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# Rapid range expansion of the Brazilian free-tailed bat in the southeastern United States, 2008–2016

Gary F. McCracken,* Riley F. Bernard, Melquisidec Gamba-Rios, Randy Wolfe, Jennifer J. Krauel, Devin N. Jones, Amy L. Russell, and Veronica A. Brown

*Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA (GFM, RFB, MG-R, JJK, DNJ, VAB)*
*Department of Ecosystem Science and Management, Pennsylvania State University, University Park, PA 16802, USA (RFB)*
*Varmint Busters Wildlife Management Services, Knoxville, TN 37922, USA (RW)*
*Department of Microbiology and Immunology, Montana State University, Bozeman, MT 59717, USA (DNJ)*
*Department of Biology, Grand Valley State University, Allendale, MI 49401, USA (ALR)*

* *Correspondent: gmccrack@utk.edu*

Brazilian free-tailed bats (*Tadarida brasiliensis*) are one of the most widely distributed bat species in the Americas, often engaging in rapid, long-distance dispersals. Here, we document that, since ca. 2007, these bats have expanded their range into western North Carolina, eastern Tennessee, and Virginia. Reports from wildlife control professionals, wildlife rehabilitators, regional submissions of bats for rabies testing, acoustic monitoring, and the presence of *T. brasiliensis* in buildings and bat houses indicate that these bats are now established in year-round colonies in areas previously thought outside their range limits. The geographic distributions of many organisms are currently shifting to higher latitudes in response to changing climate. We hypothesize that a cold-tolerant thermal physiology that allows these largely tropical bats to enter extended torpor contributes to the ability of *T. brasiliensis* to establish populations in formerly cooler regions, and propose that their rapid northward expansion is facilitated by climate change and their tendency to explore new habitats and use a wide diversity of roost sites. Because of their abundance and use of man-made structures, we anticipate that the range expansion of *T. brasiliensis* will have implications for public health, ecosystem services, and bat conservation.

Key words: bat, dispersal, extended torpor, global climate change, range expansion, *Tadarida brasiliensis*

The geographic distributions of many organisms are changing in directions that are strongly biased toward the predictions of global climate change (Parmesan et al. 2003; Root et al. 2003; Thomas 2010; Chen et al. 2011). Range shifts of terrestrial organisms, particularly shifts toward higher latitudes, also are occurring more rapidly than previously estimated (Parmesan et al. 2003; Chen et al. 2011). Although climate is not the sole factor determining range boundaries for the majority of terrestrial animal species (Thomas 2010), a number of features can contribute to a species' ability to quickly shift range boundaries in response to climate change. More rapid range shifts are expected for habitat generalists as opposed to specialists, for species that are highly mobile, and for those living in intact habitats or possessing the ability to disperse over fragmented habitats (Thomas 2010; Chen et al. 2011; Travis et al. 2013).

Several life history traits of bats suggest that they should be highly sensitive to changing climates (Sherwin et al. 2013), with bats predicted to be among the mammalian taxa most affected by climate change in the United States (Burns et al. 2003). Impacts on species distributions and species assemblages of bats have been modeled under projected climate change scenarios in Europe (Rebelo et al. 2010) and Texas (Scheel et al. 1996), and recent distributional shifts of several bat species have been attributed, at least in part, to climate change (e.g., LaVal 2004; Sachanowicz et al. 2006; Uhrin et al. 2016). However, at present, *Pipistrellus nathusii* (Lundy et al. 2010) and *P. kuhlii* (Ancillotto et al. 2016) provide the only well-documented examples of range expansions in bats that have been linked to contemporary climate change.

The expansion of new species into the existing ranges of other species will impact community structure and ecosystem dynamics in ways that can be difficult to predict (Burns et al. 2003; Rebelo et al. 2010), but it is expected that as some species spread, ranges of other more sensitive species will contract, resulting in population declines and increased risks of extinction (Thomas et al. 2004). As an example among bats, the expansion of the common pipistrelle (*Pipistrellus pipistrellus*) in western Europe, presumably due to the expansion of artificial illumination, has been implicated in the dramatic decline of the more sensitive lesser horseshoe bat (*Rhinolophus hipposideros*—Arlettaz et al. 2000a). Detecting range expansions early in the process can be important in understanding the impacts of climate change on ecosystems, the loss of species, and biotic homogenization (McKinney and Lockwood 1999).

Brazilian free-tailed bats (*Tadarida brasiliensis*) are one of the most abundant and widely distributed mammal species in the Western Hemisphere (Wilkins 1989). Both their abundance and wide distribution may be attributed to a flexible lifestyle. Some populations engage in long-distance seasonal migrations, with a banded individual currently holding the long-distance movement record for a bat (1,800 km—Villa and Cockrum 1962), whereas other populations remain year-round in the same locations or move only short distances (Krutzsch 1955; Laval 1973). Within migratory populations, some individuals remain year-round at both ends of the migratory range (Krauel and McCracken 2013). The species engages in rapid, long-distance flight and forages throughout the air column from ground level to over a kilometer above the ground (McCracken et al. 2008), where, assisted by a highly flexible echolocation call repertoire (Gillam et al. 2009), they feed on a large diversity of insects (Lee and McCracken 2005). They also are flexible in their use of roost sites, employing caves as well as a variety of man-made structures (buildings, bat houses, bridges) where their colony sizes range from a few bats to millions (Davis et al. 1962; Villa and Cockrum 1962; Laval 1973).

Free-tailed bats belong to the family Molossidae, a group of 86 bat species that are pan-tropical in distribution (Wilson and Reeder 2005). Among the Molossidae, *T. brasiliensis* in the Americas and *Tadarida teniotis* (European free-tailed bat) in the Old World are notable for their ability to penetrate into temperate zone regions. In Switzerland, *T. teniotis* lives year-round at ~46°N, apparently the highest latitude of any molossid bat (Arlettaz et al. 2000b). In the Americas, the latitudinal range limits of *T. brasiliensis* extend from ~44°N in the western United States to ~42°S in Argentina and Chile (Wilkins 1989; Barquez et al. 2013).

The physiological traits that allow survival at lower temperatures in more northern latitudes have been investigated for *T. teniotis*. Unlike most other tropical bats (McNab 1982, 2012), European free-tailed bats thermo-conform and enter torpor at low ambient temperatures (Arlettaz et al. 2000). However, compared to bats in the families Vespertilionidae and Rhinolophidae that have successfully colonized higher latitudes, European free-tailed bats maintain higher temperatures (> 10°C) during torpor and arouse more frequently between torpor bouts (Arlettaz et al. 2000b). Further, European free-tailed bats appear to select warmer roost sites so as to avoid prolonged exposure to the colder temperatures at which vespertilionid and rhinolophid bats hibernate (Arlettaz et al. 2000b). Thus, with regard to their thermal tolerance, European free-tailed bats employ a strategy that is intermediate between nonhibernating tropical species and "true" hibernating temperate zone species. Like *T. teniotis*, its congener *T. brasiliensis* also is capable of thermo-conforming to at least 10°C (Herreid 1967), and has a minimum metabolic rate at $T_a$ = 10°C (0.061 ml $O_2 \cdot g^{-1} \cdot h^{-1}$—Herreid 1963) that is nearly identical to that measured for European free-tailed bats (Herreid 1963; Arlettaz et al. 2000b). Despite an approximately 3-fold difference in body mass (10–12 g versus 30–35 g for *T. brasiliensis* and *T. teniotis*, respectively), Arlettaz et al. (2000) suggest that the intermediate wintering strategy of *T. teniotis* is likely shared by *T. brasiliensis*.

Here, we report the recent northward expansion of *T. brasiliensis* into western North Carolina, eastern Tennessee, and Virginia. Reports from wildlife control professionals, wildlife rehabilitators, regional submissions of bats for rabies testing, acoustic monitoring, and the presence of *T. brasiliensis* in buildings and bat houses indicate that these bats expanded into these areas as recently as 2007, and are now established in year-round colonies. Mitochondrial DNA sequences of bats from Tennessee and Virginia confirm species identity and reveal identical haplotypes to those obtained from the previously described species' range. We propose that the rapid northward expansion of the range of these bats is facilitated by their mobility and their proclivity for exploring new habitats and utilizing a wide diversity of roost sites. The possession of a thermal physiology that allows these largely tropical bats to penetrate colder, more northern climates suggests that with climate change these bats may be at the vanguard of faunal expansion into areas with formerly cooler climates. Because of their abundance and use of man-made structures, we anticipate that the expansion of these bats will have implications for public health, ecosystem services, and bat conservation.

## Materials and Methods

*Bats in buildings and bat houses.*—Reports of *T. brasiliensis* in buildings in North Carolina, Tennessee, and Virginia were received from certified wildlife control personnel and wildlife rehabilitators. Between 2000 and 2015, Varmint Busters Wildlife Management Services, operated by coauthor RW, conducted a total of 681 building inspections for bats in Knox County and surrounding counties in eastern Tennessee. Additional information came from personal contacts developed over the past 35 years through a variety of outreach activities by the University of Tennessee. These included presentations at local schools, civic groups, and regional nature centers. In the late 1990s and early 2000s, GFM led a Teacher's Workshop associated with the University of Tennessee's Darwin Day activities that provided in-service training for teachers. Our outreach resulted in extensive networking with the community and local middle school and high school biology teachers. These activities resulted in our being alerted to the presence of bats in buildings, invitations to visit sites with bats, and receiving photographs of bats in buildings and bat houses. News stories and social media also alerted us to the presence of bats. Outreach has been a constant part of lab activities that did not increase after *T. brasiliensis* was discovered in the region.

*Rabies surveillance.*—Since 1996, all bats submitted for rabies testing in Tennessee are collected for identification to species at the University of Tennessee College of Veterinary Medicine (Gilbert et al. 2015). Most specimens are accompanied by information on date and county of submission, possible human or animal exposure, and rabies testing status. As the condition of each submitted specimen allows, the bats are identified to species, sex, reproductive condition, and age (adult or juvenile).

*Acoustic surveys.*—As part of research investigating the impacts of white-nose syndrome (WNS) fungal disease on regional assemblages of bats, 7 SM2 Bat+ ultrasonic detectors (Wildlife Acoustics, Inc., Maynard, Massachusetts) were deployed from June through August 2012 to 2015 in riparian, forested, and urban locations in Anderson, Knox, and Jefferson counties in eastern Tennessee. A handheld D-240X bat detector (Pettersson Elektronik AB, Uppsala, Sweden) also was used to monitor bat activity at selected roost sites. Each SM2 Bat+ detector was programmed to record full-spectrum data through the night, starting 30 min before sunset and ending 30 min after sunrise. The automated identification feature in Sonobat (Arcata, California) was used to identify calls that are consistent with those of *T. brasiliensis*. Only identifications that exceeded a minimum discriminant probability of 0.95 or greater and had consistent IDs across all categories (mean classification, by vote, and by consensus) were considered a positive *T. brasiliensis* ID. All positive IDs were manually compared with voucher calls included in the Sonobat software (recorded by Dr. J. Szewczak in Arizona, California, and Texas). Acoustic activity, used as a metric of relative abundance, not true abundance, was quantified as the total number of files or bat passes identified as *T. brasiliensis*.

*Genetic analyses.*—Genetic analyses were conducted to confirm species identity and to assess haplotypes in relation to phylogeographic patterns within the established range of the species (Russell and McCracken 2006). Two-millimeter biopsies were taken from the wing membranes of 1 live bat and 24 dead bats from sites in eastern Tennessee and 1 dead bat from Virginia. DNA was extracted using DNeasy tissue extraction kits (Qiagen, Germantown, Maryland), the mitochondrial D-loop region was PCR-amplified using F(mt) and P(mt) primers following procedures similar to those described in Russell et al. (2005), and then sequenced at the University of Tennessee Genomics Core. Resulting sequences were compared to published sequences in GenBank from throughout the range of the species (Russell and McCracken 2006) by constructing a minimum-spanning network using Arlequin version 3.5.2.2 (Excoffier and Lischer 2010).

*Compliance.*—This research was approved by the University of Tennessee, Knoxville Institutional Animal Care and Use Committee (Protocols 1947 and 2026) and followed guidelines of the American Society of Mammalogists for the ethical use of wild animals in research (Sikes et al. 2016).

## Results

*Bats in buildings and bat houses.*—Since 2008, we have documented the presence of *T. brasiliensis* at 15 sites (13 buildings and 2 bat houses) in North Carolina, Tennessee, and Virginia that are located outside of the currently described range of this species (Fig. 1; Table 1).

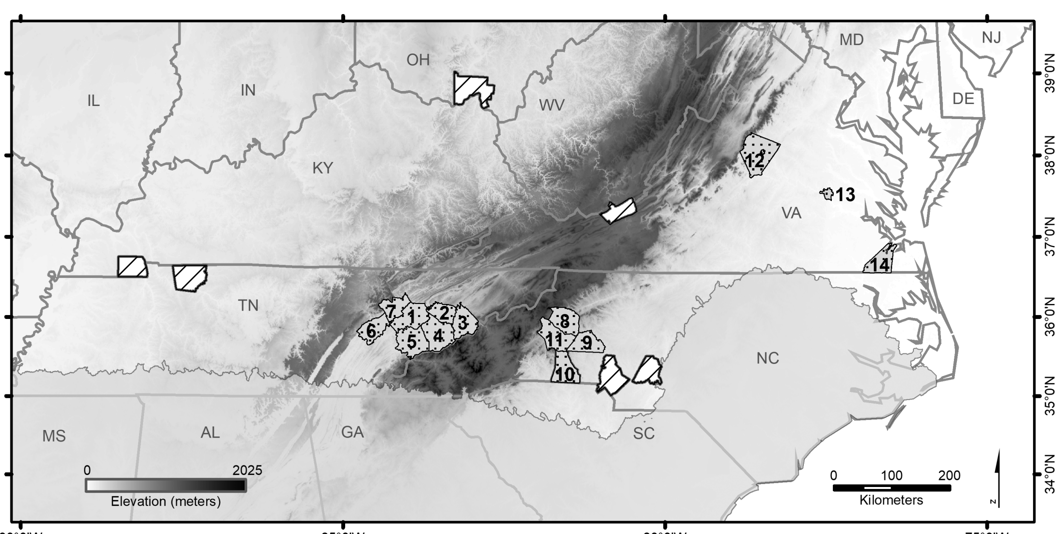


**Fig. 1.**—Range expansion of *Tadarida brasiliensis* in the southeastern United States. The light gray shaded area indicates the northern limit of the species' range from the USGS National Gap Analysis Program (GAP; gapanalysis.usgs.gov). Stippled areas are new localities reported here by county and numbered as follows: Tennessee—(1) Knox, (2) Jefferson, (3) Cocke, (4) Sevier, (5) Blount, (6) Roane, (7) Anderson; North Carolina—(8) Caldwell, (9) Catawba, (10) Cleveland, (11) Burke; Virginia—(12) Albermarle, (13) Henrico, (14) Suffolk. Stripped areas indicate county locations of vagrants reported in McCormick and Barrass (2012) and Cranford and Fortune (1994). Other shading depicts topography as elevation above mean sea level.

**Table 1.**—Occurrence of *Tadarida brasiliensis* in North Carolina, Tennessee, and Virginia, 2008–2016. Dates are months and years when bats were obtained or identified. Positive identification as *T. brasiliensis* was made from bats in-hand or unambiguous photographs. Except for a single pup (July 2014, Virginia) all bats were adults or not distinguishable in photographs from adults. EPFU refers to the big brown bat (*Eptesicus fuscus*). TWRA refers to a collection made by Tennessee Wildlife Resources Agency and TNBWG refers to a location found through the Tennessee Bat Working Group.

| Date | State | County | Roost | Estimated number | Source of report |
|---|---|---|---|---|---|
| August 2008 | North Carolina | Cleveland | Building[a] | "many" | Wildlife control |
| January 2009 | North Carolina | Burke | Building | "large" (8 collected) | Wildlife control |
| October 2009 | North Carolina | Catawba | Building | 6 collected | Wildlife control |
| November 2010 | North Carolina | Catawba | Building | Unknown | Wildlife control |
| January 2010 | North Carolina | Caldwell | Building | "several hundred" | Wildlife control |
| January 2011 | Tennessee | Knox | School A | 3 males, 3 females | Teacher |
| November 2011 | Tennessee | Knox | School A | 3 males | Teacher |
| February 2012 | Tennessee | Knox | Building A | 1 female | Wildlife control |
| March 2012 | Tennessee | Knox | School A | 1 male | Teacher |
| August 2012 | Tennessee | Knox | School A | 1 male | Teacher |
| March 2013 | Tennessee | Knox | School B | 1 male | School administration |
| April 2013 | Tennessee | Cocke | School | 2 unknown | Wildlife control |
| April 2013 | Tennessee | Jefferson | Personal residence | 1 female, 1 unknown | TWRA |
| September 2013 | Tennessee | Roane | Bat house A | 1 roosting with EPFU | Wildlife control |
| August 2013 | Tennessee | Blount | Building | 2 roosting with EPFU | Wildlife control |
| October 2013 | Tennessee | Knox | School A | 1 male | Teacher |
| February 2014 | Tennessee | Knox | School A | 2 males, 1 female | Teacher |
| Summer 2014 | Virginia | Likely Suffolk | Unknown | 1 unknown sex | Wildlife rehabber |
| July 2014 | Virginia | Albemarle | Building[a] | 1 orphan female pup | Wildlife rehabber |
| October 2014 | Tennessee | Blount | Bat house B | 2 roosting with EPFU | TNBWG |
| December 2014 | Tennessee | Blount | Bat house B | 2 dead females | Homeowner |
| January 2015 | Tennessee | Knox | Building B | At least 6 | Wildlife control |
| February 2015 | Tennessee | Knox | School A | 1 male | Teacher |
| February 2015 | Virginia | Henrico | Unknown | 1 male (died) | Wildlife rehabber |
| March 2015 | Tennessee | Knox | Building B | Several dead | Wildlife control |
| March 2015 | Tennessee | Knox | School A | 2 females, 1 male | Teacher |
| March 2015 | Tennessee | Knox | Personal residence | 1 unknown | Student |
| September 2015 | Tennessee | Blount | Bat house B | 1 roosting with EPFU | Homeowner |
| January 2016 | Tennessee | Knox | School A | 2 females, 2 males | Teacher |
| May 2016 | Tennessee | Knox | School A | 1 male | Teacher |

[a] Possible maternity roosts.

A colony evicted from a building in Cleveland County, North Carolina (Table 1) in August 2008 was at that time the farthest north and west that *T. brasiliensis* had been documented in North Carolina (Fig. 1). Building occupants reported that "many" bats had been killed at this site in 2007, and a report that this was a maternity colony is unverified. Subsequently, *T. brasiliensis* were evicted from 4 other buildings in western North Carolina between January 2009 and November 2010 (Table 1; Fig. 1). Multiple bats were captured and photos were taken confirming these as colonies of *T. brasiliensis* (Supplementary Data SD1). The sites with *T. brasiliensis* in winter and fall also contained big brown bats (*Eptesicus fuscus*), and 1 site (Caldwell County, North Carolina) also contained little brown bats (*Myotis lucifugus*).

In January 2011, we obtained 6 *T. brasiliensis* (3 females, 3 males) from a school (School A) in Knox County, Tennessee. Two of the males were alive when captured. Since then, we obtained 19 additional *T. brasiliensis* from School A (6 females, 13 males), all but 2 were found between October through March and often after freezing or near-freezing weather, and all but 1 bat were alive upon capture (Table 1; Supplementary Data SD2). Multiple big brown bats also were found at the school. On the evening of 29 November 2011, numerous bats were observed flying from access points in the exterior wall of School A, and echolocation calls were consistent in frequency and temporal characteristics with those of *T. brasiliensis*. The school was examined by coauthor RW on 21 June 2012. Staining on exterior walls and fresh guano accumulations identified numerous entry points for bats in gaps under a metal parapet that provided the bats with access to cavities in concrete blocks and spaces between the concrete blocks and brick veneer. The heads of *T. brasiliensis* were seen between the parapet and brick wall and the characteristic odor of *T. brasiliensis* was evident.

In February 2012, Varmint Busters Wildlife Management Services encountered their first *T. brasiliensis* during a building inspection in Knox County, Tennessee. Prior to that record, *T. brasiliensis* had not been found during any of the 457 inspections for bats that Varmint Busters conducted beginning in January 2000. From 2012 through 2015, Varmint Busters conducted an additional 224 inspections and documented *T. brasiliensis* in 5 buildings in 4 eastern Tennessee counties (Table 1; Fig. 1).

Between January 2011 and January 2016, we obtained a total of 35 *T. brasiliensis* from buildings and bat houses in eastern Tennessee (Supplementary Data SD2). These include the 25 bats from School A, with additional *T. brasiliensis* obtained from 2 other schools, a college administration building, a county administration building, a commercial building, 2 private residences, and a bat house. Of these bats, 25 were male and 10 were female, and 20 were alive and 15 dead when obtained (Supplementary Data SD2). We also obtained photographs, but not specimens, of *T. brasiliensis* from a private residence in Jefferson County, Tennessee, and from another bat house (Table 1; Fig. 1). At 5 sites, *T. brasiliensis* were observed roosting within colonies of a "few" to an estimated 200 big brown bats. Nineteen of the specimens were recovered when they entered interior space of buildings during winter months (December, January, February), often shortly after subfreezing temperatures (Supplementary Data SD2).

Wildlife rehabilitators in Virginia also reported several *T. brasiliensis* (Table 1). A single *T. brasiliensis* of unreported sex was found in summer 2014 in the Norfolk-Portsmouth area (likely, Suffolk County) of Virginia. A female *T. brasiliensis* pup was found outside an apartment complex in Albemarle County, Virginia in July 2014. A known roost of big brown bats is close to the location where the pup was reported, but no additional *T. brasiliensis* were found. A male *T. brasiliensis* was found near Richmond (likely, Henrico County), Virginia in February 2015, but died, presumably of hypothermia, as he was found during an ice storm.

*Rabies surveillance.*—Between 1996 and 2015, a total of 2,688 bats was submitted for rabies testing in Tennessee (Gilbert et al. 2015). Of these, 2,598 bats were identified to 16 bat species. Only 2 *T. brasiliensis* were among the bat specimens submitted from Tennessee prior to 2012. Case records show that these 2 adult female *T. brasiliensis*, submitted to the Knox County, Tennessee testing lab in 2008 (Gilbert et al. 2015), were actually obtained in northern Georgia (McCormick and Barrass 2012), within the established range of the species (Fig. 1). Since 2012, 9 *T. brasiliensis* have been submitted for rabies testing from 7 counties in eastern Tennessee, 2 each from Cocke County (March 2012) and Sevier County (March 2013 and March 2014), and 1 each from Roane County (April 2012), Knox County (March 2013), Jefferson County (February 2014), Blount County (March 2014), and Anderson County (October 2014; Fig. 1). All of these bats were rabies-negative adults, and 8 of the 9 were male.

*Acoustic surveys.*—Calls identified as those of *T. brasiliensis* were recorded at 6 of the 7 SM2 Bat+ detector sites. The sites containing the largest numbers of *T. brasiliensis* calls were in open areas near water and at the urban sites located on top of buildings on the campus of the University of Tennessee, Knoxville (UTK). Calls identified as those of *T. brasiliensis* were most abundant from the end of June through the middle of July. Over the same time frames, positive call identifications for *T. brasiliensis* recorded above the UTK campus increased from a total of 17 calls recorded in 2012, to a total of 270 calls recorded in 2013, a total of 1,230 calls recorded in 2014, and a total of 244 calls recorded in 2015.

*Genetics.*—Ten mitochondrial DNA D-loop sequences provided a 100% match to published sequences listed as *T. brasiliensis* from locations across the southeastern United States. These include South Carolina (GenBank AY348167), North Carolina (AY348158 and AY348156), western Florida (AY348134), eastern Florida (AY348126 and AY348124), Louisiana (AY348143), and eastern Texas (AY348104). The Virginia bat matches the North Carolina record AY348158. The remaining 16 haplotypes were embedded within a network describing existing variation observed throughout the North American range of the species (Russell and McCracken 2006).

## Discussion

Our results confirm that *T. brasiliensis* are now established in year-round colonies in the highlands region of western North Carolina and in the Tennessee River Valley of eastern Tennessee and indicate that they are now moving into Virginia. Further, we present multiple lines of evidence suggesting that their expansion into western North Carolina and eastern Tennessee has occurred within the last few years. Although we cannot conclusively link this recent expansion with climate change, the dynamics of the expansion are consistent with the expected effects of climate change on dispersal behavior and range expansions of generalist species with high mobility (Thomas 2010; Chen et al. 2011; Travis et al. 2013), and consistent with earlier observations of *T. brasiliensis* elsewhere in its range.

*Tadarida brasiliensis* frequently is reported outside of its established range, typically as isolated individuals that are considered vagrants. The recent (April 2011) collection of a *T. brasiliensis* in extreme southern Argentina at 52°20′S represents the current latitudinal extreme for the species and for a molossid bat (Barquez et al. 2013). This Argentine specimen joins numerous reports of apparent extralimital vagrants that are summarized elsewhere for populations of *T. brasiliensis* in the central United States (Genoways et al. 2000) and southeastern United States (McCormick and Barrass 2012).

Past studies have noted expansions regarding the range of *T. brasiliensis* within the United States, and have connected extralimital vagrants to these expansions (Lee and Marsh 1978; Saugey et al. 1988). Lee and Marsh (1978) reported the first examples of isolated, apparently vagrant individuals in coastal North Carolina in fall and winter of 1970 and 1974, and shortly thereafter the discovery in that area of a colony of *T. brasiliensis* in December 1975 and another colony in February 1977. Similarly, Saugey et al. (1988) reported the discovery of year-round colonies of *T. brasiliensis* in buildings in central Arkansas where the bats had not occurred previously, and noted that these colonies were preceded only a few years earlier by the first reports in the early 1980s of apparently isolated individuals that were mostly males found in fall. Our initial collections of bats in fall and winter were similarly male-biased (Table 1).

In compiling the large number of extralimital reports of *T. brasiliensis* in the central United States, Genoways et al. (2000) suggested that apparently isolated reports of vagrant individuals are, in fact, illustrative of the dynamics of many mammalian distributions. Specifically, Genoways et al. (2000) suggested that the distributions of most mammal species consist of 3 distinct ranges and zones of expansion: 1) a "natal range" where populations are relatively stable and individuals engage in normal reproductive activities; 2) a "pioneering range" where distributions contract and expand as population sizes change and climatic and other environmental factors relax or impose limits; and 3) a much larger "exploring zone" in which reproduction does not regularly occur but where individuals forage and investigate new habitats and occasionally become isolated and "lost." Genoways et al. (2000) argued that these distributional patterns best approximate observations for abundant, highly mobile species such as *T. brasiliensis*.

We suggest that the distributional dynamics described by Genoways et al. (2000) will be enhanced by climate change. Dispersal characteristics, themselves, are expected to respond to climate change, with increases in dispersal expected at the margins of expanding ranges (Travis et al. 2013). Meta analyses of observed shifts in species' range boundaries also document more frequent expansions at leading edges of ranges, and support suggestions that climate change is a driver for many rapid range shifts (Parmesan et al. 2003; Thomas 2010). Generalist species with high mobility are expected to be among the most responsive (Chen et al. 2011). Among bats, migratory species, those that utilize buildings as roost sites (Lundy et al. 2010; Ancillotto et al. 2016), and those that rely on aerial insect hawking (Sherwin et al. 2013) are expected to show the greatest distributional impacts in response to climate change. Because the large cave-dwelling maternity colonies of these bats in the Southwest depend on high densities of prey insects, Newson et al. (2009) proposed *T. brasiliensis* as an indicator migratory species for climate change. We agree that *T. brasiliensis* is an indicator species for climate change, but for the different reasons that we argue here. Possible impacts of climate change on the insect prey base of *T. brasiliensis* are unknown at present, but because these bats rely heavily on migratory insects (McCracken et al. 2012), and those insect migrants are themselves threatened by climate change and declining globally (Wilcove and Wikelski 2008), disruptions of their prey base are a concern (Krauel et al. 2015).

Genoways et al. (2000) emphasized that their high mobility facilitates and makes evident the exploring and pioneering dynamics of *T. brasiliensis*' range expansion, and that extralimital vagrants are part of the larger mechanism by which their range shifts occur. However, for their natal range to expand, bats must not only reach a new area but also survive and reproduce within it. Over 50 years ago, Davis et al. (1962) commented that the exploitation of buildings as roosts by *T. brasiliensis* may allow them to remain in colder climates during winter if building temperatures remain above freezing. More recent authors have speculated that the use of buildings as roosts may facilitate the expansion of *T. brasiliensis* into human-altered landscapes (e.g., Saugey et al. 1988) and, as buildings are often ephemeral roosts due to renovations and colony exclusions, the use of buildings may contribute to the bats' dispersal and exploration for new roost sites (McCormick and Barrass 2012). The recent climate change-related range expansions of *P. nathusii* and *P. kuhlii* also have been attributed to the use of buildings as roost sites. While a warming climate is allowing both European species to expand into new areas, the local availability of buildings as roosts is helping new colonies of the bats to become established (Lundy et al. 2010; Ancillotto et al. 2016). Similarly, in each case where range expansion of *T. brasiliensis* was documented, new colonies were found exclusively in buildings or, during warm weather, in bat houses.

In addition to their mobility and adaptive use of man-made structures as roosts, we suggest that the cold-tolerant thermal physiology of *T. brasiliensis* contributes to their ability to establish populations in northern areas and facilitates their expansion into formerly cooler regions. As elsewhere in much of the world, the trend toward warming climates is well documented in the region where we report the recent range expansion of *T. brasiliensis* (Fig. 2). We suggest that shifts in behavior of these bats elsewhere in their range also may be a response to changing climates. Earlier reports on the behavior of *T. brasiliensis* in the central and southwestern United States portray them as almost exclusively migratory (Davis et al. 1962; Cockrum 1969; Wilkins 1989). However, there are now numerous records of bats overwintering in the southwestern United States (Scales and Wilkins 2007; Geluso 2008) and increasing numbers of *T. brasiliensis* are remaining in the region throughout winter in caves, under bridges, and in buildings (Geluso 2008). Whereas populations of *T. brasiliensis* in the central and southwestern United States are typically thought of as cave-dwelling and migratory, and those in the Southeast are portrayed as more sedentary and roosting in buildings, the reality is far more complex. Indeed, at least subsets of the supposedly migratory populations of these bats in the central and southwestern United States behave increasingly like the more sedentary populations in the Southeast. The northward expansion and establishment of year-round colonies of *T. brasiliensis* in Arkansas and North Carolina were attributed to the putative southeastern subspecies *T. b. cynocephala.* The geography of our observations suggest that they also involve *T. b. cynocephala*; however, subsequent genetic analyses demonstrate that the southeastern populations are panmictic with the populations of *T. brasiliensis* throughout North America and that the recognition of distinct subspecies is not supported (Russell and McCracken 2006; Morales et al. 2016). The mtDNA sequence haplotypes of the bats from Tennessee and Virginia show no structure and cluster with bats from throughout the species' range in North America.

The community composition of bats in North America north of Mexico is in transition. The deaths of millions of cave-hibernating bats since 2006 from WNS (O'Shea et al. 2016) have resulted in decreased abundance of affected species, mostly broad-winged bats that feed in clutter and beneath canopy, and a proportional increase in the abundance of mostly tree-dwelling bats that tend to forage in more open areas, above canopy (Brooks 2011; Dzal et al. 2011; Ford et al. 2011). Populations of *T. brasiliensis* are now established in some of the same areas as WNS-affected species and, while it is premature to assume that *T. brasiliensis* will be unaffected by the disease, it seems likely that they will become an increasing component of the bat fauna. We should remain alert to the possibility that the recent

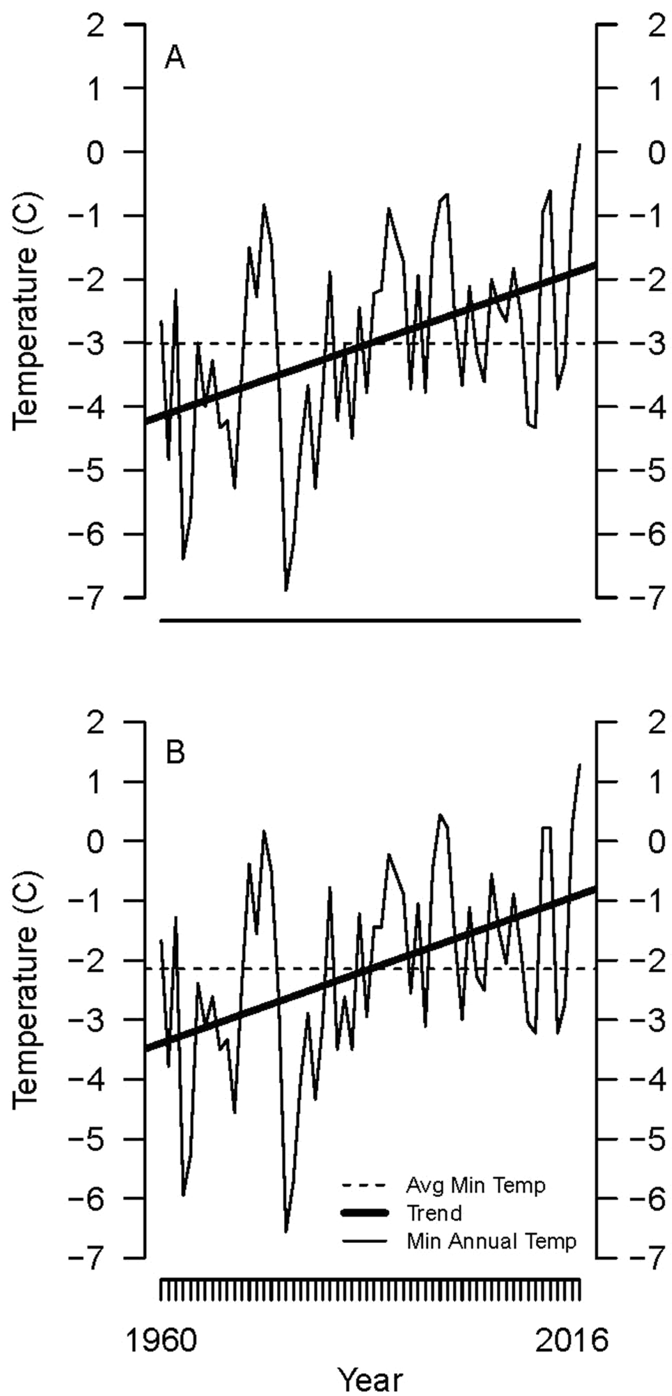


**Fig. 2.**—Averages of the minimum temperatures recorded from 1960 to 2016 during the 3 coldest months (December, January, February) of each year in A) the Western Climate Division of North Carolina, and B) the Eastern Climate Division of Tennessee. These Climate Divisions include all counties referenced in Fig. 1. The thin, solid line connects the 3-month averages of the coldest temperature observed during December, January, and February of each year. The thin, dashed line is the mean of the coldest temperatures for these 3 months from 1960 to 2016. The thick, solid line shows a warming trend of approximately 2°C in each region over the time period shown. Data are available at https://www.ncdc.noaa.gov/monitoring-references/maps/us-climate-divisions.php.

influx of *T. brasiliensis* into the WNS-affected zone will hasten the decline or inhibit any hoped-for recovery of affected bat species.

Because of their habits of roosting in buildings in large numbers, the expansion of *T. brasiliensis* into new areas will be highly visible to the public. Indeed, early attention to the documented range expansions in the southeastern United States came from public awareness, contacts with wildlife control professionals, and public health officials (see also Heidt et al. 1987). Further, although bat rabies in the United States has killed an average of 2 to 4 people per year over the last 50 years (Patyk et al. 2012), in areas where they occur, *T. brasiliensis* consistently rank first in the percentages of submitted individuals that are positive for rabies (Patyk et al. 2012). As *T. brasiliensis* populations continue to expand into new regions, increased public awareness of bats as possible nuisance species and a public health concern should be expected. Individuals who are concerned about the persecution of bats should prepare for how best to craft effective arguments for their conservation. In this regard, the value of the ecosystem services of bats are increasingly recognized (Boyles et al. 2011), and best established for *T. brasiliensis* (Cleveland et al. 2006; Federico et al. 2008; López-Hoffman et al. 2014). As these bats move into new regions, they will bring with them these previously underappreciated services. Lastly, this paper highlights the importance of documenting sightings of these and other bats at the margins of their range.

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## Supplementary Data

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

**Supplementary Data SD1.**—Photographs of *Tadarida brasiliensis* in western North Carolina and eastern Tennessee from 2008, 2009, 2010, and 2013.

**Supplementary Data SD2.**—Records of *Tadarida brasiliensis* obtained from buildings in eastern Tennessee, 2011–2016.

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