Seasonal Changes in the Active Bat Community of the Kisatchie National Forest, Louisiana

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Abstract - Few North American studies have quantified differences in bat community composition between summer and winter. In southerly regions, especially the coastal plain of the Gulf of Mexico, winters are mild and experience only short periods of freezing weather annually. In regions such as this, there may be a substantive community of bats that are active in the winter. We examined seasonality of the bat community in the Kisatchie National Forest of Louisiana. We mist-netted bats for 130 nights during winter and 51 nights during summer and caught 200 and 190 bats, respectively, from 10 different species. *Corynorhinus rafinesquii* (Rafinesque's Big-eared Bat), *Lasiurus borealis* (Eastern Red Bat), and *Lasionycteris noctivagans* (Silver-haired Bat) were more frequently captured in winter, all other species were captured more frequently in summer. Significant differences existed between summer and winter in species richness and abundance of bats, but not for Shannon's diversity index. Across the entire year and in winter, more bats were caught on nights with higher temperature than on nights with lower temperatures. Although there was much temporal variation in species composition, we found a substantial bat community that is active in the winter in the Kisatchie National Forest of Louisiana.

Introduction

Despite efforts to better characterize and understand bat communities (Stevens and Estrada-Villegas, 2020), a paucity of data exists for many regions, if they even have been surveyed at all. Such disparities in our knowledge may present obstacles to evaluating future changes, including impacts to communities associated with anthropogenic activities. For example, habitat modification is occurring globally at an unprecedented rate (Fischer and Lindenmayer 2007, Miraldo et al. 2016, Voight and Kingston 2016) and typically has a negative effect on temperate bat species (Jung and Threlfall 2016). In some North American bats, epidemics such as the outbreak of white-nose syndrome (WNS) have caused substantial decreases in populations and even changed patterns of community structure (Francl et al. 2012, Frick et al. 2010). Currently the scientific community is in need of baseline information on the structure of communities to document and improve our understanding of future changes (Malaney and Cook 2018).

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Across much of North America, fluctuations in abundance of bats at local sites are seasonal (Cryan 2003, Perry et al. 2010a), and the concept of a bat community is more nebulous during winter. At more northerly latitudes, bats either migrate to warmer regions or hibernate (i.e., long-term torpor) through much of winter (McNab 1982). Thus, the number of bat species that interact across the landscape during winter in many places is reduced or nonexistent. In temperate lower latitudes, however, bats can exhibit substantial winter activity, particularly on warm nights (Geluso 2007, 2008). Under warmer winter conditions, especially at lower latitudes, the concept of a winter bat community of interacting species becomes more relevant. Moreover, in such regions the community of active bats may be different in the winter compared to the summer (Mello 2009, Stevens and Amarilla-Stevens 2012). Therefore, baseline information on many communities should include a component of seasonality. There are other important implications of a bat community that is active in the winter, particularly in North America. Warmer temperature in winter is related to increases in insect activity (Williams 1949) and may allow bats to replenish energy reserves. Furthermore, extended activity by bats in winter (i.e., longer arousals over successive days) may affect their susceptibility to WNS by reducing infection because active bats can mount an immune response (Meteyer et al. 2012). Moreover, an important facet of conservation of many threatened and endangered bat species is management of winter hibernacula (USFWS 1995, 2007, 2009). If species are active on warm nights and use a number of roosts during winter (i.e., as opposed to a single hibernaculum), then managing multiple hibernation sites may be important.

Twelve species of bats have been reported from Louisiana (Crnkovic 2003, Lowery 1974, Stevens et al. 2017): *Corynorhinus rafinesquii* Lesson (Rafinesque's Big-eared Bat), *Eptesicus fuscus* Palisot de Beauvis (Big Brown Bat), *Lasionycteris noctivagans* Le Conte (Silver-haired Bat), *Lasiurus borealis* Müller (Eastern Red Bat), *Lasiurus cinereus* Palisot de Beauvois (Hoary Bat), *Lasiurus intermedius* H. Allen (Northern Yellow Bat), *Lasiurus seminolus* Rhoads (Seminole Bat), *Myotis austroriparius* Rhoads (Southeastern Myotis), *Myotis septentrionalis* Trouessart (Northern Long-eared Bat), *Nycticeius humeralis* Rafinesque (Evening Bat), *Perimyotis subflavus* F. Cuvier (Tricolored Bat), and *Tadarida brasiliensis* I. Geoffroy Saint-Hilaire (Brazilian Free-tailed Bat). To date, little is known of the structure and ecology of bat communities in Louisiana (Lance and Garrett 1997), especially in winter. Herein, we document the active bat community occurring in the Kisatchie National Forest and compare community structure between summer and winter seasons.

Field Site Description

The Kisatchie National Forest encompasses ~414,665 ha, of which 244,337 ha are forest land comprised of 5 ranger districts: Caney, Calcasieu, Catahoula, Kisatchie, and Winn (United States Department of Agriculture 1999). Elevation varies from ~61 to 130 m above sea level. The Kisatchie National Forest is primarily situated within the Southern Tertiary Uplands level IV ecoregion (Omernik 1995) of the Gulf Coastal Plain. Within the Kisatchie, there are 5 broad plant or

vegetation communities: *Pinus palustris* Mill. (Longleaf Pine), *Pinus echinata* Mill. (Shortleaf Pine), *Quercus* (oak)–*Carya* (hickory), mixed hardwood– *Pinus taeda* L. (Loblolly Pine), and riparian forest (United States Department of Agriculture 1999). The region generally lacks caves, abandoned mines, or other underground structures, although road culverts and cisterns are often used by some hibernating bats (Stevens et al. 2017). Mean temperatures in January and July are 9.5 °C and 28 °C, respectively (Haywood and Harris 1999, Louisiana Office of State Climatology 1995). Average rainfall is 1389 mm (Haywood and Harris 1999).

We conducted field work in the Catahoula and Winn ranger districts (Fig. 1). We obtained the minimum temperature for each night from the National Weather Service for Alexandria International Airport through Weather Underground (TWC Product and Technology LLC 2018). This weather station was located 50 km on average from our netting sites.

Methods

We sampled the bat community from July 2016 to March of 2018. Winter sampling was conducted from early December to late March, whereas summer sampling was early April to late August. We opportunistically visited each site at least once during both seasons. In total, we sampled 55 sites over 181 nights. Typically, at each site, we erected nine 12 m x 2.6 m mist nets in forest, at ground level, or above small ephemeral or permanent streams or ponds. We typically opened the nets for 4 hours beginning at dusk. We identified bats based on Lowery (1974). We followed the guidelines for capture, handling, and care of mammals of the American Society of Mammalogists (Sikes et al. 2016) and the Texas Tech University Institutional Animal Care and Use Committee Protocol No. 15062-09.

We calculated sample effort based on net-meter-hours (NMH: total linear meters of nets 2.6 m in height times the number of hours they were open; Straube and Bianconi 2002). To account for differences in sampling effort between nights and seasons, we calculated a catch-per-unit effort (CPU) as (number of individuals captured/NMH x 100). We constructed sample-based rarefaction curves (Gotelli and Colwell 2001) to determine adequacy of sampling (i.e., asymptotic rarefaction curve) in summer and winter. On 76 nights we caught no bats; therefore, rarefaction curves were based on 64 trapping nights in winter and 41 nights in summer. When rarefying, as the total number of species in a sample (i.e., summer or winter) is approached, the distribution of species richness across rarefied samples becomes more skewed. Accordingly, we displayed the median number of species given a certain number of subsamples as opposed to the mean because the median always characterizes the middle of the distribution despite its skew (Sokal and Rohlf 1995). We calculated a Spearman–Rank correlation (Sokal and Rohlf 1995) for

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Figure 1 (following page). Map of the Winn and Catahoula Districts of the Kisatchie National Forest in Louisiana (top). Distribution of 55 bat-netting sites across districts (bottom) sampled from July 2016 to March 2018. Due to close proximity of some sites, some gray cirlces represent more than 1 site.
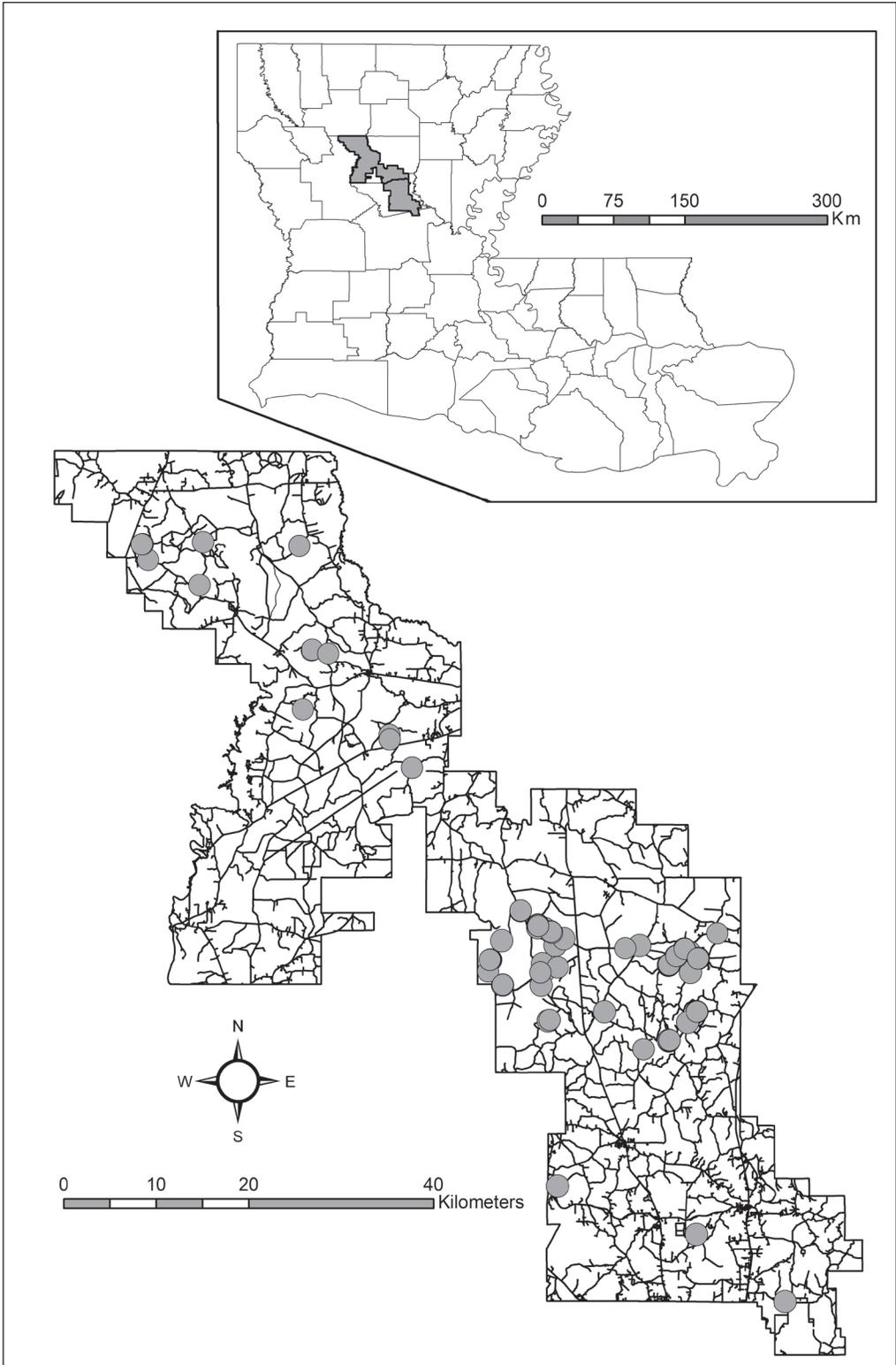
Figure 1. [See preceding page for caption.]

abundance of each species in summer and winter separately to evaluate the degree to which the rank abundance of each species changed between seasons.

We estimated 3 community-level characteristics: (1) relative abundance (CPU), (2) species richness (number of species within a sample), and (3) species diversity calculated based on Shannon' diversity index (Pielou 1975), which reflects variation in both richness and evenness of species. We examined whether these community-level characteristics were related to season or minimum temperature of each sampling night using linear models (Hoffmann 2004). All nights were used in analyses of community characteristics irrespective of whether we caught bats or not. Nights with no captures were assigned CPUs, species richness, and diversity values of 0. To examine differences between seasons, we conducted *t*-tests (Sokal and Rohlf 1995) in SPSS version 25. Variances of relative abundance were heteroscedastic between seasons. Accordingly, we used the Welch's correction to account for unequal variances (Welch 1947). To examine linear relationships between community-level characteristics and minimum nighttime temperature, we conducted generalized least-squares regression because visual inspection suggested that variates were heteroscedastic around the regression line. Accordingly, we weighted each observation based on the fixed variance error structure (Zuur et al. 2009). Generalized least-squares regressions were conducted using the 'nlme' package in R (Pinheiro et al. 2013).

Results

We mist-netted bats across 55 sites during 130 winter nights and 51 summer nights. Total effort was 67,937 NMH: 49,195 NMH during winter and 18,742 NMH in summer. We caught 390 bats of 10 species across both seasons (Table 1).

Table 1. Number and mean species diversity metrics of bats captured in summer and winter in the Kisatchie National Forest of Louisiana, 2016–2018. Numbers in parentheses represent catch-per-unit (CPU) * 100 as calculated by net meters per hour x 100. * indicates $P < 0.05$ in *t*-test, and ** indicates $P < 0.01$ in *t*-test.

| Species	Winter	Summer
Corynorhinus rafinesquii (Rafinesque's Big-eared Bat)	7 (0.014)	1 (0.005)
Eptesicus fuscus (Big Brown Bat)*	23 (0.047)	91 (0.486)
Lasiurus borealis (Eastern Red Bat)	35 (0.071)	8 (0.043)
Lasiurus cinereus (Hoary Bat)	1 (0.002)	1 (0.005)
Lasionycteris noctivagans (Silver-haired Bat)*	7 (0.014)	0 (0.000)
Lasiurus seminolus (Seminole Bat)	30 (0.061)	17 (0.091)
Myotis austroriparius (Southeastern Myotis)	10 (0.020)	10 (0.053)
Myotis septentrionalis (Northern Long-eared Bat)**	8 (0.016)	23 (0.123)
Nycticeius humeralis (Evening Bat)	65 (0.132)	31 (0.165)
Perimyotis subflavus (Tricolored Bat)	14 (0.028)	8 (0.043)
Total	200 (0.407)	190 (1.014)
CPU**	0.004	0.010
Species richness**	0.977	1.510
Shannon's diversity index	0.238	0.294

In winter, we caught no bats on 66 nights (51%), whereas in summer we caught no bats on 9 nights (18%). We caught 0.004 bats per NMH in winter and 0.010 bats per NMH in summer. All bat species were caught in both summer and winter except Silver-haired Bat, which was caught only in winter. Rarefaction curves reached an asymptote at 10 species for winter and 9 species for summer (Fig. 2). An asymptote was reached in 31 days during summer and 35 days in winter.

Significant differences in CPU between winter and summer existed for Big Brown Bat, Silver-haired Bat, and Northern Long-eared Bat (Table 1). CPUs for Big Brown Bat and Northern Long-eared Bat were greater in summer than winter, whereas the opposite was true for Silver-haired Bat. Differences between summer and winter CPUs for all other species were nonsignificant. Despite species-specific seasonal differences in CPU, the Spearman-rank correlation exhibited a positive relationship between CPU for winter and summer ($r = 0.66$, $P = 0.036$, $n = 10$), suggesting that rank in one season was a strong indicator of rank in the other season. CPU for all captures was 2.75 times higher in summer than in winter (Table 1), and this difference was significant ($t = 2.70$, df $= 56.23$, $P < 0.001$). Similarly, species richness was approximately 1.5 times greater in summer than winter ($t = 2.57$. df $= 179$, $P = 0.009$). In contrast, Shannon's diversity index exhibited no significant seasonal difference ($t = -0.831$, df $= 179$, $P = 0.407$). Species richness and CPU increased with nightly minimum temperature in winter and across the entire year (Table 2); all other regressions were nonsignificant.

Discussion

We captured fewer numbers of individuals per night in winter than in summer; however, bats in the Kisatchie National Forest exhibited considerable activity during winter. With the exception of Silver-haired Bat, all bats captured were active

Figure 2. Rarefaction curves of bat species richness in the Kisatchie National Forest, 2016–2018, for nights sampled during summer (black circles, $n = 41$) and winter (gray triangles, $n = 64$). Only nights when bats were caught were included in curves.
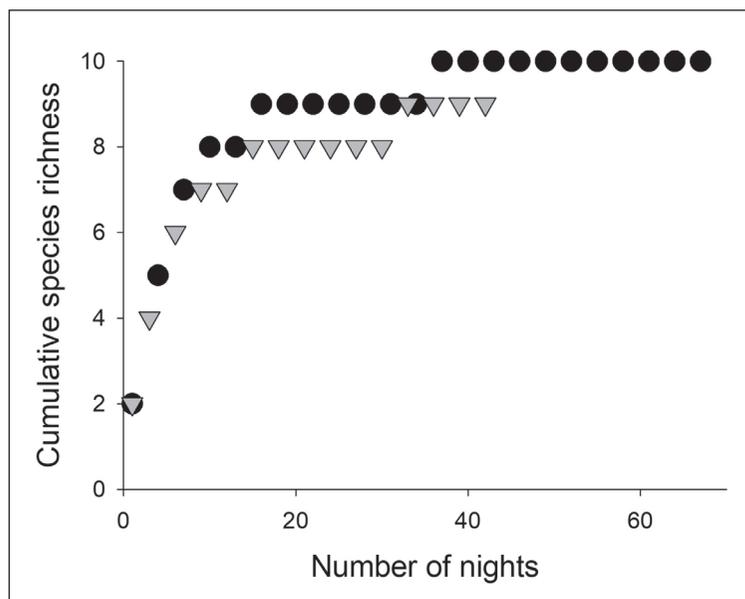
in both summer and winter. In temperate zones, especially in North America, bats are often inactive during winter and hibernate for long periods (McNab 1982) or migrate to other areas (Cryan et al. 2014, Hayward 1970, McGuire and Boyle 2013, McGuire et al. 2012, Perry et al. 2010a, Schmidly and Bradley 2016). Both hibernation (i.e., long-term torpor in response to cold temperatures) and migration are effective strategies for mitigating harsh winter conditions. Nonetheless, there are benefits and costs to both strategies. Hibernating animals may suffer from dehydration, waste accumulation, sleep deprivation, arrested reproductive development, lowered immune capabilities, and increased risk of predation due to immobilization (Czenze et al. 2017, Stawski et al. 2014, Willis 2017). Moreover, there may be only limited benefit to hibernating when ambient temperatures are not substantively lower than the thermoneutral zone of hibernating animals for long periods of time (McNab 1982). In areas where winter temperatures are generally mild, such as Louisiana, there may be little benefit to hibernation for extended periods of time. Bats also use other means to mitigate stress of cold temperatures during temporary bouts of cold weather. For example, at temperatures below ~5 °C, Silver-haired Bats increase their use of ground roosts as opposed to tree roosts (Perry et al. 2010b). Short-term torpor can also mitigate cold nights or temporary cold spells in winter (Stevens and Amarilla-Stevens 2012). Reports of seasonal reductions in bat activity related to colder temperatures are common in the literature (Barros et al. 2017, Johnson et al. 2017, Mello 2009) and reflect use of daily torpor to mitigate energetic costs.

In winter and on a nightly basis, community-level bat activity has been positively related to warmer temperatures (Barros et al. 2014). Similarly, at the species level, Tricolored Bat (Avery 1985), *Chalinolobus tuberculatus* Forster (Long-tailed Wattled Bat; O'Donnell 2000), *Nyctalus noctula* Schreber (Common Noctule Bat; Avery 1986), and *Mystacina tuberculata* Gray (New Zealand Lesser Short-tailed Bat; Christie and Simpson 2010), are also more active at higher ambient temperatures. From a physiological perspective, duration of torpor bouts is directly related

Table 2. Results from generalized least squares regression analysis evaluating the seasonal relationship of abundance (catch-per-unit [CPU]), species richness, and Shannon's diversity index with minimum nighttime temperature for captured bats in the Kisatchie National Forest of Louisiana, 2016–2018. * indicates statistical significance ($P < 0.05$).

Season	Dependent variable	r^2	df	P
Summer	CPU	0.01	48	0.385
Summer	Species richness	<0.01	48	0.641
Summer	Shannon's diversity index	<0.01	48	0.763
Winter	CPU	0.06	128	0.012*
Winter	Species richness	0.07	128	0.007*
Winter	Shannon's diversity index	0.03	128	0.079
Combined	CPU	0.09	178	<0.001*
Combined	Species richness	0.08	178	<0.001*
Combined	Shannon's diversity index	0.02	178	0.053

to ambient temperature during winter in Eastern Red Bat (Dunbar and Tomasi 2006), *Rhinolophus ferrumequinum* Schreber (Greater Horseshoe Bat; Park et al. 2003), *Myotis myotis* Borkhausen (Mouse-eared Bat; Wojciechowski et al. 2007), and *Nyctophilus bifax* Thomas (Eastern Long-eared Bat; Stawski et al. 2009). This variation in torpor duration likely reflects the flexibility of many bat species to respond to warmer temperatures in winter.

Winter activity in bat communities may not be an uncommon phenomenon (Boyles et al. 2006). In fact, substantive winter activity has been characterized at a number of geographically widespread sites across North America. Even as far north as Canada, species such as Big Brown Bat*, Myotis ciliolabrum* Merriam (Western Small-footed Bat), and *Myotis evotis* H. Allen (Long-eared Myotis) exhibit substantial activity during winter (Brigham 1987, Klug-Baerwald et al. 2017, Lausen and Barclay 2006). On the Cumberland Plateau between Kentucky and Tennessee, all bats found in summer were recorded acoustically in winter when nights were >10 °C, but activity was far less on nights when mean temperatures were <10 °C (Burns 2016). Moreover, bat activity decreased linearly with decreasing temperature. Similarly, 12 of the 29 species of bats found in New Mexico are active throughout winter in substantial numbers (Geluso 2007). In contrast, in Nebraska, only Big Brown Bat exhibited substantive winter activity, with Eastern Red Bat migrating south, and species of *Myotis* spending much of the winter in hibernacula (White et al. 2014).

Geographic variation in frequency and duration of winter activity may also influence the geographic effects of WNS. For example, differences in use of hibernation versus short-term torpor and the associated amount of winter activity may create differences in individual- and population-level survivorship and ultimately the geography of extirpation due to WNS (Reynolds et al. 2017). In New England, individual bats that were more active in winter were least impacted by WNS (Reynolds et al. 2017). In a detailed study of seasonal dynamics of WNS, Langwig et al. (2015) demonstrated that hibernation was the dominant factor determining effects of WNS; only after bats began to fully hibernate (i.e., sustained torpor) did they succumb to the disease. In areas where temperature is mitigated by geography, such as in coastal areas or those at more southerly latitudes of North America, bats may be sufficiently active so as to avoid the manifestation of advanced WNS (Grider et al. 2016). Extensive surveys of highway culverts used as roosts throughout Louisiana have found no evidence of WNS or DNA from *Pseudogymnoascus destructans* (Blehert & Gargas) Minnis & D.L. Lindner (Limon et al. 2019), even though it is widespread in surrounding states. For example, although data have not been presented, a press release by Texas Parks and Wildlife Department announced that WNS has been detected in multiple locations across Texas (TPWD 2020). Areas in North America where winters are mild may serve as important refugia from effects of WNS for a number of bat species, particularly, *Myotis lucifugus* Le Conte (Little Brown Bat), Northern Long-eared Bat, and Tricolored Bat that are experiencing the greatest effects of WNS**.** Perhaps the ability of bats to be active year-round because of higher winter temperatures and associated food availability (Williams 1949) may contribute to the absence of WNS in Louisiana. A study of the diet of Rafinesque's

Big-eared Bat in the Kisatchie National Forest found insect remains present in fresh feces throughout the year, suggesting that insect prey are available in this region during the winter months (Gregory et al. 2014).

Given the apparent frequency and variance of winter activity by bats, it may be more informative to consider winter activity as a gradient varying from deep, long-term hibernation in the coldest environments, through frequent use of daily or short-term torpor under moderate conditions, to little use of torpor in warmer environments. Our study as well as others (Bender and Hartman 2015, O'Donnell 2000, Wolbert et al. 2014) have demonstrated a general increase in activity with increasing nightly temperature. Across North America, this could translate into a dynamic mosaic of geographic variation in length and frequency of torpor use, corresponding to gradients in temperature and other climatic variables. Therefore, characterizing spatial variation in winter activity by bats is needed across the temperate zone to better understand the seasonal dynamics of bat community structure.

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