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Authors: Hristov, Nickolay I., Betke, Margrit, Theriault, Diane E. H., Bagchi, Angshuman, and Kunz, Thomas H.

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Seasonal variation in colony size of Brazilian free-tailed bats at Carlsbad Cavern based on thermal imaging

Nickolay I. Hristov,* Margrit Betke, Diane E. H. Theriault, Angshuman Bagchi, and Thomas H. Kunz

Center for Ecology and Conservation Biology, Department of Biology, Boston University, Boston, MA 02215, USA (NIH, THK)

Department of Computer Science, Boston University, Boston, MA 02215, USA (MB, DT, AB)

* *Correspondent: hristov@bu.edu*

The colony of Brazilian free-tailed bats (*Tadarida brasiliensis*) at Carlsbad Cavern, New Mexico, is a well-known example of this highly gregarious and conspicuous species in North America. For nearly a century researchers have tried to estimate the size of this colony, but different census methods and lack of repeatability have resulted in questionable estimates that have given rise to poorly understood but highly popularized, long-term population trends for this migratory species. In this study we present accurate seasonal estimates of colony size based on a recently developed census method—thermal infrared imaging and computer vision analysis. The size of the colony was estimated several times monthly from March through October 2005. Our estimates range from 67,602 to 793,838 bats, values that are orders of magnitude lower than the largest historic estimates. Consecutive estimates of nightly emergences show fluctuations of as many as 291,000 individuals, indicating that colony composition is considerably more dynamic than previously thought. Our results, combined with a quantitative analysis of emergence behavior, question the validity of early historic estimates that millions of bats once roosted in this cave and suggest that the long-term pattern of decline reported for this species might not be as severe as currently thought. DOI: 10.1644/08-MAMM-A-391R.1.

Key words: bats, census, colony dynamics, colony estimate, computer vision, historic estimates, seasonal variation, *Tadarida brasiliensis*, Three–dimensional (3D) modeling

The Brazilian free-tailed bat (*Tadarida brasiliensis*) is one of the most abundant and conspicuous insectivorous species in the United States and Mexico. It overwinters in southern and central Mexico and migrates northward each spring to northern Mexico and the southwestern United States to form enormous breeding colonies that represent some of the largest aggregations of mammals (Wilkins 1989). A major colony of this species is present from March through November at Carlsbad Cavern, New Mexico. Because of the early discovery of the cave, the colony has been the object of considerable public and scientific interest. For decades visitors have come to witness the spectacular evening flight of bats as they emerge to forage. In addition, the cavern and bats that occupy it have been the focus of studies on nightly emergence behavior and population dynamics (Allison 1937; Altenbach et al. 1979; Bailey 1928; Constantine 1967a; Route et al. 1998), feeding ecology (Best and Geluso 2003; McWilliams 2005), prevalence of rabies (Constantine 1967b), and impact of pesticides (Clark 1988; Cockrum 1970; Geluso 1981; Geluso et al. 1976; Geluso and Geluso 2004). Yet, in spite of the economic and ecological importance of Brazilian free-tailed bats (Cleveland et al. 2006), the species rarely has been considered in management plans, and little information exists on seasonal variation in colony size and structure (but see Constantine 1967a).

Colony size is an important variable for understanding the biology, ecology, and conservation of group-living organisms. However, estimating the size of large bat colonies under field conditions has been logistically and technologically challenging (Constantine 1967a; Humphrey 1971; Kunz 2003; Kunz et al. 1996; Kunz et al. 2009; McCracken 2003). Only a handful of studies have attempted to make quantitative estimates of Brazilian free-tailed bat colony sizes. With few exceptions (Betke et al. 2008; Davis et al. 1962; Humphrey 1971), most studies were conducted at Carlsbad Cavern (Allison 1937; Altenbach et al. 1979; Bailey 1928; Constantine 1967a; Route et al. 1998; Table 1). Likely because of limitations in the available methodology (but see Betke et al. 2008), these

TABLE 1.—Historical estimates of colony sizes of Brazilian free-tailed bats (*Tadarida brasiliensis*) at Carlsbad Cavern, New Mexico.

Year	Estimated size	Method	Method limitations	Source
1928	3,000,000	Emergence count	Visual estimate	Allison 1937
1936	8,741,760	Emergence count	Visual estimate	Allison 1937
1957	239,000	Roost density; mark–recapture	Variable cave surface and roost density	Constantine 1967a
1979	218,153	Emergence count	Variable emergence rate	Altenbach et al. 1979
1996–1997	79,000–353,000	Roost density	Variable cave surface and roost density	Route et al. 1998

studies produced highly variable results. Nevertheless, they suggest a general downward trend in numbers (Betke et al. 2008; McCracken 2003).

Collectively, the efforts to estimate the colony size of Brazilian free-tailed bats at Carlsbad Cavern create a seemingly detailed and complete record. However, these estimates were made by different workers, using different techniques, and sampling at different times of the year. In many cases, descriptions of techniques were incomplete or missing, making replication and validation impossible. Because of these limitations many of the published census data are at best crude estimates and have been noted by the authors themselves to be ''useful only for comparing orders of magnitude'' (Davis et al. 1962:319). In the absence of better estimates, however, these values have been perpetuated as absolute in both scientific (e.g., Kunz et al. 1995; McCracken and Gustin 1991; Wahl 1993) and popular (Ezzel 1992; McCracken 1986; Tuttle 1988) literature, and thus obscure the paucity of accurate census data. For example, it remains unknown whether the presumed decline in numbers is due to decreasing numbers of bats in the cave (Altenbach et al.1979; Route et al. 1998), inaccurate historic assessments of the size of the colony (Betke et al. 2008), or sampling biases due to seasonal variation. Clarification of these uncertainties requires accurate seasonal estimates of colony size. We contend that the questions of how many bats roost in Carlsbad Cavern, and whether there is a decline in numbers and to what extent, remain unresolved.

The objective of our study was to make noninvasive, accurate, seasonal estimates of the size of the colony and emergence behavior of Brazilian free-tailed bats at Carlsbad Cavern. We present the 1st such data using thermal infrared imaging and computer vision analysis. Unlike traditional census methods that rely on statistical sampling, our method relies on computer vision algorithms that use the thermal signature of bats to detect and track automatically each individual in flight, ultimately producing a complete census of the entire emerging colony (Betke et al. 2008; Kunz et al. 2009). Together, thermal imaging and computer vision analysis solve 2 of the most challenging caveats of traditional census methods—dependence on ambient or introduced light and need for long and tedious data processing (Hristov et al. 2008). Our method is completely noninvasive, allowing estimates that are more reliable and repeatable than methods used previously. It also allows us for the 1st time to provide quantitative assessment of nightly emergence behavior for Brazilian free-tailed bats at Carlsbad Cavern and to test the hypotheses proposed by Betke et al. (2008) that early historic estimates of colony size for this species were inflated.

MATERIALS AND METHODS

Study site.—Carlsbad Caverns National Park is located in southeastern New Mexico in the northeastern part of the Guadalupe Mountains Range (32°10′37.17″N, 104°26′27.62″W). On average the park attracts 440,000 visitors annually (2000–2008 Park Visitation Records). for Carlsbad Cavern, the largest cave in the national park, is a multilevel limestone complex that houses the Brazilian free-tailed bat colony. The cavern is accessed through a sizeable opening that also serves as the entry and exit portal for bats. A 2nd, much smaller opening east of the main entrance is not used by humans or bats. To minimize disturbance to the colony, access to the cavern by the public is permitted only during the day and is limited to areas away from roosting bats.

Brazilian free-tailed bats roost in the easternmost portion of the shallowest level of the cavern about 600 m from the main entrance. To emerge at the surface the bats fly along the length of the main corridor and spiral upward and outward through the main opening in a counterclockwise manner. The coordinated movement of thousands of emerging bats produces a spectacular tornadolike vortex. The purpose and mechanism of this formation are not entirely clear but are presumed to aid the bats in gaining altitude as they traverse the steep incline toward the entrance. Once outside the cavern the bats typically reorganize into a tight column that meanders over the landscape for several kilometers until they gain altitude and disperse widely to forage individually. Unless interrupted by inclement weather, all bats leave the cavern, and generally no bats return before the entire colony has emerged (Kunz et al. 1995). Adult females give birth to a single pup in mid- to late June, and juveniles are weaned in late July to early August. Unlike most large colonies of this species in the southwestern United States, where males typically abandon roosts after mating in the spring, males at Carlsbad Cavern remain in the roost in large numbers from spring through autumn (Constantine 1967a; Geluso and Geluso 2004).

Equipment.—We used Merlin Mid high-performance thermal cameras (FLIR/Indigo Systems, Santa Barbara, California), equipped with either a 13-mm or 25-mm lens. Each thermal infrared camera produced an image with pixel dimension of 320 × 256, captured at 60 Hz, and stored in a 12 bit per pixel digital format on an ACME Hercules HTII-

767 portable computer (ACME Portable Machines, Inc., Azusa, California). An 8-bit representation of the information was displayed to monitor the field of view of each camera and activity of bats in real time. Data from each camera were captured at a rate of 34 GB/h.

Recording technique.—Censuses were conducted monthly from late March through mid-October 2005. We attempted to record as many emergences as possible within a 10-day period, generally between the 10th and 20th day of each month. On a given night, we deployed 1–3 time-synchronized, thermal infrared cameras, depending on the direction and pattern of emerging bats observed on the previous night. Cameras were positioned at strategic locations near the top of the sinkhole entrance where the emerging bats formed a tight, unidirectional column. Best results were achieved when the optical axes of the cameras were oriented perpendicular to the flight path of the emerging bats. Camera locations were selected carefully so that they were neither too close to the cave entrance, where the spiraling bats would be counted multiple times, nor too far from it where the emerging column was less organized and more difficult to keep all bats in the fields of view of the cameras. On most dates cameras were set up south of the cave entrance (32°10′36.32″N, 104°26′27.21″W), pointing at a 248° azimuth when the bats flew in a southeasterly direction, or west of the cavern opening (32°10′36.72″N, 104°26′29.52″W), pointing at 145° when the bats flew in a southwesterly direction. Recording was started manually at the 1st sign of emerging bats and continued until bats ceased to emerge. In total, we made 32 attempts to census the colony in 2005. Accurate census estimates were computed for 20 of these attempts, resulting in at least 1 estimate for each month. The remaining 12 were not used in our analysis because of adverse weather conditions or unpredictable flight behavior.

Computer vision analysis and accuracy.—To census Brazilian free-tailed bats, computer vision algorithms were used to automatically count individuals as they emerged from the cavern. The process was completed in 2 steps by 1st automatically detecting bats in each video frame and 2nd by tracking each detected bat from frame to frame (see Betke et al. 2007, 2008). Bats successfully detected and tracked for a period of time beyond a set threshold value were tallied automatically to estimate the total number of emerging bats.

Use of the detection and tracking algorithms was restricted horizontally to a portion of the original frame size where the behavior of bats was considered optimum for censusing. In most cases the size of the analysis window was adjusted so that all bats appeared in it for 20–30 frames, whereas the tracking threshold, the number of frames in which a bat was tracked before being counted, was set to 10–15 frames (video 1, available online at http://dx.doi.org/10.1644/08-MAMM-A-391R.s1). The number of bats was tallied every minute, producing an emergence rate versus time profile for each night. The sum of the number of bats that emerged in each 1-min interval yielded an estimate of the total colony size. To evaluate the accuracy of the detection and tracking algorithms we systematically selected fourteen 1,000-frame segments from 6 census records to represent a range of emergence rates from approximately 10 to 10,000 bats/min. On average, estimates derived using the computer vision algorithms were within 3.7% of the estimates made by human observers viewing the same segments. The discrepancy between the 2 methods was smaller at lower emergence rates and increased with higher rates. In 8 of the 14 segments the computer vision estimates were higher than the manual counts. In addition, on 3 occasions, simultaneous records of the same emergences by 2 independent thermal recording systems produced an average difference of 2.4%. Based on these results, we conclude that the data reported here are accurate to within ±3.7%. We used Pearson correlation and linear regression to test and describe the relationship between colony size and duration of emergence and between emergence rate and colony size. All analyses were performed in JMP 7.0 (SAS Institute, Cary, North Carolina). Our study followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Gannon et al. 2007) and was approved by Boston University's Animal Care and Use Committee.

Visual simulation.—To evaluate the reliability of early historical estimates we created a visual simulation of emergences from Carlsbad Cavern using different scenarios of emergence rates. We reconstructed a three–dimensional (3D) graphical model of the cavern entrance using parallel survey transects. Standard LRUD (left, right, up, down) distance measurements were collected from each survey point, and the 3D model of the cave entrance was reconstructed using COMPASS, a cave data management software (www.fountainware.com). The model of the cave was imported into Autodesk Maya 8.0, a 3D modeling and visualization software (www.autodesk.com), where bats were simulated using Maya's particle dynamics environment. To reduce the computational load on the simulation, bats were represented as spheres with diameters of 0.28 m, the average wingspan of adult *T. brasiliensis* (Wilkins 1989) and the minimum volume needed for an individual to maintain flapping flight. Initial condition parameters were entered for the cross section of the effective emergence area (~120 m^2), emergence rate, and average flight speed of the emerging column through that narrowest section of the cave (4 m/s). The simulation was run for 60 s under 2 emergence rate conditions: 18,210 bats/min corresponding to the highest emergence rate recorded in 2005 and 546,360 bats/min corresponding to the estimate made in 1936 (Allison 1937). Minimum distance and overlap between the simulated bats were calculated using the size and 3D positions of the bat-modeling spheres in the narrowest section of the cave.

Results

Our results indicate large fluctuations in the number of bats at Carlsbad Cavern on a daily and seasonal basis. Over the sampling period the number of bats in the cave varied from

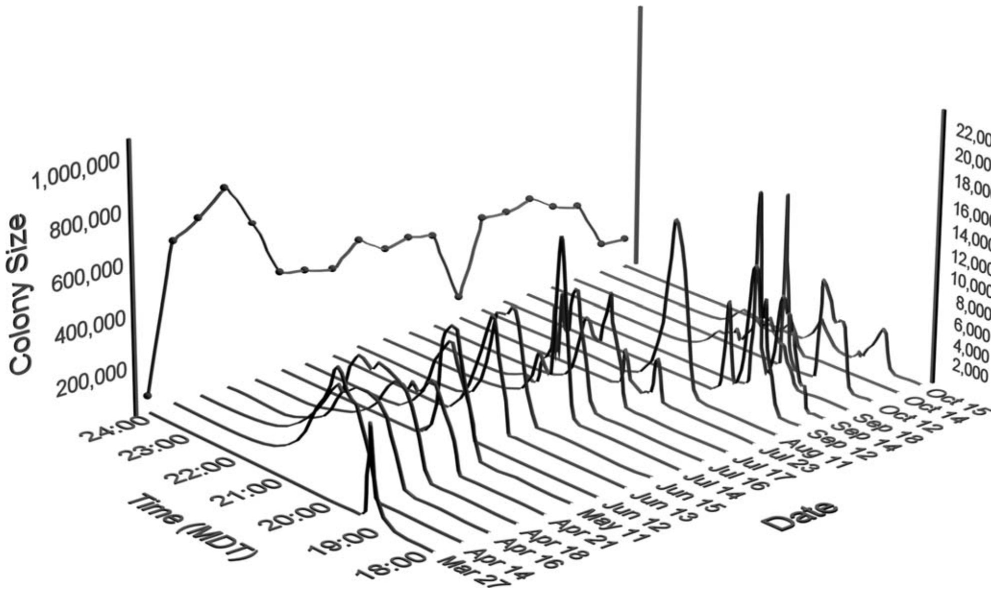

Fig. 1.—Seasonal and nightly changes in colony size, onset, duration, and rate of emergence of Brazilian free-tailed bats (*Tadarida brasiliensis*) at Carlsbad Cavern, New Mexico, based on 20 censuses in 2005 (seasonal axis not to scale).

67,602 to 793,838. The fewest bats (67,602) were recorded in March 2005 before the majority of the colony had arrived. In April 2005 the size of the colony increased sharply to 793,838, the highest count made that season. Following the spring migration period, in May, the colony decreased to 395,168 individuals. In June, when female bats typically give birth, we recorded 346,756–438,551 bats in the cave. The colony remained at the June level until a sharp decrease in size was recorded during the 2nd half of July, when only 74,202 bats were recorded exiting the cavern. By the middle of August the colony increased in size to 381,153 bats, similar to our records in early July. Throughout the rest of the season the number of bats declined. By October we counted <150,000 bats emerging from the cavern (Fig. 1; Table 2).

Multiple census records within the same month point to large daily fluctuations in colony size in 2005. We recorded changes from 40,000 to 291,000 bats within only a few days. For example, between 14 and 21 April the colony increased by approximately 150,000 bats and then decreased by approximately 170,000 bats over 3 days. Similarly, approximately 182,000 fewer bats emerged on 14 October than on 12 October 2005 during fall migration. Most notable, however, was an observed decrease by almost 291,000 bats over a 6-day period in July when the colony was expected to be most stable (Fig. 1; Table 2).

Emergence rates recorded during the nightly out-flights of bats allowed us to reconstruct the emergence profile of the colony during each census attempt (Fig. 1). Our analyses indicate considerable variation in the emergence behavior of the bats. Within the same month, and over the course of the study period, we recorded marked differences in the shape of the emergence profiles, associated with changes in colony size, onset, duration, and rate of emergence (Fig. 1).

The temporal onset of emergence ranged from 1855 to 2025 h (MDT). Daily changes followed a general pattern, where in spring (March–April) and fall (September–October) bats emerged early relative to sunset, whereas in June and July they emerged later. Generally, these changes occurred gradually over the season; however, on 3 occasions (23 July, 18 September, and 15 October) the onset of emergence changed abruptly from the preceding census.

The duration of emergence ranged from 20 to 188 min with a mean ($\pm SD$) of 103 $\pm$ 42 min. We found a significant positive correlation between colony size and duration of emergence ($r = 0.71$, $n = 20$, $P < 0.001$). In general, the larger the colony was, the longer it took for bats to emerge, although on some dates the duration of emergence was independent of colony size (Table 2; Fig. 2).

Nightly peak emergence rates varied between 2,665 and 18,210 bats/min, whereas mean emergence rates ranged from 640 to 5,307 bats/min. Emergence rates above 10,000 bats/min rarely were sustained for more than a few minutes, and in most cases the majority of the colony emerged at a lower rate. In addition, our observations of the behavior of bats during dense emergences indicate that flights at rates above 12,000 bats/min impose a cost. During such dense flights hundreds of bats were forced to land on the cave walls and wait for their turn to emerge. Others were unable to gain elevation due to the dense flight and were trapped in vegetation outside the cave where dozens of them died. These observations lead us to suggest that the maximum possible emergence rate at Carlsbad Cavern is not much greater than the maximum rate of 18,210 bats/min that we recorded in 2005. Notably, the highest emergence rates were not associated with the largest colony size. In April, when the colony was largest, bats emerged over a longer period at a moderate rate. The highest emergence rates were recorded in July and August when the colony numbered approximately 375,000 bats (Table 2; Fig. 1). We found no significant correlation between maximum emergence rate and colony size ($r = 0.30$, $n = 20$, $P = 0.21$). For example, on 12

Table 2.—Census results from the analysis of 20 emergences of Brazilian free-tailed bats (*Tadarida brasiliensis*) at Carlsbad Cavern, New Mexico, in 2005.

Date	Colony size	Emergence onset (h)	Emergence duration (min)	Average rate (bats/min)	Maximum rate (bats/min)
27 March 2005	67,602	1907	20	3,219	8,363
14 April 2005	635,674	1942	161	3,900	10,859
16 April 2005	697,905	1942	188	3,693	8,031
18 April 2005	793,838	1950	160	4,931	10,035
21 April 2005	620,154	1942	173	3,564	7,352
11 May 2005	395,168	1955	79	4,879	12,257
12 June 2005	369,108	2025	102	3,584	9,598
13 June 2005	346,756	2018	89	3,811	12,311
15 June 2005	438,551	2021	94	4,616	11,759
14 July 2005	370,894	2005	95	3,863	16,878
16 July 2005	390,664	2012	109	3,519	10,876
17 July 2005	365,202	2003	93	3,844	10,037
23 July 2005	74,202	1948	114	640	4,146
11 August 2005	381,153	1937	70	5,294	14,008
12 September 2005	376,917	1828	70	5,235	12,872
14 September 2005	403,334	1821	75	5,307	18,210
18 September 2005	333,341	1902	134	2,451	5,698
12 October 2005	308,490	1728	50	2,841	15,834
14 October 2005	126,471	1755	99	1,252	2,665
15 October 2005	117,094	1837	85	744	4,052

and 18 September the colony, although similar in size, exhibited markedly different emergence profiles (Fig. 1). On 12 September 376,917 bats emerged in 70 min with an average emergence rate of 5,235 bats/min and a peak rate of 12,872 bats/min. On 18 September the emergence of 333,341 bats lasted 134 min, and the average and peak emergence rates were 2,451 and 5,698 bats/min.

A simulated emergence of the colony through a constricted section of the cavern at 18,210 bats/min compared favorably to our observations of the flight pattern and density of bats during the highest emergence rates in 2005 (video 2, available online at http://dx.doi.org/10.1644/08-MAMM-A-391R.s2). However, at a rate of 546,360 bats/min, as derived from a 1936 estimate by Allison (1937), the assumptions of the simulation were grossly violated. The average distance between adjacent simulated bats was 0.12 m (n = 95,613

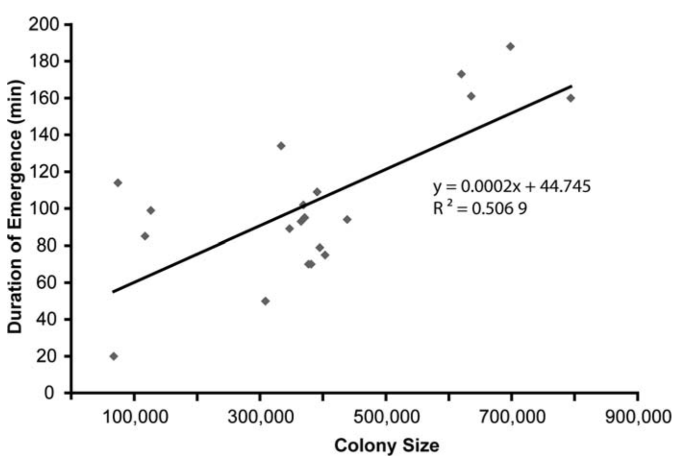

Fig. 2.—Regression of colony size on duration of emergence in Brazilian free-tailed bats (*Tadarida brasiliensis*) at Carlsbad Cavern, New Mexico, in 2005.

generated particles), resulting in an average overlap of 40% between the spheres of modeled bats (Fig. 3; video 3, available online at http://dx.doi.org/10.1644/08-MAMM-A-391R.s3). We found no overlap between adjacent bats when the average distance between them was equal to their wingspan (0.28 m). The emergence rate in this case was 240,000 bats/min.

Discussion

We demonstrated that the size of the bat colony at Carlsbad Cavern is highly variable on a seasonal and daily basis. Factors that influence the number of bats and their emergence behavior are not entirely clear, thus making predictions and forecasts difficult; nevertheless, the frequency and accuracy of our measurements indicate that these fluctuations are not a by-product of uncertain population estimates and sampling bias but rather a reflection of the complex colony dynamics of this species.

Seasonal variation in colony size at Carlsbad Cavern has been reported previously (Constantine 1967a; Route et al. 1998). However, these studies did not detect or predict daily variations as reported in the present study. The numbers most frequently quoted from these studies are the low seasonal estimates that often are cited as indicators of declining colony size (e.g., Altenbach et al. 1979; McCracken 2003; Route et al. 1998). In light of the pronounced changes in colony size recorded in 2005, we suggest that such fluctuations represent natural responses of the colony to factors such as seasonal food availability and local and large-scale weather patterns. Thus, a small colony size on a given night does not necessarily indicate a long-term decline any more than a large size suggests population increase. Rather, both are likely manifestations of seasonal responses to changing environmental conditions.

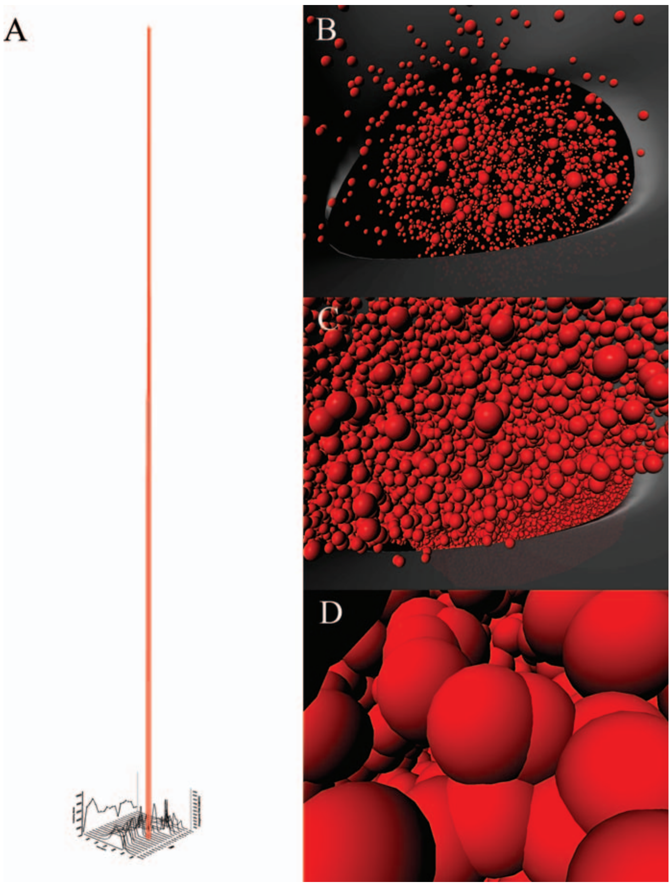

Fig. 3.—A) Comparison of emergence rate at Carlsbad Cavern, New Mexico, based on the single visual estimate of 546,360 bats/min (Allison 1937) and our estimates from thermal infrared imaging of Brazilian free-tailed bats (*Tadarida brasiliensis*) in 2005, shown in Fig. 1. B–D) Three-dimensional simulation models depicting emergence of Brazilian free-tailed bats based on B) our estimate of 18,210 bats/min—the highest we recorded in 2005, C) Allison's estimate of 546,360 bats per minute, and D) a close-up of the image modeled in C), showing overlapping spheres (simulated space for each emerging bat), suggesting that Allison's estimate is highly improbable. See text for a description of parameters used to model these estimates.

Within the same year we recorded the largest and smallest colony sizes dating back to estimates in the mid-1950s (Constantine 1967a). This variation is likely explained by specific weather patterns before and during our study (Fig. 4). The unusually wet fall of 2004 brought 635 mm of rain, 254 mm (www.met.utah.edu; Station ID BATN5 at Carlsbad Caverns National Park) above the annual average, which in the spring of 2005 transformed the Chihuahuan desert, over which the bats feed, into a lush and insect-rich landscape. We attribute the unusually large colony sizes recorded in April 2005 to the temporary presence of migrating bats exploiting the abundant food resource in the area. Constantine (1967a) reported recapturing bats during spring migration that had been banded at Carlsbad Cavern, >1,000 linear km away. The large fluctuation in estimates on consecutive days in April 2005 supports these observations and further suggests that bats arrive and depart in large groups.

By mid-July 2005 the dry and hot summer, and its effect on insect availability, is the most likely reason for the sudden decrease in colony size from 19 to 23 July when nearly 300,000 bats abandoned the cave until the arrival of monsoon rains 2 weeks later (Fig. 4). In the 8 weeks before 23 July only 25 of the average 112 mm of rain had fallen during an especially dry summer, with a total rainfall of only 117 mm compared to an average of 305 mm (www.met.utah.edu). We did not collect insect abundance data as part of our study; however, the effect of weather on insect population dynamics has been well documented (Bradford and Holyoak 1998; Lawton 1995; Tilman and El Haddi 1992; Wigly 1985). The arrival of the North American monsoons in late summer has a profound effect on the increased abundance of arthropods and especially Lepidoptera (Lee and McCracken 2005; Mackay et al. 1986; Schowalter et al. 1999). At Carlsbad Cavern, long, dry spells may force large numbers of bats to move their roosts closer to water with easier access to food (J. C. Werker and V. Hildreth-Werker, National Speleological Society, pers. comm.). We suggest that the harsh conditions of the summer and related low insect abundance forced females to advance weaning and abandon the cave with volant juveniles. The remaining 74,202 bats were likely adult males or females with nonvolant juveniles.

Highlighted by these 2 events, the overall seasonal pattern in 2005 is different from the pattern reported by Constantine (1967a) but is consistent with observations in 1996 and 1997 by Route et al. (1998). On average, the colony was largest in the spring and decreased in size during fall. We did not record an increase in numbers in the fall as reported by Constantine (1967a). Moreover, we observed no significant increase in numbers when juvenile bats became volant in late July and August, results that are consistent with observations at other colonies of Brazilian free-tailed bats in Texas (N. I. Hristov and T. H. Kunz, pers. obs.) and supporting the suggestion that adult females leave maternity colonies after weaning their young, and that most emerging bats after this period are young-of-the-year or migrants from other sites (Kunz and Anthony 1996).

The existence of large fluctuations in colony size at Carlsbad Cavern has important implications for the interpretation of historical records and the inference of long-term declines. Our study indicates that single estimates not reliable indicators of colony size and patterns of change for this species. Because of incomplete records it is not possible to determine the seasonal and daily cycles of this colony historically. However, using our estimates are of emergence rates, duration, and our simulation results, we can reexamine the claim by Allison (1937) that millions of bats once roosted and emerged from Carlsbad Cavern.

Allison (1937) described that on 16 June 1936 the evening emergence lasted 14 min in full force and 4 min at half force. He assumed that the column of emerging bats was cylindrical in shape with a diameter of 6 m (approximately 29 m^2) and moving at a rate of 8.8 m/s. His critical assumption was that each cubic foot (0.028 m^3) of space within the column was occupied by a single bat. Based on these assumptions, 9,106

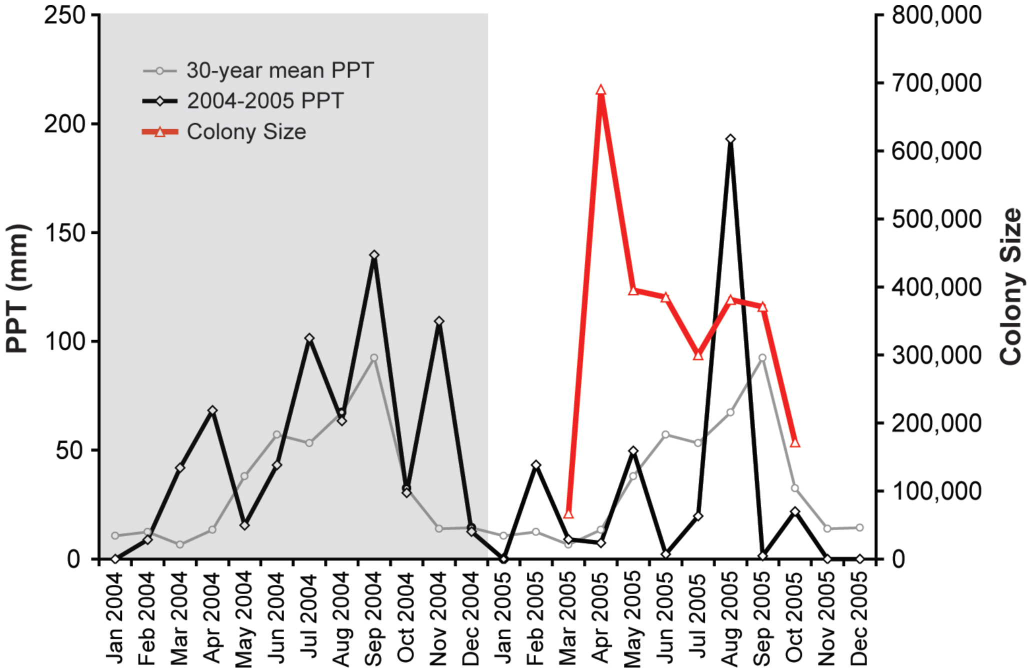

FIG. 4.—Comparison of 2004 and 2005 precipitation levels (PPT) versus 30-year mean (1971–2000) and colony size of Brazilian free-tailed bats (*Tadarida brasiliensis*) at Carlsbad Cavern, New Mexico, in 2005.

bats would have flown past an observer each second and over the course of the 14-min full-force emergence, 7,649,040 were estimated to have emerged from the cave. Using the same assumptions and half of the 9,106 bats per second estimate, he calculated that 1,092,720 bats emerged in the 2nd, less-dense 4-min period of the emergence, yielding an estimated total of 8,741,760 bats that emerged on 16 June 1936.

Our analyses of emergence behavior and flight dynamics of Brazilian free-tailed bats at Carlsbad Cavern raise questions about the validity of Allison's assumptions and ultimately his estimated number of bats. His estimates lead to an emergence rate of more than 500,000 bats/min during the full force of the emergence and more than 250,000 bats/min during the less dense part of the emergence. These estimates are nearly 2 orders of magnitude greater than the average emergence rates that we report. We found that in 2005 average emergence rates never exceeded 10,000 bats/min and peak recorded rates were never $>$ 20,000 bats/min. More important, these maximum rates occurred for short durations and accounted for a small proportion of the overall emergences. Given that duration of emergence and colony size are positively correlated, the emergence of 8.7 million bats in $<$20 min clearly deviates from this relationship. We argue that it is highly unlikely that the bats at Carlsbad Cavern emerged at the rates estimated by Allison for the following reasons. The cross section of the main natural entrance of this cavern is 204 m^2. However, 50 m inside the cavern the passage narrows to a considerably smaller cross section of only 120 m^2. To emerge, bats must pass through this constricted passage, which is one of several factors limiting the maximum emergence rate. The effective cross-sectional area of the column is even smaller because the bats do not use all of the available space to emerge but rather appear to leave at least 30% of the cross-sectional area for returning if conditions do not allow all bats to emerge at the same time. The emergence density of the column is limited further by the aerodynamic constraints of flight in groups, which dictate distances far larger than the minimum, physically possible, distance between 2 adjacent bats (Han and Mason 2005; Hedenström et al. 2007; Lissaman and Schollenberger 1970). The results of our simulations strongly suggest that these conditions do not permit more than 50,000 bats/min to emerge. Based on these arguments we suggest that 8.7 million is an extreme overestimate and does not represent the true number of bats in Carlsbad Cavern on 16 June 1936. Given the known duration of the emergence flight, maximum observed emergence rates, and the results of our simulations, a colony size of $<$1,000,000 is likely closer to the actual number of bats in the cavern at that time.

Questions about the reliability of Allison's estimate have been raised in the past. Using park records from 1936, Roemer (1996) showed that park rangers at the time classified the emergence of bats as being either ''good,'' ''fair,'' ''poor,'' or ''none.'' Most of the flights in that year were classified as poor, and as it happened, Allison made his observation on one of the few good nights, following 2 days of rain. The specific weather pattern at the time of Allison's observation is of particular importance. As was the case in 2005, the onset of emergence of Brazilian free-tailed bats is generally consistent from night to night but can vary by as much as 30–45 min on occasions (Lee and McCracken 2001). Little clear evidence exists for the cause of this variation. In our experience, periods of inclement weather are followed by relatively early, short, and unusually dense emergences on the 1st evening of good weather when bats have an opportunity to forage again. An unusually high density of the emergence of bats on 16 June 1936 might have been the reason for Allison's incorrect estimate of colony size. His estimate of flight speed and density of emergence, in particular, are higher than measured speed and density values for this location. Human numerical estimates can be distorted severely by objects with high numerical abundance and density, complex spatial configuration, and low background separation (Caughley 1974; Indow and Ida 1977; Krueger 1972; Miller and Baker 1968). These conditions characterize emergences of Brazilian free-tailed bats, making visual estimates of colony size difficult and likely inaccurate.

By the 1970s estimates of the size of the bat colony at Carlsbad Cavern appeared to drop well below earlier estimates, suggesting a drastic decline (Altenbach et al. 1979; Geluso et al. 1987; Route et al. 1998). One explanation for this trend is an actual decline in the number of bats over the intervening years. More likely, however, is that by this time better census methods provided more accurate estimates of colony size. Given the uncertainty of early estimates, the presumed decline at Carlsbad Cavern might be smaller in magnitude than previously suggested. Moreover, banding studies demonstrate that individuals can roost and sometimes move to different sites between and within years (Cockrum 1969; Constantine 1967a; Glass 1982). In addition, studies of the population genetic structure suggest that colonies in North America belong to the same large, presumably panmictic population (McCracken and Gassel 1997; McCracken et al. 1994; Russell and McCracken 2006). Thus, given the complex temporal and geographic behavior of this species, it is not clear to what extent a decrease in numbers in individual colonies indicates a decline for the entire species, because changes in numbers at one location could be compensated for by changes in another. Therefore, our understanding of the presence and magnitude of a decline at this and other colonies will depend on the correct interpretation of historical information, when it is available, and the accumulation of accurate, baseline data for the current colony size that incorporate long-term seasonal and large-scale observations.

The combination of thermal infrared imaging and computer vision analysis provides an effective method for estimating colony size and emergence behavior of Brazilian free-tailed bats. In addition, early estimates of colony size were likely inflated, and at least part of the declines reported for this species are based on faulty assumptions. Moreover, our results support the findings of Betke et al. (2008) that not as many Brazilian free-tailed bats exist in the southern United States as previously suggested. Reliable estimates of colony size are critical for evaluating the natural and anthropogenic forces that can affect current and future population trends for this and other bat species.

Resumen

La colonia de murciélagos guaneros (*Tadarida brasiliensis*) en Carlsbad Cavern es un conocido ejemplo de una especie altamente gregaria y conspicua en América del Norte. Durante casi un siglo, los investigadores han tratado de estimar el tamaño poblacional de ésta colonia, sin embargo, los diferentes métodos de estimación y la falta de repetibilidad, han dado como resultado estimaciones poco confiables que conllevan a un mal entendido pero altamente aceptado conocimiento de la tendencia población a largo plazo de ésta especie migratoria. En éste estudio presentamos estimaciones estacionales del tamaño de la colonia basadas en un método de estimación poblacional recientemente desarrollado - imágenes térmicas infrarrojas y análisis visual por computadora. El tamaño de la colonia se estimó mensualmente varias veces desde marzo hasta octubre de 2005. Nuestras estimaciones oscilan entre 67,602 y 793,838 murciélagos, valores que son órdenes de magnitud inferiores a las estimaciones históricas mas altas. Estimaciones consecutivas de la salida de los murciélagos de la cueva muestran fluctuaciones de hasta 291,000 individuos, indicando que la composición de la colonia es considerablemente más dinámica de lo que se pensaba. Los resultados, combinados con un análisis cuantitativo del comportamiento de salida, cuestionan la validez de las primeras estimaciones históricas donde millones de murciélagos se refugiaban en esta cueva y sugieren que el patrón a largo plazo del descenso poblacional reportado para esta especie, podría no ser tan grave como se pensaba.

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Supporting Information

Supporting information S1.— Thermal image sequence of emerging bats showing the application of automatic object detection and tracking algorithms.
Found at DOI: 10.1644/08-MAMM-A-391R.s1.
Supporting information S2.— Three-dimensional simulation of the emergence of bats at Carlsbad Caverns at a rate of 18,210 bats per minute — the highest recorded in 2005.
Found at DOI: 10.1644/08-MAMM-A-391R.s2.
Supporting information S3.— Three-dimensional simulation of the emergence at a rate of 546,360 bats per minute, estimated by Allison in 1937.
Found at DOI: 10.1644/08-MAMM-A-391R.s3.

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