Received: 2 March 2022 | Revised: 19 October 2022 | Accepted: 15 November 2022

DOI: 10.1002/jwmg.22364

NOTE

THE JOURNAL OF WILDLIFE MANAGEMENT

THE WILDLIFE SOCIETY

Modeling migration and movement of gray bats

Cory Holliday[1] | Joseph P. Wisby[2] | Piper L. Roby[3] | Stephen T. Samoray[4] | Jessica M. Vannatta[5]

[1]The Nature Conservancy of Tennessee, 750 Big Branch Road, Granville, TN 38564, USA

[2]The Nature Conservancy of Tennessee, 2 Maryland Farms, Suite 150, Brentwood, TN 37027, USA

[3]Copperhead Environmental Consulting, Inc, 471 Main Street, Paint Lick, KY 40461, USA

[4]Copperhead Environmental Consulting, Inc, 3908 Gallatin Pike, Nashville, TN 37216, USA

[5]California Department of Parks and Recreation, 46001 Orwin Way, Gorman, CA 93243, USA

Correspondence

Cory Holliday, The Nature Conservancy, 750 Big Branch Road, Granville, TN 38564, USA.
Email: cholliday@tnc.org

Abstract

Managing landscapes for migratory species is challenging when migratory movement patterns are unknown. Researchers have collected sufficient data to understand summer and winter habitat use for federally listed bats, but movement between these habitats in spring and fall has not been studied extensively. In addition, movement within summer habitat is less well understood than the roosting requirements. To initiate a preliminary understanding of movement patterns of gray bats (*Myotis grisescens*), we gathered all occurrence and band recovery data available within the range of the species to model movement. By weighting the pathways using the population of winter and summer locations (i.e., cave roosts), we created a heat map demonstrating the likelihood of landscape use by gray bats including nightly foraging, migration, and roost switching. The resulting map highlighted 2 major areas of use during spring and fall migration: 3 high likelihood pathways through central Tennessee and 1 primary migration route between northern Arkansas and central Missouri, USA. Although future data could influence the accuracy of this map, the representation in its current form can be used to anticipate bat presence when considering industrial development such as wind turbine siting.

KEYWORDS

gray bat, heat map, landscape use, *Myotis grisescens*, wind energy

How animals use a landscape is important for land managers to understand, especially when considering federally threatened or endangered species. Conservation of migratory animals is particularly challenging because of seasonal habitat use differences and shifting geographical areas throughout the life cycle. While migration pathways for some taxa (e.g., birds, insects) are well understood (Stervander et al. 2005, Alerstam et al. 2011), few published studies have identified migration routes of bats (Holland et al. 2006, O'Mara et al. 2019, Roby et al. 2019, Samoray et al. 2019). Bats are challenging to study because of their cryptic nature and, for many species, their small size.

Migration has evolved relatively recently but several independent times in different bat lineages as a result of diverse foraging and roosting strategies (Bisson et al. 2009). In temperate zones, a combination of decreased temperature and reduced food sources (e.g., insects) during winter deprives bats of an appropriate energy source. As a result, bats must hibernate or migrate to survive winter (Fleming and Eby 2003, Arias 2014, Fleming 2019). Migratory patterns are different among and within bat species, with different bat species using different migratory strategies (e.g., long-distance, regional, longitudinal, latitudinal) and different individuals exhibiting different levels of migratory participation (e.g., sex bias). Bats can be placed into 3 basic migration categories: sedentary in which movements are usually <50 km, regional migrants that move approximately 100–500 km, and long-distance migrants that move >500 km and up to almost 2,000 km (Fleming and Eby 2003; Cryan et al. 2004, 2014). These migration data have been collected via band recoveries (Ellison 2008), stable isotopes (Cryan et al. 2004, 2014; Hirt 2008; Arias 2014), automated radio-telemetry (McGuire et al. 2012), mapping movement phenology (Cryan 2003), population genetics studies (Burland et al. 1999, Petit and Mayer 2000, Russell et al. 2005), and radar (Horn and Kunz 2008). Regional migrants have been tracked via aerial telemetry (Roby et al. 2019, Samoray et al. 2019) resulting in the location of previously unknown maternity colonies, life-history data such as timing and speed of migration, and migration distance information.

Three myotis bats in eastern North America are regional migrants including Indiana bats (*Myotis sodalis*), little brown bats (*Myotis lucifugus*), and the federally endangered gray bat (*Myotis grisescens*). The gray bat is typically a cave-obligate species that lives year-round in caves, often migrating between summer and winter cave roosts (Harvey et al. 2011). It is estimated that only around 9 (Tuttle 1979, National Fish and Wildlife Laboratory 1980, Brady et al. 1982) to 15 (Harvey et al. 2011) caves serve as appropriate winter hibernation sites, with 95% of the population residing in those caves during winter and 25% residing in a single cave (I. Kuczynska, U.S. Fish and Wildlife Service, Missouri Field Office, personal communication). After spring migration, pregnant females congregate in maternity colonies in warm caves where they give birth to young between late May and early June after a 60–70-day gestation period (Tuttle 1976*b*, Saugey 1978, Brady et al. 1982). These maternity colonies generally consist of several caves within 70 km of each other and are associated with a river or another water source (Tuttle 1976*a*, Brady et al. 1982). Consequently, summer home ranges can be rather large: 57.9–362.2 km^2 in Arkansas (Moore et al. 2017) and 97 km^2 in Alabama and Tennessee, USA (Thomas and Best 2000). Published literature suggests that males and non-reproductive females typically roost in smaller bachelor colonies within the colony home range (Tuttle 1976*b*, Saugey 1978, Brady et al. 1982); however, anecdotal evidence from throughout the range suggests much higher incidence of sex overlap within roost sites (C. Holliday, The Nature Conservancy, personal observation; I. Kuczynska, personal communication).

In 2016, 2 new commercial wind energy developments were proposed in Tennessee, but currently, only 1 commercial wind energy site has been built. The proposed growth in this industry resulted in the consideration of regional risks associated with wind energy in the Southeast. A principal environmental risk of commercial wind energy is direct effect to long-distance migrants (Arnett et al. 2007, Thaxter et al. 2017). Gray bat conservation has been largely limited to roost site protection; however, these animals lead a dynamic life, with millions of bats taking to the air nightly during their active season and migrating regionally during spring and fall. With known migrations of 770 km and only 1 commercial wind energy site in the entire species range (Hoen et al. 2018), wind energy growth into the southeastern and Ozark Mountains regions of the United States represents a potential risk to the endangered gray bat.

This study is a descriptive analysis to guide gray bat conservation in the face of landscape threats, such as growth in the commercial wind energy sector. Whole-life-cycle conservation demands a broader view of occurrence when considering highly mobile wildlife like bats. As such, the objective of this project was to predict landscape use by gray bats when they are on the wing, outside of their roosts, year-round by building a model to predict intensity of landscape use by gray bats across the range of the species and throughout the year. We sought to map the resulting densities of the most likely migration routes and foraging ranges of gray bats to depict landscape use.

STUDY AREA

The range of the gray bat is limited to karst areas that produce caves of varying temperature and humidity conditions to accommodate roosting bats during hibernation and during the maternity season. Exceptions include significant gray bat roosts in North Carolina, USA, consisting almost exclusively man-made structures. Differential roost use can be challenging to track precisely for this highly mobile species, but the hibernation season is generally from September to April and the maternity season from May through July (Tuttle 1976*b*). This distribution ranges throughout portions of the southeastern United States, but the highest concentration of suitable roosts are throughout Tennessee, Kentucky, Missouri, and northern portions of Alabama and Arkansas, with smaller populations in southern Indiana, southern Illinois, southern Ohio, southwest Virginia, northern Georgia, northeast Oklahoma, and southeast Kansas. Historically, the range extended into northern Florida, but there are no extant populations remaining in the state (T. J. Doonan, Florida Fish and Wildlife Conservation, personal communication). The study area comprises approximately 846,000 km^2 and is within a primarily forested landscape that provides foraging and commuting opportunities. Tree roost use has been documented for gray bats during migration (Samoray et al. 2020), and this landscape can provide alternate roosting options (i.e., roosts other than caves) during cross-landscape movement. Land use analysis from the National Land Cover Database (Dewitz 2019) for the modeled gray bat range is 56% natural with 50% forest and 35% agriculture. The gray bat range described above is temperate throughout with seasonal weather that is generally cold in winter (<10°C) and warm in summer (>15°C). This study considers landscape use by gray bats throughout the year within this range.

METHODS

We first compiled a Microsoft Access (Microsoft Corporation, Redmond, WA, USA) database of all known roosts within the gray bat's range from individual state sources (Table 1). Data included in the database spanned from the 1960s through 2019. Additional 2022 gray bat census data were used to create Figure 2 but were not included in

TABLE 1 Number of gray bat roosts reported by 9 states in the United States used in the gray bat landscape use model presented. Bat roost occupancy data included varies temporally from 1965 to 2022.

State	Summer only	Winter only	Summer and winter
Alabama	41	1	1
Arkansas	50	43	1
Georgia	6	0	0
Kentucky	60	12	0
Missouri	150	45	0
North Carolina	17	0	0
Oklahoma	10	0	0
Tennessee	209	1	3
Virginia	15	0	0
Total	559	103	5

our analysis or model. States with minimal gray bat records not included in the model include Illinois, Ohio, South Carolina, Mississippi, and Florida. While Florida had a number of significant historical gray bat roosting sites, they have been completely displaced by southeastern bats (*Myotis austroriparius*; T. J. Doonan, personal communication). These data were primarily sourced from state wildlife agencies but did include additional data from the United States Fish and Wildlife Service and The Nature Conservancy (specific to Tennessee). Exact location coordinates for roost sites were provided by all states except Arkansas, which rounded coordinates to the nearest kilometer (we used these points as reported), and Missouri, which provided circular polygons approximately 8 km in diameter (we used centroid points), both of which are acceptable for the large scale of this model. Because of the vulnerable nature of these animals and their roost sites, specific roost locations will not be apparent in any part of this publication. Information provided for each site included site name, county, and state of occurrence. Data providers categorized caves as summer only, winter only, or summer and winter. Summer roosts included data for bachelor, maternity, and transitional use because these specific categories were not reported consistently for accurate independent analysis. We worked with data providers to assign use scores to each roost based on the most recent population estimates available and then placed scores into 1 of 11 population-based categories ranging from <100 to ≥1,000,000 bats (Table 2). All known roosts of significance were categorized based directly on recent population estimates. If detailed population estimates were not available, we asked data providers to categorize each roost into 1 of the 11 categories based on their personal knowledge or professional assessment.

We generated potential migration routes between roosts using maximum distances provided in Tuttle (1976*b*). It has been suggested that gray bat flight is heavily associated with traveling and foraging along water courses (Brady et al. 1982), although we could not find evidence to support this. In this model, we assumed straight line movements between seasonal roosts based on preliminary spring migration data collected during 2 years of active tracking. In spring of 2019 and 2021, we tracked gray bats during migration using a Cessna 172 Skyhawk (Cessna, Wichita, KS, USA) fitted with aircraft strut-mount assemblies (Advanced Telemetry Systems [ATS], Isanti, MN, USA) with 2 4-element Yagi directional antennas (model 13886; ATS). The aerial crew consisted of a pilot and a navigator. The pilot maintained an altitude of approximately 455 m above ground level, while the navigator monitored the transmitter signal through an ATS programmable datalogging receiver (model R4500S) and recorded bat locations on mapping software (DeLorme Topo North America 9.0, Yarmouth, ME, USA) approximately every 5 minutes. Although sample sizes were small, 3 out of 4 bats migrated in straight lines. For migrations between winter and

TABLE 2 Summer and winter roost use scores used to model dispersal of gray bats in the United States, 1965–2022, between roost sites of all roosts submitted by the 9 states that provided data for this model.

Gray bat roost size (number of bats) and seasonal use	Model score
Historical–insignificant (<100)	1
Small colony–low data confidence (100–999)	5
Moderate size–high data confidence (1,000–10,000)	10
(10,000–25,000)–high data confidence	20
(25,000) summer–(50,000) winter	50
(50,000) summer–(100,000) winter	100
(100,000) summer–(200,000) winter	200
(200,000) summer–(400,000) winter	400
(500,000) winter	500
(750,000) winter	750
(>1,000,000) winter	1,000

summer sites, we used a maximum distance of 800 km based on the maximum documented seasonal migration movement of 768 km from Tuttle (1976*b*). For summer-to-summer movements (i.e., roost switching), we used a maximum distance of 50 km supported by our active tracking foraging studies and Moore (2017). We then used queries of the data set to generate a table of roost pair combinations (individual bat roosts within 50 km of each other) and formatted the pairs of points for conversion into lines using the points to line function in ArcGIS version 10.8.1. (Esri, Redlands, CA, USA). We calculated a distance coefficient for each potential roost-to-roost route using the calculation $(D - X)/D$, where D is the maximum potential migration distance (800 km between winter and summer and 50 km for summer to summer) and X is the line length. We excluded cave pairs that exceeded the maximum potential migration distance and roost switching distance from the analysis.

To model potential spring dispersal of gray bats between winter and summer roost sites, we multiplied the distance coefficients of all summer sites within 800 km of each winter site by their summer roost use scores (Table 2), resulting in a set of potential dispersal sites weighted by proximity and roost use. For each winter site, we totaled the weights of all potential summer sites, and divided the individual summer site weights by this total to give a probability of dispersal score to that summer site. We then multiplied the probability of dispersal value for each destination summer site by the winter site use score (Table 2) and used this value as the potential migration score for the route line between that winter and summer site. By the same methodology, we also generated potential migration route scores from summer sites to winter sites and between summer sites.

We assigned all seasonal migration scores to their corresponding route lines in the geographic information system coverages. In ArcGIS, we calculated quartic kernel densities (km^2) of winter to summer, summer to winter, and summer to summer lines using the create density map function of the XTools Pro extension, with the potential migration scores of each route as population value inputs. We used a circular search neighborhood based on the type of connection. For spring and fall migrations between summer and winter sites, we stratified the radius of the search neighborhood (bandwidth; 8 values from 10–80 km, with 10-km increments) by route length (8,100-km ranges from <100 km to 700–800 km) to account for increased spatial uncertainty of travel along longer routes. For example, if the migration distance was 250 km, the search neighborhood was 30 km around that line. Separating route length into 100-km ranges resulted in 8 runs for each spring and fall density calculation (i.e., winter to summer and summer to winter). For summer-to-summer roost switching densities, we used a wider bandwidth of 20 km to account for greater spatial uncertainty associated with potential foraging during travel between roosts. Combined, these variable bandwidth metrics account for spatial uncertainties and less than perfect aerial flight paths by widening predicted flight paths in a linear fashion based on distance from a roost. In addition to using route lines connecting roosts, we also modeled foraging densities for summer roost points using population values as their use scores and a 50-km radius. We then summed density calculations for all points and lines using the raster calculator in spatial analyst in ArcGIS, resulting in an overall likelihood of presence density surface. We grouped final density values into 20 quantiles representing cumulative likelihood of presence indices for mapping.

RESULTS

Although the range of the gray bat encompasses approximately 846,000 km^2, the concentration of bat use is almost half of that area (433,000 km^2) with 2 major areas of use: the northern Arkansas and Missouri population and the Tennessee population (Figure 1). This model, as presented, assumes a high level of confidence in the roost data collected and shared by partners. In draft versions of the model, we varied roost data confidence to observe model reflections. Generally, reducing roost data confidence caused the high-density values to be over-represented and as a result, diminished observable predicted migratory corridors. While representations assuming lower confidence in the roost data protected against potential inaccuracies by prioritizing larger areas on the map, the larger resulting

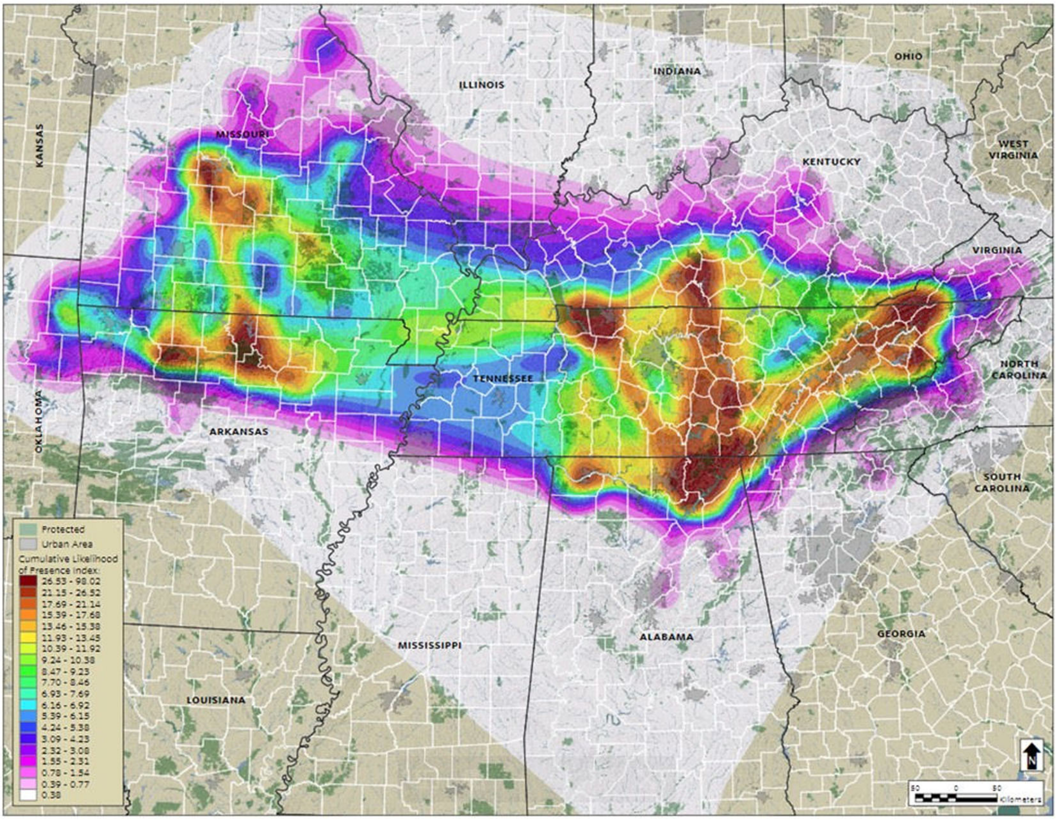

FIGURE 1 Gray bat distribution model representing the cumulative likelihood of presence indices across the range of the species, southeastern United States, year-round, based on modeled dispersal between winter and summer sites (i.e., caves), among summer sites, and between summer and winter sites.

priority zones were not useful for conservation practitioners. The presented model and final landscape use map represent our best effort to predict landscape use by gray bats without making assumptions or assertions that are not supported by the research.

DISCUSSION

The model reported here represents intensity of gray bat land use within the range of the species. In particular, the model depicts high use areas around hibernacula and maternity caves and predicts migration routes with varying levels of intensity. Data used to create this model were based on band recoveries between roost sites with no travel or behavioral information, so predicted pathways between roosting sites were created as straight lines regardless of topography or urbanization. Evidence from recent studies supports this as the most likely scenario for migrating and roost switching gray bats (S. T. Samoray, Copperhead Consulting, unpublished reports), and we validated parts of the model in a 2019 migration study in Tennessee (C. Holliday, unpublished data). All 3 gray bats tracked during spring migration were hibernating at a cave located within one of the highest density areas of the map and migrated along one of the high-density travel routes predicted in the model (S. T. Samoray, unpublished report).

Gray bats are very gregarious mammals, and the model is affected by the extremely high density at and between some of the highest populated roosts. The yellow and green shaded areas represent a moderately high likelihood of landscape use by gray bats despite being overshadowed by the red, very highly ranked zones. Gray bats do move between the 2 main areas of high bat activity (e.g., band recoveries connect northern Alabama to Arkansas [Tuttle 1976*b*]), resulting in genetic mixing.

While these cumulative heat maps indicate areas most likely used by gray bats on the landscape, they do not indicate the highest potential for activity levels over time at a given point on the map. Because of the distributive scoring used, the model indicates high potential for roost movements and migration but does not add value for time bats are using a roost during the summer. Roosts are buffered by 50 km in the model for foraging areas, and potential threats to bats within foraging distance of known bat roosts should be considered somewhat independently. A temporal component would be a good addition to this type of model, but its accuracy would depend on a large data set. The migration routes could be divided and displayed temporally to indicate short-term risks that may be useful for the periodic management of potential threats such as commercial wind turbines. Roost data confidence can be reduced to present less-specific model predictions, which protect against data deficiency or inaccuracy, but the authors found those models to be overly generalized and not as useful for resource management.

Protection of habitat and reduction of threats along migration routes play important roles in the conservation of many animal species (Wilcove and Wikelski 2008, Panzacchi et al. 2013, Lascelles et al. 2014). While we do have a wealth of roosting data for gray bats, data on migration and summer roost switching are still lacking. The model we created for gray bat land use allows for predictions of bat activity during these transition periods, providing information to land managers and conservation planners to help protect bats at this very understudied time of year.

We do not fully understand the spectrum of use and movement between seasonal roosts. As stated in the methods, for the purposes of this model, we labeled anything not harboring hibernating bats for long periods in winter as a summer site. Many of these are likely used as transition sites or short-term seasonal roosts. Researchers have reported movement between summer caves (Tuttle 1976*b*, Elder and Gunier 1978). As such, in this model we treated each summer roost equally with quantified values associated with evidenced bat use, and we created the potential for connections between these summer roosts. We feel this is the most accurate way to predict gray bat movement and landscape use with the roost information currently available. Better understanding of gray bat use of roosts and associated variables (e.g., timing, weather impacts, activity levels of bats at these sites), and more specific data for each summer roost site, may provide additional details that could influence this model. For example, we have evidence of roosts that harbor large numbers of gray bats for comparatively short periods of time outside of maternity and hibernation periods. Some of these roosts may serve as transitional hubs and would alter the weighted routes between true summer and winter roosts.

Decades of gray bat mark-recapture research, primarily using bat bands, has revealed considerable movement information for the species. Tuttle (1976*b*) extensively studied the population ecology of the gray bat by banding 40,182 individuals and recovering 19,691 bands at over 120 localities in the eastern United States. This study found that gray bats traveled anywhere between 17 km and 437 km in one direction between winter and summer caves, exhibiting strong site fidelity. Additionally, 3 banded gray bats were recovered hibernating in Missouri caves that were 689 km and 770 km west-northwest of the cave from which they were banded in Alabama. Tuttle (1976*b*) also documented 1 gray bat in a hibernaculum 668 km from the summer cave and postulates that it could have traveled 775 km in 1 direction during migration. Similarly, Elder and Gunier (1978) banded 18,768 gray bats at a winter cave in Missouri and found that bats migrated up to 640 km to their summer roosts, but most migrated within 200 km of the winter roost. During the creation of this model, we considered whether existing mark-recapture data should be used to verify our model. The majority of mark-recapture data include temporal differentials between bat captures >1 season. Elder and Gunier (1978) documented both site fidelity and site non-fidelity in their gray bat study focused on Marvel Cave in Missouri, suggesting gray bats' ability to roost shift both during and between seasons. This potential for bat site non-fidelity is supported by the variability observed in multi-year gray bat census data compiled for this study and is easily observed in the presentation of data from 3 gray bat roosts from Tennessee

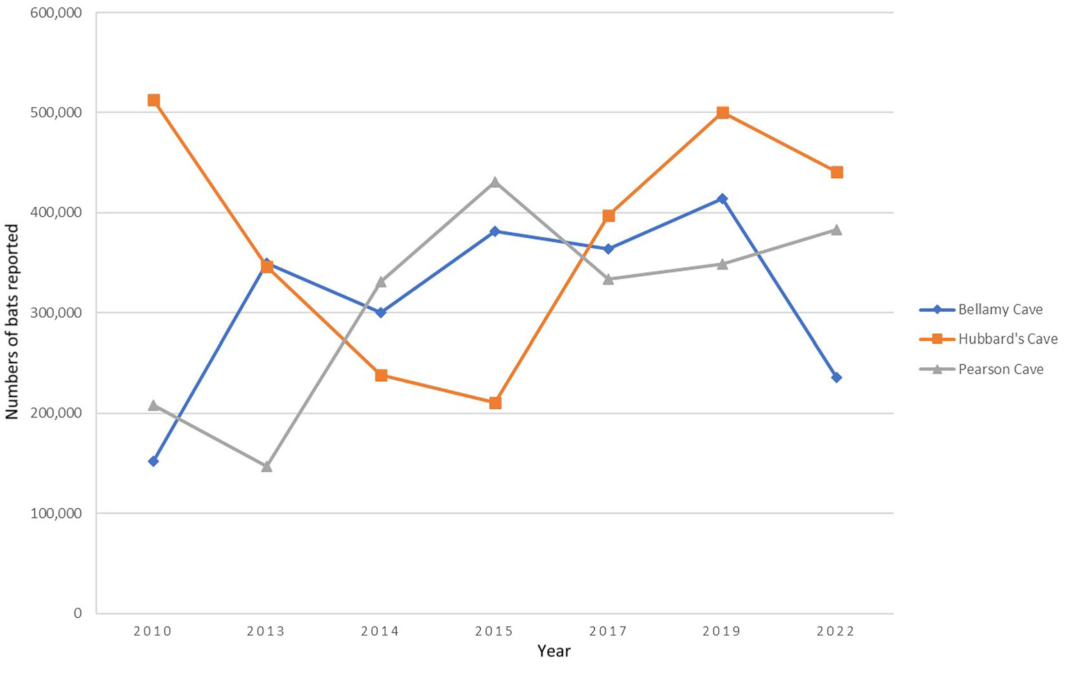

FIGURE 2 Varying gray bat census data from 2010–2022 in 3 caves with the highest populations in Tennessee, USA, indicating site non-fidelity with large fluctuations in bat numbers documented between survey years.

(Figure 2). This combination of temporal gaps between mark-recapture data, potential for site non-fidelity, and the overall limited amount of data compared to the number of bats on the landscape led us to not include mark-recapture data as an influencing factor in our model. We did, however, use mark-recapture data to determine migration movement distance thresholds.

This species-specific model is a product of combining decades of cave and bat research data; however, it is almost certainly not the final model for the species. Additional roosts within this modeled range will continue to be discovered, which might alter some aspects of this model, especially outside the core geographies. Range expansions for gray bats have been documented, notably into western North Carolina (Etchison and Weber 2020), where gray bats are using non-cave roosts. There is potential for gray bats to expand their range more through the karst of the central Appalachians, and into non-karst regions using alternative roosts, as climate change alters the suitability of habitat for myotis bats (Loeb and Winters 2012). Gray bats have been discovered in a barn (Gunier and Elder 1971), storm sewers and culverts (Hays and Bingman 1964), bridges (Johnson et al. 2002, Cervone and Yeager 2016, Powers et al. 2016, Sasse 2019, Etchison and Weber 2020), and most recently tree roosts during migration (Samoray et al. 2020).

We chose the gray bat as an at-risk regional migrant with potential for new and growing threats throughout much of its range. Ideally, complementary models and maps would be created for similarly at-risk species, especially throughout geographies most likely for development by commercial wind energy. We hope this model provides an improved idea of what the actual landscape use by gray bats is likely to be. We also hope others will use and improve upon our methodology to expand on the concept of creating full-life-cycle maps for migratory species that use available data to predict landscape use. The intent of this whole-life-cycle model is to be useful to the conservation and recovery of gray bats, assist in planning of future development projects, and to inspire similar efforts for other taxa.

MANAGEMENT IMPLICATIONS

Commercial wind energy development represents a potential emerging threat throughout much of the gray bat range. The heat map created by this model could be useful for predicting high-risk areas and to inform future development or landscape changes or threats. For conservation purposes and landscape and development planning, this model may be a useful tool for predicting likely areas used by gray bats outside of foraging ranges around roosts. The data predicted in the model could be used in wind energy siting decisions, particularly migratory corridors between seasonal roosts and high levels of activity around summer roosts. Our model attempts to fill in those knowledge gaps and identify the most likely areas gray bats will use as they traverse the landscape.

ACKNOWLEDGMENTS

This model is the result of cumulated data gathered by curious and inspired individuals recognizing the ecological value of gray bats, too numerous to name here. Individuals who contributed to data, science, and advancing technology that made the creation of this model possible include, but are not limited to, M. Armstrong, T. L. Best, E. Britzke, D. Butler, K. Caldwell, J. Campbell, S. Carr, R. L. Clawson, S. N. Colatskie, Z. Couch, R. R. Currie, T. J. Doonan, A. Elliott, W. R. Elliott, M, J. Harvey, T. Hemberger, T. H. Henry, B. Hines, M. K. Hudson, T. Inebnit, D. Istvanko, A. King, V. Kuczynska, T. H. Kunz, J. W. Lamb, T. Malabad, S. Marquardt, R. E. Melton, K. Morris, C. Ogle, W. Orndorff, P. Pattavina, D. Pelren, L. Pruitt, R. Reynolds, B. M. Sabol, D. B. Sasse, N. Sharp, C. Simpson, R. Stark, D. Thames, S. Thomas, R. Toomey, B. J. Westrich, K. Wethington, K. Womack, and G. R. Wyckoff. Of the state and federal agencies, we specifically thank personnel of the Alabama Department of Conservation and Natural Resources, Georgia Department of Natural Resources: Wildlife Resources Division, Indiana Department of Natural Resources, Kentucky Department of Fish and Wildlife Resources, Missouri Department of Conservation, National Park Service, Tennessee Wildlife Resources Agency, and the United States Fish and Wildlife Service. This work has also been made possible by a variety of scientific financial support in the public and private sectors. While we do want to protect their anonymity, we would especially like to thank the supporters of this project and The Nature Conservancy's Tennessee Cave and Karst Program.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

Authors obtained all data from existing monitoring programs. We did not handle or directly observe wild animals.

DATA AVAILABILITY STATEMENT

Analyzed data consist primarily of endangered species roost data that were shared with the authors through multiple restricted data-sharing agreements. As such, primary research data are not shared; however, other versions of the model can be created and shared. These can be used to restrict temporal periods, for example, and are available on request from the corresponding authors. The data are not publicly available because of privacy or ethical restrictions.

ORCID

Piper L. Roby http://orcid.org/0000-0002-1888-7397
Jessica M. Vannatta http://orcid.org/0000-0002-7038-3874

REFERENCES

Alerstam, T., J. W. Chapman, J. Backman, A. D. Smith, H. Karlsson, C. Nilsson, D. R. Reynolds, R. H. Klaassen, and J. K. Hill. 2011. Convergent patterns of long-distance nocturnal migration in noctuid moths and passerine birds. Proceedings of the Royal Society B: Biological Sciences 278:3074–3080.

Arias, L. C. 2014. Using stable isotope analysis to study altitudinal and latitudinal bat migration. Dissertation, Indiana State University, Terre Haute, USA.

Arnett, E. B., D. B. Inkley, D. Johnson, H. R. P. Larkin, S. Manes, A. M. Manville, R. Mason, M. L. Morrison, M. D. Strickland, and R. Thresher. 2007. Impacts of wind energy facilities on wildlife and wildlife habitat. The Wildlife Society, Bethesda, Maryland, USA.

Bisson, I. A., K. Safi, and R. A. Holland. 2009. Evidence for repeated independent evolution of migration in the largest family of bats. PLoS ONE 4:e7504.

Brady, J., T. H. Kunz, M. D. Tuttle, and D. Wilson. 1982. Gray bat recovery plan. U.S. Fish and Wildlife Service, Washington, D.C., USA.

Burland, T. M., E. M. Barratt, M. A. Beaumont, and P. A. Racey. 1999. Population genetic structure and gene flow in a gleaning bat, *Plecotus auritus*. Proceedings of the Royal Society B: Biological Sciences 266:975–980.

Cervone, T. H., and R. K. Yeager. 2016. Bats under an Indiana bridge. Proceedings of the Indiana Academy of Science 125: 91–102.

Cryan, P. M. 2003. Seasonal distribution of migratory tree bats (*Lasiurus* and *Lasionycteris*) in North America. Journal of Mammalogy 84:579–593.

Cryan, P. M., M. A. Bogan, R. O. Rye, G. P. Landis, and C. L. Kester. 2004. Stable hydrogen isotope analysis of bat hair as evidence for seasonal molt and long-distance migration. Journal of Mammalogy 85:995–1001.

Cryan, P. M., C. M. Stricker, and M. B. Wunder. 2014. Continental-scale, seasonal movements of a heterothermic migratory tree bat. Ecological Applications 24:602–616.

Dewitz, J. 2019. National Land Cover Database (NLCD). U.S. Geological Survey data release, Reston, Virginia, USA. https://doi.org/10.5066/P96HHBIE

Elder, W. H., and W. J. Gunier. 1978. Sex ratios and seasonal movements of gray bats (*Myotis grisescens*) in southwestern Missouri and adjacent states. American Midland Naturalist 99:10.

Ellison, L. E. 2008. Summary and analysis of the U.S. Government Bat Banding Program. U.S. Geological Survey Open-File Report 2008-1363, Reston, Virginia, USA.

Etchison, K. L. C., and J. Weber. 2020. The discovery of gray bats (*Myotis grisescens*) in bridges in western North Carolina. Southeastern Naturalist 19:53–56.

Fleming, T. H. 2019. Bat migration. Pages 605–610 *in* J. C. Choe, editor. Encyclopedia of animal behavior (second edition). Academic Press, Oxford, United Kingdom.

Fleming, T. H., and P. Eby. 2003. Ecology of bat migration. Pages 156–208 *in* T. H. Kunz and M. B. Fenton, editors. Bat ecology. The University of Chicago Press, Chicago, Illinois, USA.

Gunier, W. J., and W. H. Elder. 1971. Experimental homing of gray bats to a maternity colony in a Missouri barn. American Midland Naturalist 86:502–506.

Harvey, M. J., J. S. Altenbach, and T. L. Best. 2011. Bats of the United States and Canada. Johns Hopkins University Press, Baltimore, Maryland, USA.

Hays, H. A., and D. C. Bingman. 1964. A colony of gray bats in southeastern Kansas. Journal of Mammalogy 45:150.

Hirt, S. J. 2008. Analysis of stable isotopes of hydrogen to determine migrational source of silver-haired bats (*Lasionycteris noctivagans*) in Alabama. Thesis, Auburn University, Auburn, USA.

Hoen, B. D., J. E. Diffendorfer, J. E. Rand, J. T. Kramer, L. A. Garrity, and H. E. Hunt. 2018. United States Wind Turbine Database (ver. 3.1, July 2020). U.S. Geological Survey, American Wind Energy Association, and Lawrence Berkeley National Laboratory data release, Reston, Virginia, USA. https://doi.org/10.5066/F7TX3DN0

Holland, R. A., K. Thorup, M. J. Vonhof, W. W. Cochran, and M. Wikelski. 2006. Bat orientation using Earth's magnetic field. Nature 444:2.

Horn, J. W., and T. H. Kunz. 2008. Analyzing NEXRAD doppler radar images to assess nightly dispersal patterns and population trends in Brazilian free-tailed bats (*Tadarida brasiliensis*). Society for Integrative and Comparative Biology 48:24–39.

Johnson, J. B., M. A. Menzel, J. W. Edwards, and W. M. Ford. 2002. Gray bat night-roosting under bridges. Journal of the Tennessee Academy of Science 77:91–93.

Lascelles, B., G. Notarbartolo Di Sciara, T. Agardy, A. Cuttelod, S. Eckert, L. Glowka, E. Hoyt, F. Llewellyn, M. Louzao, V. Ridoux, and M. J. Tetley. 2014. Migratory marine species: their status, threats and conservation management needs. Aquatic Conservation: Marine and Freshwater Ecosystems 24:111–127.

Loeb, S. C., and E. A. Winters. 2012. Indiana bat summer maternity distribution: effects of current and future climates. Ecology and Evolution 3:103–114.

McGuire, L. P., C. G. Guglielmo, S. A. Mackenzie, and P. D. Taylor. 2012. Migratory stopover in the long-distance migrant silver-haired bat, *Lasionycteris noctivagans*. Journal of Animal Ecology 81:377–385.

Moore, P. R., T. S. Risch, D. K. Morris, and V. Rolland. 2017. Habitat use of female gray bats assessed using aerial telemetry. Journal of Wildlife Management 81:1242–1253.

National Fish and Wildlife Laboratory. 1980. Selected vertebrate endangered species of the seacoast of the United States: the gray bat. U.S. Fish and Wildlife Service, Biological Services Program; FWS/OBS-80/01.27, Washington, D.C., USA.

O'Mara, M. T., M. Wikelski, B. Kranstauber, and D. K. N. Dechmann. 2019. First three-dimensional tracks of bat migration reveal large amounts of individual behavioral flexibility. Ecology 100:e02762.

Panzacchi, M., B. Van Moorter, and O. Strand. 2013. A road in the middle of one of the last wild reindeer migration routes in Norway: crossing behaviour and threats to conservation. Rangifer 33:15–26.

Petit, E., and F. Mayer. 2000. A population genetic analysis of migration: the case of the noctule bat (*Nyctalus noctula*). Molecular Ecology 9:683–690.

Powers, K. E., R. J. Reynolds, W. Orndorff, B. A. Hyzy, C. S. Hobson, and W. M. Ford. 2016. Monitoring the status of gray bats (*Myotis grisescens*) in Virginia, 2009–2014, and potential impacts of white-nose syndrome. Southeastern Naturalist 15:127–137.

Roby, P. L., M. W. Gumbert, and M. J. Lacki. 2019. Nine years of Indiana bat (*Myotis sodalis*) spring migration behavior. Journal of Mammalogy 100:1501–1511.

Russell, A. L., R. A. Medellin, and G. F. McCracken. 2005. Genetic variation and migration in the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*). Molecular Ecology 14:2207–2222.

Samoray, S. T., S. N. Cotham, and M. W. Gumbert. 2019. Spring migration behavior of a tri-colored bat (*Perimyotis subflavus*) from Tennessee. Southeastern Naturalist 18:N16–N20.

Samoray, S. T., S. N. Patterson, J. Weber, and J. M. O'Keefe. 2020. Gray bat (*Myotis grisescens*) use of trees as day roosts in North Carolina and Tennessee. Southeastern Naturalist 19:49–52.

Sasse, D. B. 2019. Gray bat day roosts in concrete barriers on bridges during migration. American Midland Naturalist 182: 124–128.

Saugey, D. A. 1978. Reproductive biology of the gray bat, *Myotis grisescens*, in northcentral Arkansas. Thesis, Arkansas State University, Jonesboro, USA.

Stervander, M., Å. Lindström, N. Jonzén, and A. Andersson. 2005. Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and the significance of different migration routes. Journal of Avian Biology 36:210–221.

Thaxter, C. B., G. M. Buchanan, J. Carr, S. H. M. Butchart, T. Newbold, R. E. Green, J. A. Tobias, W. B. Foden, S. O'Brien, and J. W. Pearce-Higgins. 2017. Bird and bat species' global vulnerability to collision mortality at wind farms revealed through a trait-based assessment. Proceedings of the Royal Society B: Biological Sciences 284:20170829.

Thomas, D. P., and T. L. Best. 2000. Radiotelemetry assessment of movement patterns of the gray bat (*Myotis grisescens*) at Guntersville Reservoir, Alabama. Pages 27–39 *in* B. R. Chapman and J. Laerm, editors. Fourth Colloquium on Conservation of Mammals in the Southeastern United States Occasional papers of the North Carolina Museum of Natural Sciences and the North Carolina Biological Survey. North Carolina Museum of Natural Sciences, Raleigh, USA.

Tuttle, M. D. 1976*a*. Population ecology of the gray bat (*Myotis grisescens*): factors influencing growth and survival of newly volant young. Ecology 57:587–595.

Tuttle, M. D. 1976*b*. Population ecology of the gray bat (*Myotis grisescens*): philopatry, timing and patterns of movement, weight loss during migration, and seasonal adaptive strategies. Occasional Papers of the Museum of Natural History The University of Kansas 54:38.

Tuttle, M. D. 1979. Twilight for the gray bat. National Parks and Conservation Magazine 53:12–15.

Wilcove, D. S., and M. Wikelski. 2008. Going, going, gone: is animal migration disappearing. PLoS Biol 6:e188.

Associate Editor: Andrea Litt.

How to cite this article: Holliday, C., J. P. Wisby, P. L. Roby, S. T. Samoray, and J. M. Vannatta. 2023. Modeling migration and movement of gray bats. Journal of Wildlife Management 87:e22364.
https://doi.org/10.1002/jwmg.22364