

OBSERVATIONS ON THE REPRODUCTIVE BEHAVIOR OF CAPTIVE *TADARIDA BRASILIENSIS MEXICANA* (CHIROPTERA: MOLOSSIDAE)

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ABSTRACT—Descriptions of distinct behaviors and vocalizations associated with mating are available for some bat species, but similar observations have not been reported for the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*). In this paper, we describe the sequence and timing of scent marking activity, territorial defense, and vocalizations associated with pre-mating activity for two captive colonies of this species. Males in these captive colonies developed a distinctive odor and marked territories by rubbing secretions from their gular glands on surfaces of cages. These males demonstrated an obvious affinity for particular locations within the cage and appeared to defend these areas, both vocally and physically, against intrusion by other males. Two types of audible vocalizations were noted in relation to pre-mating activity by these males. The first was a buzz that may have been used to announce establishment of mating territories and to call females to these areas. The second was a faint chirping vocalization that may have functioned as a mating song or perhaps an indication of more immediate sexual intent.

RESUMEN—Existen algunas descripciones sobre distintos comportamientos y vocalizaciones asociados con el apareamiento de varias especies de murciélagos; sin embargo, observaciones similares no han sido reportadas en el murciélago mexicano de cola libre (*Tadarida brasiliensis mexicana*). En este artículo describimos la secuencia y el patrón temporal de marcaje con olores, defensa territorial y vocalizaciones asociadas con la actividad precopulatoria en dos colonias en cautiverio de esta especie. Los machos en estas colonias desarrollaron un olor característico y marcaron su territorio restregando las superficies de las jaulas con una secreción producida en las glándulas gulares. Estos machos mostraron una preferencia obvia por un sitio particular dentro de la jaula, el cual era defendido físicamente y con vocalizaciones contra la intrusión de otros machos. Se registraron dos tipos de vocalizaciones audibles en relación al comportamiento precopulatorio de los machos. El primero fue un zumbido que pudo haber usado para anunciar el establecimiento de un territorio de apareamiento y para atraer hembras hacia estas áreas. El segundo fue un débil chirrido que pudo haber funcionado como canto de apareamiento o quizás una señal de un intento sexual más inmediato.

Behaviors associated with reproduction in some bat species include scent marking with secretions from the gular gland (Horst, 1966; Rasweiler, 1987, 1988, 1992; Heideman et al., 1990), territorial defense and establishment of uni-male/multi-female groups (Kleiman and Racey, 1969; Dwyer, 1970, 1971; Bradbury and Emmons, 1974; Racey, 1974; Bradbury, 1977a, 1977b; Porter, 1979; McCracken and Bradbury, 1981; Morrison and Morrison, 1981; Gerell and Lundberg, 1985; Wilkinson, 1985; Vaughan and Vaughan, 1986). Distinctive vocalizations have also been associated with courtship, territorial defense, and copulations (Nelson, 1964; Kleiman and Racey, 1969; Roer

and Egsbaek, 1969; Khajuria, 1972; Bradbury and Emmons, 1974; Racey, 1974; Wickler and Seibt, 1976; Bradbury 1977a, 1977b; Barclay and Thomas, 1979; Porter, 1979; Miller and Degn, 1981; Gerell and Lundburg, 1985; von Helversen and von Halversen, 1994; Wilkinson, 1995).

The mating behavior of migratory populations of the Mexican free-tailed bat, *Tadarida brasiliensis mexicana* (Molossidae), has not been documented. Southwestern populations of this species leave the United States and overwinter in Mexico. They return to southwestern parts of the United States between February and April. They are known to roost in caves, mines,

bridges, and buildings. Females form large maternity colonies, mainly in caves, where young are born and raised in June and July. Males form smaller colonies. Cave populations in the southwest fluctuate widely during October, and most bats have left again by December (Barbour and Davis, 1969).

In this paper, we describe behavior associated with reproduction in two captive colonies of Mexican free-tailed bats, *T. brasiliensis mexicana*, including the sequence and timing of scent marking behavior, aggressive territorial defense, and pre-mating vocalizations.

MATERIALS AND METHODS—Two captive colonies of *T. brasiliensis mexicana* observed in this study were composed of injured or orphaned bats accumulated during wildlife rehabilitation. Colony A contained 15 males and 12 females in the fall of 1994. Additional bats were added so that the colony consisted of 17 males and 18 females in the fall of 1995. These bats were obtained from north central Texas between 1991 and 1995. Colony B contained 9 males and 14 females in the fall of 1994. Additional bats were added to Colony B so that it consisted of 10 males and 15 females in the fall of 1995. These bats were obtained from south central Texas between 1993 and 1995.

Colony A was housed in Mineral Wells, Texas, and Colony B in Austin, Texas. These colonies were housed in wooden cages measuring 1.3 m by 0.7 m by 0.6 m and 1.2 m by 0.6 m by 0.6 m, respectively. Walls were grooved horizontally, and the ceilings and doors were covered with nylon window screen to facilitate roosting and nonflight movement within the cage. Cage A was enclosed in a netted flight area (3.1 m by 6.1 m by 2.1 m); no flight area was provided for Colony B. Small padded fabric "roosting pockets," varying in dimension from 10.2 cm by 10.2 cm to 20.3 cm by 20.3 cm, were placed along the sides of each cage to create easily cleaned crevices for roosting. Cages were kept under artificial lighting for approximately 12 h per day. Colony A received both 60 watt fluorescent and 40 watt incandescent lighting, Colony B received both 100 watt incandescent light and ambient light that entered directly through a 0.6 m by 0.9 m window that received morning light and was positioned approximately 3 m from the screened cage door.

The diet of both colonies consisted of whole mealworm larvae, *Tenebrio molitor*, as well as a blended mixture of mealworm larvae, banana, and veal (see Lollar, 1994, for specifics regarding the routine care and maintenance of the bats in these colonies). Bats in Colony A were hand-fed the blended mixture twice daily, mornings and evenings. Those in Colony B were hand-fed the blended mixture once a day, in

the early evening. Bats in both colonies also had nightly access to an unlimited supply of mealworm larvae provided in feeding containers placed throughout the cages, although not all bats self-fed from this source. Individual bats in both colonies were identified by specific injuries and distinctive characteristics.

Hand-feeding sessions varied from one to two h in length, and bats in both colonies were given the opportunity to consume as much food during hand-feeding sessions as they chose. General notes on male and female roosting positions, male scent marking behavior, male/male and male/female interactions and associated vocalizations were recorded during: 1) each of the hand-feeding sessions, and 2) additional random intervals in each 24 hour period throughout the entire two years of this study. There was no protocol of randomizing observations nor for standardizing observations between the two observers. Observations were made whenever it was convenient for the observers and were intended only to provide general and introductory descriptions of specific behaviors previously observed in Colony A. Vocalizations were recorded on a TEAC W-514 tape recorder, modified frequency response 1 KHz–60 KHz, with a Panasonic WM-60AT microphone cartridge, preamped to boost high frequency. Sonographs were subsequently printed using the program Spectra Plus 3.0. Audible vocalizations emitted by the bats during territorial activity were recorded ad hoc. Specific attention was focused on males exhibiting scent marking, aggression, or territorial behavior. Visual observations of this behavior were also videotaped using a Sharp 12× VHS Slimcam. Comparisons between monthly activity records were made to determine the timing and sequence of scent marking, territorial defense, and vocalizations associated with pre-mating activity.

RESULTS—Bats in both colonies typically selected specific fabric pouches for roosting with minimal aggressive interactions except for minor disputes over roosting positions within pouches. These disputes were mostly vocal and were generally resolved in less than ten seconds.

In early November 1994, 2 of the 15 males in Colony A began roosting alone in pouches seldom used previously. They were observed rubbing their chests, throat (gular gland), pelvic, and anal areas on pouch surfaces (inside and outside) and on surrounding cage walls. Both males became aggressive and obviously defended their new roosting pouches, emitting a series of loud, audible buzzes (hereafter called "territorial buzzes"). This buzz was com-

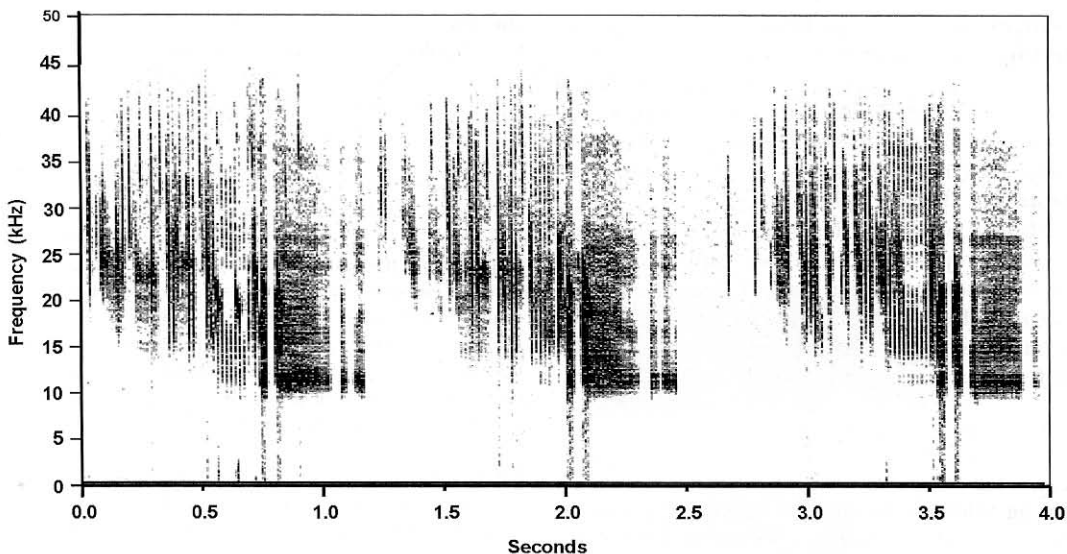


FIG. 1—Sonogram: Loud buzzes made by males that appeared to defend roosting territories.

posed of 16 vocal bursts per second, ranging from 10 to 40 kHz including harmonics. The buzz was often repeated three times within a four second interval (Fig. 1). These males chased and often bit other males, but permitted females to roost in the newly established territories. Nine females were observed roosting with one of these territorial males, A-1, be-

tween the months of November, 1994, and February, 1995. Only one of these females was observed roosting with the second territorial male, A-2, for approximately one week during the month of November before moving into A-1's pouch.

While females were in his pouch, A-1 made faint chirping vocalizations (Fig. 2) unlike the

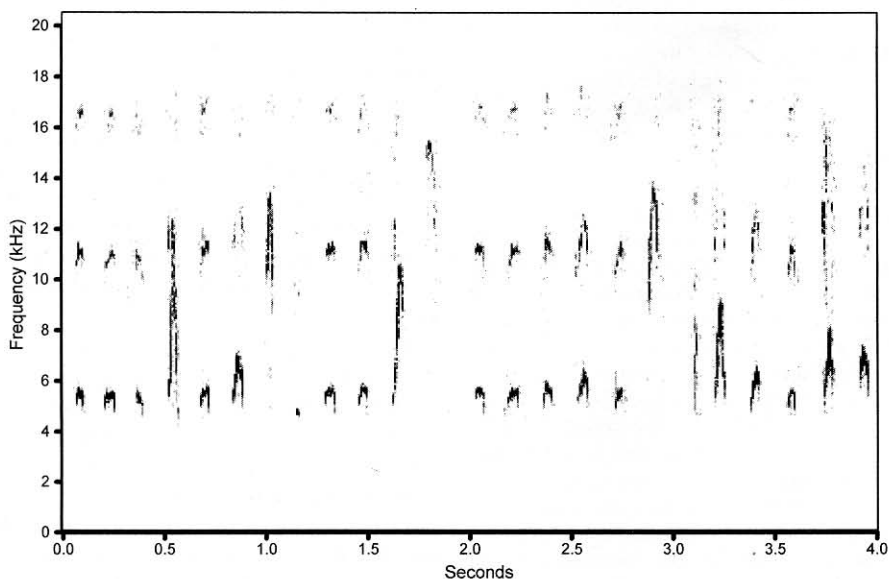


FIG. 2—Sonogram: Faint chirping vocalizations made by mating males prior to copulation.

territorial buzzes, or any other sounds normally detected from the colony. This was a four second vocalization composed of seven vocal bursts per second with three distinct harmonic tiers centered between 5 and 6 kHz, 10 and 12 kHz, and 17 and 19 kHz. This vocalization was made as he positioned himself near the pouch opening, facing a small group of females inside. When a female was removed for hand feeding, the resident male responded with territorial buzzes, often hanging from the opening of the pouch and flapping his wings until the female was returned. If the female was placed in some other section of the cage, A-1 emitted territorial buzzes until the female returned to his pouch. Aggression and associated vocalizations continued into early March 1995, when both A-1 and A-2 roosted again with the rest of the colony and resumed nonaggressive behavior.

When the two territorial males resumed roosting in communal pouches, the nine females that had roosted with A-1 moved to another pouch (here called a maternity pouch) where they roosted together. All nine females gave birth within the maternity pouch between 11 April and 30 April 1995.

Male territoriality was also observed in Colony B, although marking and aggression did not begin until January 1995, about two months after it began in Colony A. In this colony, several of the nine males became aggressive, chasing other males, but only one (B-1) was observed roosting in a pouch with females separate from communal roosting areas. Five of the 14 females in the colony were observed roosting in male B-1's pouch. This male also made faint chirping vocalizations while roosting with females. Three of these females became pregnant and subsequently moved into a different pouch (maternity pouch), again with a second male (B-2) that chased off other males attempting to enter. The three pregnant females gave birth later than those in Colony A and ranging over a two-month period. Pups born on 3 June and 10 July 1995 survived. A pup born on 7 August 1995 was stillborn.

In 1995, mating activity in Colony A began in October, a month earlier than in 1994. Eight of the 17 males in the colony established and aggressively defended territories in different pouches. These eight males emitted territorial buzzes from the openings of their pouches.

These buzzes appeared to elicit responses from females that rapidly approached and entered the calling male's pouch. All eight males emitted faint chirping vocalizations when roosting with females in their newly established territories, and male A-4 was observed copulating with a female immediately after emitting this sound. Most of the 18 females in this colony appeared to move independently from one male's pouch to another, remaining several days in each before moving to another male's pouch. One of the eight territorial males, however, was only observed roosting with a single female for approximately one week, after which, the female moved into another male's pouch.

Territorial males chased and bit non-territorial males that came within 5 to 8 cm of their respective pouches. Neighboring territorial males often moved 5 to 10 cm outside of their respective pouches onto the cage wall at their common boundary and faced one another with their noses approximately 2 to 3 cm apart, opened their mouths wide and moved their heads very slowly from side to side and up and down. On numerous occasions, territorial males were observed approaching the fabric pouches of other territorial males and ferociously biting at the pouches. On two separate occasions, a non-territorial male, A-5, entered the pouch of a territorial male, A-6. In both instances, A-6 chased the intruding male to the opening of the pouch where they engaged in an aggressive display, locking jaws and striking repeatedly at one another with folded wings while vocalizing loudly. On the first occasion, the non-territorial male moved to a communal roosting pouch, and the intruding male began rubbing his chest, throat (gular gland), and pelvic areas on the pouch and surrounding cage wall, where he remained and defended this pouch thereafter. This male, A-5, was born in captivity to female AF-1 in May 1994. AF-1 was the only female that did not continue roosting (i.e., was not subsequently observed roosting) in the pouch with male A-5.

When females left the pouches of territorial males to feed, these males emitted territorial buzzes. Females sometimes appeared to respond to these buzzes by immediately returning to the buzzing male's pouch. This male would then jump on the female as she approached, and vocalize rapidly for several sec-

onds. During this time, the female hung quietly against the cage wall with ears lowered until released by the male, at which time the female would re-enter his pouch. If a female did not respond immediately to the resident male's vocalizations by returning to his pouch, he sometimes left his pouch in an apparent attempt to "herd" her back in. On two occasions when a female that had been roosting with one territorial male was placed near the pouch of another territorial male, she was attacked by the second male, bitten and chased away.

There was a decrease in the level of aggression exhibited by territorial males beginning in early March, and all but four males had moved out of their mating territories and into communal roosting pouches by mid-March. One female aborted a partially developed fetus on 14 March. Only five females continued roosting with the four males that continued to defend mating territories into late March; the remainder of the females were roosting in communal roosting pouches at this time. Four females gave birth to live pups on 24 April, 26 April, 2 May, and 12 May.

Colony B consisted of 15 females and 10 males at the beginning of 1996. Half of the males segregated from the females on 16 January. These males were observed together in one roosting pouch. By 19 January, 7 of the 10 males in Colony B (including B-1) had moved into separate roosting pouches. Four of these seven males as well as B-3, an older male that did not establish a mating territory, emitted a pungent, musky odor (noted for individuals bats on 4, 11, and 25 January). The gular gland of two of the territorial males and B-3 had also become visibly enlarged during this month (first noted on 11 January). There was increased aggression among males in the colony, and the seven males that marked roosting areas frequently emitted territorial buzzes while in the openings of their pouches. Territorial males also frequently emitted the faint chirping vocalizations while roosting with females that began moving into their pouches. All four of these males were also observed in what appeared to be a copulatory position with roost mates immediately following vocalization. Most of the 15 females in this colony appeared to move independently from one male's pouch to another, remaining several days in each before

moving to another pouch. Four of the seven territorial males were observed roosting at one time or another with most of the females. These four males exhibited behavior similar to that of the territorial males in Colony A, including buzzing and wing flapping when females were removed from pouches for hand feedings, the apparent use of territorial buzzes to call females back to roosting pouches following self-feeding episodes, and brief displays directed at returning females immediately before the females entered these pouches.

On 25 February, two territorial males temporarily abandoned their roosting pouches and were observed roosting in alternate pouches typically occupied by non-territorial males. One of these males returned to his previous roosting pouch the following day; the other continued to roost in alternate pouches for a week before returning to his former territory. On 29 March, one female aborted a partially developed fetus. Three females gave birth on 16 May, 23 May, and 30 May. Male aggression and the frequency of territorial buzzes and chirping vocalizations began decreasing in frequency by late March. Most of the females began roosting in communal roosting pouches and territorial males also began moving back and forth between established roosting territories and communal roosting pouches at that time. Some males continued to move back and forth between established territories and communal roosting areas throughout the observation period ending July 1996.

DISCUSSION—Other investigators have suggested that male molossids develop distinctive odors (Herreid, 1960) and use the gular gland to mark roosts or females during times of reproductive activity (Horst, 1966; Quay, 1970; Rasweiler, 1987, 1988, 1992; Heideman et al., 1990). Males in the captive colonies in this study also developed a distinctive odor and marked territories by rubbing secretions from their gular glands and anal areas on surfaces of cages. These males demonstrated an obvious affinity for particular locations within the cage and appeared to defend these areas, both vocally and physically, against intrusion by other males. Similar behaviors during times when marking takes place have been reported in other molossid bats (Heideman et al., 1990). Male territorial behavior toward some females also

has been described in other species of bats (Bradbury, 1977a).

Territorial defense, courtship, and copulation have been associated with distinctive vocalizations in other bats. (Nelson, 1964; Kleiman and Racey, 1969; Roer and Egsbaek, 1969; Khajuria, 1972; Bradbury and Emmons, 1974; Racey, 1974; Wickler and Seibt, 1976; Bradbury 1977a, 1977b; Barclay and Thomas, 1979; Porter, 1979; Thomas et al., 1979; Miller and Degn, 1981; von Helversen and von Helversen, 1994; Wilkinson, 1995). We believe buzzes emitted by males in our captive colonies (Fig. 1) were intended specifically to announce establishment of mating territories and to call females to these areas. The faint chirping vocalizations emitted by these males (Fig. 2) may have been a mating song or perhaps an indication of more immediate sexual intent, as postulated in the case of the copulation call of *Myotis lucifugus* (Barclay and Thomas, 1979).

Male aggression and chirping began in October (1995) and November (1994) in Colony A, and in January (1994 and 1995) in Colony B, increased in intensity in February and early March, and began diminishing in frequency by late March in both colonies. Although male calling and territorial defense were not observed after April, some males in both of these colonies continued to move back and forth between communal roosting areas and previously established territories throughout the observation period ending in July 1996. Different feeding and housing protocols, including access to natural light, may have contributed to differences in timing of reproductive behaviors between the two captive colonies. Differences between some of the births in the captive colonies and those documented in wild populations also were likely the result of variations due to captive conditions.

Chirping vocalizations similar to those recorded in the captive colonies also were observed by the authors in 1996 preceding what appeared to be copulatory acts in wild colonies in Texas at sites that serve as summer maternity roosts for wild populations, including a building in Mineral Wells, Texas and a cave (Bracken Cave) near San Antonio, Texas on 17 March and 28 March, respectively. In that same year, a similar vocalization preceding copulation was also observed at a bridge in Williamson Co., which serves as a nursery site for

600,000 to 700,000 free-tailed bats, on 22 March (B. Keeley, pers. comm.). Of 713 free-tailed bats received from wildlife rescue organizations in Austin, Texas between 13 January and 24 January 1997, 81% were males, suggesting the majority of overwintering bats may be males. Together these observations suggest that, in some cases, males may set up mating territories in maternity roosts prior to formation of summer nursery colonies.

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