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Migration and recent range expansion of Seminole bats (*Lasiurus seminolus*) in the United States

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Bat species are facing increasing threats due to climate change, large-scale changes in vegetation, wind-power development, and white-nose syndrome, which make research on changes in bat communities essential for conservation planning in North America. The Seminole bat (*Lasiurus seminolus*) occurs throughout the southeastern United States, and recent evidence suggests they may be expanding their range in North America. I used museum records, publications, and data derived from mist-net surveys conducted by various individuals and organizations to determine changes in the seasonal and historical range of Seminole bats over the past 48 years across eastern North America. Based on records obtained, Seminole bats spend winter along the Gulf Coast, Carolinas, and southern Arkansas, but migrate as far north as Missouri and Kentucky during the summer maternity season. During the autumn juvenile-dispersal period, Seminole bats undergo widespread, long-distance movements and have been recorded in unexpected locations, including the Caribbean, Wisconsin, and New York. Over the past 48 years, the northern edge of their range has advanced 521 km and the western limit of their range has advanced 185 km, at a rate of approximately 11 km/year northward. These data suggest a recent and rapid shift northward, likely in response to climate change, and an expansion westward possibly due to changes in vegetation communities across historic grassland regions.

Key words: bats, climate change, distribution, *Lasiurus seminolus*, museum records, range expansion

Species distributions currently are in flux due to climate change and northward shifts in range are occurring more rapidly than previously predicted (Parmesan and Yohe 2003; Chen et al. 2011). Global meta-analyses of 99 species of birds, butterflies, and plants documented recent range shifts toward the poles averaging 6.1 km per decade (Parmesan and Yohe 2003). Bats in temperate areas may be especially susceptible to the effects of climate change because their life cycles (e.g., migration, food resources, and duration of hibernation) are closely linked to temperature (Humphries et al. 2002; Jones et al. 2009).

Many cave-hibernating populations of bats in North America have undergone rapid population declines since 2006 due to white-nose syndrome (WNS). The introduction of *Pseudogymnoascus destructans* (the fungus responsible for WNS) is causing population crashes and changes in community composition of bats in much of North America (e.g., Frick et al. 2010; Francl et al. 2012; Jachowski et al. 2014; Thalken et al. 2018). A rapidly changing climate, along with the effects of WNS and rapid changes in land use (Wear and Greis 2013), likely will contribute to additional changes in North American bat communities in the near future.

Bats are highly mobile, which allows them to change their distributions in a relatively short period of time in response to climate change or large-scale changes in habitat. Species such as the tricolored bat (*Perimyotis subflavus*) and evening bat (*Nycticeius humeralis*) recently have expanded their range northward and westward in North America (Geluso et al. 2005; Kurta et al. 2007; Andersen et al. 2017) and multiple species of bats have expanded their ranges northward in Europe (Arlettaz et al. 2000; Sachanowicz et al. 2006; Lundy et al. 2010; Uhrin et al. 2016). The recent and rapid expansion of Brazilian free-tailed bats (*Tadarida brasiliensis*) into the southeastern United States was attributed partially to climate change (McCracken et al. 2018). These changes in the distribution of species likely increase the potential for competition among species in newly assembled communities. Consequently, land managers and researchers need information on changes in the distributions of bats to better understand the composition of local bat communities for conservation planning.

The Seminole bat (*Lasiurus seminolus*) is a species of the southeastern United States that roosts in tree foliage during summer (Menzel et al. 1998; Hein et al. 2005; Perry and Thill 2007). They remain active year-round and only hibernate for short periods, often under leaf litter when temperatures fall below approximately 3.7°C (Hein et al. 2005). Changes in annual mean temperature may have a more profound effect on their distribution and seasonal movements than species that hibernate in more stable cave environments. For example, climate change could provide under-litter temperatures that allow survival at increasingly higher latitudes, which could result in rapid shifts northward in their distribution. Indeed, recent evidence suggests Seminole bats may be expanding their range (Wilhide et al. 1998; Lacki et al. 2014), and it is plausible that Seminole bats have expanded northward as annual temperatures have increased.

Despite their abundance across the southeastern United States, Seminole bats remain relatively unstudied compared to other bats in the eastern United States. For decades, it was believed that Seminole bats were a species of the Deep South and their distribution coincided with that of Spanish moss (*Tillandsia usneoides*—Constantine 1958; Wilkins 1987). However, radiotelemetry studies found that Seminole bats roost primarily in the canopies of pines (*Pinus* sp.), but may occasionally roost in deciduous trees (Menzel et al. 1998; Hein et al. 2005; Perry and Thill 2007). Seminole bats may be more plastic in their habitat requirements than older literature suggested, which would allow them to expand their range into additional forest ecosystems.

To determine potential range shifts for a species, it is also necessary to understand their migratory status and annual migratory movements. In temperate North America, some bats of the genus *Lasiurus* (*borealis* and *cinereus*) migrate long distances to northern regions during summer and spend winters primarily in southern regions (Cryan 2003). Other *Lasiurus* bats, such as the northern yellow bat (*L. intermedius*), are not migratory and remain in southern regions year-round. Barkalow (1948) suggested Seminole bats migrate short distances to more southerly regions during winter, which indicated they are regional migrants (migrate 100–500 km—Fleming and Eby 2003). Records of this species collected hundreds of kilometers outside their range suggested they are capable of long-distance movements, and these long-range movements may help contribute to rapid range expansion. However, little is known about movements of Seminole bats and the extent of their migration is unknown.

Using museum records, trapping data, and literature references, I sought to determine the migratory status and potential changes in distribution of Seminole bats. My goals were to: 1) determine if Seminole bats migrate northward during spring and return to more southerly areas for winter; 2) determine if Seminole bats recently have expanded their range; and 3) provide an updated distribution for this species.

Materials and Methods

Records of Seminole bat encounters were accumulated from museums, published literature, trapping permit reports from state wildlife and natural heritage agencies, and trapping data from individual researchers and managers. I contacted 61 museums either personally or by accessing their museum records online. I contacted 25 individuals who either have done extensive trapping in various regions of the Seminole bat's range or were the bat coordinators for their respective state wildlife agency. I used counties as the geographic location for each occurrence because this information was included with most collection records. When records did not indicate the county or date of capture, an effort was made to track down the original publication or data. Records without accompanying collection dates were presented in the overall distribution map, but were not included in maps presenting distribution among seasons or changes among years.

To determine seasonal changes in distribution and changes in distribution over time for Seminole bats, I plotted county locations in ArcGIS 10.3 (Environmental Systems Research Institute, Redlands, California). To determine seasonal movements and annual migration, I plotted county records for 4 seasons: summer (2 June–5 August), autumn (6 August–15 November), winter (16 November–15 March), and spring (16 March–1 June). These seasons did not correspond to meteorological seasons; instead, they corresponded to expected annual changes in bat behavior. These seasonal dates were assembled from personal observations and literature on bat migration, reproductive status of captured bats, dates of hibernation for cave-hibernating bats, and changes in annual seasonal abundance (e.g., Cryan 2003; Perry et al. 2010). Summer dates were based on the period when most female bats produce young and the young mature and become independent in the southeastern United States. Autumn dates were based on when most species undergo juvenile dispersal, migration, swarming, and enter hibernacula. Winter was when most bats remain in hibernacula in the Southeast. Spring was based on when bats emerge from hibernacula and migrate to summer areas. I also divided records into 5 historical periods: those collected in 1940 and before, those collected in 1985 and before, those collected in 2000 and before, and all reported locations up to 2018.

Results

I obtained records of Seminole bats from 33 museums (Supplementary Data SD1); 28 additional museums indicated they did not have Seminole bats in their collections or did not respond to requests. I received responses from 19 individuals or organizations (Supplementary Data SD2); 14 additional individuals indicated they did not have any Seminole bat records or they did not respond to requests. I found 38 publications that included location data for Seminole bats (Supplementary Data SD3).

I accumulated 1,548 Seminole bat records. Approximately 7% of records did not include the date of capture. In addition, 13 records did not indicate the county where the collection occurred. Records for states in the middle of the Seminole bat's distribution (Alabama and Georgia) were incomplete because they could not be obtained. For South Carolina, many of the

records were obtained from Di Salvo et al. (2002), which did not include the date of collection. County records from states that were around the periphery of the Seminole bat's range (Arkansas, Missouri, Tennessee, Kentucky, North Carolina, Oklahoma, and Texas) included all or most county records that have been reported, although a few additional counties may have been overlooked. The majority of all records occurred during summer (38%), compared to winter (18%), spring (13%), autumn (23%), and no date (7%).

Seasonal records for Seminole bats indicated their distribution during winter was confined to coastal states and southern Arkansas (Fig. 1). During spring, records suggested northward movement, and by summer, they occurred as far north as Kentucky and central Missouri during the maternity season. Seasonally, Seminole bats occurred 530 km further north in summer than during winter in western areas of their range (Arkansas and Missouri). During the post-breeding (juvenile-dispersal) season or "autumn" (6 August–15 November),

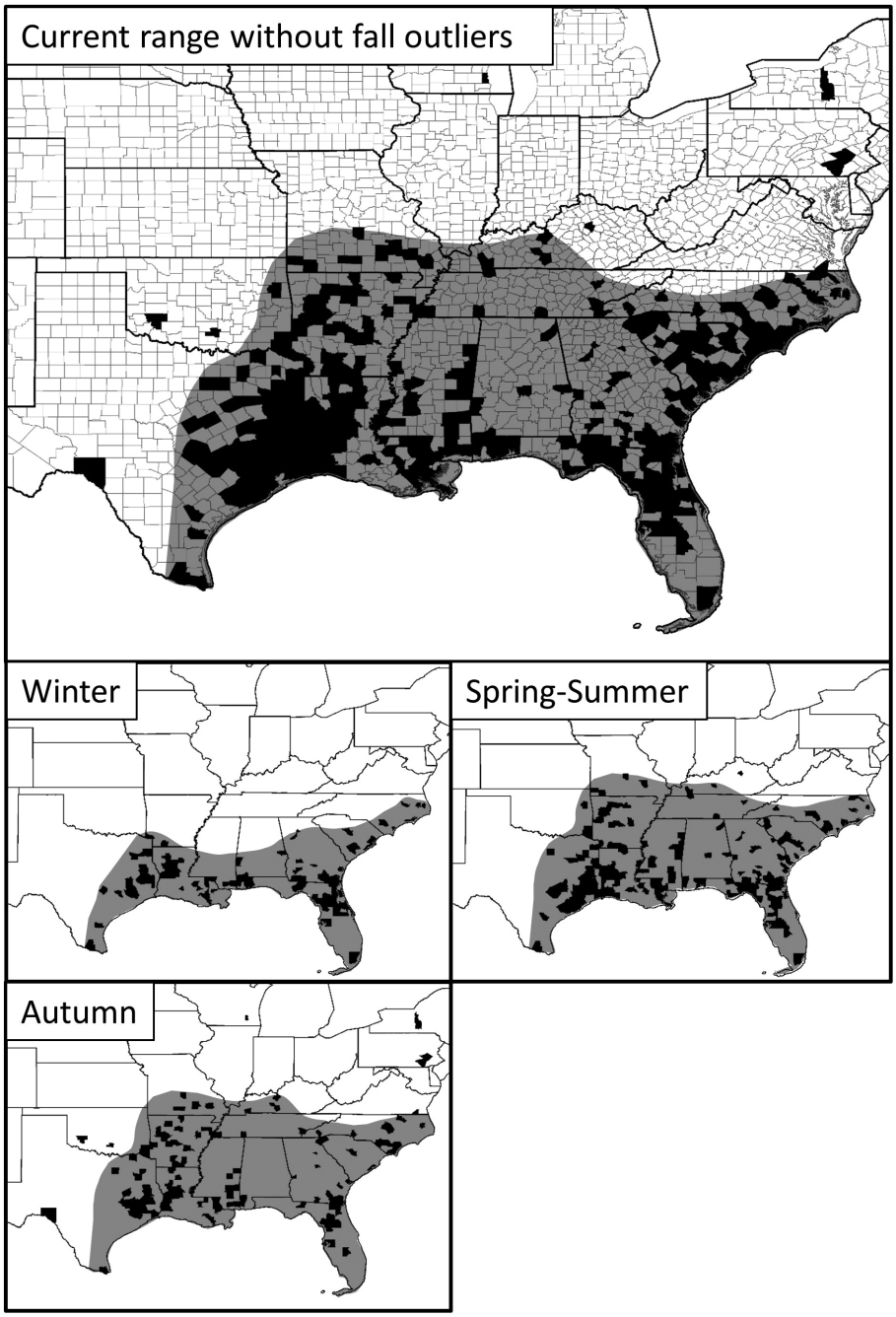

Fig. 1.—Seasonal range (gray shaded areas) of the Seminole bat (*Lasiurus seminolus*) based on county records (blackened counties) collected during winter (16 November–15 March), spring–summer (16 March–6 August), and autumn (6 August–15 November) and cumulative current range as of 2018. Counties considered outliers collected during the juvenile-dispersal period (6 August–15 November) are included on the maps but are not included in shaded distribution area.

individuals were highly mobile, with records appearing well outside their potential breeding or winter range. These locations included islands in the Caribbean (Bermuda and the Bahamas), the Mexican State of Veracruz, western Oklahoma and Texas, New York, Pennsylvania, and Wisconsin. These autumn vagrants included both males and females.

Based on collection records, the current distribution covers the eastern 1/3 of Texas, northward to Missouri and eastern Kentucky, and eastward into the southeasternmost corner of Virginia. Records that occurred outside the winter or summer maternity ranges collected during the juvenile-dispersal period of autumn were deemed vagrants and were not included in their distribution range. Some of these outlier records suggested the bats were migrating and not seasonal residents, including collections recorded during autumn from Val Verde County, Texas and Kiowa County, Oklahoma. The collection from Kiowa County, Oklahoma was at a wind turbine site surrounded by open grasslands. Another bat not included was found dead in a parking garage in north-central Kentucky (Fayette County) during summer, which suggested it may have been transported there by a vehicle (Lacki et al. 2014). A specimen collected in Murray County, Oklahoma, in the Arbuckle Mountains in late September also was not included because of the autumn collection date and the unsuitable habitat of the surrounding landscape (grassland and juniper scrub).

When analyzing collection records from 1970 to 2018, the northernmost limit of their summer maternity range moved northward approximately 521 km and their western limit moved approximately 185 km westward during the past 48 years (Fig. 2). This equates to a northward expansion rate of approximately 11 km/year. When comparing only winter records collected prior to 1970 with winter records collected up to 2018, the winter distribution of the Seminole bats appears also to have expanded northward, approximately 112 km in the western portion of their range and approximately 300 km along the East Coast into North Carolina. When records for all seasons collected prior to 1940 (438 records) were compared to those accumulated by 1970 (874 records), there was little difference in distribution, suggesting this range expansion has occurred since 1970 (Fig. 2).

Using number of new counties added per decade as a rough index of sampling effort, between 1970 and 2000, the number

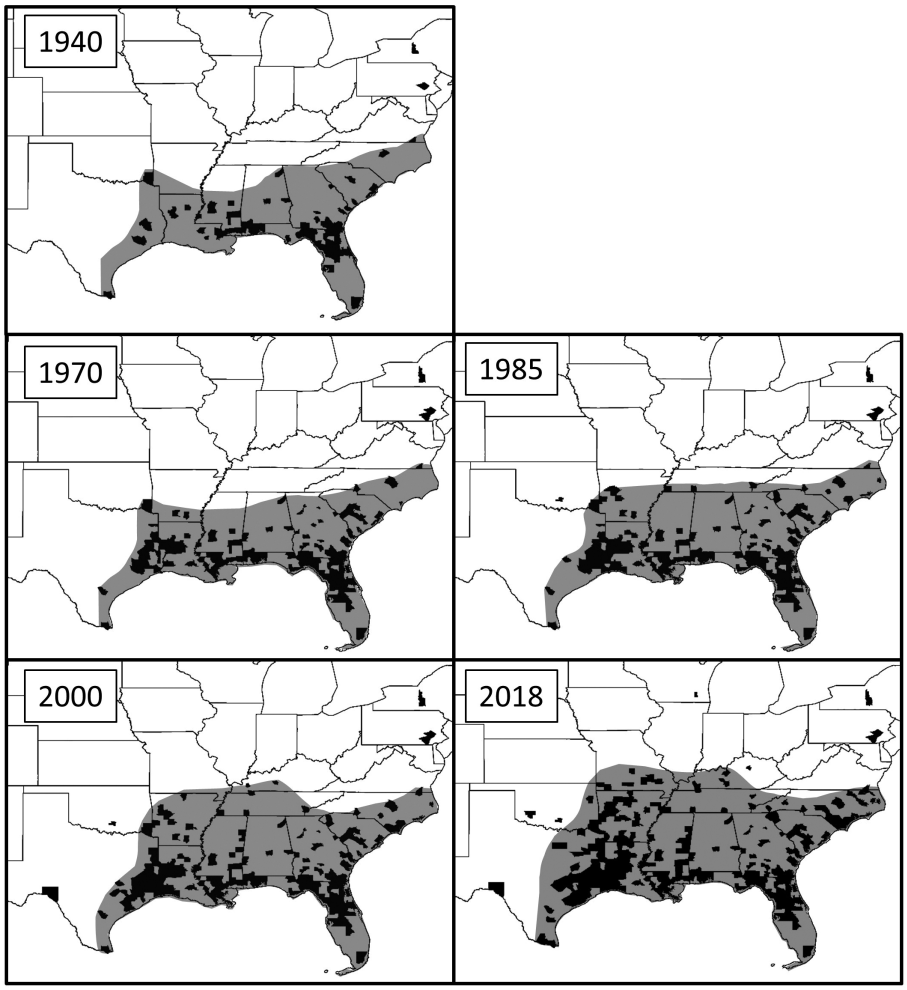

Fig. 2.—Range (gray shaded area) of the Seminole bat (*Lasiurus seminolus*) based on cumulative county records (blackened counties) in 1940, 1970, 1985, 2000, and 2018. Counties considered outliers collected during the late summer and autumn juvenile-dispersal period (6 August–15 November) are included on the maps but are not included in the shaded distribution area.

of new counties added to the distribution of Seminole bats was 15.5/decade, but the rate increased to around 43/decade between 2000 and 2018. This suggests a greater collection effort over the past 2 decades compared to collections between 1970 and 2000 (Fig. 3). However, the range of Seminole bats expanded substantially between 1970 and 2000 (Fig. 2) even with this relatively lower sampling effort.

Discussion

My results indicate Seminole bats expanded their summer maternity range northward during the past 48 years, whereas their prior range was relatively stable. Various factors could be at play in this expansion, including a changing climate, large-scale changes in vegetation communities, effects of WNS on bat community composition, or it may be a perceived expansion derived as a statistical relic of sampling and identification. Dramatic declines of forest-bat species across the eastern United States have occurred since 2006 due to WNS (e.g., Frick et al. 2010). These declines have resulted in changes in bat community composition and reproductive phenology (Brooks 2011; Francl et al. 2012; Jachowski et al. 2014). Capture rates of less-affected species may increase after WNS has invaded an area (e.g., Francl et al. 2012; Thalken et al. 2018). Reduced competition for foraging areas or other resources could allow Seminole bats greater access to these resources because Seminole bats are not believed to succumb to WNS. However, my analysis suggests the range expansion of Seminole bats began prior to the arrival of WNS in 2006. Thus, changes in climate and changes in vegetation are more likely responsible for this range expansion, although WNS may be accelerating this expansion and making newly invaded areas more favorable due to reduced competition for resources.

Seminole bats also may be expanding their range in response to large-scale changes in vegetation across the region, including expansion of forests into areas once dominated by grasslands. The current northern limit of the Seminole bat's range is mostly forested, whereas western limits are historically grasslands or open agricultural croplands with scattered trees along fencerows and in riparian areas. Historically, McCurtain County in eastern Oklahoma was the northwesternmost record for this species for decades, with records collected in 1938 and 1958 (e.g., Wilkins 1987). This county is along the historic western limit of the eastern forests biome and contains the largest expanse of virgin shortleaf pine (*P. echinata*) forest in the United States, with abundant woodlands, which are believed to be favored habitat for Seminole bats (e.g., Perry et al. 2007; Hein et al. 2008). Collections further west and after 2000 in central Texas are areas that were historically grasslands and shrublands, including the Blackland and coastal prairie ecosystem and mesquite (*Prosopis*)-chaparral ecosystems. Expansion into these areas may coincide with the invasion of forests into historic grasslands across the central United States. Woody encroachment into grassland areas has happened over a relatively short period across the Great Plains and worldwide (e.g., Ratajczak et al. 2011). This invasion has occurred due to less burning and grazing, changes in climate, and increased woody growth due to elevated CO_2 levels (Archer et al. 1995).

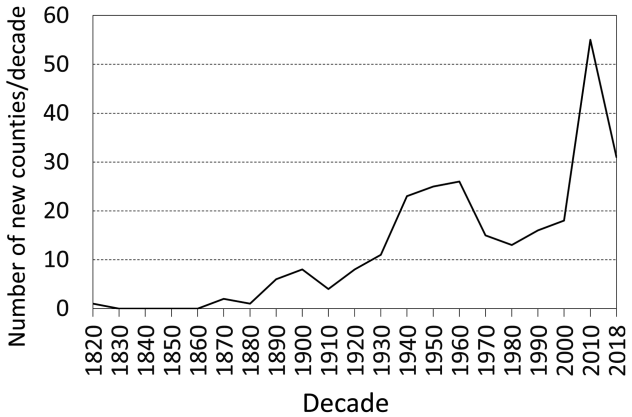

Fig. 3.—Number of new counties added to the distribution of Seminole bats (*Lasiurus seminolus*) during each decade from 1818 to 2018.

Recent studies on Seminole bat roosting during summer found them associated with pines in both Arkansas and South Carolina; they rarely roosted in deciduous trees, even when these trees were more abundant than pines (Menzel et al. 1998; Hein et al. 2005; Perry and Thill 2007). However, regions where recently they have been recorded include forests dominated by oak-hickory or other hardwood forest types. For example, areas dominated by oak-hickory forest, such as Trigg and Edmonson counties, Kentucky, have incurred multiple captures of both sexes during the summer reproductive season. Thus, Seminole bats may be adapting to roost in other forest types or they are more plastic in their roosting habits than previously believed, and additional research on roosting by Seminole bats in these non-pine ecosystems is warranted. Large-scale restoration of open woodland forests throughout states such as Missouri, Kentucky, and Tennessee (e.g., Nigh 2007) also may be providing habitat in areas that until recently contained dense, closed-canopy forests usually not preferred by Seminole bats (e.g., Perry and Thill 2007; Perry et al. 2007).

Seminole bats appear to be a regional migrant (Barkalow 1948; Fleming and Eby 2003), but do not appear to migrate the distances moved by *L. borealis* and *L. cinereus* (e.g., Cryan 2003). The lack of Seminole bat records from northern areas during winter could be a result of overwintering bats being inactive during winter or lower sampling efforts in northern areas during winter. However, Seminole bats and closely related *L. borealis* hibernate for periods typically less than a month (Hein et al. 2005; Mormann and Robbins 2007) and remain active during warmer periods of winter. In northern parts of the Seminole bat's range (e.g., Missouri), *L. borealis* remain active and commonly are encountered and captured throughout winter (Mormann and Robbins 2007), and Seminole bats are believed to have an overwinter survival and hibernation strategy similar to that of *L. borealis*. Further, Seminole bats are captured in forests throughout winter in southern portions of their range such as South Carolina (e.g., Hein et al. 2008). Thus, if Seminole bats remained in these northern areas during winter, they likely would have been encountered.

Southward migration is necessary for a species that spends winter roosting in tree foliage or under leaf litter, and likely there is a critical zone where survival is not possible above a certain latitude when roosting in these exposed conditions. My results indicate a northward shift of 100–300 km in the winter range of Seminole bats over the past 48 years. Thus, warming temperatures may have advanced this critical zone northward, where hibernating under leaf litter without freezing or exhausting energy stores may be more feasible (e.g., Perry 2013). Climate data indicate that average minimum winter temperatures have increased approximately 1.6°C between 1970 and 2018 in the southeastern United States (Fig. 4). Warmer temperatures and a longer growing season in northern areas could contribute to a longer period of high insect abundance. This longer period of insect availability also could contribute to additional fat gain, which may lead to more successful migration and overwinter survival. Root et al. (2003) indicated many species respond to climate change with changes in density, shifts in range, changes in the phenology of life-cycle events such as migration or hibernation, or changes in morphology. Consequently, a warming climate may explain the recent northward range expansion of Seminole bats into more northerly areas.

My analysis expands the distribution of Seminole bats approximately 260 km north, 185 km west, and 250 km south of the range presented in previous distribution maps (e.g., Wilkins 1987). Wilkins (1987) considered the record from southernmost Texas (Cameron County collected in autumn 1891) an outlier, but additional captures in south Texas during the maternity season and winter have since suggested that this area was, or now is, part of their distribution. Although Seminole bats may be found across their newly expanded distribution, their relative abundance throughout this area is unknown. In some areas such as Louisiana and Mississippi, Seminole bats often are one of the most abundant species encountered, whereas in other areas such as south and central Texas, Kentucky, and Missouri, they appear to be relatively rare. Prior studies suggested Seminole bats may rely on pines for roosting (Menzel et al. 1998; Hein et al. 2005; Perry and Thill 2007), and in northern and western areas that lack pines, the time Seminole bats remain in residence is unknown. In Arkansas, they frequently are captured during the growing season in the pine-dominated Ouachita Mountains, but are uncommon in the hardwood-dominated areas of the Ozarks.

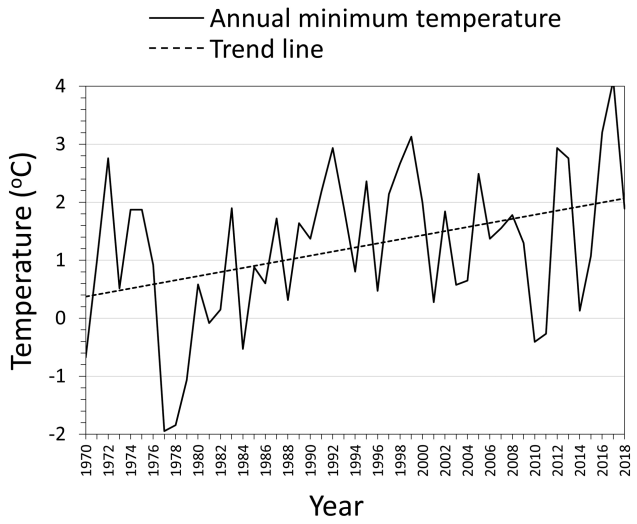

Fig. 4.—Average minimum winter (December–February) temperatures (°C) for the southeastern United States for each year between 1970 and 2017. Data derived from the National Oceanic and Atmospheric Administration, National Center for Environmental Information, Southeast and Southern Regions (https://www.ncdc.noaa.gov/cag/regional/time-series). Data are for the states of Texas, Oklahoma, Kansas, Arkansas, Louisiana, Mississippi, Alabama, Georgia, Florida, North Carolina, South Carolina, and Virginia.

All records of apparent vagrants (Fig. 2) occurred during the autumn juvenile-dispersal period, and likely were wayward migrant individuals. In migratory birds, most vagrants occur during autumn when individuals show up in unexpected places outside their typical range. These individuals may have a defect in their sense of direction (e.g., Alerstam 1990), and vagrant birds often are juveniles migrating when cloud cover obscures celestial clues (e.g., Nilsson and Sjöberg 2016). Vagrants also may result from individuals being blown off-course by storms. Post-juvenile dispersal of bats during August–September may account for these vagrant records and many of these individuals may have migrated southward later in autumn.

Expansion of the range of Seminole bats appeared to follow a pattern of individuals appearing in new areas during autumn, followed by colonization (bats collected during the maternity season) in later years. For example, all collections prior to 1985 in Arkansas were between 30 July and 9 September, but after 1985 collections occurred during all seasons. This suggests that individuals initially dispersed into new areas during late summer and autumn and some may have returned to those areas in the following years to reproduce. A similar pattern in range expansion, whereby isolated captures during late summer and autumn were followed in later years by captures of reproductive individuals during the maternity season, was demonstrated by Brazilian free-tailed bats as they expanded their range into the southeastern United States (Saugey et al. 1988; McCracken et al. 2018). Evolutionary theory predicts increased dispersal along the edges of an expanding species' range, which has been documented for a number of species (Travis et al. 2013).

My results may have been affected by missing county records, identification issues, differences in seasonal collection efforts, and changes in sampling efforts among years. Not all existing county records were obtained, although most records were included for states around the periphery of the Seminole bat's distribution. It is unlikely that additional missing data from states in the core of their distribution (Mississippi, Alabama, Georgia) would have greatly affected the outcome of my analyses, and data presented for those states were considered a subsample of the data available.

With the appearance of WNS and increased focus on bats, trapping efforts have no doubt increased dramatically across eastern North America. The rate of counties added to the distribution map was 3 times greater after 2000 than it was between 1970 and 2000, but more recent records were obtained more

easily because people who collected these data were available for contact. Changes in sampling effort over the past 200 years are unknown and not determinable, although I expected the rate of new counties added to the distribution correlated roughly with sampling effort. However, substantial range expansion occurred between 1970 and 2000, which was prior to the WNS invasion and the increased sampling efforts by land managers and researchers addressing this disease (Fig. 2). Thus, biases associated with sampling effort are a less-plausible explanation than an actual range expansion. Although unlikely, it is possible that Seminole bats always have been present in some of these more northern areas, but were not detected due to misidentification and researchers not expecting to encounter Seminole bats in more northerly regions. Undoubtedly, some records of eastern red bats were misidentified as Seminole bats because of the difficulty in distinguishing the 2 species by less-experienced biologists. Likewise, captured Seminole bats may have been misidentified as eastern red bats because they were not expected to occur in more northerly and westerly areas. Consequently, these data suggest that personnel sampling bats in these newly occupied areas should be cognizant of the potential occurrence of Seminole bats.

Although the exact cause of the range expansion of Seminole bats over the past 5 decades is unknown, preliminary evidence suggests that climate change and possibly large-scale changes in habitat are responsible. Effects of Seminole bat migration into new areas on the existing bat communities are unknown. In the South, Seminole bats and eastern red bats are the 2 species most likely to compete for roosting, although roost partitioning is likely between the 2 species (Menzel et al. 1998). Potential competition with other species for foraging areas is plausible but unknown, and competition between newly arriving species and the preexisting bat communities is possible (e.g., Arlettaz et al. 2000). Limited information is available on foraging by Seminole bats partially because their echolocation calls currently are indistinguishable from those of eastern red bats. Nevertheless, migration of Seminole bats into new areas could provide ecosystem services that previously were provided by bat species that have declined dramatically due to WNS.

Acknowledgments

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Museum collections with data on Seminole bats (*Lasiurus seminolus*) included in analysis to determine range-wide county records.

Supplementary Data SD2.—Individuals, organization, and websites contributing data on Seminole bat (*Lasiurus seminolus*) records used to determine range-wide county records.

Supplementary Data SD3.—Publications that present captures of Seminole bats (*Lasiurus seminolus*) along with location information used to determine range-wide county records.

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