Notes

Movement Patterns of Two Bat Species Active During Winter in the Southeastern United States

Reilly T. Jackson,* Emma V. Willcox, Riley F. Bernard

R.T. Jackson
Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701

E.V. Willcox
Department of Forestry, Wildlife and Fisheries, University of Tennessee, Knoxville, Tennessee 37996

R.F. Bernard
Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071

Abstract

During winter in the southeastern United States, cavernicolous bats, many species of which are susceptible to white-nose syndrome, periodically arouse from torpor and occasionally leave hibernacula. We investigated the winter movements and habitat use of two bat species persisting during the white-nose syndrome epizootic: the gray bat *Myotis grisescens* and the eastern small-footed bat *Myotis leibii*. We deployed very-high-frequency radio transmitters on individual bats captured outside hibernacula to investigate activity, which may include foraging, during winter. We tracked bats from release at the cave entrance until their transmitter signal was lost or they remained stationary for 15 min or longer. Gray bats ($n = 12$) had a core range of 1.92 km^2 and an overall range of 30.93 km^2. Eastern small-footed bats ($n = 5$) had a core range of 1.98 km^2 and an overall range of 20.22 km^2. Gray bats used open landcover types more than expected based on availability in the core range, but they selected water and forest cover types in their overall range ($P < 0.001$). Eastern small-footed bats used available landcover types as expected in the core range ($P = 0.1988$), but they selected for developed and open landcover types within the overall range ($P < 0.001$). Both species remained close to the hibernaculum and used roads when flying ($P < 0.005$), with gray bats also flying near waterways ($P < 0.001$). Habitat management and the enhancement of year-round prey availability adjacent to hibernacula may benefit bat populations, especially during winter when prey resources are low and bats are physiologically stressed due to hibernation and white-nose syndrome.

Keywords: foraging; behavior; hibernation; gray bat; eastern small-footed bat; radiotelemetry

Received: August 2022; Accepted: March 2023; Published Online Early: April 2023; Published: June 2023

Citation: Jackson RT, Willcox EV, Bernard RF. 2023. Movement patterns of two bat species active during winter in the southeastern United States. *Journal of Fish and Wildlife Management* 14(1):215–224; e1944-687X. https://doi.org/10.3996/JFWM-22-049

The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

* Corresponding author: rtj006@uark.edu

Introduction

Numerous studies on North American bats have focused on identifying spring and summer home ranges due to the energetic requirements of the maternity season (Tuttle 1976; Humphrey et al. 1977; LaVal et al. 1977; Murray and Kurta 2004; Johnson et al. 2009; Istvanko et al. 2016; Moore et al. 2017; Jonasson and Guglielmo 2019). This same effort has not been applied to investigating movement and habitat use by bats in winter, due to the perception that they enter caves for prolonged periods and hibernate without engaging in productive behaviors (Bernard and McCracken 2017). Although this "typical" behavior is often true in regions with long, cold winters (due to the high energetic needs of prolonged hibernation), bats in other areas can periodically emerge from hibernacula if ambient conditions are conducive (Thomas et al. 1990; Boyles et al. 2006; Bernard et al. 2021; Jackson et al. 2022a). Although feeding, drinking, and roost switching during winter have been documented in many bat species across North America, there have only been a handful of studies focused on the activity of cave-hibernating species during winter (Boyles et al. 2006; Dunbar et al. 2007; Geluso 2007; Ingersoll et al. 2010; Johnson et al. 2012; Bernard et al. 2021).

Because of the emergence and establishment of white-nose syndrome (WNS), a disease caused by the psychrophilic fungus *Pseudogymnoascus destructans*, the need to investigate behaviors that may influence responses to infection, such as winter activity, has become urgent. White-nose syndrome has led to significant declines in North American populations of hibernating bats in Canada and the United States (Blehert et al. 2009; U.S. Fish and Wildlife Service [USFWS] et al. 2012; Cheng et al. 2021). The fungus erodes the epidermal tissue of hibernating bats, creating lesions on the skin, muzzle, forearms, and wing membranes that lead to the disruption of homeostatic processes and frequent arousals from torpor (Cryan et al. 2010, 2013; Reeder et al. 2012). Because of these interruptions, infected bats quickly expend energy reserves that are not easily replaced due to low prey availability, leading to mortality via starvation and dehydration (Cryan et al. 2010; Reeder et al. 2012). Thus, opportunistic winter activity, which may include foraging and drinking, may be an important behavior used by bats to combat the effects of active WNS infections (Cryan et al. 2013; Verant et al. 2014; Strandin et al. 2018; Cheng et al. 2019). This is especially plausible in the southeastern United States where insect prey remains present on the landscape and bats emerge from hibernacula throughout winter due to mild ambient temperatures (Jordan 2020; Bernard et al. 2021; Jackson et al. 2022b).

As WNS has become established in portions of the southeastern United States, overwintering populations of two bat species in Tennessee have persisted—the federally endangered gray bat *Myotis grisescens* and the eastern small-footed bat *Myotis leibii*, a species of conservation concern in Tennessee—and both species maintain stable year-round populations (U.S. Endangered Species Act [ESA 1973, as amended]; Federal Register 1976; Campbell 2019; O'Keefe et al. 2019). Although research on the movement ecology of these two species is limited, a few studies have examined their movements in spring and summer. Female gray bats occupied water-associated home ranges of approximately 106–1,000 km^2 during the maternity season (Thomas and Best 2000; Moore et al. 2017), whereas eastern small-footed bats used small, largely forested home ranges during spring ($\sim$1 km^2; Johnson et al. 2009). However, winter movement patterns of these two species are relatively unknown. Although pre-WNS research assumed most hibernating bat species largely remain in hibernacula throughout the winter, several studies have shown that these two species are regularly active on the landscape throughout this period in the southeastern United States, where winters can be warm (Tuttle 1979; Best and Jennings 1997; Bernard and McCracken 2017; Bernard et al. 2017, 2021; Moosman et al. 2017; Reynolds et al. 2017; Jackson et al. 2022a, 2022b). These activity bouts during the hibernation period may present opportunities for foraging and caloric intake, which can improve the likelihood of overwinter survival for these two species in the southeastern United States (Strandin et al. 2018; Cheng et al. 2019).

We sought to investigate the movement and habitat selection of gray bats and eastern small-footed bats during the overwintering period in the southeastern United States to fill a critical knowledge gap regarding their behavior during winter (Schute et al. 2021). Our objectives were to determine 1) the home range size used by gray and eastern small-footed bats during winter and 2) the habitat use by these two species during winter movements. We hypothesized that bats were largely foraging during these active periods and that home ranges for each species during winter would be smaller and nearer the point of origin (i.e., the cave) than ranges used during the active period (spring and summer). Primarily, we presumed that bats active in winter would want to minimize energy expenditure while active during winter.

Methods

Study area and bat capture

We conducted our study at two hibernacula in northeastern Tennessee, near the Kentucky and Virginia borders, where substantial populations of gray and eastern small-footed bats occur (Figure 1). Cave names have been anonymized to county level to maintain protection of sensitive habitat, as requested by the Tennessee Wildlife Resource Agency and the Nature Conservancy. During hibernation (November–March 2016–2019), we captured gray bats at Hawkins County Cave in Hawkins County and eastern small-footed bats at Campbell County Cave in Campbell County. We used mist nets (mesh diameter: 75/2, 2.6 m high, four shelves, 4–9 m wide; Avinet Inc., Dryden, NY) at cave entrances to capture bats emerging up to four times per month on days with no rain and ambient daytime temperatures greater than 0°C. We opened mist nets approximately 30 min before civil sunset and left them open for up to 5 h or until ambient temperatures were less than 0°C. We held captured bats for no more than 30 min in individual paper bags in a large, insulated cooler with two or three hand warmers (HotHands®, Dalton, GA) before processing. For all individuals captured, we recorded age (adult or juvenile), sex, right forearm length (in millimeters), and body mass (in grams) and fitted them with a unique aluminum-lipped, narrow 2.4-mm (eastern small-footed bat) or 2.9-mm (gray bat) forearm band (Porzana, Ltd., Icklesham, East Sussex, UK).

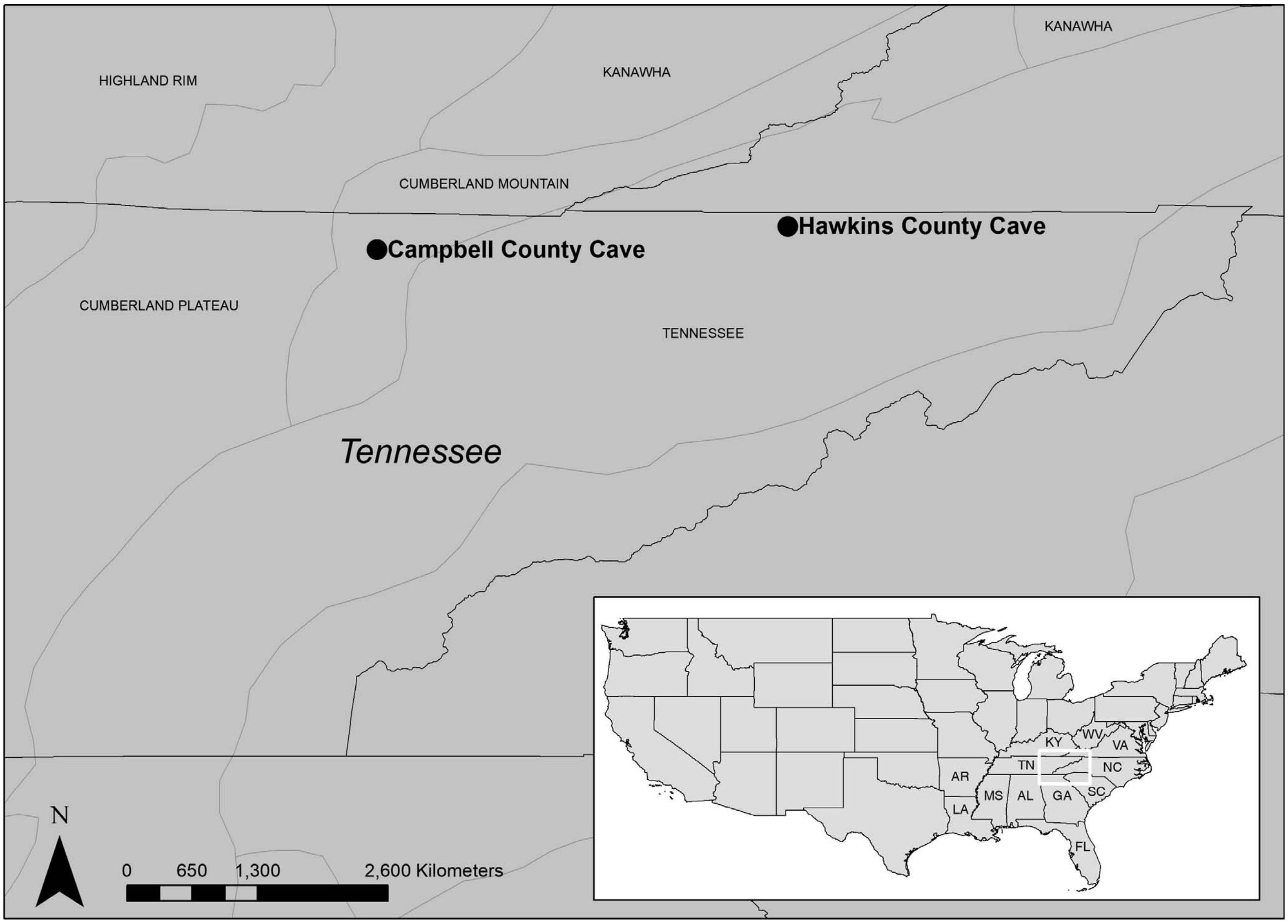

Figure 1. Two cave hibernacula in northeastern Tennessee, USA, where we captured two bat species, gray bat *Myotis grisescens* and eastern small-footed bat *Myotis leibii*, and tagged them with very-high-frequency radio transmitters. We used radio transmitters to track bat movements across the landscape during hibernation (November 1–March 31, 2016–2019).

Radiotelemetry

We applied 0.27-g (14-d) or 0.32-g (21-d) temperature-sensitive very-high-frequency radio transmitters (LB-2X, Holohil Systems Ltd., Isanti, Ontario, Canada) to captured eastern small-footed and gray bats, respectively. Data using the temperature-sensitive feature are presented in Jackson et al. (2022a). We ensured transmitters did not exceed 5–7% of the total body weight (5% for gray bats and 7% for eastern small-footed bats; Aldridge and Brigham 1988; Johnson and Gates 2008; Moore et al. 2017). We used the lightest available temperature-sensitive transmitters capable of monitoring multiple torpor bouts for eastern small-footed bats and did not exceed published weight limitations for similarly sized bats (Perry and Thill 2007; Johnson and Gates 2008). We trimmed fur just below the shoulder blades in the interscapular region to attach transmitters, away from concentrations of brown adipose tissue, by using surgical adhesive (Perma-Type, Plainville, CT; Johnson et al. 2012). We released all bats at the site of capture. The University of Tennessee Institutional Animal Care and Use Committee (2253-0317) approved all capture, handling, and transmitter application protocols, as developed by the American Society of Mammologists (Sikes et al. 2016) and authorized under scientific collection permits from the USFWS (TE35313B-3) and Tennessee Wildlife Resource Agency (3742).

We recorded ambient temperature at the capture site hourly by using a Kestrel 5500 weather meter (Kestrel Instruments, Boothwyn, PA). A flight team from Copperhead Environmental Consulting (Paint Lick, KY) tracked tagged individuals upon release from a Cessna 172 Skyhawk fixed-wing aircraft fitted with a four-element fixed Yagi directional antenna on each wing (13886; Advanced Telemetry Systems, Isanti, MI; Roby et al. 2019). The aerial crew detected VHF signals by using a data-logging radiotelemetry receiver (R4500SD; Advanced Telemetry Systems, Inc.). The aerial crew ensured independence of points by obtaining location fixes no less than every 2 min (Carter 1998). To obtain an accurate location fix, the aerial crew flew in small concentric circles above the predicted location of each bat (Seddon and Maloney 2004; Moore et al. 2017; Samoray et al. 2019). They then used mapping software (DeLorme Topo North America 9.0; Garmin International Ltd., Olathe, KS) and global positioning system navigation to view both plane and bat flight paths, as well as to determine bat location fixes (Data S1, *Supplemental Material*). The overall location accuracy of this aerial crew was 382.7 $\pm$ 44.7 m (mean $\pm$ SD; range = 5.9–1,765 m; $n = 65$ points; Roby et al. 2019). Aerial crews tracked individuals until the transmitter signal was lost, the bat was stationary for greater than 15 min, or inclement weather or low fuel forced the plane to land.

We limited aerial tracking to the night of capture because individuals from these caves were only active for a few hours each night and often returned to torpor for extended periods (<11 d) after emergence (Jackson et al. 2022a). To monitor the presence and behavior of bats with transmitters, we conducted long-term passive tracking at each site around and inside caves where we initially captured bats (Jackson et al. 2022a). Depending on the size and configuration of each cave, we deployed one to three dipole antennas (Model 13861; Advanced Telemetry Systems, Inc.) internally in September 2016 and 2017, with an additional antenna stationed outside the mouth of each cave to provide additional coverage. Internal antennas detected and recorded transmitter signals by using data-logging radiotelemetry receivers (R4500SD; Advanced Telemetry Systems, Inc.) connected to an external power source backed up to a solar power array. Antennas constantly monitored for transmitter signals and recorded when tagged bats were in the area surrounding the cave or in the cave itself. We placed all receivers for all antennae outside caves to minimize disturbance during weekly equipment inspections. We downloaded data on bat presence from each system weekly, or at minimum, biweekly. We attempted to locate tagged bats that were not logged on internal systems with occasional ground tracking within approximately 10 km of the cave by using a five-element fixed Yagi directional antenna (13886) and R4500SD radiotelemetry receiver. However, we detected no bats through landscape telemetry efforts.

Data analysis

We conducted geospatial analyses in ArcGIS PRO 2.9 (Esri, Redlands, CA) to estimate ranges for both species. Because of small samples sizes, we combined data from all individuals within a species to estimate habitat use and movement near each hibernaculum (colony level) rather than at the individual level (Moore et al. 2017). We calculated the fixed kernel density range (Worton 1989; Sparks et al. 2005; Walters et al. 2007; Johnson et al. 2009; Istvanko et al. 2016; Moore et al. 2017) for each species at each hibernaculum by using the adehabitatHR package in R (R Development Core Team 2020). We then generated a 95% percentage volume contour (PVC; i.e., geographic area that contains 95% of the probability density function from the kernel density estimate) to estimate overall range and a 50% PVC (i.e., geographic area that contains 50% of the probability density function from the kernel density estimate) to estimate core range.

To provide a comparison to the surrounding land cover, we created a "study area" buffer around each hibernation site based on the radius of the furthest distance an individual bat flew from the origin (Johnson et al. 2009). To examine landcover selection, we used the 2019 National Landcover Database (NLCD) data set to determine percent cover of four landcover types within the buffer, overall, and core ranges: developed (NLCD layers 21–24: human-developed areas ranging from open space to high intensity), open (NLCD layers 31, 52, 71, and 81–82: barren land, shrub–scrub, grassland–herbaceous, pasture, and cultivated crops), forest (NLCD layers 41–43: deciduous, evergreen, and mixed forest types), and water (NLCD layers 11 and 90–95: open water [rivers, lakes, ponds, and permanent streams] and woody and emergent herbaceous wetlands; Homer et al. 2015). To understand landcover selection in the overall range, we used a chi-square goodness-of-fit test to compare landcover composition of the buffer and the 95% PVC. Likewise, to explore landcover selection in the core range, we used a chi-square goodness-of-fit test to compare landcover composition of the 95 and 50% PVC (Aebischer et al. 1993). Last, we used a Student's *t*-test to compare the distances between bat location points and random points within the study area buffer to specific landscape features (i.e., the hibernacula of origin, roads, or waterbodies; Johnson et al. 2009). The Tennessee Department of Transportation and Tennessee Department of Ecological Conservation (http://tn-tnmap.opendata.arcgis.com/) provided road layers, and the U.S. Geological Survey's National Hydrology Dataset (https://www.usgs.gov/core-science-systems/ngp/national-hydrography) provided waterbody and waterway layers.

Results

Gray bats

We tracked 12 individual gray bats from Hawkins County Cave (Table 1) for 5–52 min (26.25 $\pm$ 4.10 min). We collected 7.66 $\pm$ 0.90 (mean $\pm$ SE) location points per individual, with a total of 92 points collected for all individuals tracked. Individuals traveled 0.12–11.40 km (2.45 $\pm$ 0.29 km) from the hibernaculum. The overall range (i.e., 95% PVC) on the colony level was 30.93 km^2, with a core range (i.e., 50% PVC) of 1.92 km^2 (Figure 2A). Gray bats spent 10.63 $\pm$ 3.49 min in the core range. Ambient ground temperature during nights of movements ranged from −1.67 to 10°C (3.45 $\pm$ 1.77°C).

In the overall range, gray bats used water and forest areas more than expected based on availability within the study area buffer, with open landcover being used less than available ($P < 0.0001$). In the core range, gray bats used open landcover types more than expected based on availability within the overall range, with water and forest being used less than available ($P < 0.001$). Within the study area buffer, gray bats flew closer to the hibernaculum ($P < 0.001$), roads ($P = 0.005$), and water (P

Table 1. Movement characteristics of two bat species aerially tracked during the hibernation season (November 1–March 31, 2016–2019) at two hibernacula in eastern Tennessee, USA. We deployed very-high-frequency transmitters on bats captured emerging from hibernacula on winter nights. We tracked bats by aerial crews the night of very-high-frequency radio transmitter attachment only. Passive telemetry surrounding and inside of hibernacula recorded transmitter signals of bats if they were in range of antenna (Jackson et al. 2022a).

			Movement characteristics			
Date	**Species**	**Sex**	**Maximum distance traveled (km)**	**Return to cave (Y/N)**	**Total no. of fixed locations**	**Total time tracked (min)**
November 11, 2016	*Myotis grisescens*	M	11.40	Y[a]	10	22
November 11, 2016	*M. grisescens*	M	0.78	Y[a]	4	9
November 11, 2016	*M. grisescens*	M	0.94	Y[a]	6	39
November 11, 2016	*M. grisescens*	M	0.66	Y[a]	5	29
February 23, 2017	*M. grisescens*	F	6.60	N	11	52
February 23, 2017	*M. grisescens*	F	0.46	Y	4	6
February 23, 2017	*M. grisescens*	F	0.45	Y	3	5
February 23, 2017	*M. grisescens*	F	5.22	N	13	34
February 26, 2019	*M. grisescens*	M	8.80	N	9	36
February 26, 2019	*M. grisescens*	F	0.59	N	10	22
February 26, 2019	*M. grisescens*	F	1.97	N	10	30
February 26, 2019	*M. grisescens*	M	5.22	N	7	31
March 9, 2017	*Myotis leibii*	M	6.84	NA	14	36
December 3, 2017	*M. leibii*	M	4.12	Y	36	109
November 18, 2018	*M. leibii*	M	5.92	N	19	197
November 18, 2018	*M. leibii*	F	1.61	N	16	77
February 3, 2019	*M. leibii*	M	4.16	N	17	68

M = male; F = female; NA = bats tagged during periods when passive long-term monitoring inside caves was not available.

[a] Passive long-term monitoring inside caves underwent technical difficulties during this time and did not allow us to determine the exact date of bat reentry into the cave, only that individuals returned between November 11 and November 20, 2016.

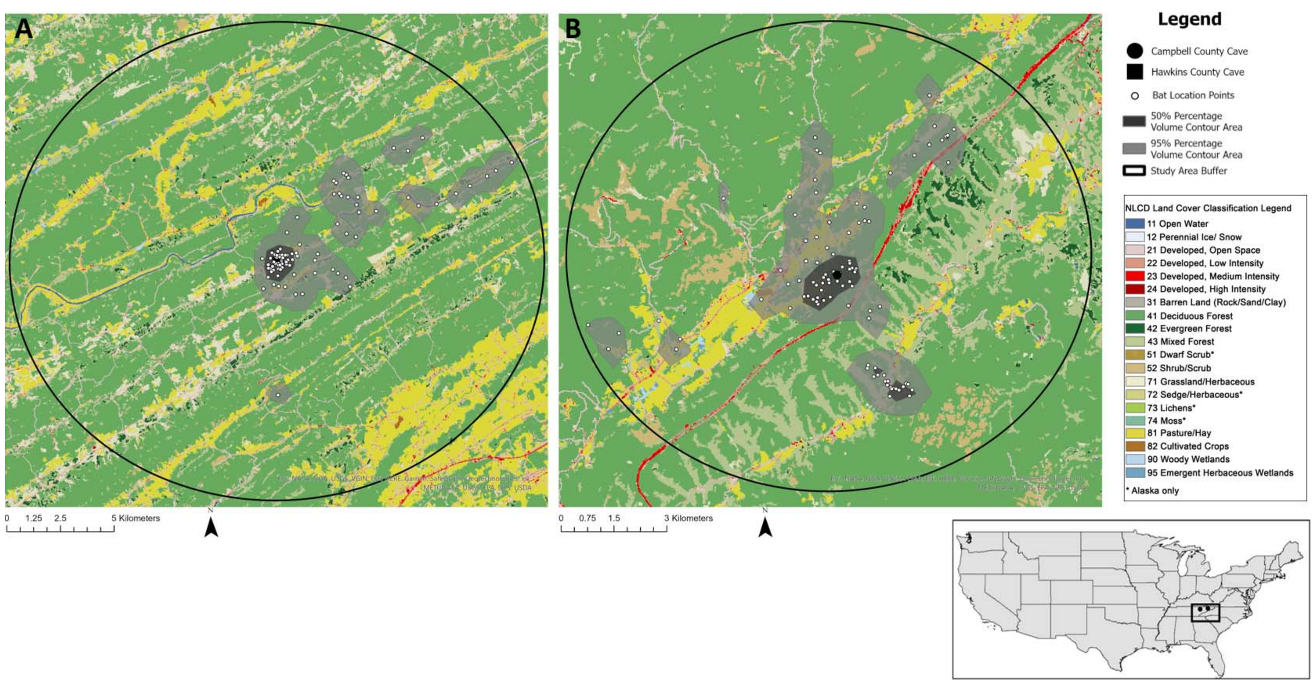

Figure 2. Locations of 12 gray bats *Myotis grisescens* (**A**) and 5 eastern small-footed bats *Myotis leibii* (**B**) captured emerging from two hibernacula in eastern Tennessee, USA, 2016–2019, based on aerial radiotelemetry. We tagged bats with very-high-frequency radio transmitters and tracked them via aerial telemetry crews during the hibernation season (November–March, 2016–2019). The 95% PVC (light gray shading) contained all bat locations to estimate the colony-level overall range of this species, with a 50% PVC (dark gray shading) determining the core range. Percent volume contours and bat locations overlay the National Landcover Database 2019. PVC = percent volume contour.

$<$ 0.001) than random. Six of the gray bats tracked returned to Hawkins County Cave during the life of the transmitter (~21 d), with two additional bats detected briefly the night after transmitter attachment.

Eastern small-footed bats

We tracked five eastern small-footed bats from Campbell County Cave (Table 1) for 36–197 min (97.40 ± 27.48 min). In total, we collected 102 location points, with an average of 21 ± 3.56 points per individual. Eastern small-footed bats traveled between 0.09 and 6.84 km (2.24 ± 0.17 km) from the cave. This species had a colony-level overall range of 20.22 km^2 and a core range of 1.98 km^2 (Figure 2B). Eastern small-footed bats spent 18.80 ± 4.93 min in the core range. Mean ambient temperature during movement ranged from −1.11 to 17.38°C (7.77 ± 3.49°C).

In the overall range, eastern small-footed bats selected for developed and open landcover types more than expected based on availability within the study area buffer, whereas they used forest less than available ($P < 0.001$). In the core range, eastern small-footed bats did not use any landcover type more than expected based on availability within the overall range ($P = 0.1988$). Eastern small-footed bats flew closer to the hibernaculum ($P < 0.001$) and used roadways more than random within the study area ($P < 0.001$). Only one of the eastern-small footed bats tracked during this study returned to Campbell County Cave during the life of the transmitter (~14 d), 2 d after transmitter attachment.

Discussion

Our study is the first account that we are aware of to investigate the winter movements of two North American bat species outside the hibernacula by using aerial radiotelemetry. Our results show that movements during winter are short and that our two focal species used different landscape characteristics and landcover types when analyzed at the colony level. Together, this information provides evidence that some bat species opportunistically emerge and move across the landscape during winter, which may provide opportunities for foraging.

Gray bats selected for water and forest in the overall range, comparable with what has been reported in summer (Moore et al. 2017). However, in contrast to summer behavior, gray bats active during winter selected for open landcover within the core range. In our study area, open landcover primarily surrounds the cave, but transitions to sparse development to the northeast, with gray bats possibly using this landcover type as a corridor to the closest major waterway. Furthermore, gray bats may not have used water landcover in the core range because of its limited distribution surrounded by forest. However, the use of water in the overall range and proximity to waterbodies indicates that gray bats largely select areas similar to those used during summer (Moore et al. 2017). In addition, gray bats also had a reduced range compared with what has been documented in summer (Thomas and Best 2000; Moore et al. 2017).

Comparatively, eastern small-footed bats selected for developed and open landcover types in the overall range, with selection of developed areas not previously recorded for the species (Johnson et al. 2009). In this area, development in the form of rural roads may be used as corridors for bats to use to reach target foraging grounds. This region is also defined by forested hills with valleys dominated by agriculture and sparse development. Bats may use low-elevation areas covered in open and developed landcover types to avoid energetically costly movements up forested hills, resulting in heavier use of these landcover types than previously recorded (Cryan et al. 2000). Interestingly, the foraging range of eastern small-footed bats during winter was similar in size to that observed in spring (Johnson et al. 2009).

Although our study provides evidence of winter activity by bats, there are likely multiple reasons driving bats to leave caves midwinter. These species demonstrated a variety of movement patterns, with at least two gray bats documented flying straight and fast, suggesting specific destinations, vs. the slower, more erratic movements in localized regions exhibited by foraging bats. Most of the movement patterns of the eastern small-footed bats were comparable with the identifiable area-restricted search patterns of foraging (Kareiva and Odell 1987; Kalko 1995; Roby et al. 2019). However, given the fast movements of some individuals and the areas in which they moved (Griffin 1945; LaVal et al. 1977; Boyles et al. 2006), as well as several tagged gray and eastern small-footed bats prolonged absence at the original hibernacula after transmitter attachment, it is possible that some bats departed this cave for extended periods and fed opportunistically on the wing (Bernard et al. 2021; Jackson et al. 2022a). Studies have shown that gray bats will switch roosts throughout hibernation and move among local hibernacula, which could explain these movements (Brack and LaVal 2006; Holliday et al. 2023). Although similar data are not available for eastern small-footed bats, summer studies have shown roost switching is frequent (Johnson et al. 2011). The areas in which we conducted this study are composed of limestone karst, with numerous cave systems surrounding the main hibernaculum, likely presenting opportunities for localized roost switching. In addition, aerial crews often abruptly lost transmitter signals of bats, which can happen when a bat reenters a subterranean roost (S. Samoray, Copperhead Environmental Consulting, Paint Lick, KY, personal communication). Although six of the gray bats and one eastern small-footed bat outfitted with transmitters returned to the cave capture site during the life of the transmitter, it is plausible that the other nine monitored individuals roosted elsewhere for extended periods after the plane lost the signals. Furthermore, ground telemetry efforts failed to locate bats that did not return to the original hibernacula.

Our results suggest that the habitat within 2 km^2 of caves is likely to be used more heavily by bats during winter. The use of areas surrounding hibernacula may indicate that movements during this period are more likely to be localized and short to conserve energy, given that flight is costly at low ambient temperatures (Tuttle 1976; Park et al. 2000). Fewer bats present on the landscape during winter may also result in decreased competition, allowing individuals to use local areas. Thus, bats may engage in more calculated, local movements during winter to reduce flight time and minimize energy expenditure during arousals. This behavior may have major ramifications for increasing survival of WNS-infected individuals. Short bouts of foraging may provide individuals with an opportunity to mitigate some symptoms of infection or avoid infection completely, if caloric intake outweighs the energetic expenditure of these movements (Cryan et al. 2010, 2013; Verant et al. 2014; Cheng et al. 2019). Furthermore, during periodic arousals, a bat's immune system is activated, potentially enabling infected individuals to mount an immune response that can be bolstered by calories gained from foraging (Prendergast et al. 2002; Dobony et al. 2011; Strandin et al. 2018; Cheng et al. 2019). The movement behavior we documented suggests that in this region of the country where winters are milder, bats may attempt to move and forage on warmer nights, and if successful, this behavior may increase their likelihood of survival. Our findings illustrate the need to maximize habitat conservation within 2 km^2 of the hibernacula so bats can engage in cost-effective foraging and potentially combat WNS infections.

Because of the numerous challenges of radio tracking bats during winter, inference based on our results is limited. Bats frequently disappeared during tracking, thereby limiting the number of locations collected per bat. We also only tracked tagged bats on the night of initial transmitter attachment. This may have biased our results to show heavy use of the area directly around the cave as bats adjusted to transmitter weight before moving out of the area (Smith 2019). In addition, the accuracy of our aerial crew varies (382.7 $\pm$ 44.7 m; range = 5.9–1,765 m; Roby et al. 2019); therefore, specific range size may differ from presented. Although there are limits to our results, this information is an important initial step toward understanding winter movements of cavernicolous bats. We suggest future studies attempt to track individuals for multiple nights, use aerial telemetry paired with ground crews, and identify secondary hibernacula to determine whether bats truly switched roosts.

By improving our understanding of the characteristics of winter behavior and presumed foraging, land managers may be able to develop actions that can increase overwinter survival of species threatened by WNS. Possible management actions may range from planting native plant species to attract insects within at least 2 km^2 of the hibernacula; reducing the use of pesticides in these areas to allow overwintering insect populations to persist; or using insect attractants, such as lights or pheromone traps. These actions may lead to a positive impact on bats engaging in foraging during winter by improving access to prey locally. Results from this study can also improve our understanding of winter roost fidelity and frequency of roost switching and help determine how bats use the landscape to maximize survival during winter.

Supplemental Material

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

Data S1. Data used to analyze the winter movement patterns of two bat species, gray bat *Myotis grisescens* and eastern small-footed bat *Myotis leibii*. We captured bats emerging from hibernacula in Tennessee, USA, during hibernation (November–March 2016–2019), tagged with radio transmitters, and tracked using aerial telemetry as they moved across the landscape.

Available: https://doi.org/10.3996/JFWM-22-049.S1 (25 KB XLSX)

Reference S1. Campbell J. 2019. Tennessee winter bat population and white-nose syndrome monitoring report for 2018–2019. Nashville: Tennessee Wildlife Resources Agency Wildlife. Technical Report 16-4.

Available: https://doi.org/10.3996/JFWM-22-049.S2 (3.534 MB PDF)

References S2. Johnson JB, Gates JE, Ford WM. 2009. Notes on foraging activity of female *Myotis leibii* in Maryland. Washington, D.C.: U.S. Department of Agriculture, Forest Service. Research Paper NRS-8.

Available: https://doi.org/10.3996/JFWM-22-049.S3 (399 KB PDF) and https://www.srs.fs.usda.gov/pubs/19840 (March 2023)

Reference S3. [USFWS] U.S. Fish and Wildlife Service. 2012. North American bat death toll exceeds 5.5 million from white-nose syndrome. News release. Washington, D.C.: USFWS.

Available: https://doi.org/10.3996/JFWM-22-049.S4 (109 KB PDF) and https://www.whitenosesyndrome.org/press-release/north-american-bat-death-tool-exceeds-5-5-million-from-white-nose-syndrome (March 2023)

Acknowledgments

We acknowledge that the lands where we conducted this study are on the ancestral home of the Eastern Band of the Cherokee, S'atsoyaha (Yuchi), and Shawandasse Tula (Shawnee) Indigenous peoples. We thank Copperhead Environmental Consulting for aerial radiotelemetry and N. House for technical support in helping design and build the antenna systems. We thank D. Thames and J. Zobel for data analysis advice and Z. David, K. Dreyer, D. Scott Hollis, M. Tate, and L. Vining for field assistance. We acknowledge the National Park Service, The Nature Conservancy, and the Tennessee Wildlife Resources Agency for assistance and cave access. We thank the

Associate Editor and two anonymous reviewers for comments on this manuscript. The USFWS (award F15AP00955-03 to E.V.W. and R.F.B.) and the National Park Service (award P18AC01279 to E.V.W. and R.F.B.) funded this study. These funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

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

References

Aebischer NJ, Robertson PA, Kenward RE. 1993. Compositional analysis of habitat use from radio-tracking data. Ecology 74:1313–1325.

Aldridge HDJN, Brigham RM. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. Journal of Mammalogy 69:379–382.

Bernard RF, McCracken GF. 2017. Winter behavior of bats and the progression of white-nose syndrome in the southeastern United States. Ecology and Evolution 7:1487–1496.

Bernard RF, Willcox EV, Jackson RT, Brown VA, McCracken GF. 2021. Feasting, not fasting: winter diets of cave hibernating bats in the United States. Frontiers in Zoology 18:1–13.

Bernard RF, Willcox EV, Parise KL, Foster JT, McCracken GF. 2017. White-nose syndrome fungus, *Psuedogymnoascus destructans*, on bats captured emerging from caves during winter in the southeastern United States. BMC Zoology 2:1–11.

Best TL, Jennings JB. 1997. *Myotis leibii*. Mammalian Species 547:1–6. Available: https://doi.org/10.2307/3504255

Blehert DS, Hicks AC, Behr M, Meteyer CU, Berlowski-Zier BM, Buckles EL, Stone WB. 2009. Bat white-nose syndrome: an emerging fungal pathogen? Science 323:227–227.

Boyles JG, Dunbar MB, Whitaker JO. 2006. Activity following arousal in winter in North American vespertilionid bats. Mammal Review 36:267–280.

Brack V Jr, LaVal RK. 2006. Diet of the gray myotis (*Myotis grisescens*): variability and consistency, opportunism, and selectivity. Journal of Mammalogy 87:7–18.

Campbell J. 2019. Tennessee winter bat population and white-nose syndrome monitoring report for 2018–2019. Tennessee winter bat population and white-nose syndrome monitoring report for 2018–2019. Nashville: Tennessee Wildlife Resources Agency Wildlife. Technical Report 16-4 (see *Supplemental Material*, Reference S1).

Carter TC. 1998. The foraging ecology of three species of bats at the Savannah River site, South Carolina. Master's thesis. Athens: University of Georgia. Available: https://sbdn.org/wp-content/uploads/2014/12/Carter-1998-Thesis-The-Foraging-Ecology-of-Three-Species-of-Bats-at-the-Savannah-River-Site-South-Carolina.pdf (March 2023)

Cheng TL, Gerson A, Moore MS, Reichard JD, DeSimone J, Willis CKR, Frick WF, Kilpatrick AM. 2019. Higher fat stores contribute to persistence of little brown bat populations with white-nose syndrome. Journal of Animal Ecology 88:591–600.

Cheng TL, Reichard JD, Coleman JTH, Weller TJ, Thogmartin WE, Reichert BE, Bennett AB, Broders HG, Campbell J, Etchison K, Feller DJ, Geboy R, Hemberger T, Herzog C, Hicks AC, Houghton S, Humber J, Kath JA, King RA, Loeb SC, Massé A, Morris KM, Niederriter H, Nordquist G, Perry RW, Reynolds RJ, Sasse DB, Scafini MR, Stark RC, Stihler CW, Thomas SC, Turner GG, Webb S, Westrich BJ, Frick WF. 2021 The scope and severity of white-nose syndrome on hibernating bats in North America. Conservation Biology 35.5:1–12.

Cryan PM, Bogan MA, Altenbach JS. 2000. Effect of elevation on distribution of female bats in the Black Hills, South Dakota. Journal of Mammalogy 81:719–725.

Cryan PM, Meteyer CU, Blehert DS, Lorch JM, Reeder DM, Turner GG, Castle KT. 2013. Electrolyte depletion in white-nose syndrome bats. Journal of Wildlife Diseases 49:398–402.

Cryan PM, Meteyer CU, Boyles JG, Blehert DS. 2010. Wing pathology of white-nose syndrome in bats suggests life-threatening disruption of physiology. BMC Biology 8:1–8.

Dobony CA, Hicks AC, Langwig KE, von Linden RI, Okoniewski JC, Rainbolt RE. 2011. Little brown myotis persist despite exposure to white-nose syndrome. Journal of Fish and Wildlife Management 2:190–195.

Dunbar MB, Whitaker JO, Robbins LW. 2007. Winter feeding by bats in Missouri. Acta Chiropterologica 9:305–310.

Federal Register. 1976. Determination that two species of butterflies are threatened species and two species of mammals are endangered species; 41 FR 17742 17747 (Schaus swallowtail; Bahama swallowtail; Mexican wolf, *Canis lupus baileyi*; gray bat, *Myotis grisescens*). Federal Register 41:17736–17741. Available: https://www.fws.gov/sites/default/files/federal_register_document/FR-1976-04-28.pdf (March 2023)

Geluso K. 2007. Winter activity of bats over water and along flyways in New Mexico. Southwestern Naturalist 52:482–492.

Griffin DR. 1945. Travels of banded cave bats. Journal of Mammalogy 26:15–23.

Holliday C, Wisby JP, Roby PL, Samorary ST, Vannata JM. 2023 Modeling migration and movement of gray bats. Journal of Wildlife Management 87:e22364.

Homer CG, Dewitz JA, Yang L, Jin S, Danielson P, Xian G, Coulston J, Herold ND, Wickham JD, Megown K. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States. Photogrammetric Engineering and Remote Sensing 85:345–354.

Humphrey SR, Richter AR, Cope JB. 1977. Summer habitat and ecology of the endangered Indiana bat, *Myotis sodalis*. Journal of Mammalogy 58:334–346.

Ingersoll TE, Navo KW, de Valpine P. 2010. Microclimate preferences during swarming and hibernation in the Townsend's big-eared bat, *Corynorhinus townsendii*. Journal of Mammalogy 91:1242–1250.

Istvanko DR, Risch TS, Rolland V. 2016. Sex-specific foraging habits and roost characteristics of *Nycticeius humeralis* in north-central Arkansas. Journal of Mammalogy 97:1336–1344.

Jackson RT, Willcox EV, Bernard RF. 2022a. Winter torpor expression varies in four bat species with differential susceptibility to white-nose syndrome. Scientific Reports 12:5688.

Jackson RT, Willcox EV, Zobel JM, Bernard RF. 2022b. Emergence activity at hibernacula differs among four bat species affected by white-nose syndrome. Ecology and Evolution 12:e9113.

Johnson JB, Gates JE. 2008. Spring migration and roost selection of female *Myotis leibii* in Maryland. Northeastern Naturalist 15:453–460.

Johnson JB, Gates JE, Ford WM. 2009. Notes on foraging activity of female *Myotis leibii* in Maryland. Washington, D.C.: U.S. Department of Agriculture, Forest Service. Research Paper NRS-8. Available: https://www.srs.fs.usda.gov/pubs/19840 (March 2023) (see *Supplemental Material*, Reference S2).

Johnson JS, Kiser JD, Watrous KS, Peterson TS. 2011. Day-roosts of *Myotis leibii* in the Appalachian Ridge and Valley of West Virginia. Northeastern Naturalist 18:95–106.

Johnson JS, Lacki MJ, Thomas SC, Grider JF. 2012. Frequent arousals from winter torpor in Rafinesque's big-eared bat (*Corynorhinus rafinesquii*). PLoS ONE 7:e49754.

Jonasson K, Guglielmo CG. 2019. Evidence for spring stopover refuelling in migrating silver-haired bats (*Lasionycteris noctivagans*). Canadian Journal of Zoology 97:961–970.

Jordan GW. 2020 Status of an anomalous population of northern long-eared bats in coastal North Carolina. Journal of Fish and Wildlife Management 11:665–678.

Kalko EK. 1995. Insect pursuit, prey capture and echolocation in pipistrelle bats (Microchiroptera). Animal Behaviour 50:861–880.

Kareiva P, Odell G. 1987. Swarms of predators exhibit "preytaxis" if individual predators use area-restricted search. American Naturalist 130:233–270.

LaVal RK, Clawson RL, LaVal ML, Caire W. 1977. Foraging behavior and nocturnal activity patterns of Missouri bats, with emphasis on the endangered species *Myotis grisescens* and *Myotis sodalis*. Journal of Mammalogy 58:592–599.

Moore PR, Risch TS, Morris KD, Rolland V. 2017. Habitat use of female gray bats assessed using aerial telemetry. Journal of Wildlife Management 81:1242–1253.

Moosman PR, Anderson PR, Frasier MG. 2017. Use of rock-crevices in winter by big brown bats and eastern small-footed bats in the Appalachian Ridge and Valley of Virginia. Banisteria 48:9–13.

Murray SW, Kurta A. 2004. Nocturnal activity of the endangered Indiana bat (*Myotis sodalis*). Journal of Zoology 262:197–206.

O'Keefe JM, Pettit JL, Loeb SC, Stiver WH. 2019. White-nose syndrome dramatically altered the summer bat assemblage in a temperate southern Appalachian forest. Mammalian Biology 98:146–153.

Park KJ, Jones G, Ransome RD. 2000. Torpor, arousal and activity of hibernating greater horseshoe bats (*Rhinolophus ferrumequinum*). Functional Ecology 14:580–588.

Perry RW, Thill RE. 2007. Tree roosting by male and female eastern pipistrelles in a forested landscape. Journal of Mammalogy 88:974–981.

Prendergast BJ, Freeman DA, Zucker I, Nelson RJ. 2002. Periodic arousal from hibernation is necessary for initiation of immune responses in ground squirrels. American Journal of Physiology 282:1054–1062.

R Development Core Team. 2020. R 3.6.1. A language and environment for statistical computing. Available: http://www.r-project.org (March 2023)

Reeder DM, Frank CL, Turner GG, Meteyer CU, Kurta A, Britzke ER, Blehert DS. 2012. Frequent arousal from hibernation linked to severity of infection and mortality in bats with white-nose syndrome. PLoS ONE 7:e38920.

Reynolds DS, Shoemaker K, von Oettingen S, Najjar S. 2017. High rates of winter activity and arousals in two New England bat species: implications for a reduced white-nose syndrome impact? Northeastern Naturalist 24: B188–B208.

Roby PL, Gumbert MW, Lacki MJ. 2019. Nine years of Indiana bat (*Myotis sodalis*) spring migration behavior. Journal of Mammalogy 100:1501–1511.

Samoray ST, Cotham SN, Gumbert MW. 2019. Spring migration behavior of a *Perimyotis subflavus* (tricolored bat) from Tennessee. Southeastern Naturalist 18:N16.

Seddon PJ, Maloney RF. 2004. Tracking wildlife radio-tag signals by light fixed-wing aircraft. Technical Series 30. Wellington, New Zealand: Department of Conservation. Available: https://www.doc.govt.nz/globalassets/documents/science-and-technical/docts30.pdf (March 2023)

Sikes RS, Animal Care and Use Committee. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 97:663–688.

Smith K. 2019. Assessing the potential impacts of radio transmitters on bat flight and behavior in a controlled environment. Master's thesis. Fort Worth: Texas Christian University.

Sparks DW, Ritzi CM, Duchamp JE, Whitaker JO Jr. 2005. Foraging habitat of the Indiana bat (*Myotis sodalis*) at an urban-rural interface. Journal of Mammalogy 86:713–718.

Strandin T, Babayan SA, Forbes KM. 2018. Reviewing the effects of food provisioning on wildlife immunity. Philosophical Transactions of the Royal Society B 373:20170088.

Thomas DP, Best TL. 2000. Radiotelemetric assessment of movement patterns of the gray bat (*Myotis grisescens*) at Guntersville Reservoir, Alabama. Occasional Papers of the North Carolina Museum of Natural Sciences and the North Carolina Biological Survey 12:27–39.

Thomas DW, Dorais M, Bergeron JM. 1990. Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus*. Journal of Mammalogy 71:475–479.

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

Tuttle MD. 1979. Status, causes of decline, and management of endangered gray bats. Journal of Wildlife Management 43:1–17.

[ESA] U.S. Endangered Species Act of 1973, as amended, Pub. L. No. 93-205, 87 Stat. 884 (Dec. 28, 1973). Available: https://www.fws.gov/sites/default/files/documents/endangered-species-act-accessible.pdf

[USFWS] U.S. Fish and Wildlife Service. 2012. North American bat death toll exceeds 5.5 million from white-nose syndrome. News release. Washington, D.C.: USFWS. Available: https://doi.org/10.3996/JFWM-22-049.S3 (109 KB PDF) and https://www.whitenosesyndrome.org/press-release/north-american-bat-death-tool-exceeds-5-5-million-from-white-nose-syndrome (March 2023) (see *Supplemental Material*, Reference S3).

Verant ML, Meteyer CU, Speakman JR, Cryan PM, Lorch JM, Blehert DS. 2014. White-nose syndrome initiates a cascade of physiologic disturbances in the hibernating bat host. BMC Physiology 14:1–11.

Walters B, Ritzi CM, Sparks DW, Whitaker JO Jr. 2007. Foraging behavior of eastern red bats (*Lasiurus borealis*) at an urban-rural interface. American Midland Naturalist 157:365–373.

Worton BJ. 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164–168.