

Testing traditional assumptions about regional migration in bats

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Abstract While some bats cover long distances during migration, moving thousands of kilometers, most migratory bats are considered regional migrants, thought to move relatively short distances (< 500 km) between hibernacula and maternity sites. However, behavior can vary considerably among species and our understanding of these movements has largely been limited to banding studies or detailed tracking of small numbers of bats by aircraft. Inferring population-wide behavior from small samples is difficult and can introduce bias. We tagged 108 Indiana bats (*Myotis sodalis*) in the Midwestern US and used a regional network of radiotelemetry receivers to study movement patterns. With this dataset, we tested the following traditional generalizations about regional migrants: (1) bats move away from hibernacula in spring in all directions with known maternity roosts, e.g., in a star-like pattern; (2) bats follow linear landscape features; (3) long-distance movements are uncommon; and (4) autumn migration comprises a single movement from summer maternity site to winter hibernaculum. In spring, bats left the hibernaculum immediately and primarily moved north despite available maternity roosts in all directions. We found no evidence that bats follow rivers, the predominant linear element in the landscape. Only six tagged bats traveled > 100 km, suggesting that longer-distance movements may be outliers. In autumn, only two bats visited multiple known hibernacula, and after swarming, some

females moved > 100 km to areas without known hibernacula. Common generalizations about regional migrant movements may not be representative of population behavior and care should be taken with respect to management decisions based on those assumptions.

Keywords Telemetry · *Myotis sodalis* · Regional migrants · Swarming · MOTUS wildlife tracking system

Introduction

While some bat species undertake latitudinal migrations of > 1000 km, as in migratory birds, most temperate migratory bat species are thought to share behaviors loosely categorized as regional migration (Fleming and Eby 2003; Griffin 1970; Krauel and McCracken 2013). In the traditional view of regional bat migration, individuals depart in spring from hibernacula and disperse in all directions across the landscape in a “star-pattern” (Griffin 1970; Hutterer et al. 2005). In autumn, individuals return to hibernacula, where mating occurs during a behavior known as swarming (Fenton 1969, 1970; Kerth et al. 2003; Veith et al. 2004). Migration distances are shorter than for long-distance migrants, typically < 500 km (Bisson et al. 2009; Fenton 1970; Kerth et al. 2003; Veith et al. 2004). Little is known about migration routes and speed, primarily due to difficulties of tracking individual bats across the landscape. Some evidence suggests that during regional migration, bats may follow landscape features, for example rivers; in Poland, *Myotis daubentonii* flew north in spring and south in autumn along a river (Furmankiewicz and Kucharska 2009), and in Spain, *Miniopterus schreibersii* used a river for orientation after release (Serra-Cobo et al. 2000). Finally, regional migrant bats may fly at faster speeds during migration than

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during foraging (Davis and Hitchcock 1965; Humphrey and Cope 1976; Tuttle 1976).

This traditional understanding of regional migration behavior includes many generalizations that may lead to bias. First, regional migration is often interpreted as synonymous with shorter-distance migration (explicitly or implicitly) and contrasting long-distance migration. However, banding data demonstrate that some individuals in regionally migratory species can travel > 500 km (*Myotis sodalis*, Rokey et al. 2013; *Myotis lucifugus*, Fenton 1970, Norquay et al. 2013; *Myotis grisescens*, Tuttle 1976; *Myotis brandtii* and *Miniopterus schreibersii*, Hutterer et al. 2005). At the species level, migration distances are often reported using the maximum documented distance, but actual movement distances by individual bats are likely to be highly variable and the extent to which these longer-distance movements represent typical behaviors is unknown. In one well-studied system (*Miniopterus schreibersii*), maximum observed migration distance is approximately 200 km, but 80% of individuals in the population moved < 60 km (Rodrigues and Palmeirim 2008). Such a highly skewed distribution suggests that describing regional migrations using maximum documented distances (Bisson et al. 2009; Fleming and Eby 2003; Krauel and McCracken 2013) may introduce a biased perspective. When allocating limited conservation resources, it is important to understand the distribution of movement behaviors in the population rather than the longest documented distances. For example, if reported longer-distance movements are common, conservation priorities may suggest allocating resources to protecting flyways. However, if movements are primarily focused at short distances around hibernacula, resources would be better allocated to local protections around hibernacula.

Another generalization of regional migration is that bats follow a typical “to-and-fro” model of migration with a single, defined start and endpoint of migration (Dingle 2014), but a growing body of literature suggests this may be an oversimplification. Many regionally migratory species are thought to hibernate at the same location used for swarming (Fenton 1969; Humphrey and Cope 1976; Laval and Laval 1980; Norquay et al. 2013; Randall and Broders 2014); thus, autumn migratory movements are often considered to end with arrival at swarming sites (Fenton 1969; van Schaik et al. 2015). However, several regional migrants appear to follow a modified to-and-fro pattern (Dingle 2014), visiting multiple hibernacula during the swarming season (Humphrey and Cope 1976; Rivers et al. 2006) and hibernating elsewhere (Rivers et al. 2006). *Myotis lucifugus* travel as far as 800 km between hibernacula in the same season (Fenton 1969) and *M. sodalis* may similarly visit multiple hibernacula during swarming (USFWS 2007). This behavior may also be sex biased, with males and females arriving at different times (Cope and Humphrey 1977; Myers 1964). Therefore, the migration track between summer habitat and ultimate hibernation site can

greatly exceed the minimum straight-line distance between mark and recovery points. Regional migration has traditionally been studied with mark-recapture methods, which do not capture more complicated movement patterns (Ellison 2008). As many authors have recognized (Fleming and Eby 2003; Griffin 1970; Hutterer et al. 2005; Krauel and McCracken 2013), band recoveries oversimplify movement patterns and are not able to detect more complex modified to-and-fro migration patterns.

Another question that remains largely unanswered is the speed of migration. Migration speed can be considered at two scales: (1) flight speed and (2) the rate at which animals travel across the landscape over the course of the entire migration, accounting for flight paths that deviate from the shortest straight-line distance, daily stopovers, and potentially extended refueling stopovers. Long-distance migrants such as *Nyctalus noctula* moved an average of 270 km/night in Germany (Hutterer et al. 2005), and simulations suggest that *Lasionycteris noctivagans* could move at a similar rate (McGuire et al. 2012). Conversely, *Pipistrellus nathusii* moved an average of 47 km/night (Hedenstrom 2009). Species differences in migration rate of long-distance migrants are poorly understood, and our understanding of regional migrants is similarly understudied. Movement decisions by regional migrants may differ from those of long-distance migrants given the relative potential nightly movement distance compared to total migration distance, and the better ability track local conditions because of the shorter distances.

Several regional migrants are classified as threatened or endangered in parts of their range (e.g., *Myotis capaccinii*, *Myotis dasycneme*, *M. grisescens*, *M. lucifugus*, *Myotis septentrionalis*, *M. sodalis*, *Perimyotis subflavus*). Thus, optimal allocation of conservation resources is particularly important, but our current interpretations of migration patterns may be prone to potential generalization-based biases. We used a regional-scale radiotelemetry array to study the movement patterns of an endangered regional migrant, *M. sodalis*, in the Midwestern US. Previous banding studies in this region have identified several movements > 400 km, connecting maternity colonies in Michigan to hibernacula in southern Indiana and Kentucky (Kurta and Murray 2002; Kurta and Rice 2002; Rokey et al. 2013; Winhold and Kurta 2006). Furthermore, movements in this region appear to follow a north-south direction (Gardner and Cook 2002; Pettit and O’Keefe 2017) rather than the star-like pattern expected for regional migrants (Griffin 1970; Hutterer et al. 2005). We examined the following traditional generalizations about regional migrants in this system: (1) bats move away from hibernacula in spring in all directions with known maternity roosts, e.g., in a star-like pattern; (2) bats follow migratory routes, possibly along linear landscape features; (3) long-distance movements documented by banding (> 400 km) are uncommon; and (4) autumn migration comprises a single movement from summer maternity site to winter

hibernaculum. In addition, we determined estimates of migratory flight speed and migration rate (movement rate across the landscape over longer time intervals) to provide further context to patterns of regional migration.

Methods

Study area

The *M. sodalis* Midwest Conservation Region includes Indiana, Ohio, Kentucky, Tennessee, Alabama, and Michigan (USFWS 2007), and we focused on a subset of that area centered on Indiana, where longer-distance regional migration movements have been documented (Gardner and Cook 2002; Kurta and Murray 2002; Rockey et al. 2013; Winhold and Kurta 2006). This area includes large tracts of forest preserves surrounding known *M. sodalis* hibernacula and maternity roosts, which comprise likely travel corridors. The dominant linear landscape elements in the study area are rivers. The Ohio River is the primary river in the region and flows within 6 km of one of our primary study sites, Wyandotte Cave in southern Indiana, one of the largest *M. sodalis* hibernacula (USFWS 2007).

Automated radiotelemetry array

We deployed a regional-scale automated radiotelemetry array to study *M. sodalis* migration. We established a network of

stationary radiotelemetry receivers deployed both locally around targeted hibernacula to capture departure and arrival behavior and regionally to capture migratory movements. We collected regional movement data at two lines of radiotelemetry receivers in east-west turnstiles across Indiana and western Ohio (Figs. 1 and 2). Towers in the turnstiles were placed approximately 26 km apart to maximize total distance covered while maintaining a high likelihood of detecting bats that flew past these towers. Detection range depends on a variety of local factors including topography and vegetation. Based on limited testing with similar equipment in a mountainous, forested area of Alaska, we were able to detect ground level transmitters at a distance of >4 km (Boyles and McGuire, pers. obs.). In a more similar geographical context to our study, the maximum detection range of a tagged animal was determined to be approximately 14 km (McGuire et al. 2012). Most of our turnstile tower locations were in very flat landscapes, comprised of extensive agricultural development (i.e., not heavily forested), and therefore, we placed our towers based on the higher end of these detection range estimates. The northern turnstile spanned 208 km, from ca. 60 km southwest of South Bend, IN, to ca. 30 km southwest of Toledo, OH. The southern turnstile was approximately 200 km to the south, spanned 200 km across most of Indiana in spring, and shifted 80 km eastward in autumn.

In addition to the main east-west turnstiles, we placed towers at known maternity roosts, hibernacula, and along rivers in Indiana, Illinois, Ohio, and Kentucky. Radiotelemetry data were collected using the automated Motus Wildlife

Fig. 1 Telemetry station deployments and bat movement in spring. The central state is Indiana. Circles represent tower locations and short thin lines represent the direction of antennas (with 5 km distances). Thick lines connect bat movements from the Wyandotte Cave tagging site to other towers where they were detected. Each line represents a bat movement; some lines represent similar movements by multiple bats. Inset shows detailed movement around Wyandotte Cave

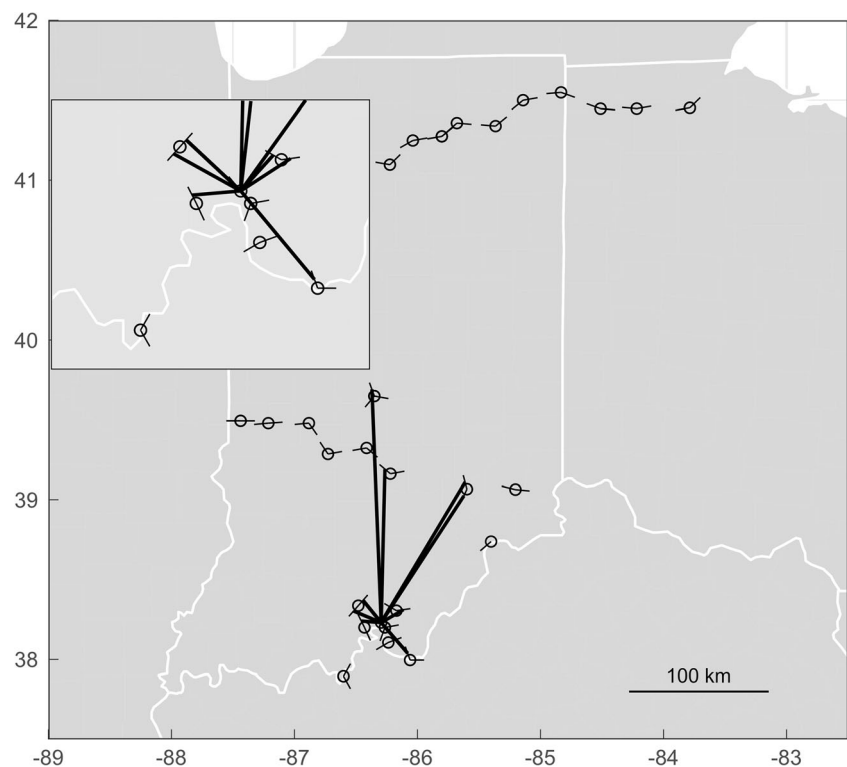
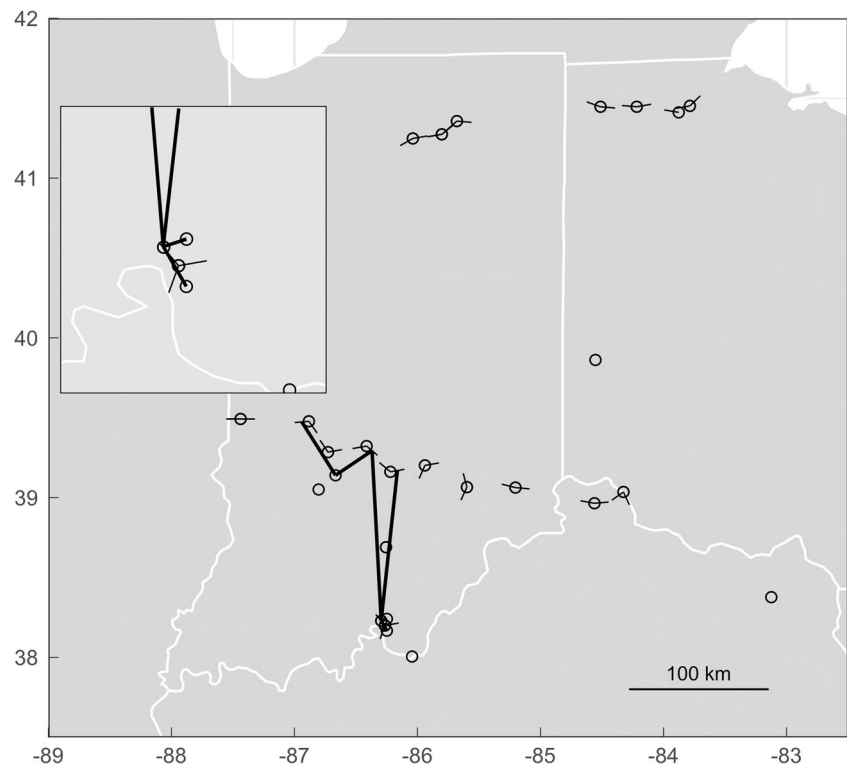


Fig. 2 Telemetry station deployments and bat movement in autumn. The central state is Indiana. Circles represent active tower locations and short black lines represent the direction of tower antennas (with 5 km distances). Open circles without antenna lines represent stations at hibernacula. Thick black lines indicate bat movement northward from the two tagging sites, Coon Cave to the north and Wyandotte Cave to the south. Inset shows detailed movement around Wyandotte cave



Tracking System (motus.org; Taylor et al. 2017). Stations across the landscape (e.g., turnstiles, along rivers, regional towers near hibernacula) consisted of a tower 8–10 m high, equipped with 2 high-gain stacked 6-element yagi antennas (Deppe et al. 2015). Stations at hibernacula and swarming sites were optimized to capture local (within ~30 m) below-canopy behavior and were generally 2–3 m tall, incorporating a single yagi antenna with 3 or 5 elements located < 50 m from and facing across the hibernaculum opening.

The two turnstiles were established in both spring and autumn migrations, and local tower deployments varied between the two seasons. In spring 2015, we deployed receivers for bats tagged upon emergence from hibernation at Wyandotte Cave (Fig. 1 inset). We placed one radiotelemetry station inside the cave entrance and a second station with 3 antennas 33 m high on a tower 4.26 km southeast of the cave entrance. Four additional stations were set up around the cave to the NE, NW, SE, and SW from 13 to 20 km away. We activated stations in March, and turnstile stations remained active until December. Stations deployed around Wyandotte Cave were active until July, when we redeployed them to hibernacula. Wyandotte Cave is 6 km from the Ohio River. To test for bats following linear landscape elements, we put three towers adjacent to the Ohio River, one downstream (64 km) and two upstream (38 km and 163 km) from the cave. Along the turnstiles, two stations each were on the Tippecanoe and Maumee Rivers, one station was on the Wabash River, and one on the Flatrock River. Finally, we placed a tower near a known maternity roost 158 km north of the cave, near the Indianapolis airport (Sparks

et al. 2005). In July 2015, we placed stations at 12 key *M. sodalis* swarming and hibernacula sites in Indiana (Coon, Endless, Jug Hole, Ray's, Twin Domes, Wallier, Wyandotte), Illinois (Blackball, Magazine), Ohio (Preble), and Kentucky (Saltpeter, Dixon) (Fig. 2; Kurta and Murray 2002; Rockey et al. 2013; USFWS 2016; Winhold and Kurta 2006).

Bat capture and tagging

In spring, we used a harp trap to capture bats as they emerged from hibernation at Wyandotte Cave. During autumn swarming, we captured bats at Wyandotte Cave and at Coon Cave, 106 km northwest of Wyandotte Cave. At Wyandotte Cave, we used a harp trap at the mouth of the cave, and at Coon Cave, we used mist nets around the cave entrance. Upon capture, we weighed each bat and recorded species, sex, and forearm length. We attached small, digitally coded radiotransmitters (0.29 g, < 5.3% of body mass; NTQB-1 Lotek Wireless) by trimming a small amount of fur in the intrascapular region and affixing the transmitter with veterinary grade cyanoacrylate (Gluturo Topical Adhesive, Abbott Laboratories). Radiotransmitters were factory configured with a 20-s pulse interval and 12/12 programming (active for 12 h at night and dormant during the daytime hours) to extend battery life (expected > 40 days). All animal capture and handling methods complied with the US Fish and Wildlife Services WNS decontamination protocols (USFWS 2016). All research activities were approved by Animal Care protocols from

Southern Illinois University (14-034) and Texas Tech University (15039-05), with all relevant state and federal permits.

Data analysis

Radiotelemetry data were downloaded from each station regularly during the study period and then uploaded to a database clearinghouse responsible for maintaining data across the Motus system. We conducted post-processing of data, including tag identification, tower location, antenna direction, signal strength, date, and time using default settings in the SensorGnome R package (Brzustowski 2016) to identify unique detections and screen for false positives. We conducted all analyses using the program R (version 3.2.3, R Core Team 2016). We calculated distances between station locations using the R package geosphere (Hijmans 2015). We estimated theoretical minimum power speed and maximum range speed for *M. sodalis* by generating a power curve using the program FLIGHT (Pennycuik 2008) based on our observed body mass values in spring and wing morphology from Norberg and Rayner (1987). We accepted all default values other than entering body mass, wing area, and wing span.

Results

We attached transmitters to 55 *M. sodalis* (all female) in spring at Wyandotte Cave and 69 *M. sodalis* (48 female, 21 male) during swarming in autumn at Wyandotte and Coon caves. After tagging, we re-detected 52 of the bats tagged in spring and 48 of the bats tagged during swarming; 29 bats were detected at sites away from their tagging location.

We tested the generalization that bats depart in spring in random directions by comparing departure detections at four towers 12–20 km around the hibernaculum. All but one bat left the Wyandotte Cave area within 22 min of tagging and did not return; the only exception was one bat detected 2 days after tagging and not detected thereafter. Bats departed primarily to the north and not in random directions (Rayleigh & Watson's tests $p < 0.01$). The towers NE and NW of the cave detected 13 bats, while the towers to the SE and SW only detected 1 bat (binomial test, $p = 0.0018$). There was no directional pattern among the bats that departed to the north (4 detected NE, 9 detected NW, binomial test $p = 0.27$).

We examined the importance of linear landscape features during migration using detections at towers along rivers. No bats were detected at any of the six turnstile stations adjacent to rivers. In spring, two bats traveled 32 km southeast to a station along the Ohio River, one briefly in passing but the other bat was detected repeatedly over 25 days. Neither bat

was detected by towers near the hibernacula, subsequently further up or down the river, nor at any other stations.

We used the number of tagged bats detected > 400 km from the hibernaculum, and also detections at stations farther than 100 km apart, to assess how common such long-distance movements were. No bats were detected after traveling > 400 km from the hibernaculum. Six bats traveled > 100 km during the study. In spring, one bat traveled 158 km northward from Wyandotte Cave, two other bats covered 111 km, and a fourth moved 104 km (Fig. 1). During autumn swarming, two females flew north (121 and 104 km, respectively) away from swarming sites and were detected along the southern turnstile (Fig. 2). These bats were not recorded at any swarming sites after initial tagging.

If autumn migration comprises a single movement from summer maternity site to winter hibernaculum, then bats should not move across the landscape after swarming at hibernacula. We placed transmitters on bats at a high-use swarming site and looked for detections of those bats at other known swarming sites at distances ranging from 4 to 480 km from the tagging site. Bats tagged during swarming at Wyandotte Cave were repeatedly detected at that site on many subsequent nights over 3 weeks following tagging. Male bats were more likely to revisit swarming sites than females (64% of tagged males, 12% of tagged females). Only two bats visited multiple hibernacula. Both bats were male and each visited one adjacent hibernacula. One bat briefly visited a cave 4.3 km to the northeast and the second bat visited a site 8 km to the southeast (Fig. 2 inset).

While only two bats visited multiple hibernacula, we found other evidence that some bats move greater distances in autumn than would be expected in the simple to-and-fro migration model. Four bats tagged during autumn swarming were subsequently detected at sites to the north, away from any known swarming locations (Fig. 2). Two bats made long-distance trips from Wyandotte (104 and 121 km N), and two bats tagged at Coon Cave were detected 42 km NW and 30 km N, respectively.

We estimated flight speeds during migration using bats with detections at multiple towers. Because both multi-night and very short distance flights could introduce errors related to detection range, we restricted analysis of flight speed to same-night intermediate-range flights that minimize the likelihood of detection-range-based outliers. We have two records of bats that traveled intermediate distances: both traveled a distance of 32 km, over a period of approximately 2 h (137 and 118 min). The flight speed of these movements was 3.91 and 4.53 m/s, respectively. The flight power curves we generated predicted a maximum range speed of 11.2 m/s and minimum power speed of 5.50 m/s. There was considerable variation in the migratory rate for bats covering > 100 km, with bats moving 6.9–92.5 km/day.

Discussion

This study was one of the largest to date to attempt to track migrating bats at a regional scale (Davis and Hitchcock 1965), and the results challenge some traditional assumptions about behavior of regional migrants. We found little support for some expected behaviors, and we observed unexpected movement patterns. Because our study was designed to optimize detection of specific behaviors, the lack of evidence of those behaviors suggests regional migration is more complicated than simply short-distance movements radiating into, and away from, a central hibernaculum.

In spring migration, bats left the hibernaculum primarily northward (Fig. 1) despite presence of known maternity colonies within 50 km south of the hibernaculum. This is consistent with earlier studies showing a northward bias in spring movements (summarized in Gardner and Cook 2002). With no lines of towers south of the cave (compared with the two lines of towers to the north), it was not possible for us to detect long-distance movements to the south. However, there was clear directionality in departure direction indicated by the towers near the hibernaculum. While many bats generally appear to depart northward during spring migration, we cannot determine if bats follow a common migratory route. Detections were approximately equal to both the northeast and northwest. We also found no evidence that bats follow rivers, the dominant linear landscape features in the study area. The paucity of detections at towers near rivers suggests *M. sodalis* disperse across the landscape during migration rather than following rivers or other routes.

The goal of a regional-scale radiotelemetry study is to describe movements probabilistically, by tagging large numbers of individuals and considering both detection presences and absences (Taylor et al. 2017). Based on previous band recoveries for bats in the study area (Kurta and Murray 2002; Rockey et al. 2013), we expected some bats to cross our turnstile lines while migrating > 400 km between hibernation and summer areas to the north. However, we detected few bats making movements > 100 km, and the longest detected movement was only 158 km. If long-distance movements were common, we might not detect the full extent of those movements, but we would expect to pick up a greater number of bats at towers located at intermediate distances away from the hibernaculum. Our study was designed to detect such movements, and because so few were detected, our results suggest those long-distance movements are uncommon. There are limitations with this technology such that if bats migrate in a manner that limits detection (e.g., if they use valleys or heavily wooded areas to migrate, or during daylight hours when transmitters were not active), we may have missed them. However, such obstacles were most common at the sites around Wyandotte Cave, where we detected many bats. Many of the towers in the turnstiles were in landscape with flat terrain,

where detection distance and probability would be maximized. Detections of other species (Gómez et al. 2017) on our towers confirm the efficacy of the towers. Thus, our data suggest that common movement distances are similar to those observed in other parts of the species' range (< 100 km, USFWS 2007). Britzke et al. (2012) found high variability in catchment sizes for even small hibernacula, suggesting that generalizing movement distance based on longest documented distance or even regional species averages may lead to bias in conservation strategies.

There are many outstanding questions about behavior during migration, including foraging activity and the use of extended stopovers (McGuire et al. 2012). Migratory flight behavior may differ from foraging behavior in multiple ways, including flight speed, altitude, linearity, and duration, but there is very little information about migratory flight behavior in any bat species (Hedenstrom 2009). We estimated one aspect of that behavior, flight speed, over an intermediate distance. If this flight was not linear, the speeds of 3.91 and 4.53 m/s would be underestimated. They are much closer to our predicted minimum power speed, 5.50 m/s, than the predicted maximum range speed of 11.2 m/s. Theoretical estimates suggest bats would use minimum power speed for foraging and maximum range speed for commuting or migration (Fleming and Eby 2003; Grodzinski et al. 2009; Hedenstrom 2009). Contrary to generalizations about speed used by regionally migrating bats (Davis and Hitchcock 1965; Humphrey and Cope 1976; Tuttle 1976), our results suggest that *M. sodalis* does not fly faster during migration than while foraging. However, the rate at which bats travel across the landscape is more relevant than simple flight speed. Our results indicate that regional migrants are capable of maintaining migratory flight for extended periods. One bat flew 111 km in 1.2 days, suggesting that some bats cover > 50 km/night.

Previous studies have suggested swarming behavior might complicate bat movement across the landscape during autumn migration (Fenton 1969; Humphrey and Cope 1976; Laval and Laval 1980; Norquay et al. 2013; Randall and Broders 2014). Movements among hibernacula during swarming appear to be uncommon. Still, we did detect a few movements across the landscape during the swarming period, supporting the idea that autumn migration is more complex than a simple to-and-fro movement. Two males were detected at hibernacula near the swarming site where they were tagged. Conversely, four females tagged at swarming sites were subsequently detected at stations to the north, away from known hibernacula. Such movements have been documented in the past (Humphrey and Cope 1976; Myers 1964), but it is still unclear if they are common or what the purpose of such movements might be. Males visiting multiple hibernacula may be seeking to increase varied mating opportunities. However, the reasons for females to migrate to a hibernaculum and to then fly 100 km away from known hibernacula are unclear.

Finally, our results provide additional insight into regional migration behaviors and strategies. One possible explanation for our low detection rates is that *M. sodalis* migrate near the ground. Flying close to the ground in a forested region, as *M. sodalis* are known to do while foraging (Laval and Laval 1980), is likely to limit detection distances. Migrating silver-haired bats (*Lasiorycteris noctivagans*, Jonasson 2017; Jonasson and Guglielmo 2016; McGuire et al. 2012), hoary bats, and eastern red bats (*Lasiurus cinereus* and *L. borealis*, Jonasson 2017; McGuire, unpublished) are all readily detected by automated radiotelemetry stations such as those we deployed. More importantly, high-flying migratory birds tagged in other MOTUS network studies (Gómez et al. 2017) were detected by many of our stations, demonstrating the effectiveness of our towers. Thus, we conclude the lack of detections was not related to faulty equipment, but rather a biological phenomenon. If migrating *M. sodalis* remain close to the ground, it may partially explain the lack of long-distance movements that we observed.

Conservation implications

This study has important conservation implications for *M. sodalis* and potentially other regional migrant bat species. First, our results support previous work showing that long-range movement of regionally migrating bats is relatively uncommon (Rodrigues and Palmeirim 2008). Migration distances are likely to be highly skewed, with most individuals traveling short distances, while only a small number of individuals make longer-distance movements. Thus, descriptions or classifications based on maximum migration distance are likely to be, at best, misleading and may skew conservation efforts toward protecting a small number of individuals who are outliers in migration behavior. If most bats in a population remain closer to hibernacula, conservation efforts based on limited funds may be better allocated by protecting a larger buffer around hibernacula rather than attempting to cover extensive flyways. As with other skewed distributions (e.g., age distributions), it is important to recognize that each detection of an increasing maximum provides progressively less information about the distribution as a whole and must be carefully interpreted.

Second, variation in migratory flight behavior may represent risk to bats beyond those expected under traditional regional migration assumptions. If the longer travel times documented in our study represent bats moving more slowly across the landscape, bats migrating through areas including wind farms would be vulnerable during a larger window of time and space. If bats are flying close to the ground, they may be more sensitive to land use changes and habitat fragmentation across their migratory route.

Third, we detected several long-distance movements after swarming. This behavior may intensify the impacts of

wind development in the region because bats may have to navigate wind farms multiple times. This risk is further compounded if such movements are female biased (as they were in our study), as female mortality will have a strong negative effect on population dynamics. Such female-biased movements are an excellent example of the necessity of studying migration patterns within demographic groups rather than assuming a similar migration pattern for the entire population.

Finally, long-distance movements among, or away from, hibernacula during swarming may contribute to increased transmission of WNS among hibernacula. Individual bats may be infected with *P. destructans* either from substrate at swarming sites, where the fungus is known to persist (Lorch et al. 2013), or from interactions with other bats (Langwig et al. 2015). Thus, movements of potentially infected bats across the landscape can contribute to increased transmission of the fungus among hibernacula, consistent with the rapid spread of the fungus to all known hibernacula in newly affected regions (Frick et al. 2010).

The goal of a regional-scale radiotelemetry study is different than the goal of traditional airplane and automobile tracking of bats. In this framework, which describes movements probabilistically, a lack of detections also provides important data. For this reason and others, the potential inference of studies using this approach far exceeds the potential inference of traditional projects based on tracking a single individual in detail. Regional migration in bats is common and yet more complex than traditionally assumed, and the application of a regional-scale telemetry array offers promise for answering questions important for effective management.

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Compliance with ethical standards All applicable international, national, and/or institutional guidelines for the care and use of animals were followed, including the US Fish and Wildlife Services WNS decontamination protocols (USFWS 2016). All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted: Southern Illinois University (14-034) and Texas Tech University (15039-05).

Conflict of interest The authors declare that they have no conflict of interest.

References

- Bisson IA, Safi K, Holland RA (2009) Evidence for repeated independent evolution of migration in the largest family of bats. *PLoS One* 4. <https://doi.org/10.1371/journal.pone.0007504>
- Britzke ER, Loeb SC, Romanek CS, Hobson KA, Vonhof MJ (2012) Variation in catchment areas of Indiana bat (*Myotis sodalis*) hibernacula inferred from stable hydrogen (delta H-2) isotope analysis. *Can J Zool* 90(10):1243–1250. <https://doi.org/10.1139/z2012-093>
- Bruzostowski J (2016) Tools for the sensorgenome project. R package version 1.0.43. https://sensorgnome.org/Post-Processing_Telemetry_Data
- Cope JB, Humphrey SR (1977) Spring and autumn swarming behavior in Indiana bat, *Myotis sodalis*. *J Mammal* 58:93–95. <https://doi.org/10.2307/1379736>
- Davis WH, Hitchcock HB (1965) Biology and migration of the bat, *Myotis lucifugus*, in New England. *J Mammal* 46:296–313. <https://doi.org/10.2307/1377850>
- Deppe JL et al (2015) Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. *Proc Natl Acad Sci U S A* 112:E6331–E6338. <https://doi.org/10.1073/pnas.1503381112>
- Dingle H (2014) *Migration: the biology of life on the move*, 2nd edn. Oxford University Press, New York
- Ellison LE (2008) Summary and analysis of the U.S. government bat banding program. U.S. Geological Survey open-file report 2008–1363, Reston, p 117
- Fenton MB (1969) Summer activity of *Myotis lucifugus* (Chiroptera—Vespertilionidae) at hibernacula in Ontario and Quebec. *Can J Zool* 47:597–602. <https://doi.org/10.1139/z69-103>
- Fenton MB (1970) A technique for monitoring bat activity with results obtained from different environments in Southern Ontario. *Can J Zool* 48:847–851
- Fleming TH, Eby P (2003) Ecology of bat migration. In: Kunz TH, Fenton MB (eds) *Bat ecology*. University of Chicago Press, Chicago, pp 156–208
- Frick WF et al (2010) An emerging disease causes regional population collapse of a common North American bat species. *Science* 329: 679–682
- Furmankiewicz J, Kucharska M (2009) Migration of bats along a large river valley in southwestern Poland. *J Mammal* 90:1310–1317
- Gardner JE, Cook EA (2002) Seasonal and geographic distribution and quantification of potential summer habitat. In: Kurta A, Kennedy J (eds) *Indiana bat: biology and management of an endangered species*. Bat Conservation International, Austin, pp 9–20
- Gómez C et al (2017) Fuel loads acquired at a stopover site influence the pace of intercontinental migration in a boreal songbird. *Sci Rep* 7: 3405. <https://doi.org/10.1038/s41598-017-03503-4>
- Griffin DR (1970) Migrations and homing of bats. In: Wimsatt WA (ed) *Biology of bats*, vol 1. Academic Press, New York, pp 233–264
- Grodzinski U, Spiegel O, Korine C, Holderied MW (2009) Context-dependent flight speed: evidence for energetically optimal flight speed in the bat *Pipistrellus kuhlii*? *J Anim Ecol* 78:540–548. <https://doi.org/10.1111/j.1365-2656.2009.01526.x>
- Hedenstrom A (2009) Optimal migration strategies in bats. *J Mammal* 90: 1298–1309. <https://doi.org/10.1644/09-mamm-s-075r2.1>
- Hijmans RJ (2015) Geosphere: spherical trigonometry. R package version 1.5–1. <https://CRAN.R-project.org/package=geosphere>
- Humphrey SR, Cope JB (1976) Population ecology of the little brown bat, *Myotis lucifugus*, in Indiana and north-central Kentucky. *Special Publ Am Soc Mammal* No 4, 1976:1–81
- Hutterer R, Ivanova T, Meyer-Cords C, Rodrigues L (2005) Bat migrations in Europe: a review of banding data and literature. Federal Agency for Nature Conservation, Bonn
- Jonasson KA (2017) The effects of sex, energy, and environmental conditions on the movement ecology of migratory bats. Dissertation, The University of Western Ontario
- Jonasson KA, Guglielmo CG (2016) Sex differences in spring migration timing and body composition of silver-haired bats *Lasionycteris noctivagans*. *J Mammal* 97:1535
- Kerth G, Kiefer A, Trappmann C, Weishaar M (2003) High gene diversity at swarming sites suggest hot spots for gene flow in the endangered Bechstein's bat. *Conserv Genet* 4:491–499. <https://doi.org/10.1023/a:1024771713152>
- Krauel JJ, McCracken GF (2013) Recent advances in bat migration research. In: Adams RA, Pedersen SC (eds) *Bat evolution, ecology, and conservation*. Springer Science Press, New York, pp 293–314
- Kurta A, Murray SW (2002) Philopatry and migration of banded Indiana bats (*Myotis sodalis*) and effects of radio transmitters. *J Mammal* 83: 585–589
- Kurta A, Rice H (2002) Ecology and management of the Indiana bat in Michigan. *Michigan Academician* 34:175–190
- Langwig KE et al (2015) Host and pathogen ecology drive the seasonal dynamics of a fungal disease, white-nose syndrome. *Proc R Soc B Biol Sci* 282:7. <https://doi.org/10.1098/rspb.2014.2335>
- Laval RK, Laval ML (1980) *Ecological studies and management of Missouri bats, with emphasis on cave-dwelling species*. Missouri Department of Conservation, Terrestrial Series 8:1–52
- Lorch JM, Muller LK, Russell RE, O'Connor M, Lindner DL, Blehert DS (2013) Distribution and environmental persistence of the causative agent of white-nose syndrome, *Geomyces destructans*, in bat hibernacula of the eastern United States. *Appl Environ Microbiol* 79: 1293–1301
- McGuire LP, Guglielmo CG, Mackenzie SA, Taylor PD (2012) Migratory stopover in the long-distance migrant silver-haired bat, *Lasionycteris noctivagans*. *J Anim Ecol* 81:385
- Myers RF (1964) Ecology of three species of myotine bats in the Ozark plateau. Dissertation, University of Missouri
- Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia, Chiroptera)—wing adaptations, flight performance, foraging strategy and echolocation. *Proc R Soc B* 316: 337–419
- Norquay KJO, Martinez-Nuñez F, Dubois JE, Monson KM, Willis CKR (2013) Long-distance movements of little brown bats (*Myotis lucifugus*). *J Mammal* 94:506–515. <https://doi.org/10.1644/12-MAMM-A-065.1>
- Pennycuik CJ (2008) *Modelling the flying bird*, Theoretical ecology series. Elsevier Academic Press Inc, San Diego, pp 1–480
- Pettit JL, O'Keefe JM (2017) Impacts of white-nose syndrome observed during long-term monitoring of a midwestern bat community. *J Fish Wildl Manag* 8:69–78
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna URL <https://www.R-project.org/>
- Randall J, Broders HG (2014) Identification and characterization of swarming sites used by bats in Nova Scotia, Canada. *Acta Chiropt* 16:109–116
- Rivers NM, Butlin RK, Altringham JD (2006) Autumn swarming behaviour of Natterer's bats in the UK: population size, catchment area and dispersal. *Biol Conserv* 127:215–226
- Rockey CD, Stumpf JP, Kurta A (2013) Additional winter recoveries of Indiana bats (*Myotis sodalis*) banded during summer in Michigan. *Northeast Nat* 20:N8–N13. <https://doi.org/10.1656/045.020.0306>
- Rodrigues L, Palmeirim JM (2008) Migratory behaviour of the Schreiber's bat: when, where and why do cave bats migrate in a Mediterranean region? *J Zool* 274:116–125. <https://doi.org/10.1111/j.1469-7998.2007.00361.x>
- Serra-Cobo J, Lopez-Roig M, Marques-Bonet T, Lahuerta E (2000) Rivers as possible landmarks in the orientation flight of *Miniopterus schreibersii*. *Acta Theriol* 45:347–352

- Sparks DW, Ritzl CM, Duchamp JE, Whitaker JO (2005) Foraging habitat of the Indiana bat (*Myotis sodalis*) at an urban-rural interface. *J Mammal* 86:713–718
- Taylor PD et al (2017) The Motus wildlife tracking system: a collaborative research network to enhance the understanding of wildlife movement. *Avian Conserv Ecol* 12. <https://doi.org/10.5751/ACE-00953-120108>
- Tuttle MD (1976) Population ecology of the gray bat (*Myotis grisescens*): Philopatry, timing and patterns of movement, weight loss during migration, and seasonal adaptive strategies. *Occasional Papers Mus Nat Hist Univ Kans* No 54:1–38
- USFWS (2007) Indiana bat (*Myotis sodalis*) draft recovery plan: first revision. U.S. Fish and Wildlife Service, Fort Snelling
- USFWS (2016) National white-nose syndrome decontamination protocol, version 04.12.2016. https://www.whitenosesyndrome.org/sites/default/files/resource/national_wns_decon_protocol_04.12.2016.pdf
- van Schaik J, Janssen R, Bosch T, Haarsma AJ, Dekker JJA, Kranstauber B (2015) Bats swarm where they hibernate: compositional similarity between autumn swarming and winter hibernation assemblages at five underground sites. *PLoS One* 10. <https://doi.org/10.1371/journal.pone.0130850>
- Veith M, Beer N, Kiefer A, Johannesen J, Seitz A (2004) The role of swarming sites for maintaining gene flow in the brown long-eared bat (*Plecotus auritus*). *Heredity* 93:342–349. <https://doi.org/10.1038/sj.hdy.6800509>
- Winhold L, Kurta A (2006) Aspects of migration by the endangered Indiana bat, *Myotis sodalis* bat. *Res News* 47:1–6