ~ sinuosity + (1 | transect)]. In Model 3, we modeled sinuosity as a fixed effect and with slope \neq 1 [count ~ sinuosity + (sinuosity | transect)]. When we assumed a Poisson distribution in our models, we detected significant overdispersion and, hence, we ran our final models with a negative binomial distribution, which assumes conditional means \neq conditional variance (Lindén and Mäntyniemi 2011). After running the models, we conducted an analysis of variance in R to test the 3 negative binomial distribution models against one another and present chi-squared values to compare model significance.

Habitat use

We used occupancy models rather than conducting an analysis of relative abundance because most segments had ≤ 1 detection for each phonic group (Low, Mid, *Myotis*). For each phonic group, we created a binary detection history (1 = detected, 0 = not detected) for the segment and each of the 4 surveys. We considered a phonic group present along a segment if ≥ 1 call file was detected. Noting that bats might randomly occupy the transects we surveyed, we interpret modeled occupancy estimates as indicators of probability of habitat use (MacKenzie 2005). To facilitate comparisons of important predictors of habitat use among the phonic groups, we tested the same suite of probability of detection and occupancy covariates for each phonic group.

We developed hypotheses based on published literature (Furlonger et al. 1987, Jones 2000, Elmore et al. 2005, Loeb and O'Keefe 2011, Kaiser and O'Keefe 2015b) and selected covariates for probability of detection (p) and occupancy (ψ) models to test our hypotheses (MacKenzie et al. 2018). Temporal probability of detection covariates included mean temperature ($^{\circ}\text{C}$), day of the year, and year (2014 or 2015). We expected more detections on warmer nights (Kaiser and O'Keefe 2015b). We did not include other weather covariates, as we only conducted surveys during times of low wind and no precipitation. We used day of year as a detection covariate, expecting more detections once juveniles were volant later in the year (Jones 2000). We tested single-season occupancy

models with year as a detection covariate to account for interannual variation. Initially, we tested year as an occupancy covariate, however year produced unreliable parameter estimates and lowered model weights; therefore, we excluded year from our final occupancy analyses. We did not detect any significant changes in available habitat from 2014 to 2015 and, thus, we did not expect occupancy to vary by year over our study. We chose single-season occupancy models rather than multiple-season models because our objective was to assess patterns of habitat use within season, we had limited temporal replication, and we were not interested in occupancy dynamics (i.e., extinction and colonization; Fuller et al. 2016). To test for covariate correlation, we used Spearman's rank tests (R v3.3.2; R Core Team 2015) and visually assessed plots. Detection covariates were not highly correlated ($|r| < 0.2$).

We used the following spatial covariates in our occupancy models: proportion of forest and proportion of agriculture in the 250-m buffer surrounding the segment, distance to lakes/streams (m; water), distance to city or

TABLE 1 Ranked Akaike's Information Criterion (ΔAIC_c), model weights (w_i), and number of model parameters (K) for 6 detection models per phonic group for bat acoustic data collected during 12 mobile transect surveys in northeastern Tennessee, USA, June to July 2014–2015. We tested each detection model with a 3-variable occupancy (ψ) model containing proportion of forest in a 250-m buffer on each side of the road (for), distance to city boundary (m, city), and mean elevation (m, elev). Probability of detection (p) covariates were temperature (temp), day of year (date), and year. The null model lacked detection covariates.

Model	ΔAIC_c	w_i	K
Low			
ψ (for + city + elev), p (temp + date + year)*	0	0.63	8
ψ (for + city + elev), p (date)*	1.85	0.25	6
ψ (for + city + elev), p (date + year)	3.31	0.12	7
ψ (for + city + elev), p (temp)	18.9	<0.001	6
ψ (for + city + elev), p (year)	19.24	<0.001	6
ψ (for + city + elev), p (.)	19.51	<0.001	5
Mid			
ψ (for + city + elev), p (date + year)*	0	0.71	7
ψ (for + city + elev), p (temp + date + year)*	1.99	0.26	8
ψ (for + city + elev), p (date)	6.83	0.02	6
ψ (for + city + elev), p (year)	9.13	0.007	6
ψ (for + city + elev), p (.)	20.65	<0.001	5
ψ (for + city+elev), p (temp)	21.37	<0.001	6
Myotis			
ψ (for + city + elev), p (date)*	0	0.40	6
ψ (for + city + elev), p (date + year)*	0.68	0.28	7
ψ (for + city + elev), p (temp + date+year)*	0.84	0.26	8
ψ (for + city + elev), p (.)	5.48	0.02	5
ψ (for + city + elev), p (year)	5.93	0.02	6
ψ (for + city + elev), p (temp)	6.99	0.01	6

*Plausible set.

town (m; all $\leq \sim 66,000$), and elevation (m). Two pairs of covariates were correlated: proportion of forest and agriculture ($|r| > 0.49$, $P < 0.001$), and distance to water and elevation ($|r| > 0.5$, $P < 0.001$). We did not include the correlated variables in the same models. We normalized all spatial covariates using the `normalize` function in program `Presence` (v.12.17, v.13.13; Hines 2016).

Using `Presence` (Hines 2016), we fit 6 probability of detection models, each with 1–3 detection covariates and a set of 3 non-correlated occupancy covariates (MacKenzie et al. 2018); we also tested a null model (Table 1). We required models to have substantial support ($\Delta AIC_c \leq 2.0$) to be included in the plausible set. From plausible models, we identified informative detection covariates as those for which 85% confidence intervals for parameter estimates did not cross zero (Arnold 2010); informative covariates were used in occupancy models. For low-frequency bats, date was in both plausible detection models and temperature was only in one model (Table 1); given that warmer nights occur later in the summer, we opted to use only date as a detection covariate in occupancy models. Date and year were in both plausible detection models for mid-frequency bats, and both were retained as detection covariates. For *Myotis* bats, date was in all 3 plausible models and year was in 2 of 3 plausible models. There was model uncertainty and the effect of year was ambiguous; therefore, we only retained date as a detection covariate.

For each phonic group, we fit 10 probability of occupancy models with 1–3 covariates each, plus a null model (Table 3). We followed the same requirements described above for models to be included in the plausible set of models. To identify important factors predicting habitat use, we evaluated estimates for parameters in plausible models (Burnham and Anderson 2002; Table 4). A parameter was considered important if the 85% confidence interval values of the parameter estimate did not cross zero. We present means ± 1 standard error where appropriate.

RESULTS

We drove 2,328 km total in 73 hours of active surveying. Over the entire length of all transects, most call files recorded were in the low-frequency group (51% of all files), followed by the mid-frequency group (42%), and *Myotis* (7%; Appendix C). Transects T3, T2, T1, and T5 had the highest activity; all had ≥ 75 call files for at least one transect survey night or nearly 2 bat call files/km. Although *Myotis* detections were low overall, T1 and T2 had the highest *Myotis* activity (0.4 and 0.5 call files/km, respectively; Appendix C). On average, we identified 5 call files per segment (range 0–23).

Sinuosity

Segment sinuosity ranged from 0 to 1 ($\bar{x} = 0.77$), with the segment being straighter as the value approached 1 (Figure 1). Across all transects, the mode for sinuosity within a segment ranged from 0.53 (T5) to 0.95 (T4) and the mean sinuosity by segment ranged from 0.71 (T3) to 0.89 (T4). Sinuosity did not affect the number of calls recorded in each segment, as there was no significant difference between the model that did not account for sinuosity (Model 1) and models that did (Model 2 $\chi^2_{(4)} = 0.5472$; Model 3 $\chi^2_{(6)} = 0.5053$). As models did not differ, we did not consider sinuosity in the detection and occupancy analyses.

Probability of detection and use

Low-frequency phonic group

For low-frequency bats, date had a clear, positive effect in both models (Table 2). The probability of detecting low-frequency bats was higher later in the summer, and survey-specific detection estimates were 0.21–0.61 in the top-ranked occupancy model. Proportion of agriculture was a covariate in all 3 plausible occupancy models (Table 3)

TABLE 2 Estimates, standard errors (SE), and 85% confidence levels for parameters in plausible probability of detection models (see Table 1). Date was important for all phonic groups as 85% confidence intervals for this parameter did not cross zero.

Model	Intercept		Temp Estimate		Date Estimate		Year Estimate	
	Estimate	SE	(85% CI)	SE	(85% CI)	SE	(85% CI)	SE
Low-frequency								
ψ (for + city+elev), p(temp + date+year)	-8.81	1.41	0.28 (0.12-0.43)	0.11	0.68 (0.50-0.87)	0.13	0.26 (-0.01-0.54)	0.19
ψ (for + city+elev), p(date)	-6.47	1.12			0.69 (0.51-0.87)	0.13		
Mid-frequency								
ψ (for + city+elev), p(date + year)	-5.24	1.03			0.50 (0.33-0.67)	0.12	0.54 (0.28-0.80)	0.18
ψ (for + city+elev), p(temp + date+year)	-5.32	1.33	0.01 (-0.14-0.17)	0.11	0.50 (0.33-0.67)	0.12	0.55 (0.27-0.82)	0.19
Myotis-frequency								
ψ (for + city+elev), p(date)	6.75	2.52			-1.04 (-1.47- -0.62)	0.29		
ψ (for + city+elev), p(date + year)	5.89	2.52			-0.97 (-1.39- -0.56)	0.29	0.49 (-0.13-1.12)	0.43
ψ (for + city+elev), p(temp + date+year)	2.61	3.44	0.40 (0.003-0.79)	0.27	-1.00 (-1.44- -0.56)	0.30	0.73 (0.06-1.39)	0.46

and was the only informative covariate (Table 4). As the proportion of agriculture within a 250-m buffer around the transect segment increased, the probability of use by low-frequency bats decreased (Figure 2A).

Mid-frequency phonic group

For mid-frequency bats, the estimated effects of date and year were similar (Table 2). The probability of detecting mid-frequency bats was higher later in the summer and during the second year of surveys; detection estimates were 0.23–0.58 in the top-ranked occupancy model. All occupancy models had low AIC_c weight (≤ 0.17) and there was uncertainty as to the best model, as 8 of 11 models were plausible based on ΔAIC_c values, including the null model (Table 3). Further, none of the parameters were informative regarding habitat use by mid-frequency bats (Table 4).

Myotis phonic group

For *Myotis* bats, date had a clear negative effect (Table 2). In contrast to what we observed for low and mid-frequency bats, we were less likely to detect *Myotis* bats on later survey dates within a season. Detection estimates for *Myotis* bats were 0.03–0.30 in the top-ranked occupancy model. We excluded 2 models (city and agriculture + water + city) from model comparisons and rankings due to convergence failures and negative standard errors; this problem likely arose due to the overall low detection rates for *Myotis*. Although there were 8 plausible occupancy models containing various parameters (Table 3), forest was the only informative parameter (Table 4). The proportion of forest within a 250-m buffer surrounding the transect segment had a positive effect on habitat use by *Myotis* bats (Figure 2B).

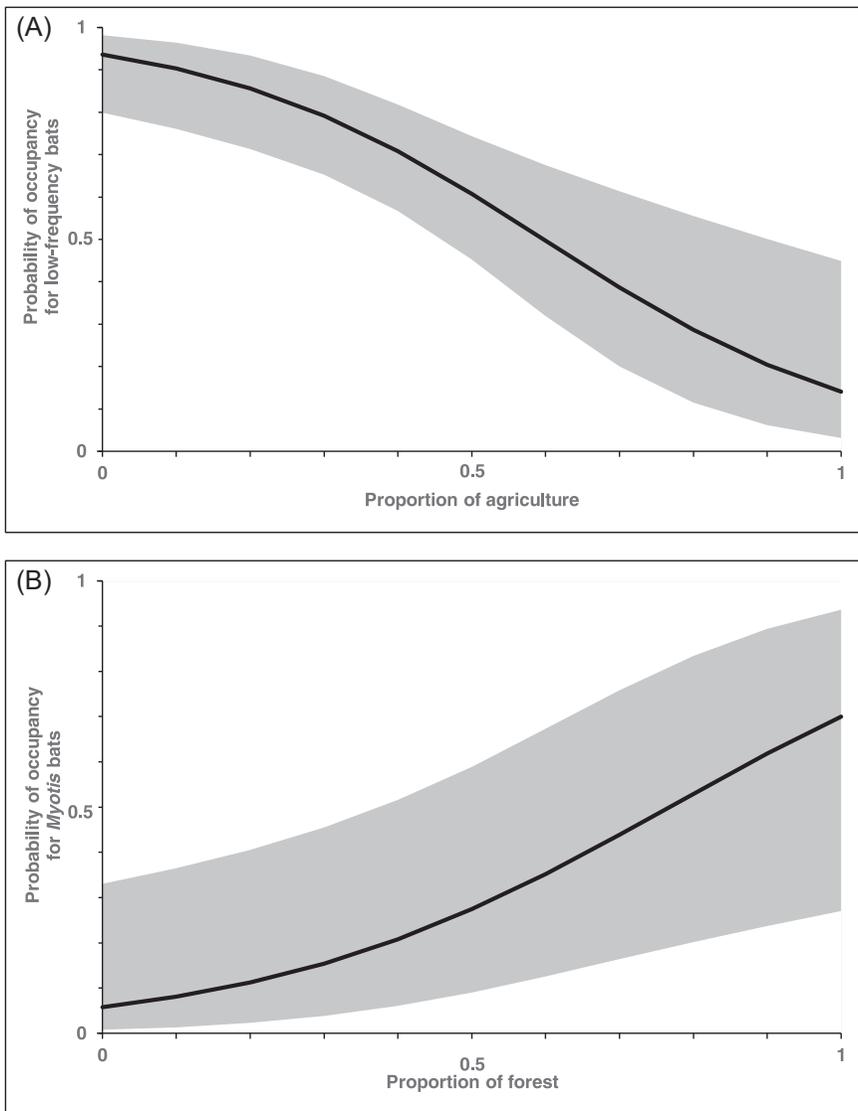


FIGURE 2 Proportion of agriculture within a 250-m buffer around transect segments, an important predictor of habitat use for low-frequency bats, is shown as non-normalized values in relation to probability of occupancy estimates for the highest ranked model (A). Proportion of forest within a 250-m buffer around transect segments, an important predictor of habitat use for *Myotis* bats, is shown as non-normalized values in relation to probability of occupancy estimates for the highest ranked model (B). Occupancy analyses were based on acoustic data from mobile transect surveys in northeastern Tennessee, USA, June to July 2014–2015.

DISCUSSION

Surveying bats across mountainous terrain introduces many challenges. Mobile acoustic surveys, paired with occupancy modeling, offer an efficient way to assess the temporal and spatial patterns of habitat use by bats in large, rugged landscapes. Dividing transects into segments, as demonstrated by Roche et al. (2011) and Fisher-Phelps et al. (2017), allows an assessment of land-cover effects. We showed that sinuosity did not affect the number of call files detected, which should assuage concerns about conducting mobile transects in mountainous terrain. For *Myotis* and

TABLE 3 Ranked Akaike's Information Criterion (ΔAIC_c), model weights (w_i), and number of model parameters (K) for 11 occupancy models per phonic group for bat acoustic data collected during 12 mobile transect surveys in northeastern Tennessee, USA, June to July 2014–2015. We tested these occupancy (ψ) covariates using data for alternating transect segments: proportion of forest (for) and agriculture (ag) in a 250-m buffer on each side, distance to city boundary (m; city) and nearest lake or river (m; water), and mean elevation (elev). Day of year (date) was a detection (p) covariate in each model; year was also included in mid-frequency bat models. Null models lacked occupancy covariates.

Model	ΔAIC_c	w_i	K
Low			
ψ (ag + water), p (date)*	0	0.38	5
ψ (ag), p (date)*	0.10	0.36	4
ψ (ag + water+city), p (date)*	0.88	0.25	6
ψ (for + water), p (date)	10.22	<0.01	5
ψ (for), p (date)	10.97	<0.01	4
ψ (for + elev), p (date)	11.15	<0.01	5
ψ (for + city+elev), p (date)	12.81	<0.01	6
ψ (city), p (date)	13.98	<0.01	4
ψ (.), p (date)	15.17	<0.01	3
ψ (elev), p (date)	15.38	<0.01	4
ψ (water), p (date)	15.95	<0.01	4
Mid			
ψ (.), p (date + year)*	0	0.17	4
ψ (water), p (date + year)*	0.29	0.15	5
ψ (ag), p (date + year)*	0.49	0.14	5
ψ (ag + water), p (date + year)*	0.71	0.12	6
ψ (for), p (date + year)*	1.2	0.10	5
ψ (for + water), p (date + year)*	1.39	0.09	6
ψ (elev), p (date + year)*	1.66	0.08	5
ψ (city), p (date + year)*	1.96	0.06	5
ψ (ag + water+city), p (date + year)	2.63	0.05	7
ψ (for + elev), p (date + year)	3.02	0.04	6
ψ (for + city+elev), p (date + year)	5.01	0.01	7
Myotis			
ψ (for), p (date)*	0	0.35	4
ψ (for + water), p (date)*	0.97	0.21	5
ψ (for + elev), p (date)*	1.99	0.13	5
ψ (ag), p (date)	2.39	0.10	4

(Continues)

TABLE 3 (Continued)

Model	ΔAIC_c	w_i	K
ψ (for + city+elev), p (date)	2.78	0.09	6
ψ (ag + water), p (date)	3.56	0.06	5
ψ (.), p (date)	4.64	0.03	3
ψ (elev), p (date)	6.18	0.02	4
ψ (water), p (date)	6.31	0.01	4

*Plausible set.

mid-frequency bats, habitat use followed our predictions based on ecomorphology (Norberg and Rayner 1987), but this was not true for low-frequency bats.

Sinuosity of a transect segment did not affect the number of call files detected. Transects had varying degrees of sinuosity but dividing transects into segments allowed the issue of sinuosity to be addressed more precisely. There is concern that surveys conducted on sinuous routes risk detecting an individual bat more than once, thus inflating the number of calls in sinuous segments and reducing the efficacy of mobile transects for estimating bat abundance in mountainous terrain (Britzke and Herzog 2009, Loeb et al. 2015). However, in our study, sinuous segments did not have inflated numbers of call files relative to straighter segments. We recommend additional testing of mobile transects along sinuous routes in other landscapes.

Probability of detection estimates along segments in top occupancy models were higher for low- and mid-frequency bats than for *Myotis* bats. Date (day of year) was an informative detection parameter for all phonic groups. We expected detections to be higher later in the summer due to the presence of volant young of the year (Jones 2000). Low- and mid-frequency bat detections were higher later in the summer; however, we were less likely to detect *Myotis* later in summer. Lower detection rates for *Myotis* bats could be related to within-summer declines in *Myotis* bats, as was observed for a population of little brown bats (*Myotis lucifugus*) affected by white-nose syndrome (Reichard and Kunz 2009). Year also had a positive effect on detection of mid-frequency bats. There was no apparent explanation for the differences among years, as temperatures and captures of mid-frequency bats were similar between years during a concurrent study (average 21°C and 20 bats vs. 22°C and 23 bats in 2014 and 2015, respectively, Rojas et al. 2019). In that study (2013–2015), nearly all mid-frequency captures were eastern red bats (*Lasiurus borealis*, $n = 94$), except 4 eastern tri-colored bats (*Perimyotis subflavus*). We agree with Li and Wilkins (2014) and Loeb et al. (2019) that it may be important to conduct surveys at least twice each year to account for within-season variation in detection.

Complete transects passed through multiple land-cover types but dividing transects into segments allowed us to assess the effects of land cover on habitat use and to reduce spatial autocorrelation bias. We used an average segment length (1.6 km) that was equal to segment length for mobile surveys in Ireland (Roche et al. 2011); their approach was to survey 15 individual 1.6-km segments from a 24-km survey. Future studies could consider how varying segment lengths affect the perceived relationship between land cover and habitat use.

Factors that affected habitat use largely matched our expectations based on ecomorphology, although this was not the case for low-frequency bats. Capture data from a concurrent study showed that big brown bats were the most common low-frequency bat in our study area (Rojas et al. 2019). We expected that proportion of open area would have a positive effect on low-frequency bat use, but in fact low-frequency bats were less likely to occupy segments with higher proportions of agricultural land cover (mainly pastureland in this region). Our results are consistent with the negative effect of cultivated crops on big brown bat acoustic activity in North Carolina (Li et al. 2019). Low-frequency bats may avoid agricultural areas if such areas are void of suitable roosting habitat

TABLE 4 Estimates, standard errors (SE), and 85% confidence levels (CI) for parameters in plausible probability of occupancy models (see Table 3). Agriculture was the only important parameter for low-frequency bats and forest was the only important parameter for *Myotis*, as 85% confidence intervals did not cross zero for either parameter. No parameters were important for mid-frequency bats.

Model	Intercept		Forest		Agriculture	
	Estimate	SE	Estimate (85% CI)	SE	Estimate (85% CI)	SE
Low-frequency						
ψ (ag + water), p (date)	1.84	0.47			-1.06 (-1.51- -0.61)	0.31
ψ (ag), p (date)	1.74	0.43			-1.02 (-1.46- -0.56)	0.31
ψ (ag + water+city), p (date)	1.85	0.49			-1.01 (-1.45- -0.56)	0.31
Mid-frequency						
ψ (.), p (date + year)	1.88	0.42				
ψ (water), p (date + year)	1.91	0.44				
ψ (ag), p (date + year)	1.96	0.54			0.57 (-0.37-1.51)	0.65
ψ (ag + water), p (date + year)	2.01	0.57			0.62 (-0.39-1.62)	0.70
ψ (for), p (date + year)	1.88	0.43	-0.32 (-0.88-0.24)	0.39		
ψ (for + water), p (date + year)	1.92	0.45	-0.34 (-0.89-0.22)	0.38		
ψ (elev), p (date + year)	1.87	0.42				
ψ (city), p (date + year)	1.88	0.42				
<i>Myotis</i> group						
ψ (for), p (date)	-0.37	0.75	0.94 (0.34-1.54)	0.42		
ψ (for + water), p (date)	-0.05	1.21	1.14 (0.15-2.13)	0.69		
ψ (for + elev), p (date)	-0.37	0.77	0.94 (0.29-1.59)	0.45		
Model	Water		City		Elevation	
	Estimate (85% CI)	SE	Estimate (85% CI)	SE	Estimate (85% CI)	SE
Low-frequency						
ψ (ag + water), p (date)	0.40 (-0.03-0.83)	0.30				
ψ (ag), p (date)						
ψ (ag + water+city), p (date)	0.38 (-0.05-0.82)	0.30	0.30 (-0.12-0.72)	0.29		
Mid-frequency						
ψ (.), p (date + year)						
ψ (water), p (date + year)	-0.40 (-0.84-0.04)	0.31				
ψ (ag), p (date + year)						
ψ (ag + water), p (date + year)	-0.41 (-0.86-0.04)	0.31				
ψ (for), p (date + year)						
ψ (for + water), p (date + year)	-0.41 (-0.85-0.03)	0.31				
ψ (elev), p (date + year)					-0.17 (-0.58-0.23)	0.28
ψ (city), p (date + year)			-0.06 (-0.53-0.41)	0.33		
<i>Myotis</i> group						
ψ (for), p (date)						
ψ (for + water), p (date)	-0.53 (-1.64-0.58)	0.77				
ψ (for + elev), p (date)					-0.003 (-0.39-0.39)	0.27

(Brigham and Fenton 1986) and far from preferred patches of roosting habitat. Low-frequency bats may favor foraging along road corridors within forested areas because such edge habitat is uncluttered relative to the forest interior but offers similar insect abundance to the forest (Grindal and Brigham 1999).

As expected, mid-frequency bats, which were most likely to be eastern red bats in our study area, were detected across a variety of land-cover types; however, we did not identify any informative parameters regarding habitat use. Eastern red bats are capable of foraging in a variety of land-cover types (Furlonger et al. 1987), with varying preferences dependent upon the landscape context. For example, in an intensively managed pine landscape in Mississippi, eastern red bats do not show a preference for stand type, given the options of young and open pine, closed canopy pine, thinned pine, unmanaged mixed pine/hardwood, and mature pine/hardwood (Elmore et al. 2005). In southwestern Ontario, eastern red bats are more active in forests and fields than over open water (specific feature types not specified; Furlonger et al. 1987), while in forests in Kentucky, eastern red bats forage over aquatic habitat (streams, ponds, and lakes) more often than expected (Hutchinson and Lacki 1999). Probability of habitat use by *Myotis* increased with higher proportions of forest in transect segments. Increased use was expected for these clutter-adapted species, as *Myotis* bats tend to forage in more forested areas (Henderson and Broders 2008, Loeb and O'Keefe 2011).

We were not able to use individual species identifications but instead based our analyses on phonic groups. In areas where bats are difficult to detect and calls may be poor quality (e.g., highly cluttered areas), the use of phonic groups may be a more feasible approach. The use of phonic groups allows the use of less conservative call identification settings (e.g., using a 3-pulse rather than 5-pulse minimum per call file) and enables a surveyor to quickly parse calls into groups. Our approach allows resource managers to quickly identify areas where a phonic group of interest is present, following up with acoustic, mist net, or roost surveys. For example, the majority of *Myotis* detections on our mobile surveys were aggregated along certain segments of just a few transects, mainly in the more forested southwestern region of the NCF. Mist net surveys confirmed *Myotis* presence near some of these segments (Rojas et al. 2019), but detections along other segments point to potential sites for future mist net surveys.

MANAGEMENT IMPLICATIONS

Mobile transects are an efficient way to survey a relatively large landscape and can be used in areas with a mixture of private and public lands. Further, mobile transect surveys allow the estimation of relative abundance whereas individual point surveys do not (e.g., Evans et al. 2021). Estimating relative abundance may be impossible when bat detections are particularly low. In such cases occupancy modeling may be a viable alternative. When mobile acoustic surveys are conducted across a range of land-cover types, occupancy models can be used to assess general bat-habitat relationships. To account for temporal variation in detection probability, we recommend that surveys be conducted both early and late in the summer, and across multiple years. Because sinuosity of the route did not affect the number of calls recorded in our study, it is possible that sinuous roads in mountainous terrain can be included in future NABat monitoring efforts. Using mobile acoustic surveys to assess spatiotemporal patterns of habitat use by phonic groups or species in mountainous regions should aid in monitoring the status of bat populations and informing conservation decisions.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

We conducted our research under federal (ID: TE206872-9) and state (TN ID: 3148) permits following an Institutional Animal Care and Use Committee protocol (ID: 531861-4).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Vanessa G. Rojas  <https://orcid.org/0000-0003-0173-2708>

Susan C. Loeb  <https://orcid.org/0000-0002-9264-3614>

Joy M. O'Keefe  <https://orcid.org/0000-0001-9074-6268>

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APPENDIX A: PHONIC GROUPS

Species recorded during mobile acoustic transects in the northern ranger districts of the Cherokee National Forest, Tennessee, June to July 2014–2015. Data were assigned to phonic groups (Low, Mid, *Myotis*) based on average minimum frequency, slope, average frequency at the knee of the call, and duration using Bat Call Identification (v2.7c, BCID 2016) software. Bats that occur in this region are shown according to phonic group.

Phonic group	Scientific name	Common name
Low-frequency	<i>Corynorhinus rafinesquii</i>	Rafinesque's big-eared bat
	<i>Eptesicus fuscus</i>	Big brown bat
	<i>Lasionycteris noctivagans</i>	Silver-haired bat
	<i>Lasiurus cinereus</i>	Hoary bat
	<i>Tadarida brasiliensis</i>	Mexican free-tailed bat
Mid-frequency	<i>Lasiurus borealis</i>	Eastern red bat
	<i>Nycticeius humeralis</i>	Evening bat
	<i>Perimyotis subflavus</i>	Tri-colored bat
<i>Myotis</i> group	<i>Myotis grisescens</i>	Gray bat
	<i>Myotis leibii</i>	Eastern small-footed bat
	<i>Myotis lucifugus</i>	Little brown bat
	<i>Myotis septentrionalis</i>	Northern long-eared bat
	<i>Myotis sodalis</i>	Indiana bat

APPENDIX B: RECLASSIFIED LAND COVER

National Land Cover Database types reclassified as 3 dominant types found along mobile acoustic transects in the northern ranger districts of the Cherokee National Forest, Tennessee surveyed June to July 2014–2015.

Reclassified land-cover type	Original land-cover type
Agriculture	Pasture/Hay
	Row Crop
Developed	Developed, Low Intensity
	Developed, Medium Intensity
	Developed, High Intensity
Forest	Evergreen Plantation
	Southern Ridge and Valley Dry Calcareous Forest - Hardwood Modifier
	Northeastern Interior Dry Oak Forest-Hardwood Modifier
	Northeastern Interior Dry Oak Forest - Virginia/Pitch Pine Modifier
	Appalachian Hemlock-Hardwood Forest

Reclassified land-cover type	Original land-cover type
	Central and Southern Appalachian Spruce-Fir Forest
	Southern Appalachian Low Mountain Pine Forest
	Southern Piedmont Dry Oak-(Pine) Forest - Hardwood Modifier
	Southern Piedmont Dry Oak-(Pine) Forest - Mixed Modifier
	Southern Appalachian Montane Pine Forest and Woodland
	Central and Southern Appalachian Montane Oak Forest
	Central and Southern Appalachian Northern Hardwood Forest
	Allegheny-Cumberland Dry Oak Forest and Woodland - Hardwood Modifier
	Southern and Central Appalachian Oak Forest
	Southern and Central Appalachian Oak Forest - Xeric
	South-Central Interior Mesophytic Forest
	Southern and Central Appalachian Cove Forest

APPENDIX C: TRANSECT CALL FILE SUMMARY

Number of call files of Low, Mid, and *Myotis* phonic groups for each of 12 mobile acoustic transects in the northern ranger districts of the Cherokee National Forest, Tennessee, surveyed June to July 2014–2015. Transects were surveyed twice each year, early and late summer to account for pre- and post-volancy periods (A and B, respectively). Unidentified call files are labeled as unknown (Unkn).

Transect	2014					2015				
	Low	Mid	<i>Myotis</i>	Unkn	Total	Low	Mid	<i>Myotis</i>	Unkn	Total
T1-A	11	12	8	6	37	23	22	25	15	85
T1-B	14	22	1	7	44	12	20	6	10	48
T2-A	6	8	10	8	32	7	5	4	2	18
T2-B	35	21	10	2	68	27	20	21	14	82
T3-A	19	2	2	0	23	6	15	3	3	27
T3-B	85	35	2	1	123	93	13	0	4	110
T4-A	11	4	0	0	15	16	10	3	3	27
T4-B	15	20	0	2	37	22	26	0	4	50
T5-A	23	7	0	0	30	40	19	0	16	75
T5-B	24	29	2	4	59	39	25	0	5	69
T6-A	6	5	2	2	15	7	12	2	0	21
T6-B	22	3	2	5	32	35	19	2	3	59
T7-A	8	11	2	4	25	3	12	2	1	18
T7-B	0	2	0	0	2	4	23	2	4	33

(Continues)

Transect	2014					2015				
	Low	Mid	Myotis	Unkn	Total	Low	Mid	Myotis	Unkn	Total
T8-A	10	27	3	3	43	15	29	1	2	47
T8-B	22	38	7	5	72	24	24	3	1	52
T9-A	8	10	0	0	18	8	8	0	0	16
T9-B	21	13	2	4	40	35	32	0	3	70
T10-A	5	3	0	0	8	20	15	0	13	48
T10-B	10	13	0	1	24	17	34	0	2	53
T11-A	7	6	0	3	16	11	12	0	0	23
T11-B	8	10	0	1	19	14	22	0	23	59
T12-A	25	8	0	1	34	7	9	2	0	18
T12-B	15	6	0	0	21	28	20	0	1	49
Total	410	315	53	59	837	513	446	74	124	1157