



Nine years of Indiana bat (*Myotis sodalis*) spring migration behavior

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The endangered Indiana bat (*Myotis sodalis*) congregates in large hibernation groups in winter and travels after spring emergence to form summer maternity colonies, but information on migration behavior in this species remains limited to mostly band recovery observations. We tracked female Indiana bats in spring migration toward summer grounds using aerial radiotelemetry. Adult female Indiana bats were radiotagged in spring from 2009 through 2017, with 15 individuals successfully tracked to summer grounds and an additional 11 bats located in summer grounds via aerial telemetry after migration was complete. This resulted in the location of 17 previously unknown summer grounds for female Indiana bats, including adding Georgia, Alabama, and Mississippi to the summer maternity range. Two of the colonies identified in this study were south of the previously known southernmost colony in Tennessee, expanding the summer maternity range for the species by 178 km. Time-stamped location fixes along the migration path provided information about nightly and overall distances traveled, duration of travel, migration speed, and weather-related influences on bat behavior. Bats traveled 164.6 ± 26.2 km ($\pm SE$) on average from hibernacula to summer grounds and were migrating for an average of 7.3 ± 1.4 calendar nights. Bats alternated between foraging and traveling throughout each night of their migration route. Nightly migration rate was 9.9 ± 0.8 km/h and bats were active on the landscape for an average of 6.1 ± 0.4 h/night. Lower nighttime temperatures and lower barometric pressure correlated with use of layover areas during a migration night. Understanding bat behavior during migration can provide pertinent information for land managers to consider in efforts to conserve potential migration corridors, foraging areas, and roosting habitats of species in decline.

Key words: aerial radiotelemetry, bat migration, bat movement, Chiroptera, endangered species, Indiana bat, *Myotis sodalis*

The definition of animal migration has been debated and there is no consensus of its definitive meaning (Fryxell et al. 2011). However, for bats, it is generally defined as seasonal movement between two habitats that each provide climatic advantages (Fleming and Eby 2003). Migration of bats is not well understood for many species, partly due to the difficulty in tracking them over long distances at night. Regardless, movement of bats on the landscape has been studied for decades (summarized in Voigt et al. 2017) using wing-banding studies (Hall 1962; LaVal and LaVal 1980; Kurta and Murray 2002; Winhold and Kurta 2006; Ellison 2008; Rockey et al. 2013), stable hydrogen isotopes (Cryan et al. 2004; Britzke et al. 2009, 2012; Sullivan et al. 2012; Fraser et al. 2017), and automated telemetry (Holland et al. 2011; McGuire et al. 2012; Taylor et al. 2017). However, there are shortcomings for each

of these methods. For example, band recovery data have been collected since the 1930s in the United States (Ellison 2008) and in Europe (Hutterer et al. 2005) and have provided an origin point and an end point, but with limited information on timing or behavior in between. Band recoveries provide data on minimum distance traveled (assuming a straight-line flight) and, potentially, the minimum amount of time to complete the journey (e.g., Tuttle 1976), but they are limited by low recovery rates (e.g., Griffin 1940; Ellison 2008).

The Indiana bat (*Myotis sodalis*) has been listed as federally endangered since 1967. The majority of the species congregates in large colonies (> 10,000 bats) in 23 hibernacula (i.e., Priority 1 hibernacula) across seven states (USFWS 2007). This high concentration of bats is likely to require more resources on the landscape than are available immediately around the hibernacula

in the summer. Therefore, Indiana bats engage in female-biased partial migration (Fleming and Eby 2003), where females can migrate up to 673 km (Butchkoski and Bearer 2016), but males often remain near hibernacula or migrate shorter distances (USFWS 2007). The average distance, estimated from band recoveries, of migration by Indiana bats in the central part of the range is 401.9 ± 29.6 ($\pm SE$) km (Hall 1962; Davis 1964; LaVal and LaVal 1980; Gardner and Cook 2002; Kurta and Murray 2002; Winhold and Kurta 2006; Rockey et al. 2013; Butchkoski and Bearer 2016). Migration distances, as determined by radiotracking, of populations near the periphery of the range in northeastern United States are much shorter, with an average of 62.5 ± 11.9 km (Butchkoski and Bearer 2016; C. Butchkoski and G. Turner, Pennsylvania Game Commission, pers. comm., July 2009). Factors influencing timing and speed while traveling these distances are likely related to regional weather differences and animal health upon spring emergence.

Bats transfer heat easily, so nighttime weather conditions are likely to influence if, when, and how far bats migrate in a night. Spring weather conditions in the southern United States can be volatile and unpredictable, creating a challenge for nighttime-flying animals. Bats are heterothermic mammals with high surface area-to-volume ratios (Speakman 2000). This equates to thermoregulatory challenges that can be exacerbated by weather conditions, including cold (e.g., Racey and Swift 1981; O'Shea et al. 2016) and heat (e.g., Welbergen et al. 2008; O'Shea et al. 2016). Bats emerging from hibernation are vulnerable because they have depleted fat stores over the winter (Bernard and McCracken 2017), but still must have enough in reserve to start migrating to maternity colonies. Bats likely forage while migrating to supplement lost fat reserves (Fleming and Eby 2003; Hedenström 2009), and certain weather conditions are required to ensure prey availability along migration routes (Paige 1995; Kunz 1988). Therefore, weather is likely a contributing factor to spring migration behavior of Indiana bats.

We tracked individual female Indiana bats during spring migration using aerial telemetry to describe migration behavior in this species. We predicted that bats would migrate north from hibernacula to maternity colonies based on data from band recoveries (Winhold and Kurta 2006; USFWS 2007). We further predicted that Indiana bats would not migrate > 400 km. This distance threshold was used to distinguish between long-distance and regional migration of the noctule bat (*Nyctalus noctula*) in Europe (Lehnert et al. 2018), is the average distance documented by band recoveries as stated above, and is supported by Gardner and Cook (2002), who postulated that Indiana bats would not migrate "large distances." Lastly, we predicted that migration behavior of bats would be influenced negatively by weather conditions such as lower temperatures, stronger winds, and heavier amounts of precipitation (USFWS 2007; McGuire et al. 2014; Weller et al. 2016; Pettit and O'Keefe 2017).

MATERIALS AND METHODS

Study area and use of hibernacula.—Karst topography has resulted in an abundance of caves throughout the southeastern

portion of the United States, including central parts of Indiana, Kentucky, Tennessee, and Alabama (Weary and Doctor 2014). We attached radiotransmitters to female Indiana bats from ten different cave hibernacula in three states: Tennessee ($n = 8$), Indiana ($n = 1$), and Alabama ($n = 1$). We visited five of the caves once, four caves twice, and one cave in central Tennessee (referred hereafter as TN1) in 7 consecutive years (2010–2016). Typically, we visited more than one cave in a year, resulting in 20 bat collection events over 9 years (2009–2017). Start dates were based on the known timeframe of natural emergence of Indiana bats from hibernation, but we chose nights forecasted with favorable weather conditions that permitted aerial tracking at night (i.e., no rain, low wind speeds, and temperatures remaining above 10°C until at least midnight). Other factors for selection of start dates included the geographic location of a cave, the number of bats hibernating inside a cave, and the acoustic activity recorded at a cave entrance in previous years. The land cover around the caves was mostly deciduous forest on public or private land, with scattered residences and very little agricultural use. The number of hibernating Indiana bats in sampled caves ranged from two individuals to > 60,000, with most caves housing fewer than 100 bats.

Bat capture.—In the spring of 2009 through 2017, we hand-collected Indiana bats from inside hibernacula ($n = 8$ caves), or bats were caught in harp traps ($n = 2$ caves) as they emerged at dusk. We identified bats to species, measured mass (g) and right forearm length (mm), and banded them with aluminum-lipped uniquely numbered bat bands (Porzana Ltd., Icklesham, East Sussex, United Kingdom). We used beeper VHF radiotransmitters from Holohil Systems Ltd. (Carp, Ontario, Canada) and coded VHF radiotransmitters from Lotek Wireless Inc. (Newmarket, Ontario, Canada) to radiotag select females by trimming hair from between the scapulae and securing transmitters with surgical cement (Perma-Type Co Inc., Plainville, Connecticut). We released bats individually near hibernacula in coordination with aerial crews circling overhead. The mass of transmitters used ranged from 0.29 to 0.42 g, but the majority (75.8%) were < 0.35 g.

All methods followed the American Society of Mammalogy guidelines for use of wild animals in research (Sikes et al. 2016) and were approved by the University of Kentucky Institutional Animals Care and Use Committee (protocol #2017-2787). All protocols were conducted under Endangered Species Act Section 10(a)(1)(A) permits for endangered species (TE070584-4 and TE94849B-0) and appropriate state permits for the years in which work was conducted.

Radiotelemetry.—We conducted aerial tracking using a Cessna 172 Skyhawk fixed-wing aircraft fitted with Advanced Telemetry Systems (ATS, Isanti, Minnesota) aircraft strut mount assemblies and a 172-3FB 4-element ATS Yagi directional antenna on each wing. All aircraft pilots and navigator data collectors were trained bat biologists. We detected transmitter signals using an ATS receiver-datalogger (model R4500CD) while the plane maneuvered in tight circles above the bat's mobile position. We used mapping software (Delorme Topo North America 9.0) loaded to laptop computers with

installed GPS (Panasonic Toughbook, Newark, New Jersey) to view the location of the plane and for the navigator to manually place location fixes (i.e., waypoints) on the map based on the signal strength from either or both antennas. We placed waypoints on the map that were automatically time-stamped with the computer's internal clock. Using three navigators and two pilots resulted in an overall location accuracy of 382.7 ± 44.7 m ($n = 65$ points, range: 5.9–1,765 m).

For the purposes of this document, "migration" encompasses the entire process after emergence from hibernacula to the arrival at summer grounds. Summer grounds indicate the areas where female Indiana bats are congregating before 15 May to form maternity colonies (USFWS 2007). During migration, bats travel (move away from the hibernaculum toward the summer grounds), forage (engage in an erratic flight pattern), roost (inactive inside a roost for one day), or use a layover area (inactive inside a roost or using multiple roosts in the same area for > 1 day). Tracking of travel and foraging were conducted during nighttime hours (i.e., approx. 19:00–07:00 h) on a single radiotagged bat at a time. We monitored other active bat frequencies periodically to determine if target bats were migrating with other radiotagged bats. Ground support crews tracked bats throughout the night and maintained contact with bats when the plane was temporarily unavailable for refueling during the night. Vehicles were equipped with telemetry receivers and long-range 5-element Yagi antennas to maintain contact with radiotagged bats. Contact between aerial and ground crews was maintained by two-way radios and text messaging with cellular telephones.

We placed temperature data loggers (iButton, Maxim Integrated, San Jose, California) on the roofs of field vehicles for collecting ambient temperature (T_a) data at night and on trees near roosting bats to collect T_a during days and nights. From 2013 through 2017, interpulse periods emitted by temperature sensitive transmitters were stored in an ATS receiver-datalogger to determine skin temperature of bats (T_{sk}) during post-processing.

Since multiple bats were radiotagged at each tracking event, we conducted daytime searches of known maternity colonies to document use by the remaining radiotagged bats, as well as flying predetermined transects with the intent of locating radiotagged bats at previously undocumented maternity colonies. We determined that a bat had arrived at its summer grounds when: 1) the bat did not continue to migrate in favorable weather, 2) it began roosting with other bats to form a maternity colony, and 3) it was roosting in habitat typical for summer roosting Indiana bats, e.g., dead or dying standing trees with sloughing bark typically within riparian areas or bottom-land habitat surrounded by contiguous forest (USFWS 2007).

Data analysis.—We imported time-stamped waypoint files representing bat location fixes into ArcGIS v.10.5 (ESRI, Redlands, California) and overlaid them onto topographic and aerial maps to determine distance and direction of bat flights and to quantify behavior. We evaluated linear flight distances (between start and end points) in this study, which included distances from hibernacula to summer grounds and lengths of behavioral segments, i.e., traveling or foraging.

We used Oriana v 4.02 (Kovach Computing Services, Anglesey, Wales) software to determine the direction bats migrated. We calculated a circular-linear correlation between direction and distance traveled in Oriana. Data used in these analyses were the straight-line azimuth and distance calculated in ArcGIS from the bat's hibernaculum of origin to the first roost at the summer grounds. We used Rao's spacing goodness-of-fit test (or Rao's U) to test the prediction that bats migrate north (Bergin 1991). We conducted a one-way analysis of variance (ANOVA) to determine if the size of the hibernating population affected the distance that bats migrated. We also used a one-way ANOVA to determine the relationship, if any, between the distance from hibernacula to summer grounds and the number of nights a bat spent migrating.

We classified flight behavior based on patterns of sequential GPS locations (Fig. 1). We characterized closely spaced points that did not form a linear pattern as foraging, while we characterized sequential points that moved away from an origin (i.e., hibernaculum, roost, or foraging area) as traveling. We conducted cluster analysis in the R environment (R Development Core Team 2017) to validate the manual classification of each point using X–Y coordinates, date–time stamp, and the distance from origin hibernaculum. The distance from origin hibernaculum did not add to the predictive power of the model, therefore, we only used location coordinates and the date–time information in separating foraging from migration traveling. The accuracy value describing how often the classifier is correct was 0.84 ± 0.01 (range: 0.77–0.98) for 18 bats.

Because the data were not normally distributed, we used separate Student's *t*-tests (Zar 1999) for unequal variances to determine differences in the amount of time bats spent traveling versus foraging, bat speed before and after the use of a layover area, and nightly distance traveled before and after the use of a layover area. The overall amount of time bats spent traveling per night was normally distributed, therefore we used Student's *t*-tests to determine differences in these activities before and after a layover event.

To determine if the number of nights migrating was affected by weather, we conducted analysis of T_a and T_{sk} to assess whether bats were torpid or normothermic on a given night. Calibration points were provided by the manufacturer for each temperature-sensitive transmitter, which we then used to create individual polynomial equations for determining T_{sk} from the collection of interpulse periods. Subsequently, we paired T_a and T_{sk} by timestamp for further analysis. We determined torpor onset temperature for roosting bats with bat mass (BM) and T_a in the equation described by Willis (2007) using model parameters minus 1 SE:

$$T_{sk-onset} \text{ 1SE} = (0.041) * \text{BM} + (0.04) * T_a + 31.083$$

We compared individual recorded T_{sk} values to the torpor onset value to determine if the bat was normothermic ($T_{sk} > T_{sk-onset} - 1 \text{ SE}$) or torpid ($T_{sk} < T_{sk-onset} - 1 \text{ SE}$).

We obtained data on weather factors that could potentially affect bat behavior during migration from Weather Underground (www.wunderground.com). These included minimum temperature

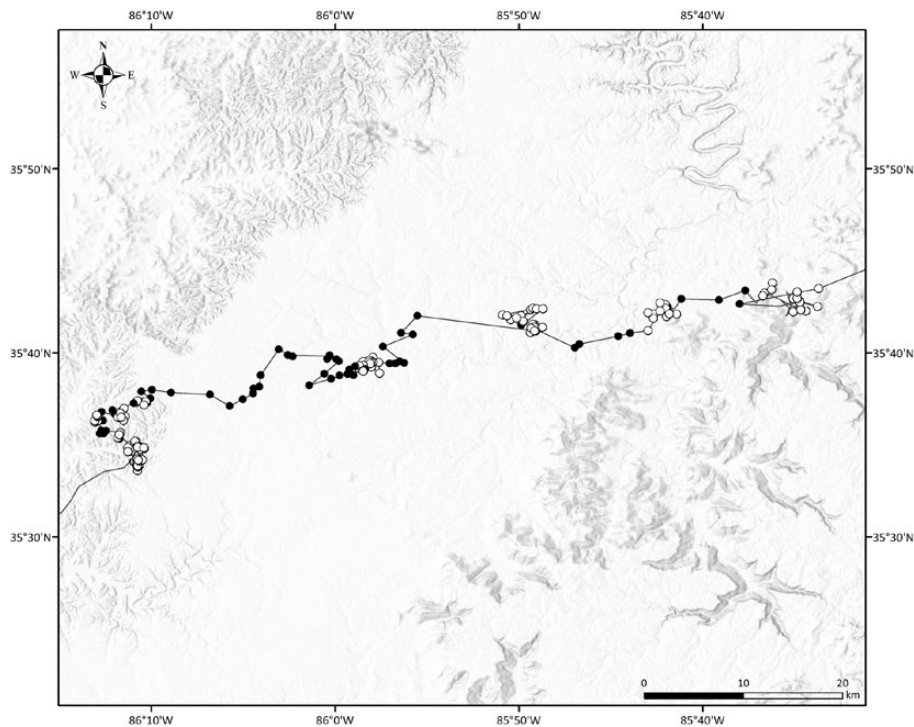


Fig. 1.—Visual representation of an Indiana bat (*Myotis sodalis*) traveling (closed circles) and foraging (open circles) during migration.

(nearest 1°C), precipitation (0.1 mm), wind speed (1.0 km/h), barometric pressure (1.0 hectopascal [hPa]), and absolute humidity (1%). We used data recorded from 19:00 to 07:00 h each night at the nearest weather station to a tracked bat. From these data, we derived Pearson correlations for 11 weather metrics using a pairwise method: low temperature, precipitation, high wind speed, average wind speed, gust wind speeds, high barometric pressure, average barometric pressure, low barometric pressure, high humidity, average humidity, and low humidity. Correlated variables (Pearson's $|r| > 0.20$) were removed and the three remaining uncorrelated variables were used in further analysis. These were low temperature, low pressure, and high humidity.

For each night of tracking, we assigned bat behavior to one of the categories defined in "Radiotelemetry" based on the behavior that dominated throughout the night: travel ($n = 39$ nights), foraging ($n = 8$ nights), or layover ($n = 26$ nights). We conducted one-way ANOVAs to determine how nightly weather variables affected nightly bat behavior.

We assessed possible differences in mass of radiotagged bats and those not tagged using a Student's t -test. Both data sets were normally distributed and possessed equal variances. We used Student's t -test for unequal variances to determine if body mass of bats that migrated the first night after release differed from those that did not migrate the first night. Except for the cluster analysis in Program R stated earlier, we conducted remaining analyses in JMP (Version Pro 14. SAS Institute Inc., Cary, North Carolina, 1989–2007). For all statistical tests conducted, $\alpha = 0.05$.

RESULTS

Bat capture.—A total of 260 transmitters were deployed on 372 adult female Indiana bats captured at hibernacula typically

during the first week of April each year. However, start dates ranged from 20 March to 17 April depending on the onset of spring from one geographic location to another. This included 288 individuals radiotagged once and 51 individuals radiotagged two to four times each throughout the 9-year study period. Regardless of capture frequency, migration data were only collected on an individual once. Most bats ($n = 239$) were radiotagged from TN1 and largely outnumbered all captures combined from the other nine caves (sum = 133). Mean mass of captured bats was 6.7 ± 0.03 g (range: 5.0–9.0 g), with radiotagged bats heavier ($\bar{x} = 6.8 \pm 0.04$ g; range: 5.5–9.0 g) than bats not radiotagged ($\bar{x} = 6.3 \pm 0.06$ g; range: 5.5–7.8 g; $t_{370} = 7.22$, $P < 0.01$). Mean transmitter mass was 4.8 ± 0.04 % (range: 3.7–6.7%) of body mass. Of the 51 recaptured bats, 46 were radiotagged multiple times and 26 were radiotagged with transmitters weighing $> 5\%$ of the bat's body mass, either once or twice. Of these 26 bats, 22 were recaptured in following years after having carried a transmitter that exceeded 5% of the body mass.

Radiotelemetry.—We collected 4,398 location fixes on 20 individual bats tracked from eight hibernacula. Of these, 3,429 location fixes were collected on 15 bats that were tracked to their summer grounds with an average of 228.6 ± 46.9 fixes per bat (range: 39–777 fixes). The remaining 969 fixes were collected on bats that were tracked during incomplete migration routes but which still provided behavioral information. The majority of bats (82.4%) foraged after release either before starting migration travel or during staging behavior. We defined staging as the behavior when bats foraged and roosted within 5 km of the hibernaculum, based on known distances of roosts from hibernacula used by bats after spring emergence (Gumbert et al. 2002). Some bats may have engaged in staging

without being detected due to the tracking crew following a migrating bat, but those bats that were documented to remain near the hibernaculum the first night ($n = 22$ bats) did not differ in mass ($\bar{x} = 6.8 \pm 0.1$ g) from those that migrated the first night ($n = 20$ bats; $\bar{x} = 6.9 \pm 0.2$ g; $t_{34.4} = -0.6$, $P = 0.53$). There was no difference in ambient temperature on nights when bats migrated ($n = 7$ nights, $\bar{x} = 15.9 \pm 1.9^\circ\text{C}$) from nights when bats staged ($n = 6$ nights; $\bar{x} = 14.6 \pm 6.0^\circ\text{C}$; $t_{5.8} = -0.5$, $P = 0.63$). Once migration had begun, bats foraged upon emerging from a roost 58.1% of the time and then began traveling toward summer grounds. During the other 41.9% of the time, bats commenced traveling upon emergence from a roost without a detectable foraging bout. A larger majority of the time (85.7%), bats foraged before roosting for the day, whereas bats did not forage before roosting only 14.3% of the time.

Data for the entire migration route were collected on 15 individual bats that traveled 6.3–368.1 km between hibernacula and summer grounds or confirmed maternity colonies ($\bar{x} = 164.6 \pm 26.2$ km). Distance and direction from the hibernaculum were not correlated ($r = 0.3$, $P = 0.07$). Nightly migration distance was 59.8 ± 5.2 km (range: 2.2–153.3 km) and bats were active for 6.1 ± 0.4 h (range: 1.4–9.7 h) per night of migration. This resulted in an average nightly migration rate of 9.9 ± 0.8 km/h (range: 0.7–20.1 km/h). These distances are the minimums measured for bats in flight, with the total distances flown likely being much longer.

During migration, bats alternated between foraging and traveling throughout a night. The mean distance that bats traveled between foraging areas was 16.2 ± 1.5 km, but the range of these values was wide (1.3–69.4 km). The distribution was not normal (Shapiro–Wilk $W = 0.81$, $P < 0.01$) and it was heavily weighted to short-distance movements (Fig. 2). Migrating bats used 3.3 ± 0.3 foraging areas per night on average (range: 1–8 foraging areas) and 2.8 ± 0.3 traveling bouts per night (range: 1–7 traveling bouts). Bats spent more time in individual traveling bouts ($\bar{x} = 1.3 \pm 0.1$ h) than in foraging bouts ($\bar{x} = 0.6 \pm 0.1$ h; $t_{156.3} = 5.1$, $P < 0.01$) and spent more time traveling per night ($\bar{x} = 3.9 \pm 0.3$ h) than foraging ($\bar{x} = 2.2 \pm 0.2$ h; $t_{66.7} = 4.3$, $P < 0.01$). In addition, bats spent more time traveling per night after a layover event ($\bar{x} = 4.5 \pm 0.6$ h) than during the nights at the onset of migration ($\bar{x} = 2.8 \pm 0.6$ h; $t_{20.4} = -2.13$, $P = 0.046$). Although nightly flight speed was not significantly faster after

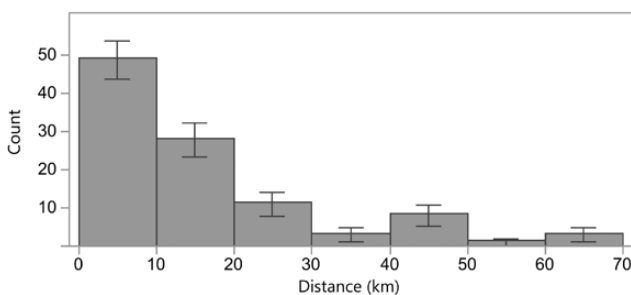


Fig. 2.—Distribution of distances traveled (km) between foraging bouts by spring-migrating female Indiana bats (*Myotis sodalis*) from hibernacula to summer grounds. The majority of distances were short (< 20 km).

a layover event ($\bar{x} = 10.7 \pm 1.0$ km/h) than before the use of a layover ($\bar{x} = 8.1 \pm 1.2$ km/h; $t_{22.8} = -1.64$, $P = 0.11$), the distance traveled in a night was longer after a layover ($\bar{x} = 68.5 \pm 9.9$ km) than before a layover ($\bar{x} = 42.9 \pm 6.1$ km; $t_{21.2} = -2.2$, $P = 0.04$).

The mean duration of bat activity was 6.0 ± 0.4 h each night of migration (range: 1.0–10.8 h). Bats were tracked on average for 7.3 ± 1.4 nights (range: 1–22 nights), but they actively traveled along the migration route for 2.7 ± 0.4 nights (1–5 nights). The overall linear distance a bat traveled was highly correlated with the number of migration nights ($R^2 = 0.8$; $F_{1,13} = 55.8$, $P < 0.01$).

Although 15 bats were actively tracked, we located an additional 11 bats in their summer grounds via aerial telemetry after the completion of migration. The direction from hibernacula to summer grounds of all bats located in their summer grounds ($n = 26$ connections) was not random ($U = 159.78$, $P < 0.05$) and the mean cardinal direction was west ($278.9 \pm 15.9^\circ$, 95% $CI = 247.7^\circ$ – 310.2° ; Fig. 3). Population size of hibernating bats did not have an effect on migration direction ($F_{13,57} = 1.68$, $P = 0.09$). For example, the only two female Indiana bats hibernating in a cave in northwest Tennessee migrated in different directions to different summer grounds (northwest and north), and two female bats radiotagged from a hibernaculum housing 60,000 bats in Indiana also each migrated in different directions (southwest and northeast).

Bats did not travel in a straight line from hibernacula to summer grounds. Therefore, the migration path for each bat was determined by measuring the farthest deviation from

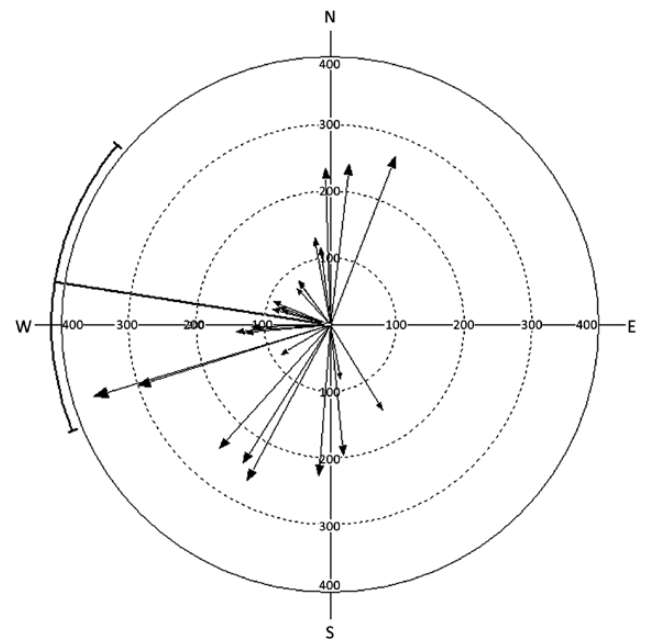


Fig. 3.—Direction and distance traveled by 26 female Indiana bats (*Myotis sodalis*) migrating in the spring from hibernacula to summer grounds. We actively tracked 15 individuals, but 11 bats were located via aerial telemetry in summer grounds after migration was completed. Bats traveled in a westerly direction on average (dark black line). Direction values: 0 = north, 90 = east, 180 = south, 270 = west. Values within the circles represent distance in kilometers.

a straight line connecting the hibernaculum and summer grounds. The mean migration path width from hibernacula to summer grounds was 24.8 ± 4.2 km (range: 2.7–55.3 km). Five bats were tracked from two hibernacula to the same summer grounds in northeastern Alabama (Fig. 4), effectively creating a migration corridor measuring 23.5 km wide. Although there was variability in the exact path, the collective routes of these five bats converged at a point in northwestern Georgia (Fig. 4, inset), before diverging to cross Weiss Lake in Alabama and again reconvene near the confirmed maternity roost in eastern Alabama.

No bat radiotagged multiple times was actively tracked in multiple years, but three were located again in their respective known maternity colonies during targeted searches. Radiotagged bats were never documented migrating together

and were always documented roosting alone until they reached the summer grounds. We identified connections between eight hibernacula and 20 summer grounds across eight different states for a total of 26 connections, including some summer grounds connected to multiple hibernacula (Fig. 5). Of the 20 summer grounds and maternity colonies, 17 were previously undocumented including adding Alabama, Georgia, and Mississippi as new states to the known maternity range. Of these, Alabama now houses the southernmost colony known to date that extends the summer range of the species by 61 km (Redinger 2006; USFWS 2007). However, this summer record reported by Redinger (2006) is from a cave that was surveyed multiple times in 2005, and only males and non-reproductive females were captured. Prior to the current study, the southernmost maternity colony of Indiana bats known was in southern

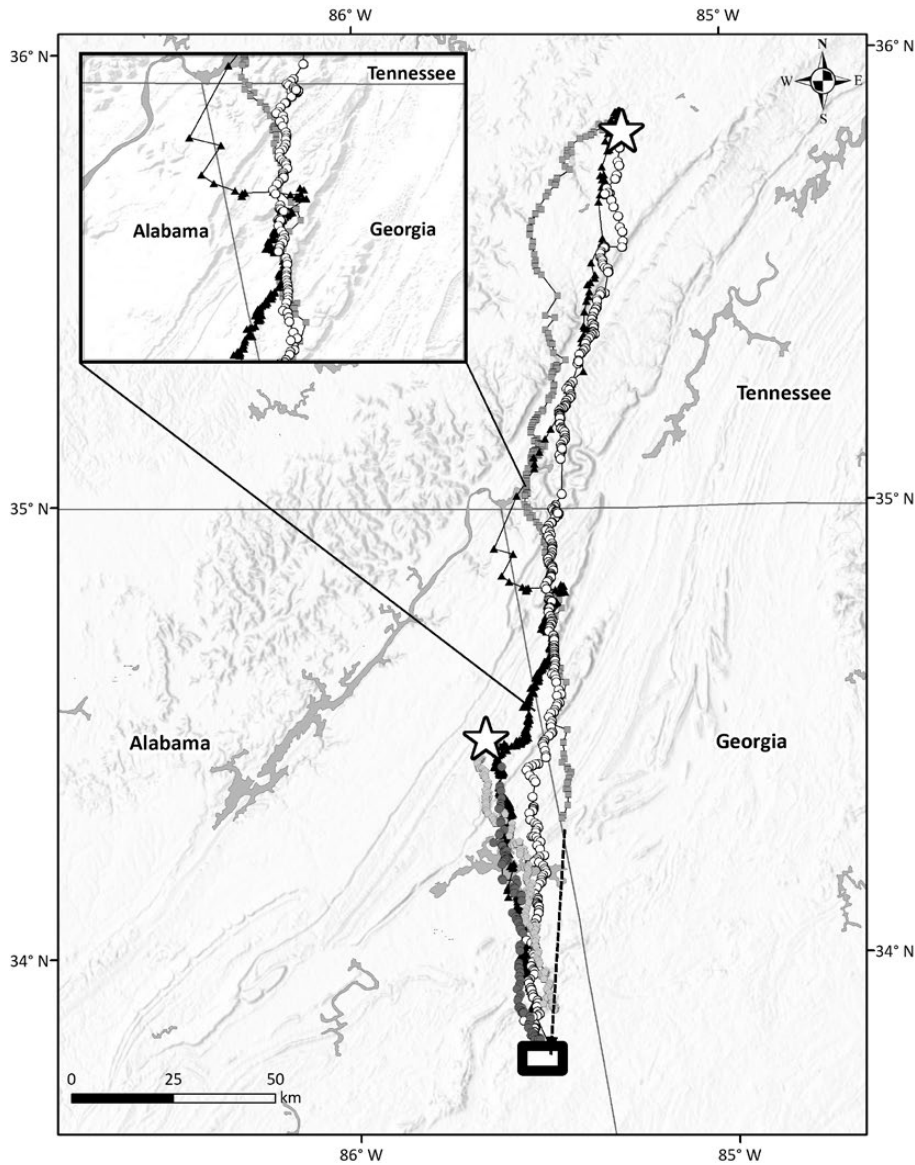


Fig. 4.—Travel paths comprised of location fixes for individual female Indiana bats (*Myotis sodalis*) aerially radiotracked during spring migration. Each large white star is a hibernaculum and each smaller symbol represents a different individual ($n = 5$ bats). All bats traveled south from hibernacula during spring migration to their shared maternity area (rectangle at the bottom of the migration paths). Filled gray irregular polygons represent lakes. Inset: overlapping migration paths.

Tennessee. Therefore, our southernmost colony located in Alabama extends the maternity range by 178 km. Arrival date to summer grounds ranged from 24 March in central Tennessee to 2 May in northeastern Indiana.

Effects of weather.—Pearson correlation filtering resulted in three uncorrelated weather variables for evaluating bat behavior: low temperature, low pressure, and high humidity. High humidity did not affect behavior ($F_{2,70} = 0.45, P < 0.64$), but low temperature ($F_{2,70} = 7.63, P = 0.001$) and low pressure ($F_{2,70} = 18.49, P < 0.0001$) varied among the three behavior types. There was no difference between foraging and layover behavior for either of these variables, but migrating behavior was different from both foraging and layover behavior ($P < 0.05$ post-hoc Tukey’s HSD). Mean low temperature during a travel night ($\bar{x} = 11.3 \pm 0.8^\circ\text{C}$) was higher

than during a layover ($\bar{x} = 7.1 \pm 0.8^\circ\text{C}$) and during a foraging night ($\bar{x} = 6.9 \pm 1.7^\circ\text{C}$). Mean low pressure was higher during migrating ($\bar{x} = 995.9 \pm 0.9$ hPa) than during a layover ($\bar{x} = 988.7 \pm 1.5$ hPa) or a foraging night ($\bar{x} = 983.0 \pm 2.0$ hPa). Bats typically were not active when T_a was $\leq 10^\circ\text{C}$, even if T_{sk} was normothermic. Only 9.1% of the data points revealed that bats were normothermic at temperatures below 10°C (Table 1). One exception was an individual that foraged for up to 2 h when T_a was 9°C on two separate nights.

Precipitation events and high wind nights (i.e., > 10.3 m/s as determined for safety by pilots during this study) grounded aircraft, requiring the team to rely on ground monitoring. However, ground monitoring of radiotagged bats during those nights or the following days typically recorded little bat movement. An exception was the loss of a transmitter signal the day following severe storms and the subsequent location of this bat within its summer grounds 180 km away 6 days later.

DISCUSSION

The migration pattern used by Indiana bats once they exit hibernacula is composed of alternating steps of linear and concentrated flights. Some bats migrated the first night, while others remained near the hibernaculum, i.e., engaged in staging behavior. It is unknown why some bats used the staging area for ≥ 1 night while others migrated after release, but there are likely many factors. Although four of the five bats caught in harp traps during natural emergence from hibernacula migrated on the night of capture, the majority of the bats radiotagged in this study were hand-collected from within the cave. Some of the hand-collected bats migrated the first night whereas others remained in the staging area the following day. There was no difference in body mass of bats that staged and those that started migrating the first night, a phenomenon also documented by Dechmann et al. (2017). However, there could still be a physiological difference that would influence timing of migration, such as physically imperceptible impairment due to white-nose syndrome (WNS), a devastating disease caused by the fungus *Pseudogymnoascus destructans* that is reducing bat populations throughout the eastern United States and Canada (Frick et al. 2010). Although no physiological measurements were taken, staging bats may not retain enough fat reserves from the winter due to any number of factors (e.g., arousing too often, not enough fat during the onset of hibernation, roosting in sub-optimal temperatures, etc.). The amount of time animals remain in hibernation is regulated by “an endogenous circannual clock” (Wang and Wolowyk 1988) and females

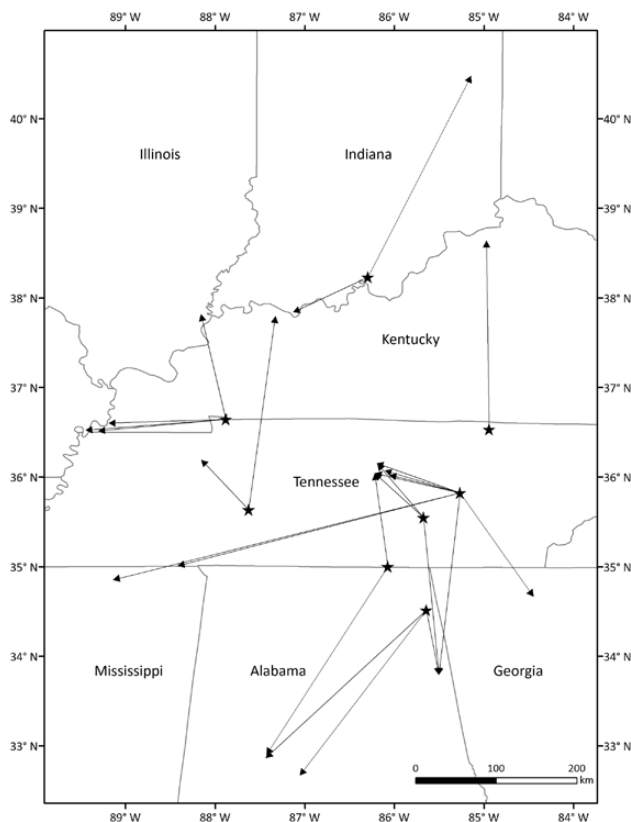


Fig. 5.—Connections between winter hibernacula (black stars) and summer grounds (arrow heads) for radiotagged female Indiana bats (*Myotis sodalis*) identified by aerial radiotracking during spring migration. Arrows indicate the direction of travel away from hibernacula during spring migration.

Table 1.—Measurements of Indiana bat (*Myotis sodalis*) skin temperatures (T_{sk}) and associated ambient air temperatures (T_a) during day and night, and energetic states, 2013–2017.

Day or night energetic state	Mean T_a ($^\circ\text{C}$)	Range of T_a ($^\circ\text{C}$)	Mean T_{sk} ($^\circ\text{C}$)	Range of T_{sk} ($^\circ\text{C}$)
Day				
Normothermic	24.4	13.0–27.0	33.1	32.0–34.4
Torpor	21.8	5.0–34.5	24.3	12.1–32.4
Night				
Normothermic	16.2	4.5–23.0	33.0	31.5–35.1
Torpor	12.5	4.5–23.0	21.9	11.9–32.1

require hibernation for the storage of sperm (McNab 1974). Therefore, because bats do not all enter hibernation at the same time, neither do they emerge at the same time. Bats that staged may have entered hibernation later than ones that migrated. In addition, individuality among bats cannot be ruled out; not all bats behave the same way.

Regardless if bats staged or began migrating the night of release, they generally utilized a foraging bout initially. Once bats began moving away from hibernacula toward summer grounds, they alternated between migration flight and foraging flight. This alternating pattern persisted until weather became unfavorable to continue migrating (i.e., temperature dropped or storms were encountered) or until sunrise, when bats often foraged before selecting a diurnal roost. Indiana bats also used layover areas consisting of a multi-night inactive period that was occasionally accompanied by foraging. This pattern of travel, foraging, and layovers continued until bats arrived at summer grounds, when only nightly foraging occurred during favorable weather.

Although the number, frequency, and duration of foraging bouts varied among bats, all individuals engaged in this behavior during migration and frequently before selecting a roost. This is in contrast to the postulation that silver-haired bats (*Lasionycteris noctivagans*) do not forage along migration routes (McGuire et al. 2014) but is in agreement with the theoretical model by Hedenström (2009). Indiana bats spend up to 6 months in hibernation resulting in their lowest body condition in the spring (Bernard and McCracken 2017). Their fat reserves acquired in the autumn months are used for homeostasis and to support their arousal every 12–15 days during hibernation (Speakman and Thomas 2003). Consequently, prey items must be consumed upon emergence from hibernation to replenish fat stores and acquire needed calories for the imminent migration (Sapir et al. 2011).

After initial foraging in the staging area and foraging bouts in subsequent nights, bats spent more time traveling and traveled farther after using a layover than at the onset of migration. Presumably bats had acquired or conserved sufficient energy requirements during a layover and therefore were able to fly for longer traveling bouts and use fewer foraging bouts during the last leg of their journey. Arriving at summer grounds early is likely advantageous for several reasons. Bats could potentially reduce the amount of time and effort exerted during migration, would arrive in an area of familiarity for ease of foraging and roosting opportunities, and could begin establishing the maternity colony to prepare for pregnancy.

Band recovery data for Indiana bats has revealed migration pathways in a north-south direction (USFWS 2007; Rockey et al. 2013). However, in portions of the Midwestern United States, band recoveries document bats traveling southwest, southeast, east, and west (Gardner and Cook 2002). Spring-migrating bats in Pennsylvania were actively tracked along both north-south and east-west pathways (Butchkoski and Bearer 2016; Hart and Brenner 2016; C. Butchkoski and G. Turner, Pennsylvania Game Commission, pers. comm., July 2009). Indiana bats in our study favored a westerly migration

path on average, rejecting our prediction of northward spring migration. This suggests that there may be variation in the general migration direction across geographic regions. This is supported by band recovery data of many species of bats (Baker 1978). The variation in migration pathways and lack of clearly defined linear flyways also suggests that the whole range of the Indiana bat should be considered potential flyway habitat. The locations of < 10% of maternity colonies of this species are known (USFWS 2007), so bats could be migrating in any direction from a given hibernaculum. Therefore, it would be unreasonable to consider any part of the range devoid of Indiana bat activity during at least some portion of the year.

Bats in our study migrated relatively short distances (i.e., < 400 km). Other studies have reported band recoveries documenting longer migration distances (i.e., 575 km in Winhold and Kurta 2006; 673 km in Butchkoski and Bearer 2016), indicating that individuals of the species are capable of migration movements > 400 km. We respectfully disagree with Krauel et al. (2017), who used automated radiotelemetry to conclude that Indiana bats that travel farther than 100 km are outliers. In our study based on aerial radiotelemetry tracking, 67% of the bats traveled farther than 100 km from hibernacula, suggesting that these are not outliers.

Air temperature was a significant factor determining Indiana bat behavior on a given night. Bats did not migrate at lower temperatures, and essentially no activity was recorded when air temperature was lower than 10°C. This value is generally accepted as the temperature at which bat activity during the summer months is reduced (USFWS 2018) and when bats start to enter hibernacula in the fall (Hall 1962; Myers 1964). This provides a starting point for understanding how temperature might affect bat migration activity, and further research is needed to determine different levels of torpor and the effect of transition temperatures between two behavioral states, i.e., normothermy and torpor. Low atmospheric pressure was also a significant indicator of layover use in our study, as documented in previous studies (Cryan and Brown 2007; Baerwald and Barclay 2011; Wolcott and Vulinec 2012; Bender and Hartman 2015). Even though wind speed was not a predictor of behavior, wind speeds sufficient to ground the aircraft also tended to deter bat movement. This is in agreement with McCracken et al. (2016), who found that Mexican free-tailed bats (*Tadarida brasiliensis*) adjusted their flight behavior depending on wind speed. Springtime weather appears to be an important external cue for migrating bats of many species (Park et al. 2000; Smith and McWilliams 2016; Jonasson 2017), including Indiana bats.

The dates of arrival at maternity roosts in our study are within the range of earliest arrival (17 March–15 April) and colony formation (8 April–14 May) found by Pettit and O'Keefe (2017) at a large Indiana bat colony in central Indiana. Geographic location, distance traveled, and weather all influence this wide range of travel dates. Summer habitat used by Indiana bats from 15 May to 15 August is protected under the Endangered Species Act. However, with the use of maternity areas in the transition period between migration and official establishment of maternity colonies, we agree with Pettit and O'Keefe (2017) that the

time periods before 15 May and after 15 August are equally important for land managers to protect bat habitat. Tree clearing is allowed from 15 October to 31 March (USFWS 2018), but empirical data demonstrate that at least some Indiana bats are using trees outside of these dates.

The general lack of information on bat migration behavior has resulted in insufficient conservation efforts for bat species during these critical transition periods. Most information collected on endangered bat species in the United States has primarily been habitat use in the summer maternity season and population estimates gained through winter hibernacula counts. While these data are important to the protection of the species, many questions still exist, including habitat use of migrating bats, landscape use and avoidance, energetics, and the effects of weather during dynamic times of year. Answers to these questions are needed to help mitigate losses of these nighttime keystone predators.

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