Brazilian free-tailed bats (*Tadarida brasiliensis*: Molossidae, Chiroptera) at high altitude: links to migratory insect populations

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Synopsis Existing information on the activity of bats in the aerosphere is restricted almost exclusively to altitudes that are within a few tens of meters above the ground. We report a total of 50.2 h of ultrasonic recordings made using radio microphonic bat detectors suspended from free-floating helium balloons and from kites. The data include a total of 22 353 echolocative calls from ground-level to 1118 m above ground level (AGL). These calls are attributed to Brazilian free-tailed bats based on acoustic features and the large numbers and high-altitude aerial dispersion of these bats over the local landscape. Bat activity varied significantly throughout the air column and was greatest at 400–500 m AGL and near ground level. Feeding buzzes, indicating feeding on aerial prey, were most abundant near ground level and at 400–500 m, and were detected to altitudes of ~900 m AGL. The peak activity of bats at 400–500 m AGL is concordant with the altitude of the atmospheric boundary layer and the seasonal formation of the low-elevation southerly wind jet that has been identified as a major aeroecological corridor for the nocturnal dispersal of noctuid moths and other insects.

Introduction

Because the ultrasonic signals emitted by bats attenuate within a few tens of meters (Griffin 1971), most field studies monitoring the echolocative calls of insect-eating bats have been restricted to activity occurring close to the ground (Acharya and Fenton 1992; Barclay et al. 1999; Gillam and McCracken 2007). Exceptions are two studies that employed radio microphonic bat detectors suspended beneath helium-filled kite balloons to document the orientation and feeding calls of bats at altitudes of up to 600 m above ground level (AGL) (Griffin and Thompson 1982; Fenton and Griffin 1997). Others have used radio microphones (Menzel et al. 2005) or bat detectors mounted on towers (Kalcounis et al. 1999) to document bat activity at altitudes of up to 30 m AGL above forest canopy. None of these previous studies provided information on the insects that may be available at high altitudes; information that may be critical to understanding the altitudinal distribution of bat activity. A recent dietary study showing that the bat *Nyctalus lasiopterus* preys aloft on migrating songbirds (Popa-Lisseanu et al. 2007) illustrates the limitations of our current knowledge regarding the feeding activity and resources that are available to bats at higher altitudes.

Brazilian free-tailed bats, *Tadarida brasiliensis*, occur in enormous numbers throughout Mexico and the southern portions of the United States, with over 100 million of these bats estimated to inhabit 10 large caves in South Central Texas during spring and summer months (Wahl 1993, McCracken 2003). Visual triangulation from the ground (Davis et al. 1962) and radar (Williams et al. 1973) show that dense columns of bats emerging from these caves near nightfall ascend to altitudes of up to 3000 m AGL. Average flight speeds were estimated at 40 km/h, and their nightly flight range at over 100 km (Davis et al. 1962; Williams et al. 1973). With the implementation of (U.S.) National Weather Service NEXRAD WSR-88D Doppler radars in Texas in the mid-1990s, the earlier observations of rapid, long-distance, high-altitude flight by enormous numbers of bats were confirmed (Fig. 1). The presence of such large numbers of bats and their propensity to ascend to great heights provides an excellent opportunity to investigate altitudinal patterns of bats' foraging activity.

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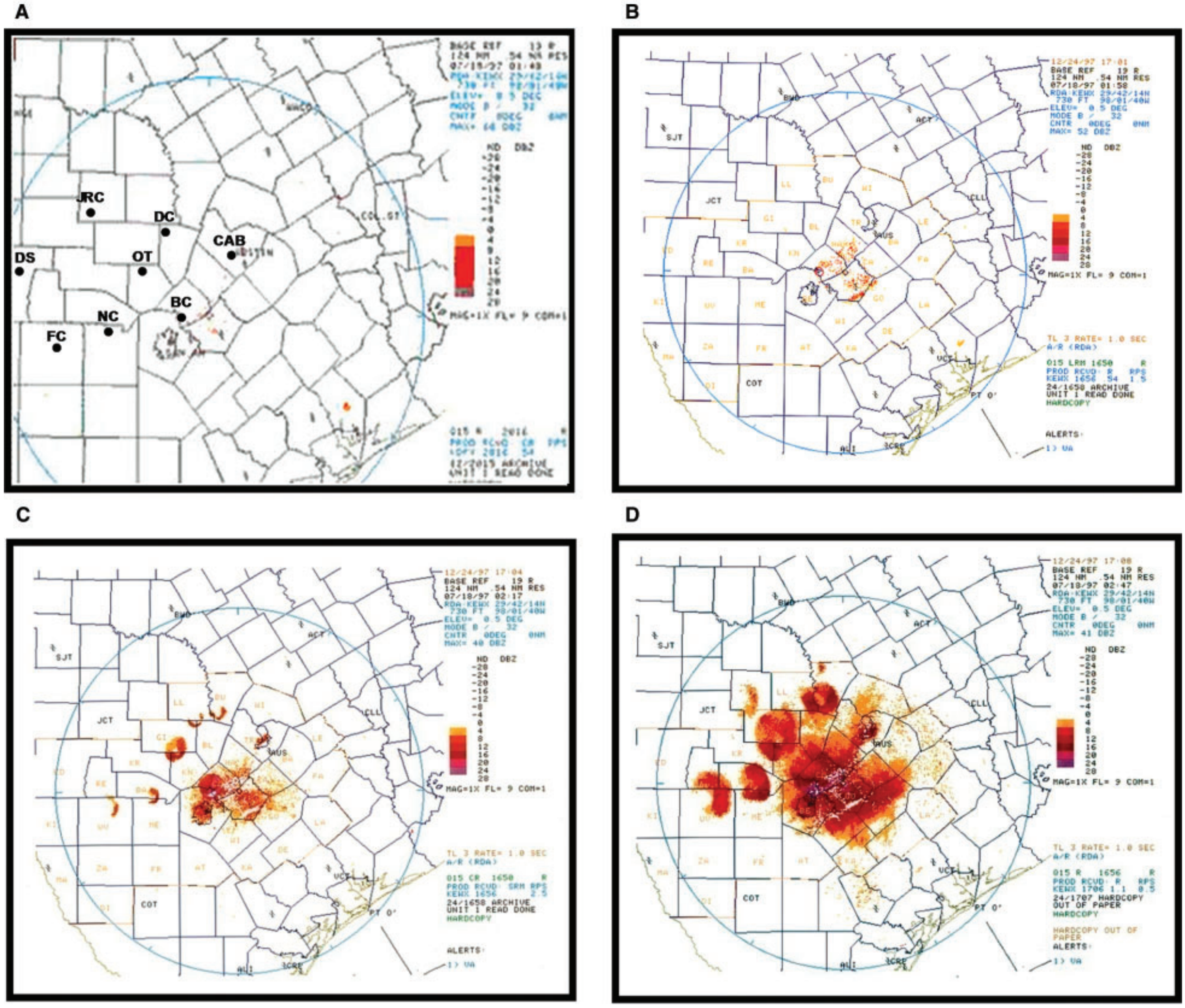

Fig. 1 Locations of large roosts of Brazilian free-tailed bats in central Texas. Reflectivity images from NEXRAD WSR-88D Doppler radar at New Braunfels, TX, **(A)** showing emergence and movements of Brazilian free-tailed bats from major roost sites in clear weather on the night of July 18, 1997, (**B**) ~15 min, (**C**) 30 min, and (**D**) 45 min after the onset of the bats' emergence. DS, Devil's Sinkhole; FC, Frio Cave; NC, Ney Cave; JRC, James River Cave; OT, Old Tunnel; DC, Davis Cave; BC, Bracken Cave; CAB, Congress Avenue Bridge.

The reasons for high-altitude flight by the bats in Texas have not been determined. Davis et al. (1962) speculated that the bats may feed aloft or, alternatively, that they ascend to select winds that assist their travel to favored foraging locations near the ground. The radar studies of Williams et al. (1973) showed that the aerial dispersion of the bats was nonrandom and that the direction of flight did not correspond with prevailing winds, suggesting that movements were actively directed. Williams et al. (1973), however, did not believe that the bats engaged in substantial feeding aloft. In observations from a helicopter, Williams et al. (1973) inferred from their flight paths that bats were feeding at altitudes below 200 m, but not above 200 m. Williams et al. (1973) also observed many insects below 200 m, but rarely saw insects above 200 m.

Many insects are known to migrate and disperse at night at high altitudes (Drake and Gatehouse 1995). Because many migratory insects are important agricultural pests, attention has been given to documenting the magnitude, sources, emergence schedules, and long-distance movement of these insect populations. Since the 1980s, agricultural researchers have documented the seasonal migrations of billions of moths (Lepidoptera; Noctuidae), including corn earworms (*Helicoverpa zea*) and fall armyworms (*Spodoptera frugiperda*) from crops in the Lower Rio Grande Valley of northern Mexico and southern Texas (Hartstack et al. 1982; Raulston et al. 1990; Wolf et al. 1990; Lingren et al. 1994; Johnson 1995; Westbrook et al. 1995; Westbrook et al. 1997; Westbrook 2008). Upon emergence, adult moths

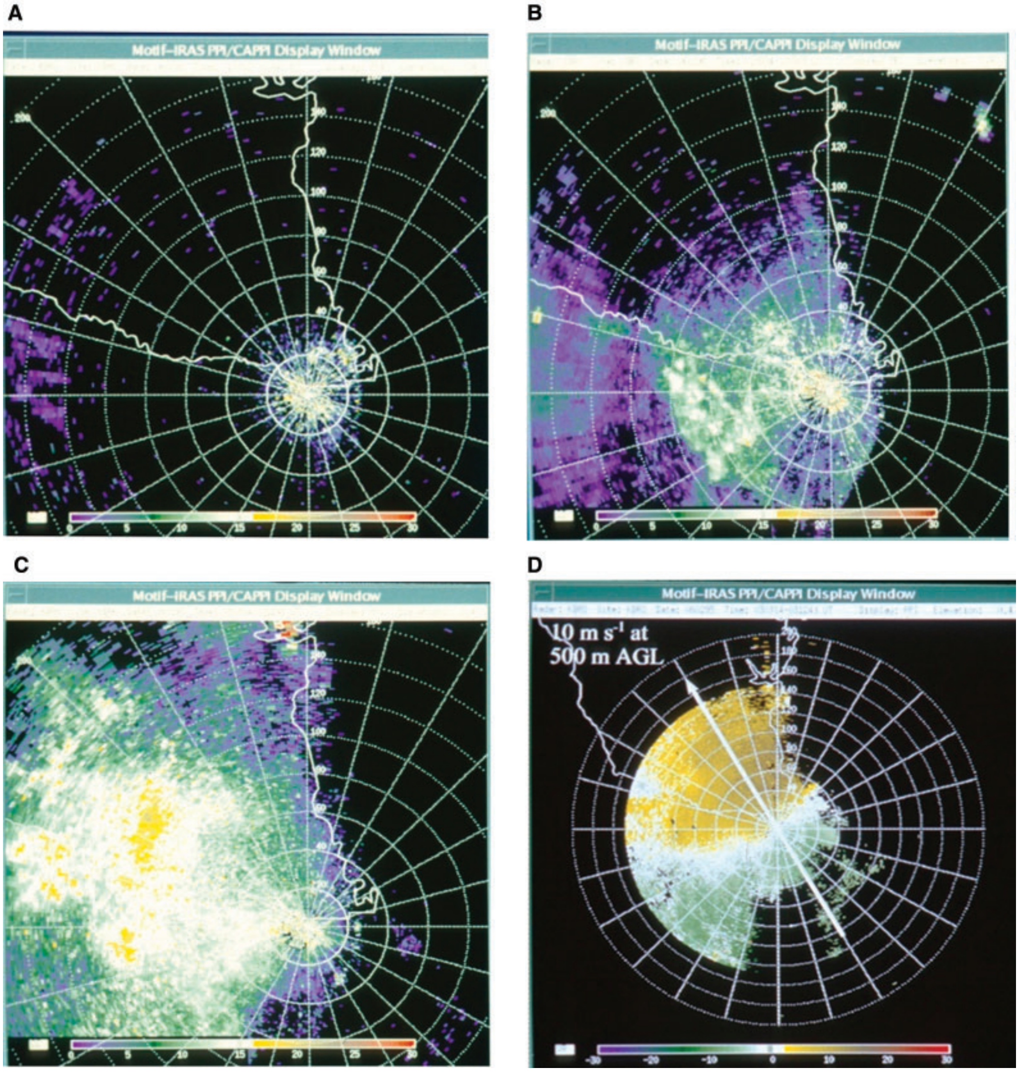

Fig. 2 Reflectivity images taken at **(A)** 20:00 CDT, **(B)** 21:00 CDT, **(C)** 22:00 CDT from the NEXRAD WSR-88D Doppler radar at Brownsville, TX, showing moth migration from the Lower Rio Grande Valley in clear weather on the night of June 1, 1995. **(D)** Net vector of north-northwestward movement of the moth population at 24:00 (or 0:00 CDT) on June 1, 1995.

ascend to altitudes of several hundred meters where southerly winds assist their long-distance migration. Following a single night's displacement, these large moth populations are within the foraging range of the south-central Texas bat populations (Wolf et al. 1986, 1990; Westbrook et al. 1995). As with the bats, NEXRAD radar documents the nightly emergences and northward displacements of migrating moths (Fig. 2).

Studies of the diets of the Brazilian free-tailed bats in Texas reveal a striking increase in consumption of moths that correlates with the emergence and availability of the migratory moth populations (Whitaker et al. 1996; Lee and McCracken 2002, 2005). While many of these moths may be eaten close to ground-level, the occurrence of billions of moths at the same altitudes and locations as millions of bats suggests a motivation for the high-altitude flights of the bats. Here we record echolocative calls of bats in south-central Texas from ground level to >1000 m AGL, and investigate whether the activity patterns of the bats are associated with the altitudinal distribution of the migratory moth populations.

Materials and methods

Radio microphones

As with Griffin and Thompson (1982), Fenton and Griffin (1997) and Menzel et al. (2005), radio microphonic bat detectors were used to monitor the echolocative calls of bats aloft. The radio microphones were constructed from the electret microphone and circuit board of Pettersson Elektronik AB, D-230 bat detectors, and custom-made 145–149 MHz,

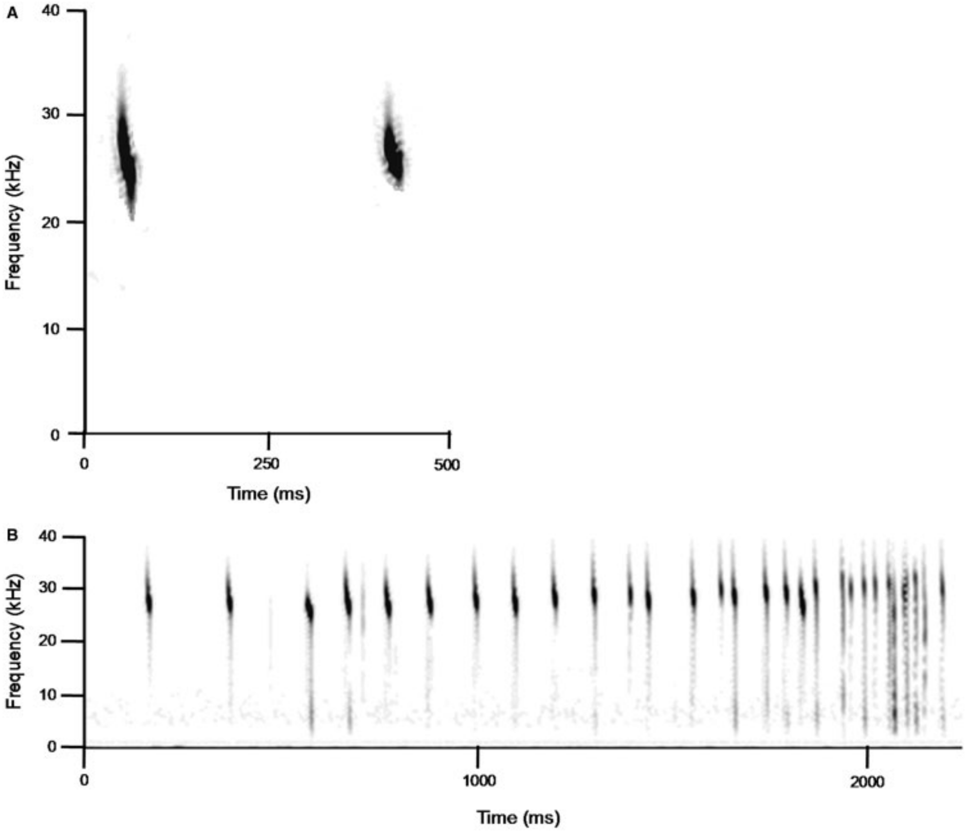

Fig. 3 Example of radio microphonic recordings of echolocative calls. **(A)** Timefrequency plot (sonogram) of two search phase calls. **(B)** Call sequence including approach phase calls and feeding buzz. Calls were recorded by a radio microphone suspended from a kite at (A) 191 m and (B) 200 m (AGL).

FM radio-transmitters (Holohil Systems Ltd.). The divide-by-ten circuit of the Pettersson D-230 detector transforms the ultrasonic calls of foraging bats to audible frequencies, and preserves information on duration of call, repetition rates, and dominant-frequency domains (Fig. 3A). To conserve battery power, the transmitter was activated by a sound-actuated circuit from the output of the D-230 detector, and was designed to turn off after 10 s with no signal. The units were powered by three fused Li1/2 C-cell batteries (CSC93, Electrochem Industries) and placed within foam insulation for mechanical protection. Thus configured, the radio microphones weighed ~200 g and had an operational life of *ca.* 20 h of continuous transmission. Transmitted signals were monitored and recorded at ground-level using a 3-element Yagi antenna connected to a narrow-band FM scanner (AOR Model AR300) and cassette recorder (Sony WM-D6C, Marantz PMD221, Awia HS-F150).

Tetrahedral balloons (tetroons)

On the nights of July 8 and 10, 1996, a single radio microphone was tethered to a 2 m^3, helium-filled, mylar tetroon. Tetroons also carried a strobe light for aircraft safety, a radiosonde that transmitted information on altitude, barometric pressure, air temperature, relative humidity, and wind velocity, and a 0.9 g radio transmitter (Holohil Systems Ltd. BD-2) to assist in relocating the equipment after descent. Tetroons were ballasted to drift with prevailing winds at 750 m above ground level, an altitude that was previously determined as typical for migrating moths (Wolf et al. 1990; Westbrook et al. 1995) and that was sufficiently high for consistent radio detection. Tetroon launches were synchronized with previously determined schedules of moth emergence. Tetroon positions, altitudes, speeds, and directions of drift were monitored continuously during flight from a tracking vehicle that was equipped with an on-board navigation system and receivers for signals from the radiosonde and the radio microphone. The tetroon and vehicle-tracking systems were the same as used to investigate migrations of noctuid moth populations from the Lower Rio Grande Valley, as described by Westbrook et al. (1995). Exceptions were that: (1) a larger (2 m^3) tetroon was used to accommodate the weight of the radio microphone,

(2) a custom electronic device was programmed to release the helium and force the tetroon's descent after 3 h of flight, and (3) the Yagi antenna was attached in parallel with the existing steerable antenna on the tracking vehicle. Immediately prior to each launch of a tetroon, a pilot balloon (pibal) with an attached airsonde was released to assess prevailing winds and to calculate air density at the altitudes to which the tetroon was to be ballasted (Westbrook et al. 1995). Notices to Airmen (NoTAMS) were requested and issued by the Federal Aviation Administration (FAA) to make pilots aware of the planned altitudes and trajectories of the tetroon flights.

Tetroons with attached radio microphones were launched from Pearsall, TX (28° 49′ 38″ N, 99° 06′ 46″ W) between 21 : 05 and 21 : 12 CDT. Pearsall, TX is located near the southern edge of the Winter Garden agricultural region, an area that is dominated by field crops of corn and cotton, and is ~100 km SE of Frio Cave (29° 26′ 30″ N, 99° 40′ 30″ W) with an estimated population of 8 million Brazilian free tailed bats (Wahl 1993; McCracken 2003). The tetroon launches were after the peak migration of corn earworm moths from the LRGV, but during the time of emergence and dispersal of moths from local corn fields, and the flights were designed to intercept moths as they emerged and migrated from local crops (Westbrook et al. 1995). Tetroons were timed to deflate after 3-h flights that would carry the radio microphones to the vicinity of Frio Cave.

Kites

Radio microphones were suspended from the tether lines of kites on nine nights between July 10 and 19, 1997. The kite experiments all were conducted from a fallow field (29° 26′ 30″ N, 99° 41′ 30″ W) located ~25 km north of Uvalde, TX, and 12 km south of Frio Cave. This site is at the northern edge of the Winter Garden agricultural region. The kite studies also occurred after the peak migration of corn earworm moths from the Lower Rio Grande Valley, but during the time of peak emergence and dispersal of moths from local crops.

The experimental kite system was originally developed for atmospheric research and is described by Balsley et al. (1992, 1994). Depending on wind speeds, our experiments used a 9 m^2 (heavier winds) or 12.5 m^2 (lighter winds) nylon parafoil kite attached to a 6-km length of 430 kg-test woven Kevlar tether. A radiosonde attached to the tether 50 m below the kite provided continuous information on altitude, speed, and direction of the wind, temperature, and atmospheric pressure. For aircraft safety, strobe lights were attached to the tether at 100 m intervals. Notices to AirMen (NoTAMS) were requested and issued to make pilots aware of the location of operation and a safe radius around the moored kite.

On the nights of 10, 11, and 12 July a single radio microphone was attached to the tether 100 m below the kite. These flights were aborted due to various problems, including noise from wind that interfered with the reception of ultrasonic signals. In subsequent flights, the radio microphones were placed in plastic funnels with the microphone facing out of the larger (30 cm) open end of the funnel. As the funnel vaned in the winds aloft, the microphone was oriented in the wind shadow of the funnel, effectively alleviating wind noise. On the night of July 14, two radio microphones transmitting at different frequencies were attached to the kite 100 and 600 m below the kite. On the nights of 15, 16, 17, and 18 July three radio microphones transmitting at different frequencies were attached to the tether at 100, 400, and 700 m below the kite. On all nights, kites were launched at *ca.* 19 : 00 CDT and equipment was operating by *ca.* 21 : 00 CDT. Our intention was to operate until *ca.* 6 : 00 CDT on the following morning, unless interrupted by technical problems, inclement weather or wind exceeding 30 km/h aloft. Throughout the nights, the kites were occasionally lowered and raised, as needed, to check or fix equipment, or due to vicissitudes of the wind aloft. Raising and lowering the kites allowed us to approximate a vertical transect of the activity of bats from 0 to 1100 m AGL.

Activity of bats

Similar to other automated echolocation-detection systems (Johnson et al. 2002), the sound-actuated feature of the radio microphones resulted in the acquisition of echolocative calls in files of varying duration. We define "file duration" as the time from the detection of the first call in a sequence to the beginning of the next consecutive actuation and detection of calls from the same radio microphone. Thus, file duration reflects the length of a recording that includes the period of no activity until the next consecutive call is recorded. Files where the radio microphone actuated and then shut down without transmitting calls were discarded from the dataset. Calls were visualized using Batsound-Pro Software (Pettersson Elektronik AB) and the numbers of calls in each file were counted manually. Relative "bat activity" was summarized by altitude as the number of calls per minute (calls in a file/file duration), irrespective of signal quality.

Although, it is standard to assess activity of bats as number of "bat passes" per time (Johnson et al. 2002), others have measured activity as number of calls per time (Britzke et al. 1999; Tibbels and Kurta 2003). We report bats' activity as calls per minute because files frequently contained such high levels of activity that it was not possible to discern individual passes. Pseudoreplication is often an issue in biological research (Hurlbert 1984). In studies monitoring the echolocative calls of bats either as bat passes per time (Johnson et al. 2002) or as calls per time (Britzke et al. 1999; Tibbels and Kurta 2003) data must be interpreted as relative indices of bat activity, and not as measures of the numbers or abundance of bats.

The characteristic shortening of call duration and inter-pulse interval and the increase in frequency modulation that occurs as a bat approaches and attacks an insect provide evidence that bats are feeding aloft. We define a feeding buzz as a series of approach-phase calls with interpulse intervals of 50–150 ms, that transition into a close succession of terminal-phase calls with interpulse intervals < 50 ms. We searched all files for feeding buzzes and tallied these by altitude and time of night.

For the purpose of our analyses, we treated all calls having time and frequency domains that were within the range of variation known for the calls of Brazilian free-tailed bats (Gillam and McCracken 2007) as the calls of these bats. We justify this on the basis of (1) the extremely large numbers of these bats above the landscape of our study area, (2) the fact that the calls of Brazilian free-tailed bats comprise > 95% of all bats' calls recorded in the vicinity at ground level, and (3) of the calls transmitted from aloft for which time and frequency domains could be measured, ~98% were consistent with calls recorded at ground level from bats confirmed as *T. brasiliensis* (Gillam and McCracken 2007; Gillam et al., manuscript in preparation).

Statistical analysis

SigmaPlot (Systat Software, Inc., San Jose, CA) and NCSS (Number Cruncher Statistical Systems, Kaysville, UT) were used for all statistical analyses. We conducted a polynomial regression analysis to determine whether bats' activity, defined as echolocative calls per minute, was associated with altitude. We also used analysis of variance (ANOVA) to determine if average numbers of calls per minute differed by altitude when the data pooled over all nights were partitioned into 100-m altitude intervals. We examined our recordings by time of night to investigate whether the altitudinal distribution of bats' activity differed during the peak periods of activity that occur in the evening (21 : 00–1 : 00 CDT) and morning (4 : 00–7 : 00 CDT).

Results

Tetroons

During the flight of July 8, a file containing a sequence of 10 echolocative calls was transmitted from 680 m AGL, after which the tetroon continued to ascend to over 1300 m and radiosonde contact was lost without reception of other calls (Fig. 4A). The equipment later was located in Sonora, TX, ~250 km northwest of the launch site. The radio microphone launched on July 10, transmitted six separate files of echolocative calls from altitudes of 490–930 m AGL (Fig. 4A). During a flight lasting 1 h 25 min, this tetroon traveled ~60 km west-northwest to the vicinity of Batesville, TX where the equipment was recovered.

Kites

A total of 50.2 h of recordings was obtained from radio microphones suspended from kites on the nights of July 14–18, 1997. The data consist of 208 files (mean file duration = 33.4 min; range = 2.5–193.7 min) containing a total of 22 353 calls from ground level to 1118 m AGL (Fig. 4B; Table 1). Three short files with calls at higher frequencies than known for Brazilian free-tailed bats were eliminated from analysis. Regression analysis reveals a significant fourth-order polynomial fit of calls per minute to altitude ($R^2 = 0.13$, $P < 0.0001$), with the highest levels of activity at ground level and at 400–600 m AGL (Fig. 5A). When the data are partitioned into 100 m altitudinal categories (Table 1), ANOVA also shows significant differences in bats' activity at different altitudes ($F = 4.35$, $P < 0.0001$), with the average of 105 calls/min recorded at 400–499 m AGL exceeding call activity at all other altitude intervals, including the average of 76 calls/min observed at 0–100 m AGL.

Bats' activity throughout the night was strongly bimodal with peak activity occurring from the start of the evenings' recordings until 1 : 00 CDT and from 4 : 00 to 6 : 30 CDT (Fig. 6A). The highest levels of activity were observed in morning, at altitudes of 400–600 m AGL (Fig. 6A and B). Datasets from both morning and evening showed significant fourth-order polynomial fits of calls per minute versus altitude ($R^2 = 0.20$, $P < 0.0001$ morning $R^2 = 0.13$, $P < 0.0001$, evening), with an apparently stronger fit

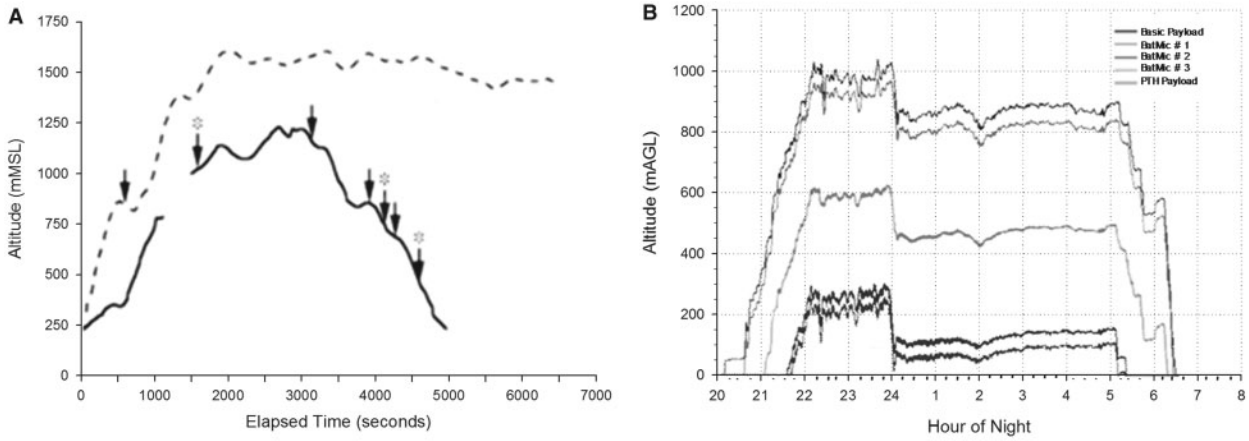

Fig. 4 Vertical profiles of **(A)** free-floating tetroon flights on July 8 and 10, 1996; arrows indicate times and altitudes at which echolocation calls were detected and arrows with ∗ are call sequences that included a feeding buzz or partial buzz and (**B**) kite recordings on July 17–18, 1997; the top line indicates the altitudinal profile of the kite with attached radiosonde and the three lines below the kite are the profiles of the radio microphones at the highest, middle, and lowest altitudes.

Table 1 Activity of bats summarized by 100-m altitude intervals (AGL)

Altitude (m)	Recording time (min)	Average calls/min	Total no. of calls	Feeding buzzes	Partial buzzes
0–99	402	76.4 (14.2)	6245	12	29
100–199	282	17.0 (4.2)	1382	1	6
200–299	771	17.4 (6.2)	2022	5	4
300–399	390	11.5 (2.8)	1755	0	4
400–499	440	105.2 (25.3)	4798	4	10
500–599	179	62.9 (15.0)	3056	2	3
600–699	152	5.0 (1.8)	285	0	0
700–799	102	42.6 (20.5)	1262	0	7
800–899	282	21.8 (7.9)	1532	2	5
900+	14	1.1	16	0	0
Total	3014	49.4 (5.9)	22 353	26	68

ANOVA: $F = 4.35$, $P < 0.0001$.

Calls were recorded by radio microphones suspended from kites on July 14 – 19, 1997. Recording time refers to the total number of minutes recorded for each altitudinal interval, including periods of silence and periods when bats were calling. We also report average calls per minute (standard error), total number of recorded calls, and total number of feeding buzzes and partial buzzes recorded for each altitudinal interval. ANOVA results reveal significant differences among altitudinal intervals in the average number of calls per minute. Note that no standard error is reported for the 900 + altitude interval as this includes only one file.

demonstrated by the bats' activity in morning (Fig. 6B).

Feeding buzzes were most abundant near ground level, but were detected to altitudes of 847 m (Table 1, Fig. 3B). In addition to typical feeding buzzes, we also detected many call sequences that included approach-phase calls and the beginning of the feeding buzz, but did not include the most terminal portion of a buzz, which is a characteristic train of short-duration calls with very small inter-pulse intervals. We dubbed these sequences "partial buzzes", as to our knowledge they have not been previously described in the literature. Similar to feeding buzzes, partial buzzes were detected throughout the range of altitudes sampled (Table 1), with the highest recorded at an altitude of 860 m.

Discussion

Our results concur with those of others that, at least for some species of bats, activity above the ground can equal or exceed activity at ground level. Griffin and Thompson (1982) reported up to five orientation calls per second at 200 m AGL over Utah and Nevada that they attributed either to Brazilian free-tailed bats or to a related species of free-tailed bat,

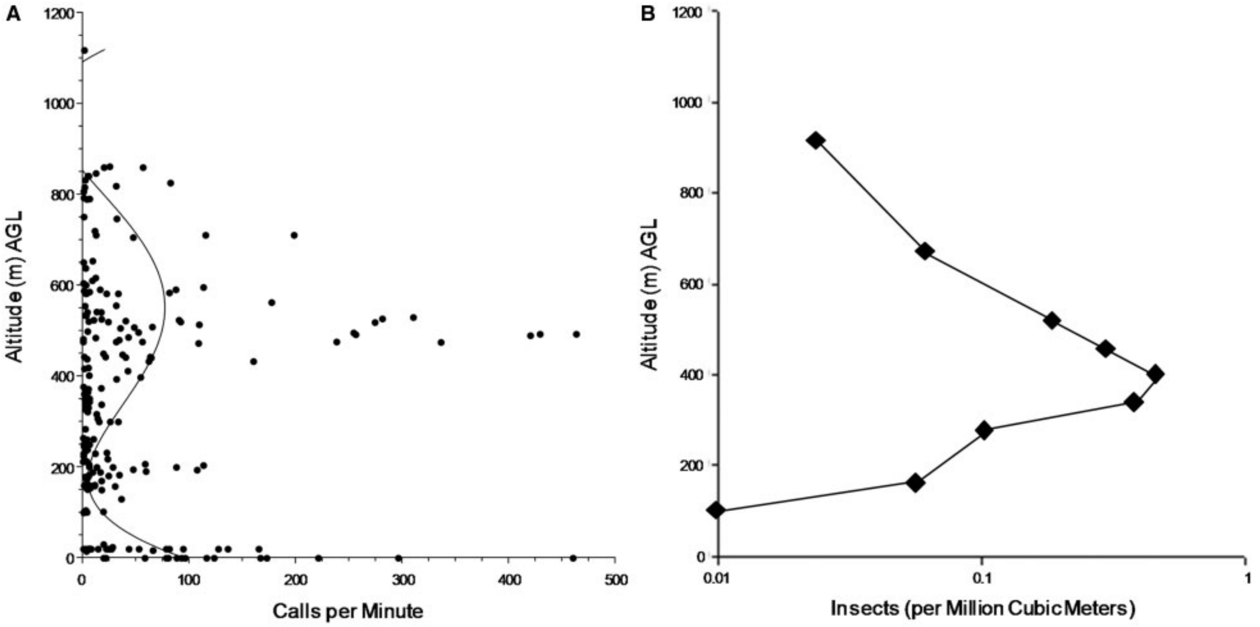

Fig. 5 (A) Altitude versus calls per minute recorded by radio microphones suspended from kites. Data show a significant fourth-order polynomial fit of calls per minute versus recording altitude ($R^2 = 0.13$, $P < 0.0001$, $Y = 94.80 - 1.219x + 0.00523 \times 2 - 7.36E - 6 \times 3 + 3.22E - 9 \times 4$), with the highest levels of bat activity at ground level and at 400–600 m AGL. While altitude is the independent variable for this regression, it is shown on the *Y*-axis for comparison to **(B)**. (B) Altitude versus noctuid moth densities as estimated from X-band radar. Peaks of bat activity and moth density correspond at the altitude that is typical for the low-level wind jet in central Texas.

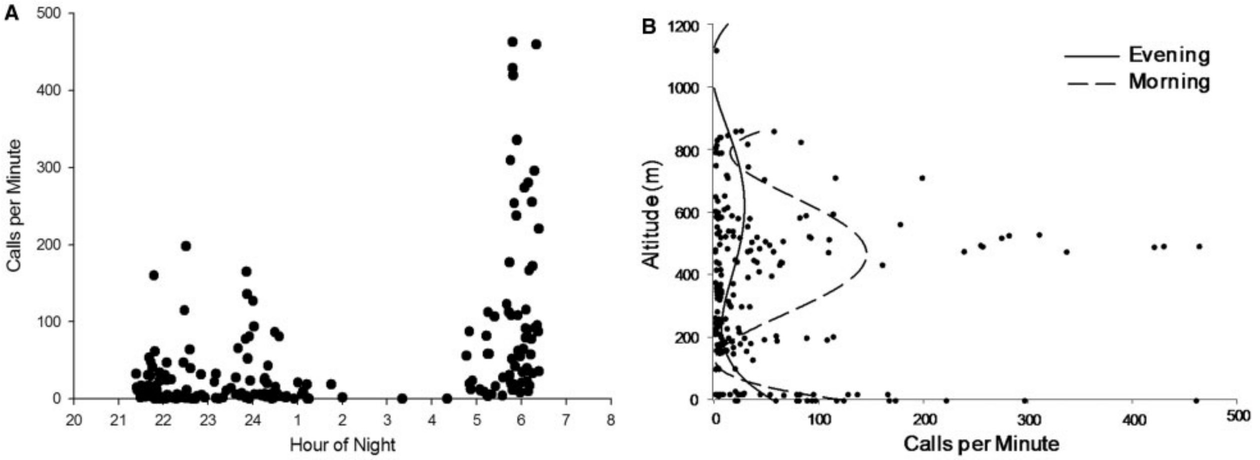

Fig. 6 (A) Bat activity in calls per minute versus time of night for recordings made from kites showing bimodal pattern with peak activity before 1:00 CDT (night) and between 4:00 and 6:30 CDT (morning). **(B)** Bat activity versus altitude partitioned into the evening and morning recordings. Significant fourth-order polynomial fits of calls per minute versus recording altitude are demonstrated for both sets of data (evening, $R^2 = 0.13$, $P < 0.0001$, $Y = 56.03 - 0.52x + 0.00181x2 \times 2.21E - 6x3 + 8.65E - 10x4$; morning, $R^2 = 0.20$, $P < 0.0001$, $Y = 122.26 - 2.19x + 0.0122x2 - 2.13E - 5x3 + 1.16E - 88x4$).

Nyctinomops macrotis. In Australia, the same authors recorded feeding activity at 200 m AGL attributed to other species of free-tailed bats that was more than twice that typically recorded at ground-level at nearby streetlights. The average activity that we observed at 400–499 m AGL also exceeded that observed closer to the ground at 0–100 m AGL (Table 1). However, because most studies of echolocative activity by bats are conducted at ground level, we attempted to better estimate activity at ground level by truncating this lowest category of altitude to include only the calls recorded within 30 m of the ground, which is the maximum distance that the echolocative calls of Brazilian free-tailed bats can be detected by a hand-held Pettersson D230 bat detector (GFM & EHG, personal observation).

We obtained an average of 76 calls/min at ground level, still below that obtained at 400–499 m AGL (Table 1). The highest activity observed in our study was almost 500 calls/min, recorded at 490 m AGL (Fig. 5A) which exceeds the peak activity recorded over Utah by Griffin and Thompson (1982).

This peak in activity at 400–600 m AGL shows striking convergence with the altitude of the atmospheric boundary layer (ABL) that results in the formation of a low-level, southerly wind jet that occurs at night and typically extends from southern Texas to the upper midwestern United States. The atmospheric conditions responsible for this seasonal wind jet, and the research identifying it as a major aeroecological corridor for the nocturnal dispersal of billions of noctuid moths and other organisms are summarized and described by Westbrook (2008). Although we do not have observations on the winds aloft or on movements or densities of moths that are coincident with the dates of our kite studies, the ABL is well defined in the region of our study by climatological research (Bonner 1968; Bonner and Pagel 1970), as is the concentrated presence within it of huge populations of dispersing noctuid moths (Wolf et al. 1990; Westbrook et al. 1995; Westbrook 2008). The altitudinal convergence of bats and moths (Fig. 5A and B) at the ABL supports the hypothesis that the distribution of the bats is determined by the distribution of the moths.

The hypothesis that bats go where the insects are implies that they go there to eat them. Our data and others' data demonstrate that bats feed at high altitudes. For example, Fenton and Griffin (1997) recorded echolocative calls, including feeding buzzes, in Zimbabwe at up to 500 m AGL, that they attributed to six species of bats belonging to the family Molossidae and to one species of emballonurid bat (*Taphozous mauritianus*). Similarly, foraging by *Taphozous spp.* at high altitudes in India was inferred from observations of erratic flight paths that are typical of feeding by bats (Siefer and Kriner 1991). However, in 50.2 h of recordings we are confident only in reporting 26 feeding buzzes and 68 partial buzzes (Table 1) and, although we recorded buzzes to over 800 m AGL, we must consider why we do not document higher rates of feeding. Feeding buzzes, and particularly the terminal phase of the buzz, are more difficult to detect than are orientation or approach-phase calls. Feeding buzzes are characterized by progressively decreasing pulse duration, decreasing amplitude, and increasing frequency, all features that result in attenuation of the signal over shorter distances. The more rapid attenuation of terminal pulses of the buzz may account for some of the apparent partial buzzes. This problem may have been exacerbated because the wind-noise protection we implemented resulted in the radio microphones suspended from kites being highly directional, causing rapid attenuation or even "loss" of signals from bats flying past the open end of the funnel. Such directional effects would not be as severe in typical ground-level recordings that are made in more benign winds. Another possibility that deserves further attention involves issues of scale and sampling volume. Because of their limited range, ultrasonic detectors at ground level are essentially sampling airspace in two dimensions, whereas air volume expands exponentially with increasing altitude, making it increasingly less likely that successful foraging will occur within range of a bat-detector's perception. The densities of migrating noctuid moths recorded in entomological radar studies rarely exceed 10^3 moths/10^6 m^3, which, if evenly distributed would equal one moth in a cube of airspace 10 m/side. While moths are typically at densities that are one or two orders of magnitude $<10^3$ moths/10^6 m^3, unpublished simulations show that even at such diffuse density in such voluminous airspace a bat hunting at random should have no difficulty encountering insects at rates sufficient to satisfy its' daily energetic demands. However, an ultrasonic detector with a maximum detection range of 30 m may only rarely perceive these encounters.

Finally, it is impossible to eliminate the possibility that bats were attracted to the equipment that we placed aloft and that calls we recorded resulted from their investigating kite lines, tetroons, or the radio microphones. Recent studies show that high-flying bats investigate objects placed in their airspace, such as wind turbines (Horn et al. 2008) and this may account, at least in part, for fatal impacts of bats with turbines (Arnett et al. 2008). If bats were investigating the kite system, partial buzzes, in particular, are a possible artifact of such behavior. However, the heightened call activity and higher numbers of partial buzzes at altitudes corresponding with the ABL are not expected from this artifact hypothesis, but are predicted from the hypothesis that bats are feeding aloft on migrating moths.

At 1182 m for orientation calls, and 862 m for feeding buzzes, we claim the AGL altitude records for echolocations and documented foraging activity by bats. During our studies with kites, the winds aloft abated each night at *ca.* 1000 m AGL, limiting our ability to place equipment at altitudes above 1200 m (Fig. 5B). Thus, we detected bat activity to altitudes as high as we were able to operate the bat detectors. Radar in Texas documents that large numbers of

Brazilian free-tailed bats fly as high as 3000 m AGL (Williams et al. 1973). Other reports also support the occurrence of high-altitude flights by bats, including an airplane strike with a hoary bat at 2438 m AGL (Peurach 2003). There is no reason to suspect that we have as yet recorded the maximum altitudes above the ground at which bats fly and feed.

Many bats are known to fly above canopies in open, uncluttered airspace. These bats typically have wings with high aspect ratio and high wing loading, characteristics that allow for rapid flight in unobstructed airspace (Norberg and Rayner 1987; Norberg 1990). Species in the families Molossidae, such as *Tadarida spp.*, and Emballonuridae, such as *Taphozous spp.* (Fenton and Griffin 1997) fit this syndrome, as do some members of the family Vespertilionidae, including *N. lasiopterus*, the migratory bird-eater in Europe (Popa-Lisseanu et al. 2007) and North American bats of the genus *Lasiurus.* Calls in three files recorded at altitudes of 105–476 m AGL by radio microphones suspended from kites had minimum frequencies ranging from 31 to 40 kHz. This is higher than is typical of the calls of Brazilian free-tailed bats (Gillam and McCracken 2007), but consistent with expectations for the calls of red bats (*Lasiurus borealis*) (Obrist 1995), another migratory, high-flying species. In the absence of a call library for the bats in the region, attributing these calls to red bats is speculative.

While there is evidence that many bats are adapted for feeding at high altitudes, so is there evidence that many insects occur at these same altitudes. Yet, the use of this aerosphere as a foraging habitat by bats has received little study. The long-distance, seasonal transport of large populations of insects, many of them important crop pests, has been documented on every continent where the topic has been examined (Drake and Gatehouse 1995). The consumption of crop pests by Brazilian free-tailed bats provides significant agronomic and ecological services (Cleveland et al. 2006; Federico et al. 2008), much of it occurring well above the ground. While unusual in their numbers and, perhaps, in opportunities for study, there are no reasons to expect that the behavior or ecological significance of bats in the aerosphere above Texas is unique.

Acoustic monitoring provides a "window" to the behavior of bats, but the view has been largely restricted to a few tens of meters above the ground. The ability to place radio microphonic bat detectors aloft expands this view and allows us to investigate the activity of bats in an important habitat that is increasingly impacted by human technology, particularly by communication towers and the proliferation of wind-power turbines (Kunz et al. 2007; Arnett et al. 2008; Horn et al 2008). In addition to linking the activities of bats and insects aloft, we anticipate that the use of radio microphones will provide a better understanding of migratory behaviors and the local movements of bats in relation to weather, wind patterns, and local and regional topographies, with the goal of ameliorating impacts of technology on bat populations.

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