



Thermal Imaging Reveals Significantly Smaller Brazilian Free-Tailed Bat Colonies Than Previously Estimated

Authors: Betke, Margrit, Hirsh, Diane E., Makris, Nicholas C., McCracken, Gary F., Procopio, Marianne, et al.

Source: Journal of Mammalogy, 89(1) : 18-24

Published By: American Society of Mammalogists

URL: <https://doi.org/10.1644/07-MAMM-A-011.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

THERMAL IMAGING REVEALS SIGNIFICANTLY SMALLER BRAZILIAN FREE-TAILED BAT COLONIES THAN PREVIOUSLY ESTIMATED

MARGRIT BETKE,* DIANE E. HIRSH, NICHOLAS C. MAKRIS, GARY F. MCCrackEN, MARIANNE PROCOPIO, NICKOLAY I. HRISTOV, SHUANG TANG, ANGSUMAN BAGCHI, JONATHAN D. REICHARD, JASON W. HORN, STEPHEN CRAMPTON, CUTLER J. CLEVELAND, AND THOMAS H. KUNZ

Department of Computer Science, Boston University, Boston, MA 02215, USA (MB, DEH, MP, ST, AB, SC)

Department of Mechanical Engineering, Massachusetts Institute of Technology, Cambridge, MA 02139, USA (NCM)

Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA (GFM)

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

Department of Geography and Environment, Boston, MA 02215, USA (CJC)

Using data collected with thermal imaging technology, we found a major reduction in population estimates of colony size in the Brazilian free-tailed bat (*Tadarida brasiliensis*) from 54 million, obtained in 1957 without this technology, to 4 million in 6 major cave colonies in the southwestern United States. The 1957 census was based on human visual observations of cave emergence flights that were subject to potentially high errors. The recent census was produced using an accurate, reproducible counting method and based on complete temporal records of colony emergences. Analysis of emergence flights from dusk through darkness also revealed patterns in group behavior that would be difficult to capture without thermal infrared technology. Flow patterns of bats during emergence flights exhibited characteristic single, double, or triple episodes, with the peak flow during the 1st episode. A consistent rhythmic pattern of flow episodes and pauses was revealed across colonies and was independent of emergence tempo.

Key words: bats, censusing, detection, group behavior, image analysis, population estimate, thermal infrared imaging, tracking

The Brazilian free-tailed bat (*Tadarida brasiliensis*) is a seemingly abundant migratory species, forming colonies that may be the largest aggregations of mammals in the world (McCracken 2003). It is a predator of the moth *Helicoverpa zea*, one of the most destructive agricultural pest species in North America (Cleveland et al. 2006), and thus a decline in population size may lead to increased use of pesticides, which could have detrimental consequences for the environment, economy, and human health. This species likely has a central role in “continental-scale” ecological processes (Cleveland et al. 2006), providing incentive to understand its current population size.

We report the results of censuses taken of Brazilian free-tailed bat colonies at 8 caves conducted between 2000 and

2006. Six of these colonies are considered to be among the 11 largest colonies of this species in North America (McCracken 2003). The combined population estimate of 4 million bats is more than an order of magnitude lower than the number of bats, 54 million, estimated to have roosted in the same 6 caves in the summer of 1957 (Constantine 1967; Davis et al. 1962).

Our estimate was produced with an image analysis method that we developed to detect and track bats in video records of cave emergence flights. We obtained the video records using thermal imaging, which is ideally suited for censusing nocturnal homeothermic animals (Frank et al. 2003; Sabol and Hudson 1995). Previous censusing approaches were limited by low ambient light conditions during the later part of the emergence period (Altenbach 1988; McCracken 2003). They included trapping methods, visual assessment by observers positioned near cave entrances, or retrospective analysis of photographs or videos, recorded without thermal imaging technology.

Qualitative visual inspection of emergence counts at cave entrances in the past may have resulted in serious censusing errors. Davis et al. (1962) provided most of the historic population

* Correspondent: betke@cs.bu.edu

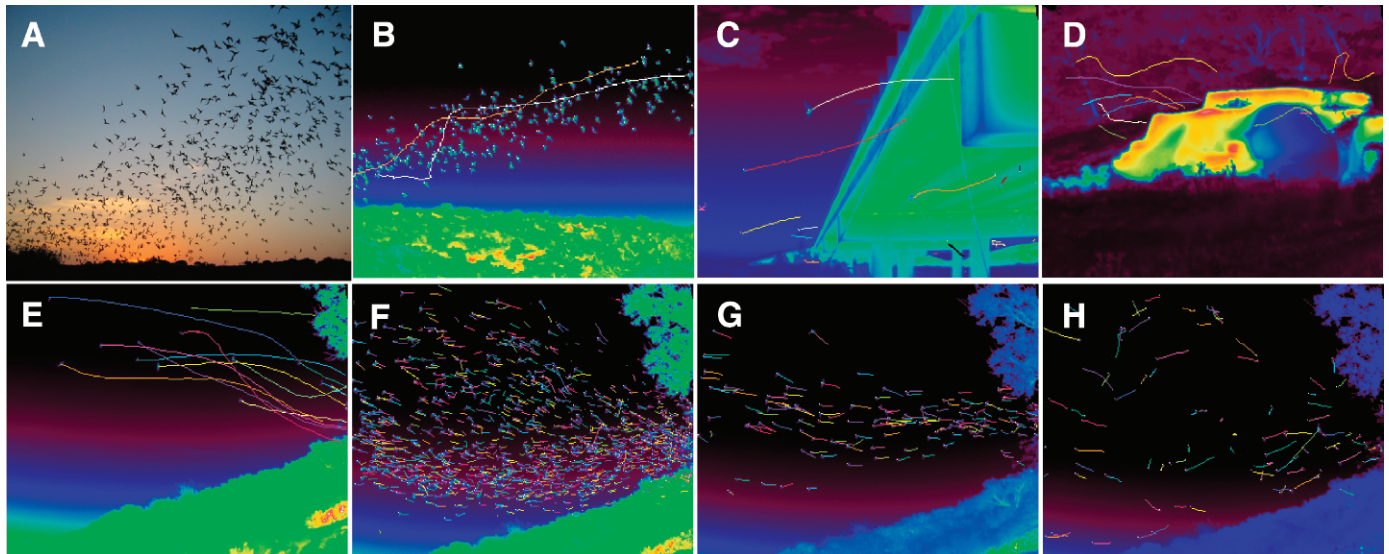


FIG. 1.—Brazilian free-tailed bats (*Tadarida brasiliensis*) emerging from roosts at A) Frio Cave, B) Eckert James River Cave, C) Seco Creek Bridge, D) Selah Chiropterium, and E–H) Davis Cave. Bats detected in thermal images and their automatically tracked flight paths are shown in B–H. Emergence and foraging situations were automatically distinguished by evaluating the angular deviation of detected flight paths from the average projected direction of flight. The deviation was small during emergence flights (B–G) and high during foraging (H). The length of the colored trails in frames E–H corresponds to 1 s, 1/60 s, 1/30 s, and 5/30 s of the bats' flight paths. Frames are shown at the beginning of the emergence (E) with 12 bats (17° deviation), at the 1st emergence peak (F) with 698 bats (25° deviation), at the 2nd emergence peak (G) with 135 bats (27° deviation), and during foraging (H) with 48 bats (75° deviation). Vegetation and sky were cooling down during the evening of recording at Davis Cave and slowly appeared darker (E–H).

estimates (13 colonies) but cautioned that their estimates should serve for relative comparisons only. We suggest that much of the order-of-magnitude difference between current and historic census estimates could be due to overestimation of colony sizes in 1957. Nonetheless, the decrease we found also may be explained by a population decline or shift.

We begin by describing our image analysis method, its accuracy, and how we assessed the accuracy of historic estimates. Our image analysis method also enabled us to investigate group behavior of bats during emergence and foraging flights. We describe the discovery of a characteristic rhythm of flow episodes and pauses in emergence. We then report our current estimates and make a projection for the total midsummer cave population of the Brazilian free-tailed bat in the southwestern United States.

MATERIALS AND METHODS

Video recording.—We used Merlin Mid infrared cameras (Indigo Systems, Goleta, California) that store thermal data as 12-bit intensity values in 320×240 digital video images directly onto computer hard drives at video rates of up to 60 frames per second. For most censuses, we placed a single camera with a 25-mm lens outside cave entrances so that, during emergence, bats flew across the field of view, approximately perpendicular to the camera's optical axis (Figs. 1 and 2, video 1, available at <http://www.cs.bu.edu/faculty/betke/videos/bats1.avi>). In some instances, the bats emerged from more than 1 entrance or markedly changed flight direction during the emergence period. Under these conditions, we used 2 or 3 cameras to ensure a complete emergence record (e.g., 3 cameras at Bracken Cave).

Image analysis method.—Our method tracked each bat that emerged from the cave as it flew through the field of view of the camera (video 2, available at <http://www.cs.bu.edu/faculty/betke/videos/bats2.avi>). The method was successfully applied under a wide range of field conditions when it could be ensured that the apparent size of the bats in the images was sufficient (a few pixels) and the apparent density and range of size were small enough so that bats occluded each other only briefly (at most a few frames). If these conditions could not be met during a recording, another censusing attempt was made with a different camera setup the following evening.

To automatically detect bats from the thermal imaging data, our method analyzed the intensity profile of clusters of bright pixels, ranging from a few bright pixels to several hundred. Clusters in which the warm vegetation appeared had relatively flat intensity profiles. Clusters of bright pixels formed by bats contained high-intensity values that corresponded to the warm thorax of bats and lower-intensity values that corresponded to their cooler parts such as wings. The number of intensity peaks contained in a cluster of bright pixels was therefore used to estimate the number of bats represented in the cluster. To find clusters of bright pixels, we could not simply use a fixed intensity threshold. Distant bats had lower intensity values than close bats, and these lower values also could be found in image regions in which bats did not appear (e.g., the sky near vegetation). Thus, we developed an adaptive filtering method that built a dynamical model of the intensity values measured at each pixel over time (Hirsh 2004). With this model, the current value of a pixel could be compared to the mean and standard deviation of recently measured values. A difference between

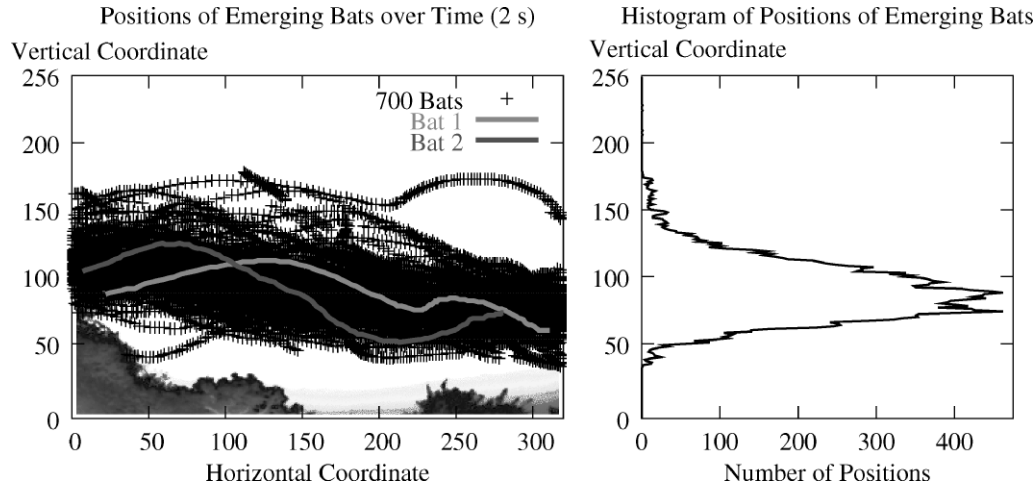


FIG. 2.—Analysis of flight paths of 700 Brazilian free-tailed bats (*Tadarida brasiliensis*) emerging from Davis Cave on 4 July 2004. Left) The positions (crosses) of bats detected in 2 s are shown overlaid onto a thermal infrared image of the scene. The sinusoidal paths of 2 bats are highlighted. Right) A histogram of the vertical coordinates of the positions shown on the left was generated by counting the number of times each bat was in a particular vertical position during the 2 s, regardless of its horizontal position.

the current and mean values that was larger than a fraction of the standard deviation indicated that a bat appeared at that pixel. Smaller differences were caused by noise from the camera or other changes in the environment such as moving vegetation or clouds.

Tracking was accomplished by recursive Bayesian filtering (Betke et al. 2007). Each bat was tracked by estimating its position in the current frame from its position in previous frames. The algorithm assigned observations of bats, detected in the current frame, to previously established tracks in an efficient manner. This data-association algorithm significantly pruned the large number of possible observation-to-track assignments with the technique of gating. Gating restricts the algorithm to consider only those observations that are close to the predicted position of a bat. As a result, the computational complexity of the tracking process was linear in the number of observations.

With the combined detection, tracking, and data-association methods, we were able to detect and track hundreds of bats simultaneously and evaluate multiple-track hypotheses automatically when track crossings and occlusions occurred. The average processing rate of the combined image analysis method was 10.8 Hz.

Accuracy of video analysis.—For each data set for which we provided a colony census (Table 1), we verified the accuracy of the image analysis method by manually detecting and tracking bats in the video record to establish their “true” flight paths. We implemented a video-marking tool to simplify this laborious process.

For the Selah Chiroptorium colony (3 July 2004), we were able to compare the census based on our “ground truth” inspection of the entire video record with the census computed by the image analysis method. The output of our method, 7,056 tracked bats, compares favorably with the manual estimate of 7,007 bats—a difference of only 0.78% (Betke et al. 2007). For large colonies, we tested the accuracy of the tracking component of our method by checking representative samples

of at least 200 flight paths per data set. We chose the samples systematically in each video record. The number of bats automatically detected in a fragment of a video was divided by the number of frames in which a manually tracked bat appeared in this fragment. We then summed the ratios that were computed for each video fragment in this manner to obtain a total census. This semiautomatic method and our automatic census method provided consistent results when applied to the same data sets, with an average census difference of only 3.2%, and a maximum difference of 7%. Thus, we estimate that the censuses data reported here are accurate within $\pm 7\%$.

To evaluate the accuracy of the detection component of our census method, we compared bats-per-frame estimates with estimates made by 5 independent human volunteers with expertise in image analysis. We systematically chose 27 frames, approximately 5 min apart (every 5,000 frames), from the 2.5-h emergence video collected at Frio Cave on 26 June 2000 and asked the observers to take as much time as they needed to estimate the number of bats in each frame. None of the observers knew the estimates of the other observers—or the estimate of our census method. Over all sample frames, the observers identified an average of 4,181 bats and the detection algorithm identified 4,215 bats. The difference between these 2 estimates is only 0.8% of the average observer count. The minimum and maximum numbers of bats identified by the observers were 3,498 and 4,882, respectively. The minimum observer count was 14.3% smaller than the average observer estimate and the maximum observer count was 16.8% larger than the average observer estimate. Thus, because the differences between extreme and average observer estimates were much larger than the difference between the estimate derived from the detection algorithm and the average observer estimate, we conclude that an estimate by the detection algorithm was at least as reliable as an estimate by a human observer.

Our procedures followed the guidelines of the American Society of Mammalogists for the use of wild mammals in

TABLE 1.—Census results obtained by analysis of emergence videos of 8 cave colonies in the United States.

Cave	Date	Length of emergence period (h)	No. emergence episodes	Peak flow rates (bats/min)	No. tracked bats
Bracken ^a	7 Jun. 2006	2:04	3	31,319	464,890
Carlsbad	11 Aug. 2005	1:10	1	11,956	341,026
Chiroptorium	2 Jul. 2004	0:03	1	889	7,056
Davis	16 Jul. 2004	1:26	3	36,483	431,205
Eckert James River	29 Jun. 2000	2:05	2	14,115	591,386
Eckert James River	25 Jul. 2004	2:15	2	25,749	1,312,027
Frio	26 Jun. 2000	2:11	3	28,945	653,845
Frio	25 Jun. 2001	2:20	1	24,082	1,008,796
Lava Beds	10 Jul. 2003	0:29	1	10,668	95,325
Ney ^a	10 Jun. 2004	1:13	1	6,237	219,721
Ney	30 Jun. 2005	1:31	3	33,151	397,846

^a The colonies at Bracken and Ney caves may not have fully formed in early June. Intra-seasonal variations in colony size can be expected.

research (Gannon et al. 2007) and were approved by Boston University's Animal Care and Use Committee.

RESULTS

Current and historic census estimates.—We conducted 9 censuses between 2000 and 2006 of colonies at Bracken, Davis, Eckert James River, Frio, and Ney caves in Texas and Carlsbad Caverns in New Mexico, which are considered to be among the 11 largest colonies in North America (McCracken 2003; Table 1). We compared historic and recent estimates of the number of bats in these colonies (Fig. 3). We found an

order-of-magnitude reduction from the combined census of 54 million bats estimated to have roosted in the 6 caves in the summer of 1957 (Constantine 1967; Davis et al. 1962) to our combined census of 4 million bats. The observed decrease may be explained by a population decline, a population shift, and/or an overestimate of the population in 1957.

Accuracy of historic estimates.—Before imaging technology became available to census bat colonies, emergence counts at caves were performed by qualitative visual assessment by observers positioned near cave entrances. Observers monitoring a column of emerging bats estimated the average density (i.e., number of bats per unit volume), the volume of a unit cross section, the exit speed of an individual bat, and the durations of the emergence episodes (Allison 1937; Davis et al. 1962). For a typical cave, Davis et al. (1962) reported exit speeds of 8.9–15.6 m/s and column densities of 200–500 bats in a 30-cm-wide cross section of the column. Using the lower values, 8.9 m/s and 200 bats per cross section, we computed a flow rate of 5,933 bats/s or 355,980 bats/min. This number and the even higher estimate of average flow rate provided by Allison (1937), 546,360 bats/min, are an order of magnitude higher than the highest flow rate we observed with thermal infrared technology, 36,483 bats/min (Table 1).

Using the estimated flow rate of 355,980 bats/min, we established that 21.4 million bats would have emerged during a 1-h period from the typical cave that Davis et al. (1962) described. Davis et al. (1962) also reported emergence durations of several hours, with the 1st episode lasting nearly to the end of the 2nd hour. In this case, almost 42.8 million bats would have emerged from the typical cave during the 1st episode. This number is more than twice the largest colony size estimated by Davis et al. (1962)—20 million bats at Bracken Cave. This lack of consistency may be explained by the additional methods that Davis et al. (1962) used to estimate colony sizes. They combined their estimates based on emergence counts with estimates derived from capture rates and estimated roost densities.

Overestimation of column density seems to be a plausible explanation for the order-of-magnitude difference between historic and current estimates of average flow rates. For example, if a human observer underestimated the length scale between closely packed bats in a rapidly undulating column by 50%, the

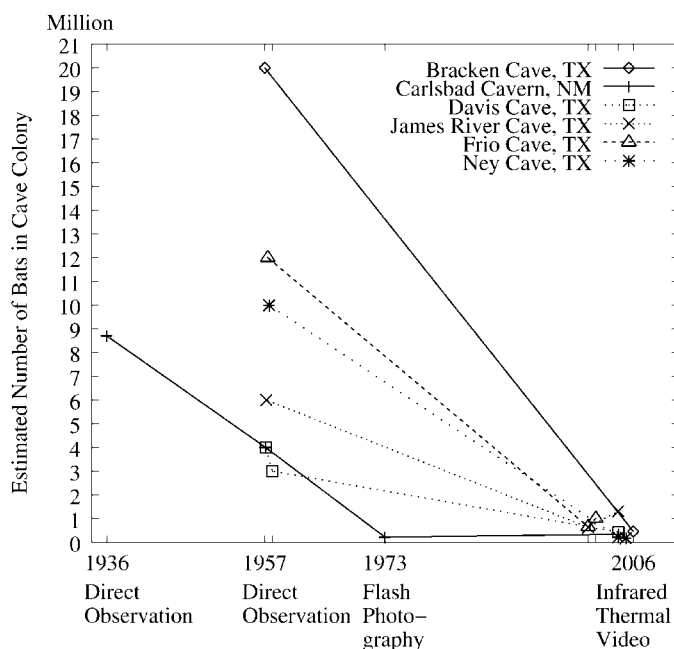


FIG. 3.—Historic and recent estimates of the number of bats (*Tadarida brasiliensis*) at 6 major roost sites in Texas and New Mexico. Estimates of colony sizes in 1936 and 1957 were based on observations of emergence flights (Allison 1937; Davis et al. 1962) and roost densities (Constantine 1967; Davis et al. 1962). The census estimate of the 1973 colony at Carlsbad Caverns was obtained with flash photography (McCracken 2003). The average reported size of a cave colony was 9 million bats in 1957 and 0.6 million bats in 2000–2006.

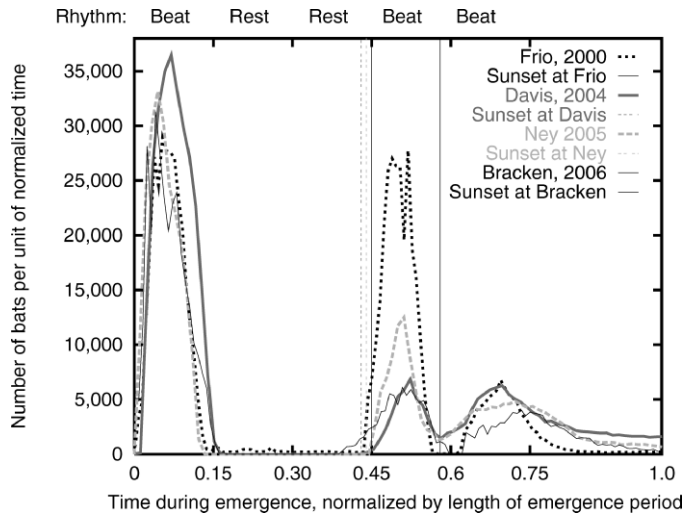


FIG. 4.—The number of bats (*Tadarida brasiliensis*) tracked during triple-episode emergences at 4 caves shows a similar pattern when the time axis is normalized by the respective durations of emergence (the duration range was 86–131 min). On this normalized axis, the episode durations and peaks approximately coincide for all 4 caves, showing a characteristic rhythm of “beat, rest, rest, beat, beat.” Sunset time coincided with the beginning of the 2nd or 3rd emergence episode. The strongest flow of bats occurred during episodes before sunset.

corresponding overestimate in density would be 337%. Thus, a colony estimated to consist of 10 million bats may in fact only total 3 million individuals.

To evaluate the hypothesis that historic estimates were indeed overestimates, we conducted an experiment that evaluated how difficult it may be to estimate colony size based on visual assessment and a clock alone. We asked 16 volunteers (11 scientists and 5 nonscientists) to estimate the number of emerging bats in a 1-min infrared video recorded at Davis Cave during a dense emergence episode. We ensured that the volunteers did not see any still images, which would have simplified estimation of column density, and did not know the estimate computed by our image analysis method. The volunteers provided a median estimate of 6,000 bats/min, a mean estimate of 11,420 bats/min, and a large standard deviation of 11,398 bats/min. (Mean and standard deviation of the estimates of scientists were lower than those of the nonscientists.) Our automated image analysis provided an estimate of 19,367 bats/min, whose accuracy we verified by frame-by-frame inspection of representative flight paths. Thus, among the 16 volunteers, 3 overestimated and 13 underestimated the number of bats in the 1-min video. This result weakens the hypothesis that historic estimates were overestimates.

Emergence patterns.—Analysis of the flow of bats during complete emergence periods revealed patterns independent of the location or size of the colony. These patterns involved single, double, or triple emergence episodes with the peak flow during the 1st episode. In triple-episode emergences, the observed duration of an episode ranged from 12 to 22 min. The 1st and 2nd episodes were separated by a pause in activity, whereas the 2nd and 3rd episodes followed in succession, with no marked

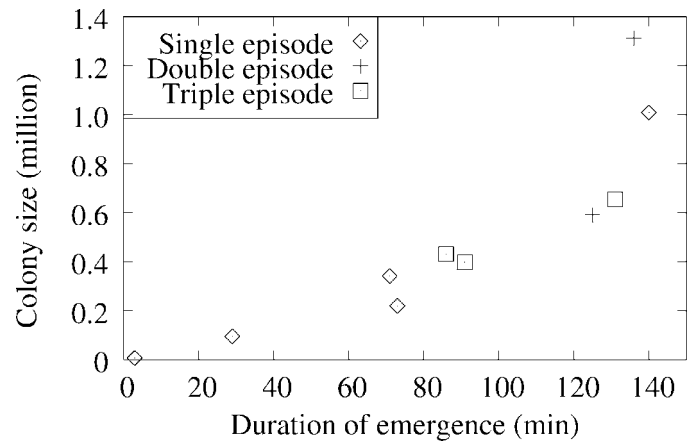


FIG. 5.—Eleven colonies of Brazilian free-tailed bats (*Tadarida brasiliensis*) with single- (5), double- (2), or triple-episode (4) emergences. Colony size is plotted against duration of emergence.

intervening pause between them (Fig. 4). For a given emergence, the duration of the 1st and 2nd episodes was approximately equal and the duration of the pause was approximately twice as long as each emergence period. Triple-episode emergences thus seem to have a characteristic rhythm that corresponds to a strong initial beat, a 2-beat rest, and 2 more beats. This natural rhythm of flow episodes and pauses appeared to be independent of the emergence tempo. This phenomenon was observed by plotting the number of emerging bats per unit of time for each colony against a time axis that was normalized by the respective durations of emergence.

Regardless of the overall size of the colony, the peak of the 1st episode occurred during the 1st quarter of the emergence period. The 2nd peak occurred during the middle of the emergence period and the 3rd after 71% of the emergence time had passed. The length of the single- or multipisode emergence period increased nonlinearly with colony size (Fig. 5). The tempo of emergence decreased with colony size.

Estimation of current population size.—The nightly emergence of bats from their roost sites can be detected in NEXRAD Doppler radar images used for weather forecasting. This imagery has been used to identify major colonies and to compare relative colony sizes (Cleveland et al. 2006). The data corroborate that Bracken, Davis, Eckert James River, Frio, and Ney caves and Carlsbad Caverns are roosts with major colonies. The combined census data obtained from the 6 colonies, 4 million, was divided by 54 million, the number of bats that was estimated to roost in the same 6 caves in the summer of 1957 (McCracken 2003). We multiplied this ratio, 0.07, by the historic censuses of 9 other colonies in the southwestern United States to project their current sizes (Table 2). We made this projection under the assumption that the same decline or overestimate occurred at these 9 caves as we have measured for the 6 caves we censused. The sum of the projected censuses and additional information from 3 other caves, Eagle Creek Cave, Valdina Sink Hole, and Reed Bat Cave, is 5 million (Table 2). Combining this projection with our 4-million census data yields a projection of 9 million bats for the total midsummer cave

TABLE 2.—Estimates of sizes of Brazilian free-tailed bat (*Tadarida brasiliensis*) colonies in the southwestern United States. The historic estimates of the colony sizes of 12 caves were reported by McCracken (2003). We computed projected estimates under the assumption that the same decline or overestimate occurred at these caves than the decline or overestimate that we measured for the 6 caves listed in Table 1.

Roost site	Historic estimates (millions)	Year	Projected estimates (millions)
Eagle Creek Cave	20–50	1963	0.1 ^a
Goodrich Cave	14–18	1957	1.2
Rucker Cave	12–14	1957	1.0
Fern Cave	8–12	1957	0.7
Devil's Sink Hole	6–10	1957	0.6
Valina Sink Hole	4	1957	0 ^b
Quarry Colony	5	1989	0.3
Vikery, Selman, Merrihew, and Connor caves	>3	1952	0.2
Webb Cave	<0.6	1957	<0.1
Wilson Cave	<0.6	1957	<0.1
Y-O Ranch Cave	<0.6	1957	<0.1
Reed Bat Cave	0.5–1	1993	0.75 ^c
Total projected estimates (millions)			5

^a The colony at Eagle Creek Cave was found decimated in 1967 (McCracken 2003).

^b Valdina Sink Hole was found abandoned in 1987 (McCracken 2003).

^c The average colony size reported at Reed Bat Cave (McCracken 2003) was used as the projected estimate.

population of the Brazilian free-tailed bat in the southwestern United States. This suggests that the current population is only 6% of the population that was estimated to consist of 150 million bats in the late 1950s.

DISCUSSION

It is possible that much of the order-of-magnitude difference between current and historic census estimates reflects a population decline. Reasons for a decline may be food-chain poisoning and the deterioration of feeding and roosting habitats. Exposure to pesticides has previously been associated with high mortality in bat species (Clark 2001; Cockrum 1970; Geluso et al. 1996). The toxicity of DDT, in particular, has been attributed to the decline of bat populations. DDT was developed as an organochlorine insecticide in 1939 and used extensively in agriculture in the 1950s and 1960s. Peak production occurred in 1961, and it was banned in 1972. A study of organochlorine residues among preserved samples of bats collected at Carlsbad Cavern during the last 70 years revealed significantly greater levels of DDT compounds in the 1950s and 1960s than in the 1970s (Clark 2001). This suggests that the lethal effects of DDT-derived compounds probably played a major role in the population decline observed during the 1960s (Clark 2001).

Disturbances of cave roosts include vandalism, mining of bat guano for use as fertilizer, and cave commercialization, and the impact on bat colonies is documented. Mining of bat guano for use as fertilizer has occurred for many decades. It is still ongoing in some of the privately owned caves in Texas, such as

Frio Cave, and may disturb colonies. In the spring of 2000, a primary entrance to Frio Cave was altered and trees removed to allow vehicular access for guano extraction years (B. Walker, Frio Cave guide, pers. comm.). Experienced bat observers corroborated that the summer of 2000 was highly unusual, with far fewer bats observed at Frio Cave than in previous or subsequent years (B. Walker, Frio Cave guide, pers. comm.). We censused this colony in June 2000 and recorded 653,845 bats. The population increased to 1,008,796 in June 2001. Another example of the impact of roost disturbances occurred at Valdina Sink Hole, which was abandoned by the bats after the sinkhole was modified to increase the recharge of surface water to the Edwards Aquifer (McCracken 2003).

Disturbances may have caused bats that would have roosted in natural cave habitats to select alternative human-made roost sites, for example, the crevices of bridges or culverts (Keeley and Tuttle 1999). Bridge roosts were not included in the early census studies (Davis et al. 1962) but are important at present because of their increasing numbers and a shift to construction practices that accommodate bats (Keeley and Tuttle 1999). It is unlikely that migration, which occurs in the spring and fall, contributes to the order-of-magnitude difference between current and historic estimates because they were made in midsummer, at a time when colony size is expected to be most stable. The differences in numbers of bats we censused at Ney Cave in 2004 and 2005 and at Eckert James River Cave in 2000 and 2004 may show typical intra-seasonal variations in numbers of bats in a Brazilian free-tailed bat colony. In both cases, the higher counts were obtained a month later in the season than the lower counts.

It is not understood why Brazilian free-tailed bat colonies emerge in 1 or more nightly emergence episodes. Examination of our data shows that the beginning of the 2nd or 3rd emergence episode coincided with sunset (Fig. 4). This confirms that light is an important environmental cue that synchronizes the emergence rhythm. It corroborates previous observations that emergence behavior of the Brazilian free-tailed bat relates to light levels (Davis et al. 1962; Erkert 1982; Lee and McCracken 2001; Wilkins 1989). Reproductive female bats tend to emerge earlier than males and nonreproductive females, presumably because of their higher energetic demands (Kunz et al. 1995; Lee and McCracken 2001). The different energetic demands of these cohorts of bats may contribute to the characteristic rhythm of flow episodes and pauses observed here, allowing reproductively active females additional time to fly to and disperse into their foraging habitats.

It is important to describe emergence episodes and pauses quantitatively for accurate colony censusing. Estimating the flow of bats during the peak of a presunset emergence episode and, based on this estimate, extrapolating the number of bats emerging in the dark could lead to invalid generalizations. Using thermal infrared technology, we can avoid inadequate sampling schemes and instead analyze the complete record of a colony emergence. The historic census estimates obtained without this technology may have been too high, and it is quite plausible that a combination of overestimation and population decline occurred.

Colony censuses obtained using our image analysis method can serve as a base for comparison for future censuses of colonies for which there are no published estimates (e.g., Bat Cave, Lava Beds National Monument, California, and Selah Chiroptorium, Texas, the latter of which is an artificial cave created to serve as a roost for Brazilian free-tailed bats; Table 1). The censuses also may be used to estimate the economic value of the pest control service provided by Brazilian free-tailed bats in the southwestern United States. Using the conservative estimate that 1 million bats consume 1.5 million *H. zea* per night in an 8-county region in southwestern Texas during the early stages of the cotton crop, Cleveland et al. (2006) estimated that the development of 5 million moth larvae is impeded per night and thus 1, and perhaps 2, applications of pesticides are prevented. This yielded an annual estimate of the avoided cost of pesticide use of up to \$200,000 for this region, which we can here update. We estimate that at least 2.5 million bats forage in this 8-county region, based on our estimates of the number of bats roosting at Bracken, Frio, and Ney caves and Devil's Sinkhole (and likely more if bridge colonies were included). Using the same static model of pest control assessment as used by Cleveland et al. (2006), in which the avoided cost of pesticide use in cotton crop scales linearly with the number of bats present, we computed that the value of the annual pest control service of these bats may reach \$500,000.

Our census method makes it feasible for future studies to assess subtle changes in intra- and interseasonal colony levels and to quantify the impact of changes in feeding and roosting habitats on this species. Using thermal infrared technology, a similar image analysis method could be developed to census other crepuscular or nocturnal species of bats and birds.

ACKNOWLEDGMENTS

We thank L. Allen, J. Frank, K. Fuhmann, and S. Petronio for field assistance; B. Walker for access to Frio Cave; M. and D. Bamberger for access to the Selah Chiroptorium; D. Davis for access to Davis Cave; K. Fuhmann for access to Lava Beds National Monument; D. Snodgrass for access to Eckert James River Cave; L. and T. Barnett and T. Keyes for access to Ney Cave; and R. West for hospitality and support at Carlsbad National Park. We also are grateful to L. Premerlani, E. Immermann, J. Burger, E. Carrel, T. Castelli, and C. Ng for computational assistance. This study was supported by grants from the National Science Foundation (EIA-ITR 0326483 to THK, MB, and GFM, DBI-9808396 to THK and CJC, DBI-0216349 to THK, and IIS-0093367 and EIA-0202067 to MB), the Office of Naval Research (N000140110444 to MB), the National Park Service (PMIS 69606 and LABE-2003-SCI007 to THK), and the Computing Research Association (DMP to MB).

LITERATURE CITED

- ALLISON, V. C. 1937. Evening bat flight from Carlsbad Caverns. *Journal of Mammalogy* 18:80–82.
- ALTENBACH, J. S. 1988. Techniques for photographing bats. Pp. 125–140 in *Ecological and behavioral methods for the study of bats* (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.
- BETKE, M., D. E. HIRSH, A. BAGCHI, N. I. HRISTOV, N. C. MAKRIS, AND T. H. KUNZ. 2007. Tracking large variable numbers of objects in clutter. Proceedings of the IEEE Computer Science Society Conference on Computer Vision and Pattern Recognition. Minneapolis, Minnesota, June 2007:1–8.
- CLARK, D. R., JR. 2001. DDT and the decline of free-tailed bats (*Tadarida brasiliensis*) at Carlsbad Caverns, New Mexico. *Archives of Environmental Contamination and Toxicology* 40: 537–543.
- CLEVELAND, C. J., ET AL. 2006. Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. *Frontiers in Ecology and the Environment* 4:238–248.
- COCKRUM, E. L. 1970. Insecticides and guano bats. *Ecology* 51:761–762.
- CONSTANTINE, D. C. 1967. Activity patterns of the Mexican free-tailed bat. *University of New Mexico Publications in Biology* 7: 1–79.
- DAVIS, R. B., C. F. HERREID II, AND H. L. SHORT. 1962. Mexican free-tailed bats in Texas. *Ecological Monographs* 32:311–346.
- ERKERT, H. G. 1982. Ecological aspects of bat activity rhythms. Pp. 201–242 in *Ecology of bats* (T. H. Kunz, ed.). Plenum Press, New York.
- FRANK, J. D., T. H. KUNZ, J. HORN, C. J. CLEVELAND, AND S. M. PETRONIO. 2003. Advanced infrared detection and image processing for automated bat censusing. Proceedings of the SPIE Conference on Infrared Technology and Applications XXIX 5074: 261–271.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- GELUSO, K. N., J. S. ALTENBACH, AND D. E. WILSON. 1996. Bat mortality: pesticide poisoning and migratory stress. *Science* 194: 184–186.
- HIRSH, D. E. 2004. Evaluation of computer vision methods for analyzing infrared thermal video and censusing Brazilian free-tailed bats. Work for Distinction in the Department of Computer Science. Boston University, Boston, Massachusetts.
- KEELEY, B. W., AND M. D. TUTTLE. 1999. Bats in American bridges. Resource Publication 4. Bat Conservation International, Inc., Austin, Texas.
- KUNZ, T. H., J. O. WHITAKER, JR., AND M. D. WADANOLI. 1995. Dietary energetics of the Mexican free-tailed bat (*Tadarida brasiliensis*) during pregnancy and lactation. *Oecologia* 101:107–115.
- LEE, Y.-F., AND G. F. MCCracken. 2001. Timing and variation in the emergence and return of Mexican Brazilian free-tailed bats. *Zoological Studies* 40:309–316.
- MCCracken, G. F. 2003. Estimates of population sizes in summer colonies of Brazilian free-tailed bats (*Tadarida brasiliensis*). Pp. 21–30 in *Monitoring trends in bat populations of the U.S. and territories: problems and prospects* (T. J. O'Shea and M. A. Bogan, eds.). United States Geological Survey, Biological Resources Discipline, Information and Technology Report, USGS/BRD/ITR-2003-003:21–30.
- SABOL, B. M., AND M. K. HUDSON. 1995. Technique using thermal infrared-imaging for estimating populations of gray bats. *Journal of Mammalogy* 76:1242–1248.
- WILKINS, K. T. 1989. *Tadarida brasiliensis*. *Mammalian Species* 331: 1–10.

Submitted 11 January 2007. Accepted 25 April 2007.

Associate Editor was R. Mark Brigham.