

PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Ongoing changes in migration phenology and winter residency at Bracken Bat Cave

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Funding information

Marshall Sherfield Fellowship

Abstract

Bats play an important role in agroecology and are effective bioindicators of environmental conditions, but little is known about their fundamental migration ecology, much less how these systems are responding to global change. Some of the world's largest bat populations occur during the summer in the south-central United States, when millions of pregnant females migrate from lower latitudes to give birth in communal maternity colonies. Despite a relatively large volume of research into these colonies, many fundamental questions regarding their abundance—including their intra- and interseasonal variability—remain unanswered, and even estimating the size of individual populations has been a long-running challenge. Overall, monitoring these bat populations at high temporal resolution (e.g., nightly) and across long time spans (e.g., decades) has been impossible. Here, we show 22 continuous years of nightly population counts at Bracken Cave, a large bat colony in south-central Texas, enabling the first climate-scale phenological analysis. Using quantitative radar monitoring, we found that spring migration and the summer reproductive cycle have advanced by approximately 2 weeks over the study period. Furthermore, we quantify the ongoing growth of a newly-established overwintering population that indicates a system-wide response to changing environmental conditions. Our observations reveal behavioral plasticity in bats' ability to adapt to changing resource availability, and provide the first long-term quantification of their response to a changing climate. As aerial insectivores, these changes in bat phenology and propensity for overwintering indicate probable shifts in prey availability, with clear implications for pest management across wider regional agrisystems.

KEYWORDS

bats, migration, overwintering, phenology, radar, remote sensing, *Tadarida*

1 | INTRODUCTION

Large bat colonies such as those residing in caves and bridges across the south-central United States are a source of public fascination, yield millions of dollars annually in ecotourism, and are integral to the regional economy through the billions of dollars in agricultural ecosystem services they provide (Bagstad & Wiederholt, 2013; Boyles, Cryan, McCracken, & Kunz 2011; Cleveland et al., 2006). Among these bat populations, the summer maternity colony

of Brazilian free-tailed bats (*Tadarida brasiliensis*) roosting in Bracken Cave in suburban San Antonio, Texas is widely regarded as one of the largest aggregations of mammals on Earth (Figure 1a–c), but basic information about its population including size, persistence, and change over time remains unknown (Frick, Chilson, Fuller, Bridge, & Kunz, 2013). Surveys of Bracken Cave in the 1950s produced some of the most cited population estimates from extrapolated roost densities, yielding an average population of 20 million bats and summertime maxima approaching 40 million

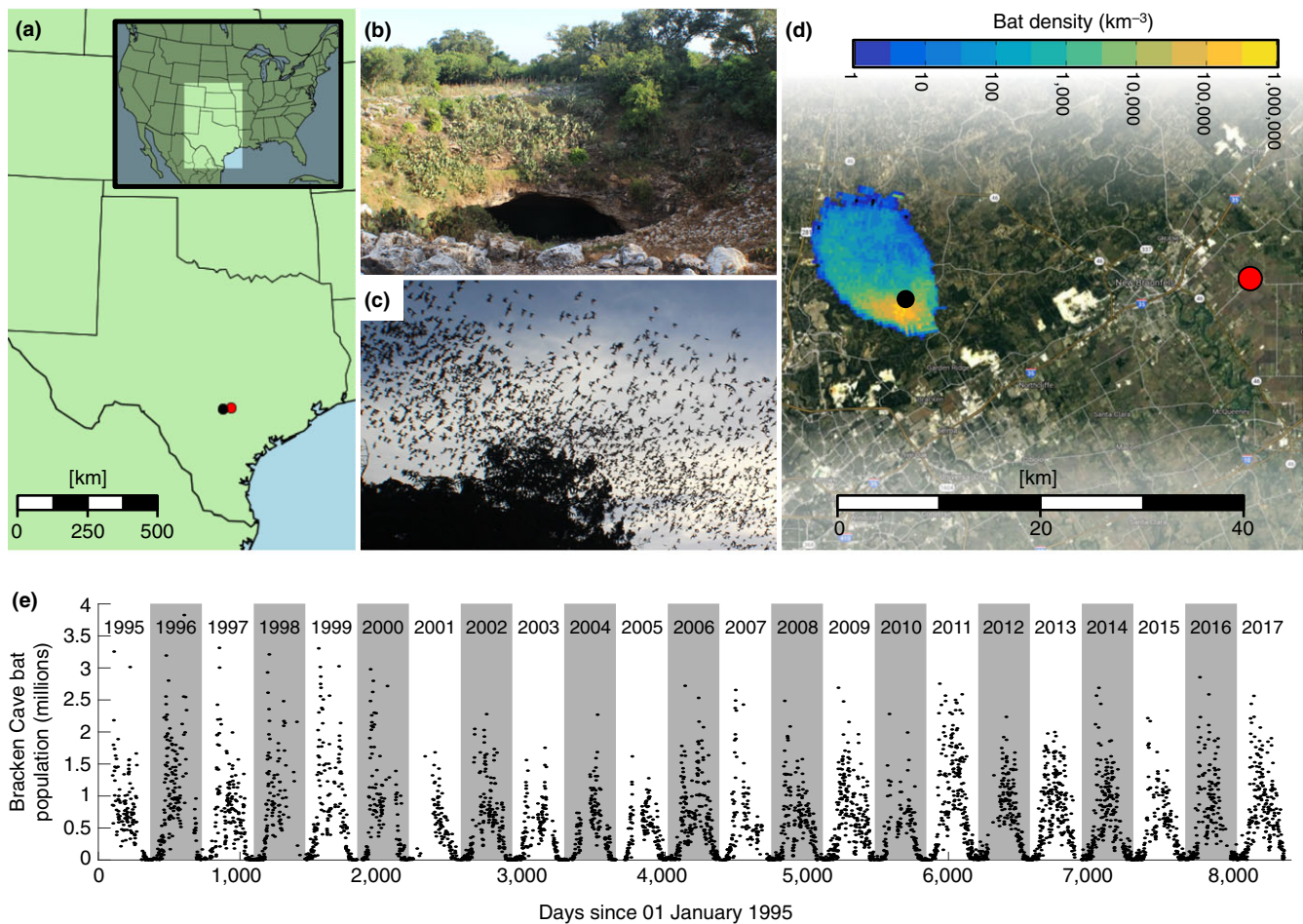


FIGURE 1 Two decades of nightly colony counts at Bracken Cave. (a) We monitored the population dynamics of the Brazilian free-tailed bat colony (*Tadarida brasiliensis*) at Bracken Cave in suburban San Antonio, Texas, USA (black circle) using a nearby weather surveillance radar (red circle). (b) The population spends the day roosting inside the cave, emerging en masse at dusk. (c) Bats maintain high aerial densities within the emergence column, communally climbing to high altitudes before dispersing to forage. (d) The concentrated ascent of the population away from the Bracken Cave entrance (black circle) forms a “cloud” of bats that is detected by the local weather radar (red circle), enabling enumeration. (e) Nightly emergences captured on radar provide an objective time series of the Bracken Cave population over 22 years, enabling historical analysis and real-time monitoring. Population measurements span March 20, 1995 through November 30, 2017 ($n = 4,481$). Photographs were taken on July 05, 2016 at (b) 01:23 UTC and (c) 01:28 UTC, immediately preceding the pictured radar scan (d) at 01:33 UTC [Colour figure can be viewed at wileyonlinelibrary.com]

individuals (Davis, Herreid, & Short, 1962; McCracken, 2003). Subsequent studies presented significantly smaller numbers, leading some to diagnose a major population crash, while others questioned the precision and accuracy of former estimation techniques (Betke et al., 2008; McCracken, 2003). Further complicating the matter, these bat populations are highly mobile—taking part in both semiannual long distance migrations to wintering grounds in Mexico, as well as nightly regional movements among neighboring caves and bridge roosts (Horn & Kunz, 2008; Humphrey, 1971; McCracken, 2003). Advanced thermal imaging techniques have revealed the most accurate depictions of nightly population counts for several caves (Betke et al., 2008) and the variability in a single colony over one season (Hristov, Betke, Theriault, Bagchi, & Kunz, 2010), but in general, bat migration and population dynamics—especially within large colonies—has remained a difficult phenomenon to study (Cryan & Diehl, 2009; Humphrey, 1971;

McCracken, 2003), resulting in large knowledge gaps in nightly, seasonal, and interannual variability in colony size.

Ecosystems around the globe have been changing in response to anthropogenic stimuli (Walther et al., 2002), but with the inherent challenges in quantifying fundamental characteristics of bat ecology, detecting trends in these changing migration systems has remained infeasible (Cryan & Diehl, 2009; Sherwin, Montgomery, & Lundy, 2012; Voigt & Kingston, 2016). Most studies of anthropogenic change have focused on avian migration (e.g., Both, Bouwhuis, Lessells, & Visser, 2006; Cotton, 2003; Kelly et al., 2012; Krauel & McCracken, 2013; Schmaljohann & Both, 2017), and birds have remained a convenient analog for bats in lieu of a direct alternative. With the ongoing rise in threats to bats such as habitat fragmentation, human encroachment, wind energy development, climate change, and the spread of infectious diseases such as white nose syndrome, establishing baseline population measurements and real-

time monitoring systems is vital for guiding management strategies and informing conservation policy (Loeb et al., 2015; Voigt & Kingston, 2016).

Remote sensing technology has proven invaluable for providing long-term quantitative ecological measurements with high spatiotemporal resolution and broad coverage, and the application of satellite observational infrastructure has helped shape modern studies of plant phenology (e.g., Buitenwerf, Rose, & Higgins, 2015; White et al., 2009). Operational ground-based weather surveillance radar networks hold similar potential for making systematic phenological measurements for airborne biota (Kelly et al., 2012, 2016), and use of these observational platforms for monitoring bats in flight has been advocated by chiropterologists for 50 years (Cryan & Diehl, 2009; Frick et al., 2013; Kunz et al., 2007; McCracken, 2003; McCracken et al., 2008; Williams, Ireland, & Williams, 1973). Despite this potential, few studies have applied weather radar for monitoring bat populations (Frick et al., 2012; Horn & Kunz, 2008) and none have attempted to quantify animal numbers. The goal of this study is to use long-term radar measurements to produce the first multi-decadal set of nightly population counts of a large bat colony, providing an objective yardstick with which to quantify population dynamics, as well as migratory and reproductive phenology of the Bracken Cave colony.

2 | MATERIALS AND METHODS

2.1 | Radar site and system specifications

The US national network of operational weather surveillance radars (NEXRAD) provides continuous real-time measurements of the airspace that have been archived in a long-running database since the early 1990s, and routinely detects the dusk emergence of bat colonies as they depart from their roosts en masse to forage for insects on the wing (Frick et al., 2012; Horn & Kunz, 2008). These nightly exodus events present the ideal opportunity for radar-based censuses of bat colonies (Betke et al., 2008; Horn & Kunz, 2008). The nearest weather surveillance radar to Bracken Cave (cave entrance: 29.6870°N, 98.3525°W, 314.6 m AMSL; black circle in Figure 1a,d) is located at the Austin/San Antonio National Weather Service office (International Civil Aviation Organization site identifier: KEWX) at the New Braunfels Regional Airport. The KEWX radar installation is located at 29.7039°N, 98.0283°W with an antenna height of 29.7 m above ground level and 222.7 m above mean sea level (red circle in Figure 1a,d). At 31.43 km from Bracken Cave, the center of the lowest beam is 240.5 m above the entrance to the cave and extends down to the surface at the periphery. The KEWX radar operates at S-band, with a radio frequency of 2,880 MHz and 10.41-cm wavelength. The operating parameters and scan patterns follow the operational NEXRAD specifications (Diehl & Larkin, 2005; NEXRAD Operational Support Facility, 1996). General background on the basics of radar theory, specifically focusing on NEXRAD for ecological applications, can be found in several primers (Chilson et al., 2012; Diehl & Larkin, 2005; Larkin & Diehl 2012). Radar alone

cannot provide species-level classification of bats, and generally relies on complementary acoustic monitoring or site surveys to determine species composition (Cryan & Diehl, 2009). For Bracken Cave, numerous site studies over several decades have repeatedly confirmed the dominant inhabitants as a single subspecies of Brazilian free-tailed bat (*Tadarida brasiliensis mexicana*), commonly referred to as the Mexican free-tailed bat (Davis et al. 1962; Eads, Wiseman, & Menzies, 1957; McCracken, 2003).

2.2 | Radar data processing

The full historical archive of NEXRAD data is hosted on the Amazon Web Services Cloud and is continuously appended with current measurements in real time with average data latency of less than 10 min (<https://aws.amazon.com/public-datasets/nexrad/>). For the KEWX site, data are available from March 20, 1995 through the present date (November 30, 2017). For each night in this period, we downloaded all KEWX volume scan data files from 21 UTC through 03 UTC—a time span encompassing local sunset, civil twilight, and the early hours of the night at Bracken Cave. In total, this 22-year analysis involved downloading, processing, and analyzing over 351,000 volume scan files, exceeding 28 terabytes of information. For each volume scan, we converted measurements of equivalent radar reflectivity factor (Z_e ; Figure 2a–f) to reflectivity (η) following Chilson et al., (2012). We used the mean radar cross section of a Brazilian free-tailed bat at S-band (4.519 cm²), obtained from an electromagnetic model (Mirkovic, Stepanian, Kelly, & Chilson, 2016), to convert reflectivity to aerial bat density (Chilson et al., 2012). We calculated the volume of individual sampling voxels from beam geometry, assuming a one-degree rotationally symmetric circular conical frustum in legacy resolution and one-degree (elevation) by half-degree (azimuth) elliptical conical frustum after the site upgrade to super-resolution on July 11, 2008. We calculated the number of bats aloft within each voxel by applying the aerial bat densities to the corresponding sample volumes, and summed the resulting bat numbers for the 0.5–4.5 degree elevation angles over a 20 km by 20 km domain centered on the cave entrance (Figure 2a–f, red box) to get an instantaneous snapshot of bats in the airspace over the cave region. Finally, for each night we found the greatest instantaneous number of bats aloft between 21 UTC and 03 UTC as an estimate of the cave population (Figure 2g). Knowing that all bats are likely not simultaneously present at altitude within this domain, this estimate is more appropriately a lower bound on the true population. To ensure the accuracy of these measurements, we manually inspected the radar images from each night (Figure 2a–f) to screen for missing data, weather, clutter, and other biological contamination from migrating birds, insects, or neighboring caves. If any of these conditions were identified, the night was removed from the analysis. The result of this quantitative radar surveillance technique is a time series of Bracken Cave population estimates spanning over 22 years, from March 20, 1995 to November 30, 2017 (Figure 1e).

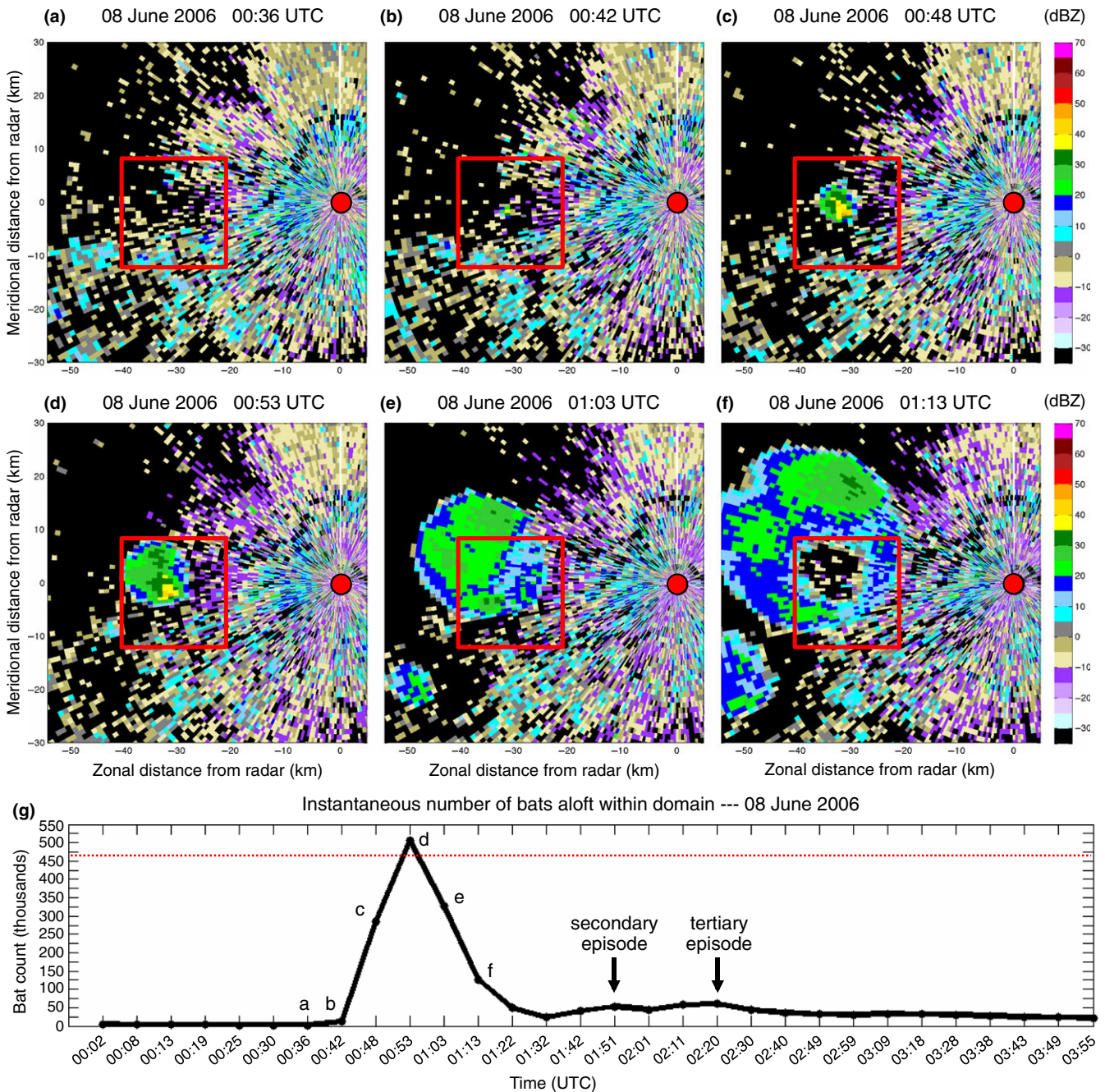


FIGURE 2 Extracting nightly bat population from radar measurements. (a–f) Six successive images of radar reflectivity factor from the San Antonio/Austin weather surveillance radar (red circle) on the night of June 07, 2006 showing the 20 km by 20 km analysis area (red box) centered on the entrance to Bracken Cave. (g) Each volume scan of reflectivity factor measurements is converted to bat numbers and summed over the three-dimensional analysis volume, yielding an instantaneous estimate of the number of bats aloft (black line). The maximum instantaneous number (506,191 bats; d) is taken as the population estimate, and the corresponding radar image (d) is checked to ensure no contamination from weather or other clutter. This particular case was sampled by the Boston University bat group using a thermal imaging exodus census, yielding a count of 464,890 bats (red dotted line) [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Validating population estimates against a thermal imaging survey

While high precision of radar measurements is assured across long time spans through the strict operational calibration requirements maintained by the National Weather Service (<1 dBZ at signal-to-

noise ratios >10 dB; NEXRAD Operational Support Facility, 1996), the accuracy of bat population estimates requires validation. The Boston University Bat Lab conducted a survey of a dusk emergence of Bracken Cave on June 07, 2006 using a sophisticated thermal imaging technique (Betke et al., 2008), which is unquestionably the most accurate single measurement of the population to date. The

census yielded a count of 464,890 bats and reports a count certainty within $\pm 7\%$ of manual human inspection of the video frames (Betke et al., 2008). We compared this count to our concurrent radar estimate of 506,191 bats on the same evening (Figure 2), resulting in a percent difference of 8.5%. In this particular case, the majority of the population emerged in a single primary exodus episode, with minor secondary and tertiary episodes occurring afterward (Betke et al., 2008). The timing and relative magnitude of these three emergence episodes match across both radar (Figure 2) and thermal imaging censuses (see Fig. 4 in Betke et al., 2008). While the first emergence episode typically contains most of the population (Betke et al., 2008), it is possible that in some cases the population may be split more evenly among exodus episodes, yielding a snapshot that misses a portion of the colony and underestimates the population for the night. As with all emergence surveying techniques, these two methods only detect bats leaving the cave and will inherently omit pups that remain in creches until their first exodus flights (Betke et al., 2008; McCracken, 2003).

2.4 | Validating population estimates against winter photographic surveys

A site survey of Bracken Cave was conducted in December 2010 and 2011, providing two valuable estimates of overwintering population numbers (Weaver, Simpson, Baccus, & Weckerly, 2015). Population estimates were obtained using photographs of roosting clusters of bats to determine their coverage density over the surveyed surfaces, and extrapolating these densities over polygons of roost surface area (Weaver et al., 2015). The population estimates from these two surveys, as well as their 95% confidence intervals based on extrapolation techniques, are reported as $15,233 \pm 1,223$ bats for December 2010 and $88,334 \pm 2,232$ bats for December 2011. By comparison, our radar estimates for December 2010 ranged from zero (i.e., no emergence detected) to 29,013 bats, with the detected emergences having a monthly mean of 8,610 bats and median of 4,595 bats ($n = 16$). December 2011 ranged from zero to 163,825 bats, with a monthly mean of 38,409 bats and median of 25,984 bats ($n = 20$). Inspection of radar images has revealed periodic intermixing among roosts during the winter, with surrounding colonies amalgamating into the Bracken Cave population. These temporary increases in cave inhabitancy contribute to the right-skewedness of the radar-derived winter population distributions and likely did not occur on either of the two site surveys conducted by Weaver et al. (2015). Aside from actual variability in the size of the winter population occupying the cave, another possible cause for differences between estimates is that photographic roost surveys sample all bats present, while exodus surveys only sample bats that leave the cave to forage. Moreover, radar surveys require bats to reach altitudes within radar coverage. This interpretation is consistent with descriptions that winter foraging is contingent on weather conditions (Weaver et al., 2015), and may result in staggered or erratic emergence schedules among individuals. It is likely that opportunistic weather conditions may lead to episodic mass emergence events during the

winter, which would yield radar estimates of the true population, but in general, the absolute numbers of individuals obtained in winter radar exodus surveys are probably underestimates of the true population numbers. While nightly variability inhibits direct comparison between the two methods, the surveyed population estimates do fall within the range of daily radar estimates for the corresponding months. Perhaps a more relevant comparison is the percent-increase in overwintering population between years, reported as 480% by site survey (Weaver et al., 2015), vs. our radar estimates of 346% (by monthly means), 465% (by monthly medians), and 465% (by monthly maxima). This general agreement suggests that radar surveys do provide a reasonable depiction of interannual variability in winter residency, and that the maximum monthly counts are likely sampling emergence events involving a high percentage of the population.

2.5 | Validating radar-derived phenology

Systematic radar sampling of animal aggregations has been shown to contain phenological signals (Kelly et al. 2012), but interpreting these embedded signals requires knowledge of the natural history of the sampled system. In this case, the annual cycle of the colony revealed by radar (Figure 3a) can be interpreted by comparing life history accounts of the species across seasons (e.g., Davis et al., 1962; Eads et al., 1957; Horn & Kunz, 2008; Humphrey, 1971; Reichard et al., 2009), thereby linking the intra-annual variability in population to distinct stages in migration and reproduction. In January and February a small overwintering population of bats remains active at Bracken Cave, evidenced by their regular foraging flights. Spring migration begins at the start of March and peaks in April, during which time stopover migrants temporarily inflate the population (Figure 3a). The spring migration season wanes through May as the stopover population steadily departs the region, leaving the summer population of pregnant females as the primary cave inhabitants (McCracken, 2003; Reichard et al., 2009). Around 10 June, mothers give birth to a single pup and must forage heavily to maintain energy for lactation (Davis et al., 1962; Kunz & Robson, 1995; McCracken & Gustin, 1991; Reichard et al., 2009). The population effectively doubles during this short period, but emergence censusing does not detect the flightless pups that remain in the maternity roost. It does, however, detect a sudden increase in exodus activity associated with the birth of the pups, evidenced by the population increase in mid-June (Figure 3a). After approximately 6 weeks (c. 22 July), the pups are first capable of flight and begin to forage independently (Kunz & Robson, 1995; Reichard et al., 2009). We associate the perceived population maximum in early August with these exodus flights that now include volant pups (Figure 3a). Also during this period, the mothers begin to leave their pups, dispersing from Bracken Cave (Eads et al., 1957). Through August and September the fully grown pups continuously disperse from Bracken Cave when they are first able (Glass, 1982). While it is likely that fall migrants use Bracken Cave for stopover during this period, no clear population spikes are observed like those in spring (Figure 3a), possibly due to a slower pace and staggered timing of fall migration. It is also possible that

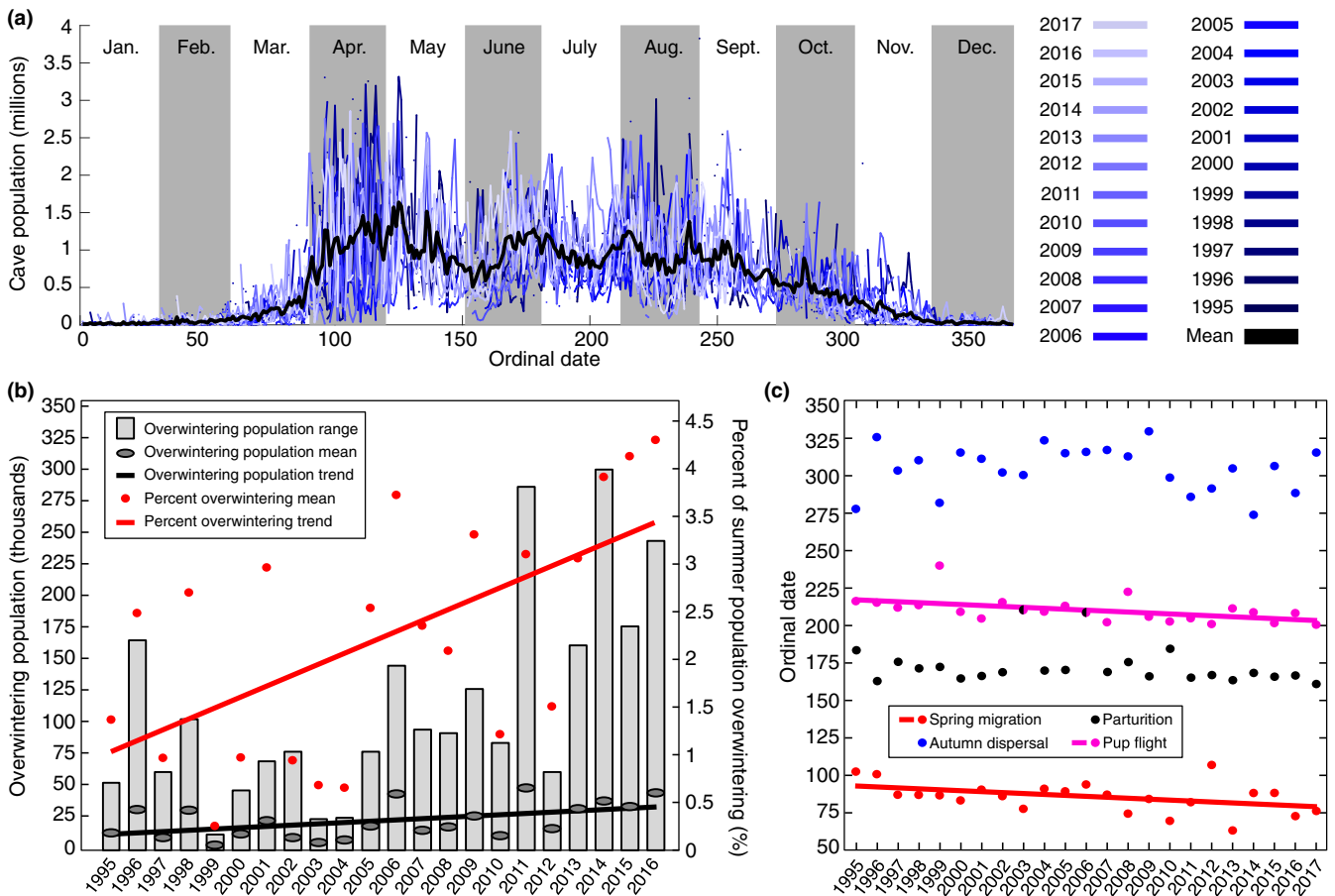


FIGURE 3 A shifting annual cycle in migratory bats. (a) Seasonal cave population dynamics reveal distinct stages in migration and reproduction (black line). While yearly variability in abundance and timing exists among the 23 years (blue lines), each follows a common phenology (black line). (b) Over the winter there is nightly variability in population (gray bars), but the yearly mean overwintering population (gray ovals) is increasing at a rate of 1,081 bats per year (black line). When considering these overwintering numbers as a percent of the summer population (red dots), winter inhabitation is increasing at a rate of 0.12% per year (red line). (c) Phenophases are defined for spring arrival (red), parturition (black), pup flight (pink), and autumn dispersal (blue). Advancing phenology is detected in spring migration (-0.66 days/year; red line) and pup flight (-0.63 days/year; pink line), while no significant trend is observed in parturition or fall dispersal. All test statistics are provided in the main text [Colour figure can be viewed at wileyonlinelibrary.com]

fall migrants prefer alternative stopover sites such as highway bridges (Horn & Kunz, 2008), perhaps to avoid noxious cave conditions following the densely populated summer season. Reduced competition for resources at smaller roosts may also motivate vacation of large maternity caves in the postbreeding season (Reichard et al., 2009). From October onward, the population continues to disperse until by early December only winter residents remain (Figure 3a). Within this context, we identify four detectable phenophases: the onset of spring migration, parturition, pup flight, and autumn dispersal.

2.6 | Statistical methods and definitions

We define the summer population of each year as the mean population over July and August. Similarly the winter population of each year is defined as the mean population over December of that year and the following January. The propensity for overwintering at Bracken Cave is taken as the proportion of mean winter residents

with respect to the preceding summer mean population. For the phenological analysis, we increase the temporal resolution by including 971 additional points that were excluded from the population abundance analysis due to missing scans or light clutter within the night, and linearly interpolating the time series to fill missing dates. Traditionally, phenophases have been defined in a manner to be easily detected by qualitative human observations (e.g., first arrivals, egg dates, budburst, etc.), enabling confident repetition. In remote sensing studies with quantification of phenomena, phenophases are not bound by these limitations, allowing quantitative thresholds to serve as objective benchmarks for comparison (see Buitenwerf et al., 2015; Kelly et al., 2012; Kelly and Horton, 2016). With this flexibility in mind, we define phenophases as changes in population with respect to an annual standard: the summer mean population. Analysis relative to the summer mean, as opposed to fixed population thresholds, serves as normalization across years, accounting for variability in interannual abundance. The phenophases are defined using the following conventions. The start of spring migration metric is

defined as the first date surpassing 50% of the summer mean population. The end of fall dispersal metric is defined as the final date surpassing 50% of the summer mean population. The parturition date metric is defined as the first occurrence after ordinal date 159 (c. 08 June) surpassing 125% of the summer mean population. We define the pup flight metric as the first occurrence after ordinal date 199 (c. 18 July) surpassing 125% of the summer mean population.

Taking each year as an independent sampling unit, we test for long-term trends in abundance and phenology using simple linear regression implemented using the MATLAB 2017b statistics toolbox. Taking the slope of the regression as the measure of the long-term trend, we use the *t* test embedded within the regression function to determine whether the slope is significantly different from zero (i.e., no long-term change). We will use the convention of reporting the regression slope with the 95% confidence intervals, followed by the coefficient of determination (R^2), *t*-statistic (*t*), degrees of freedom (dof), and *p*-value (*p*).

3 | RESULTS

3.1 | Changes in seasonal residency

Over the past 22 years, the mean population of bats overwintering at Bracken Cave (Figure 3b, gray ovals) has been increasing at a rate of $1,081 \pm 798$ bats per year (Figure 3b, black line; $R^2 = .261$, $t = 2.656$, dof = 20, $p = .015$). Similarly, the maximum annual winter inhabitancy (Figure 3b, gray bars) has been increasing at $7,637 \pm 4,305$ bats per year ($R^2 = .377$, $t = 3.477$, dof = 20, $p = .002$). In comparison, the mean summer population shows no significant annual trend ($-5,841 \pm 14,026$ bats per year; $R^2 = .031$, $t = -0.816$, dof = 21, $p = .424$), although summertime maxima do appear to be showing a significant decline ($-49,686 \pm 32,873$ bats per year; $R^2 = .295$, $t = -2.962$, dof = 21, $p = .007$). When considering the proportion of winter residents with respect to the preceding summer population (Figure 2b, red circles), winter residency has increased at a rate of $0.115 \pm 0.068\%$ per year (red line; $R^2 = .358$, $t = 3.340$, dof = 20, $p = .003$).

3.2 | Changes in migration and reproductive phenology

Over the analysis period, spring migration has advanced at an average rate of 0.658 ± 0.577 days per year (Figure 3c, red; $R^2 = .192$, $t = -2.235$, dof = 21, $p = .036$), accumulating a total shift of approximately 2 weeks. This change is synchronized with corresponding shifts in the date pups become volant, which is advancing at 0.630 ± 0.459 days per year (Figure 3c, pink; $R^2 = .257$, $t = -2.235$, dof = 21, $p = .014$). While we might expect parturition date to be constrained by these two stages, we did not detect a significant annual trend in the date pups are born (Figure 3c, black; -0.388 ± 0.806 days per year; $R^2 = .041$, $t = -0.945$, dof = 21, $p = .356$). Neither was there a significant annual trend in the date of fall dispersal (Figure 3c, blue; -0.259 ± 0.954 days per year; $R^2 = .013$, $t = -0.532$, dof = 21, $p = .600$).

4 | DISCUSSION

This first look at long-term trends in a migratory bat system presents a new perspective on adaptation to global change, answering some long-standing questions while raising many more. Overwintering appears to be a relatively recent behavioral shift in this region (Weaver et al., 2015), with early cave surveys by Eads et al. (1957) reporting, "Our observations of Bracken Cave over a 3 year period [1954–56] supplemented by numerous visits to the other free-tailed bat retreats indicated. . . no discernable bats present during the latter part of November, December, January and most of February." With winter foraging flights evident in our earliest radar records (i.e., 1995), it is clear that an overwintering population must have developed during the 39-year interim. It is currently unclear whether this winter population is comprised of the same summer residents that inhabited Bracken Cave and chose not to migrate, or whether Bracken Cave has become a wintering ground for bats migrating from higher latitudes. In either case, the decision to occupy Bracken Cave throughout the winter indicates the presence of requisite resources and environmental conditions to support overwintering. Furthermore, the steady increase in the total number of overwintering bats in Bracken Cave, as well as the increasing propensity for overwintering in this region may indicate an expanding winter range of common prey such as noctuid moths (Krauel, Westbrook, & McCracken, 2014; Weaver et al., 2015). Systematic foraging flights throughout the winter indicate year-round presence of food sources in this region of Texas, and a modeling study supports this range expansion in the corn earworm (*Helicoverpa zea*; Diffenbaugh, Krupke, White, & Alexander, 2008), an important prey species and crop pest of the region (Lee & McCracken, 2005; McCracken et al., 2008, 2012).

While annual migration from Bracken Cave is still by far the most prevalent mechanism for winter survival, migratory bats are demonstrating marked changes in their phenology (Figure 2c). The ongoing shift in spring arrivals illustrates plasticity in migration timing, suggesting a facultative onset in response to an environmental cue. Potential cues could include meteorological conditions that support migratory flight (e.g., tail-wind assistance; Dechman et al. 2017) or the availability of requisite resources (e.g., prey insects; Krauel et al., 2014; McCracken et al., 2012). If such a cue—or combination of cues—does exist, two implications follow. First, the cue must be perceptible to the bats prior to arrival; second, the cue must be advancing. We believe these criteria hold promise for designing future studies to identify drivers of the onset of migration.

An ongoing shift in phenology is not only apparent in migration through advancing spring arrivals at the cave but also exists in the developmental cycle leading to pups' first flights (Figure 3c, pink). Intuition would dictate that the corresponding advances in spring arrival and pup flight would necessitate a similar advance in parturition, but no significant trend was detected (Figure 3c, black). It is possible that our definition of the parturition phenophase may have influenced this result, and additional statistical inference will be necessary to gain a complete understanding of long-term changes in

reproductive phenology. Foraging flights of volant pups mark the completion of the summer cycle, and it follows that autumn migration to wintering grounds could share these advancing trends. In contrast, resources such as prey insects are remaining abundant later into the year (Diffenbaugh et al. 2008; Venugopal & Dively, 2017), enabling the possibility of delayed autumn migration. Our results provide no clear trend in autumn departure decisions, and show large yearly variability (Figure 3c, blue). Furthermore, it is unclear whether autumn decreases in the population correspond with fall migration, or if bats are persisting locally in smaller peripheral caves or bridge roosts until a later departure (Eads et al., 1957; Horn & Kunz, 2008). It is also possible that summer residents of Bracken Cave are continuously replaced with stopover migrants from higher latitudes, and that this autumn phenophase represents migration phenology of the last bats to move through the region. Overall, understanding cave use later in the year will require similar analysis of additional cave and bridge roosts, in conjunction with complementary field efforts (e.g., banding, biologging, site surveys).

Robust quantification of bat populations is a pressing need in conservation, particularly outside of the breeding season (Loeb et al., 2015; Weller, Cryan, & O'Shea, 2009), and Bracken Cave has been shown to be the most important single roost in the United States for the population viability of Brazilian free-tailed bats (Wiederholt et al., 2015). Similar analyses are still needed for neighboring cave and bridge roosts throughout this region to determine whether these trends are unique to Bracken Cave, or representative of the regional population as a whole. Such studies could provide new insights into nightly and seasonal regional movements, use of bridge habitats, and overall population trends (Horn & Kunz, 2008). There are myriad threats to migratory bats in a changing climate (Sherwin et al., 2012), including the risk of asynchrony between migration timing and availability of prey species (Krauel et al., 2014; McCracken et al., 2012; Sherwin et al., 2012), but so far the bats of Bracken Cave are showing plasticity through behavioral changes. Despite current adaptation, it is unclear whether these behavioral shifts can keep pace with evolving climatic conditions, and at what stage these adaptations will no longer suffice. Under global warming scenarios, increasing summer daytime temperatures and drought stress will continue to place pressure on bat populations (Adams, 2010; Frick et al., 2012; Jones, Jacobs, Kunz, Willig, & Racey, 2009; Sherwin et al., 2012). These same changes are forecasted to promote seasonal and geographical expansion of migratory agricultural pest insects, while strengthening their resistance to pesticides and transgenic crops (Diffenbaugh et al. 2008; Venugopal & Dively, 2017). Bats have the capacity to provide natural pest management, directly increasing profitability of both natural and genetically engineered field crops (Federico et al. 2008). Moreover, synchronization in migratory timing between bats and volant insects can promote *en route* pest suppression by these comigrating populations (Krauel & McCracken, 2013; Krauel et al., 2014; McCracken et al., 2012). In this light, the bats of Bracken Cave may serve the role of sentinels, regulating the passage of insects through the region, and reducing the impact of future generations downwind (Federico et al. 2008; Krauel et al., 2014).

Given the high economic value of the ecosystem services provided by the bats in this agricultural region (Boyles et al., 2011; Cleveland et al., 2006) and the important role of the bats as bioindicators (Jones et al., 2009; Newson et al., 2009; Sherwin et al., 2012), monitoring large bat colonies is imperative for diagnosing change at lower trophic levels in surrounding agrisystems (Cleveland et al., 2006; Federico et al., 2008). These new baseline measurements, combined with continuing real-time radar surveillance, ensure that future changes in the population of Bracken Cave will be readily diagnosed, and conservation efforts can be applied efficiently and effectively. Finally, weather radar networks are key infrastructure around much of the world, and provide standardized observations that hold the promise of providing continental surveillance of bat populations (Bauer et al., 2017), as well as their ongoing responses to global change.

ACKNOWLEDGEMENTS

This project was supported by a Marshall Sherfield Fellowship. Rothamsted Research is a national institute of bioscience strategically funded by the UK Biotechnology and Biological Sciences Research Council. Bracken Cave is owned and maintained by Bat Conservation International, a charitable NGO dedicated to conserving bats and their habitats. We gratefully acknowledge D. Mirkovic for development of the electromagnetic model used in this analysis, and G. McCracken for enabling a site visit to Bracken Cave, during which time the photographs appearing in this manuscript were taken. This work benefitted from early conversations with W. Frick, G. McCracken, and the University of Oklahoma Aeroecology Group, particularly J. Kelly, D. Mirkovic, and P. Chilson. We also thank D. Reynolds, M. Menz, K. Lim, and J. Kelly for providing internal review on an initial version of this manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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How to cite this article: Stepanian PM, Wainwright CE.

Ongoing changes in migration phenology and winter residency at Bracken Bat Cave. *Glob Change Biol.* 2018;00:1–10. <https://doi.org/10.1111/gcb.14051>