

Library of Social Communication Calls of the Mexican Free-tailed Bat, (*Tadarida brasiliensis*)

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Introduction

The authors (BF and AL) have maintained two captive colonies of Mexican free-tailed bats (*T. brasiliensis*) over a period of several years. Both colonies are composed of injured or orphaned bats that could not be released. At least a portion of the buzzes, chirps, and clicks used by these bats during social interactions are audible to the human ear and over time we have come to recognize the behaviors associated with many of them (Lollar, 1994, 1995; French and Lollar, 1998, 2000; French et al., 2000).

Bats in colony A originated from north central Texas and included 15 males and 12 females in 1994, 17 males and 18 females in 1995, and 32 males and 45 females in 1999. Bats in colony B originated from south central Texas and included 9 males and 14 females in 1994, 10 males and 15 females in 1995, 40 males and 18 females in 1999. In 2003, colony B was separated into a bachelor colony with 29 males and a reproductive colony with 14 males and 16 females.

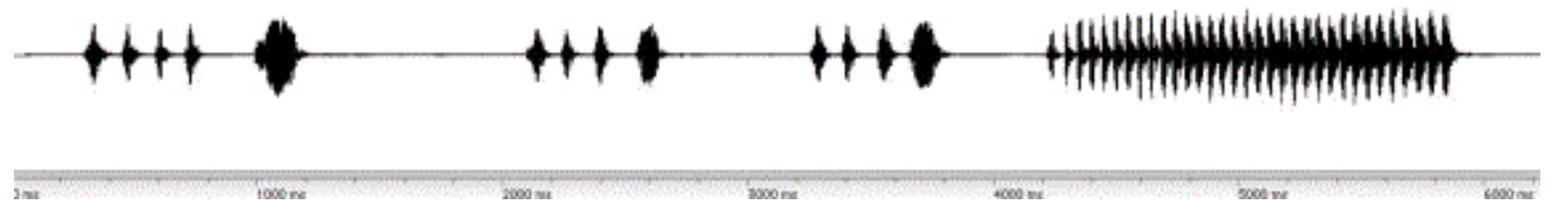
Bats in both colonies A and B were housed and cared for as described in Captive Care and Medical Reference for the Rehabilitation of Insectivorous Bats (Lollar and Schmidt-French, 2002). Both colonies exhibited predictable activity patterns which included periods of social interaction, daily torpor, two night-time feeding bouts separated by a period of rest when many of the bats clustered in alternative night roosting areas. Hand-feeding sessions varied from one to two hours in length. Notes on male and female roosting positions, male scent marking behavior, male/male, male/female, female/female, and mother/pup interactions, and associated vocalizations were recorded in both colonies during hand-feeding sessions and at random intervals from 19 February, 1999 through 1 August, 2000. There was no protocol of randomizing observations nor for standardizing observations between the two observers (BF and AL).

Audible vocalizations emitted by the bats were recorded ad hoc in both colonies from 19 February, 1999 through 1 August, 2000. Additional vocalizations and visual records were recorded in colony B from January through April, 2003. In 1999-2000, vocalizations were recorded on a TEAC W-514 tape recorder, modified frequency response 1 kHz-60kHz, with a Panasonic WM-60AT microphone cartridge, preamped to boost high frequency. In 2003, vocalizations were recorded using a B&K 1/2-inch microphone type 4133 and a B&K preamplifier model 2669; the signal was passed through a custom built 8X expander and then recorded at a sample rate of 44.1 kHz on a Macintosh powerbook. Attention was focused on vocalizations that were repeatedly associated with specific behaviors; behaviors were documented with a Sony Night-Shot camcorder. A total of 20 distinctive calls were recorded in both colonies. Samples of each call type and descriptions of associated behaviors are given

below.

Results

1. Territorial announcement buzz—This buzz was emitted by reproductively active males observed marking mating territories. The male dabbed its anus and penis on a roosting pouch or surrounding cage surface, leaving a small secretion, and then repeatedly rubbed his gular gland on the same surface, and sometimes rubbed the top of his head in the marked area. These males emitted territorial buzzes and often flapped their wings in the areas they marked. They also emitted the buzz when another male approached, generally chasing the intruder away. Territorial males sometimes bite and locked jaws with intruding males. A territorial male also emitted this buzz while hanging from the opening of his roosting pouch and flapping his wings whenever a female left or was removed from his pouch. Territorial buzzes ranged from 8 to 40 kilohertz. (Graph shows call slowed 8 times.)

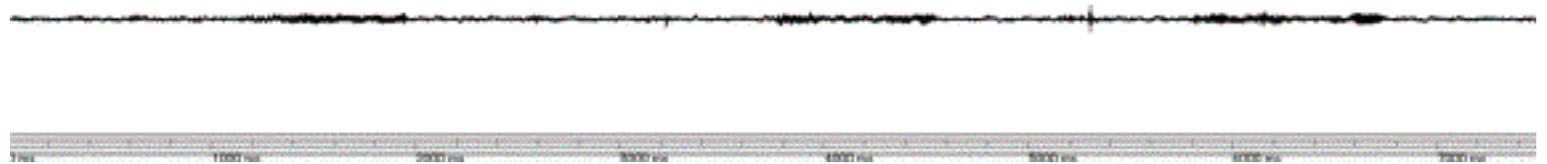


2. Warning call—This call consisted of a series of loud clicks emitted in the roost when two bats confronted one another, face to face with lips drawn back and teeth bared (see photo). Bats often bobbed their heads up and down and from side to side while in this position. These calls generally took place either inside of, or just outside of, roosting pouches used by territorial males. Although the call appeared to be associated with territorial behavior, it was mainly a ritualistic display that did not generally result in physical aggression. Warning calls ranged from 16 to 26 kilohertz. (Graph shows call slowed 8 times.)



3. Screeching—This was a "screeching" sound emitted by two bats engaged in actual physical confrontation with jaws locked onto one another. These disputes always involved at least one, sometimes two, reproductively active males and started within a short distance (10cm) of one of the male's mating territories. Like the warning call, this vocalization was associated with territorial disputes, but screeching was accompanied actual physical aggression.

4. Courtship or Marking Call—This was a soft, musical sound emitted by reproductively active males while females were roosting with them in their established territories. The male sometimes raised and lowered his wings slightly while emitting the call. Females did not generally appear to resist copulatory acts initiated by males inside of established territories. Courtship calls ranged from 5 to 6 kilohertz. (Graph shows call slowed 8 times.)

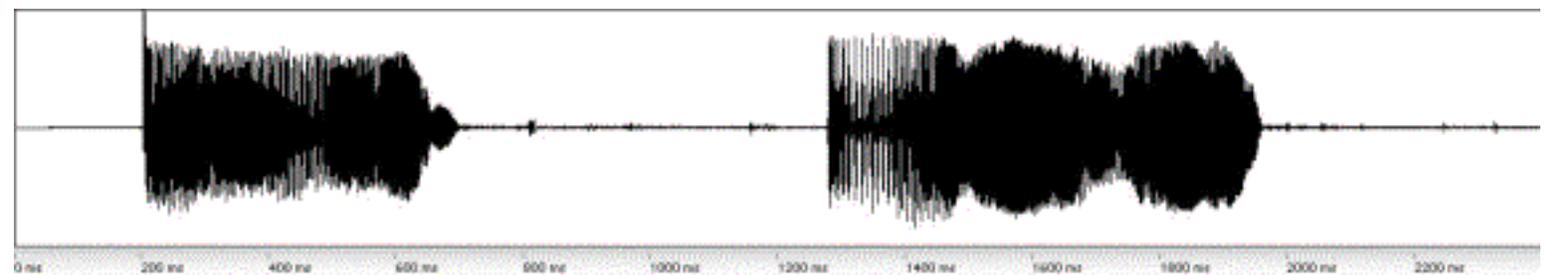


5. Female response call—This call was a quiet sound emitted by reproductively active females in response to (immediately following) male territorial calls and dominance scolds. Females often emitted the call when they approached a calling male's territory. Females also emitted the call immediately following copulation with a territorial male. Female response calls ranged from 15 to 30 kilohertz. (Graph shows call slowed 8 times.)



6. Dominance scold—A male often met a female approaching his territory by jumping on the female's back, and repeatedly jerking his entire body as he pressed his face into the female's shoulders while emitting this series of notes. The female took on a passive posture during this call, lying crouched against the cage wall with ears lowered. When the vocalization stopped, the

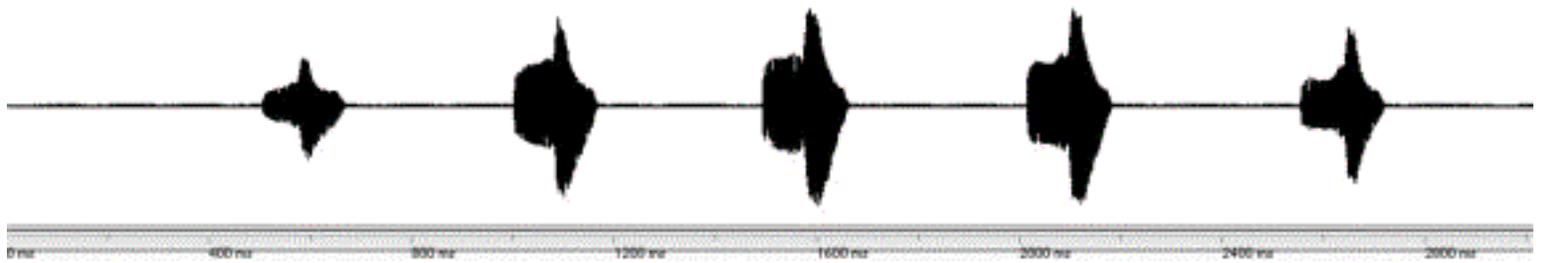
female often emitted the female response call. Then the female entered the male's roosting pouch, followed by the male. Young males less than one year of age often jumped onto the back of other bats, both females and males, and pressed their muzzles into the other bats' shoulders. During this time, they emitted a sound very similar to the dominance scold made by reproductively active males. Dominance scolds ranged from 1 to 35 kilohertz. (Graph shows call slowed 8 times.)



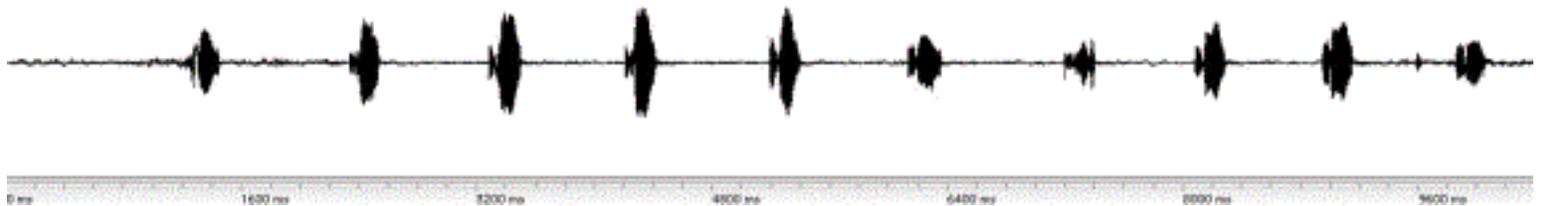
7. Herding buzz—This call consisted of a series of buzzes emitted by territorial males while inside their roosting pouches. The male emitted the buzz while forcefully pushing his face into the bodies of the females that shared his roosting pouch and chasing them around until they formed a tight cluster in one corner. The call was also emitted by males when they caught reproductively active females outside of established territories. A male grabbed a female at the scruff of the neck or ear with his teeth while emitting this buzz. Females struggled against copulatory attempts outside of established male territories. If the female did not escape, copulation took place when the female was caught. Herding buzzes ranged from 18 to 33 kilohertz. (Graphs shows call slowed 8 times.)



8. Directive call—This sharp repetitive call was emitted by some females during the birthing process and by all females immediately after giving birth. A female emitted the call while facing her newborn infant and intermittently as she rubbed her muzzle back and forth from side to side across the infant's face and body. Females also emitted the call in response to their infants' isolation calls as they approached their young to nurse. In addition, females who gave birth to stillborn pups continued to emit these calls periodically for up to four days following the birth. Directive calls ranged from 8 to 47 kilohertz. (Graph shows call slowed 8 times.)



9. Isolation call—This sharp repetitive call was emitted by neonates immediately following birth in response to the mother's directive call and by pups prior to weaning whenever their stomachs were empty. The call changed somewhat as the infant matured. Milk was visible through the translucent skin of the abdomen after pups nursed. Pups did not emit the call when isolated from their mothers at times when their stomachs were full. Mothers responded to these calls with directive calls, which they repeated as they approached their infants to nurse them. Isolation calls range from 12 to 40 kilohertz. (Graph shows call slowed 8 times.)



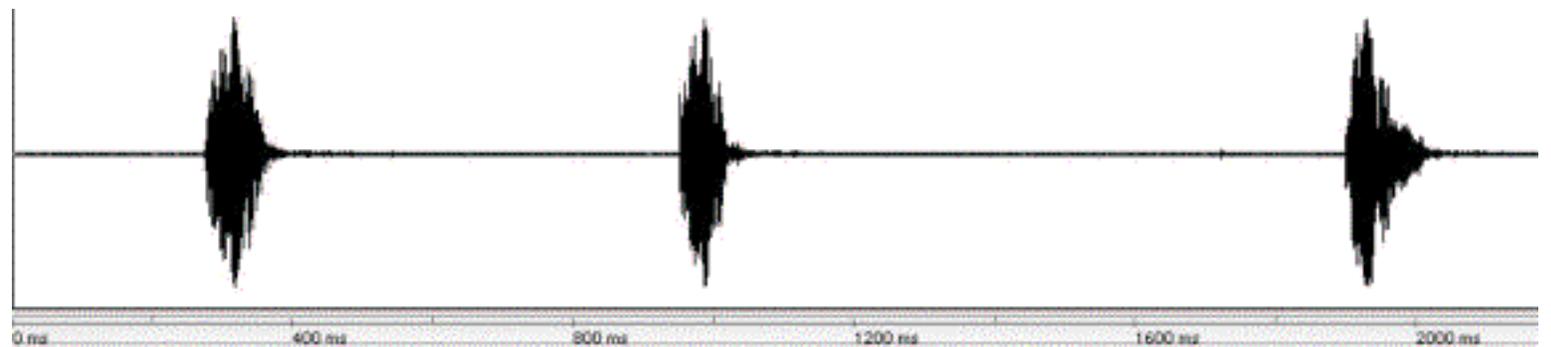
10. Practice flight call—This call was a soft "fluttering" sound emitted by pups between three to five weeks of age, prior to the time they were able to fly, and were emitted during episodes of rapid wing flapping. (Call below has been slowed 3 times.)



11. Chattering—This was a relatively soft "chattering" sound emitted by both males and females during periods of physical contact when bats were at rest. Bats often rubbed their muzzles against one another when making this sound. Chattering was composed of 2 harmonics and ranged from 16 to 50 kilohertz. (Graph shows call slowed 8 times.)



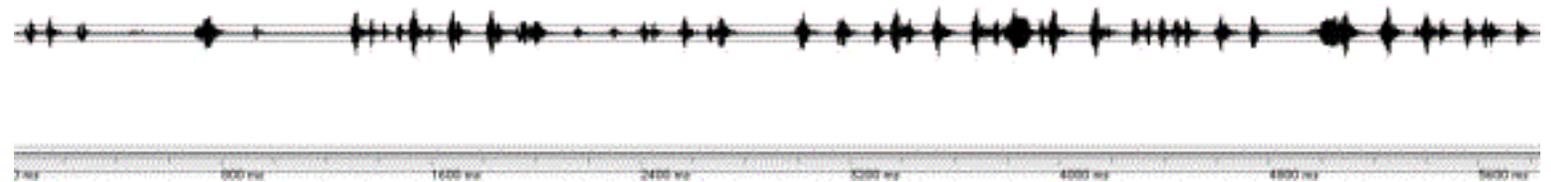
12. Exaggerated chittering—This was a somewhat modified or exaggerated version of chittering emitted by both males and females during periods of nonaggressive physical contact. While emitting this sound, a bat sometimes hopped a few centimeters forward towards another bat or turned its head toward another bat, firmly pressing its muzzle into and quickly back and forth from side to side across the other bat's body. These bats also sometimes gently tapped the other bat with a folded wing while making this call, although no real aggression took place during the encounter. Exaggerated chittering ranged from 7 to 35 kilohertz. (Graph shows call slowed 8 times.)



13. Questioning call—This call was emitted by both males and females when disturbed in the roost by an outside source. A bat emitted the series of soft clicks as it approached the intruder (human caretaker) and sometimes actually touched the human hand with its nose before turning and rejoining the cluster of bats. Questioning calls ranged from 22 to 45 kilohertz. (Graph shows call slowed 8 times.)



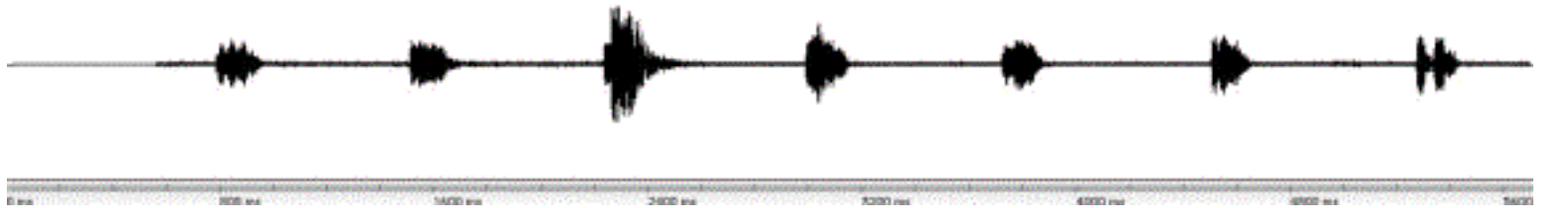
14. Escape cry—This call consisted of a series of clicks or flutter-like calls emitted by males and females running or flying out of a roosting pouch or corner of a roosting cage when sufficiently disturbed by an outside source. While initial intrusion into a roost area would initiate the questioning call, continued disruption or manipulation to the roost would result in the escape cry and associated fleeing activity. Escape cries ranged from 17 to 38 kilohertz. (Graph shows call slowed 8 times.)



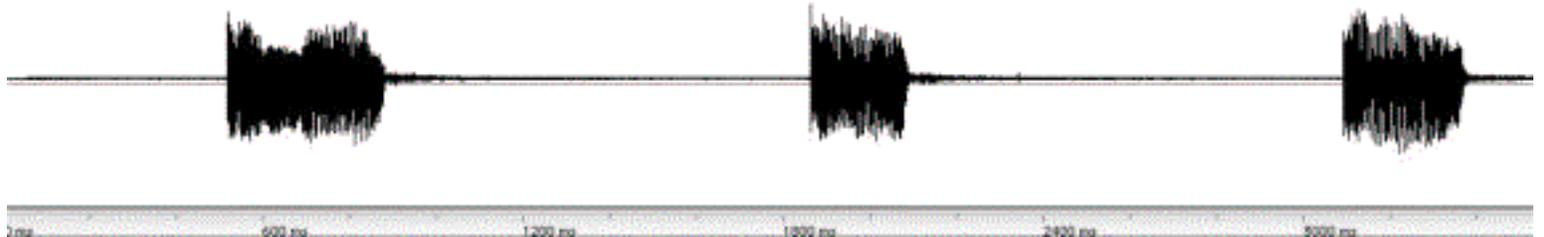
15. Irritation buzz—Bats emitted these calls in communal roosts while butting heads. This buzz was emitted by both males and females whenever they were physically disturbed in the roosting cage (i.e. handled) by the authors for the purpose of hand feeding, roosting pouch maintenance, or routine physical examinations. Irritation buzzes ranged from 18 to 60 kilohertz. (Graph shows call slowed 8 times.)



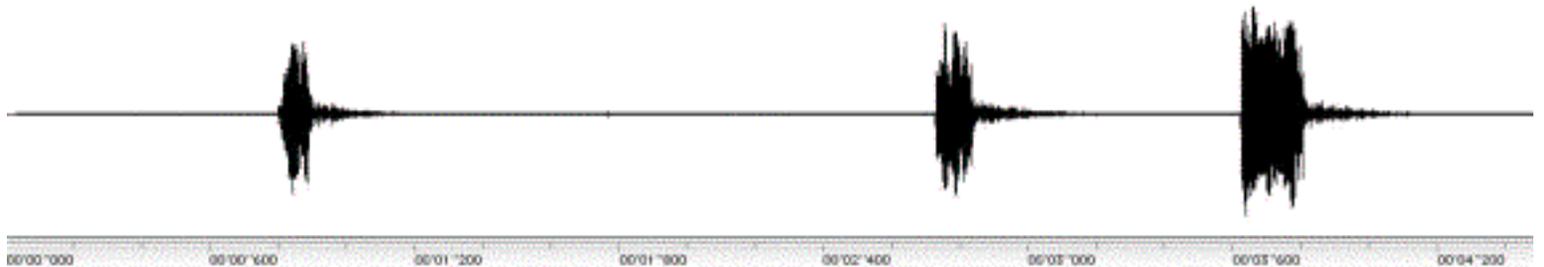
16. Squabbling—often emitted by multiple bats simultaneously, including both males and females, as they appeared to jostle for roosting positions, forcefully pushing their bodies into one another. Squabbling sometimes deteriorated into protest squeals. Squabbling ranged from 21 to 29 kilohertz. 17. Protest squeal—This was either single or multiple sharp squeals emitted by both males and females in response to aggression by another bat (e.g. bite), or sometimes in response to treatment of an injury by the caretaker. Protest squeals were also emitted by females attempting to resist copulatory acts by aggressive males. (Graph shows call slowed 8 times.)



17. Protest squeal—This was either single or multiple sharp squeals emitted by both males and females in response to aggression by another bat (e.g. bite), or sometimes in response to treatment of an injury by the caretaker. Protest squeals were also emitted by females resisting copulatory attempts by non-territorial males. Protest squeals range from 1 to 48 kilohertz. (Graph shows call slowed 8 times.)

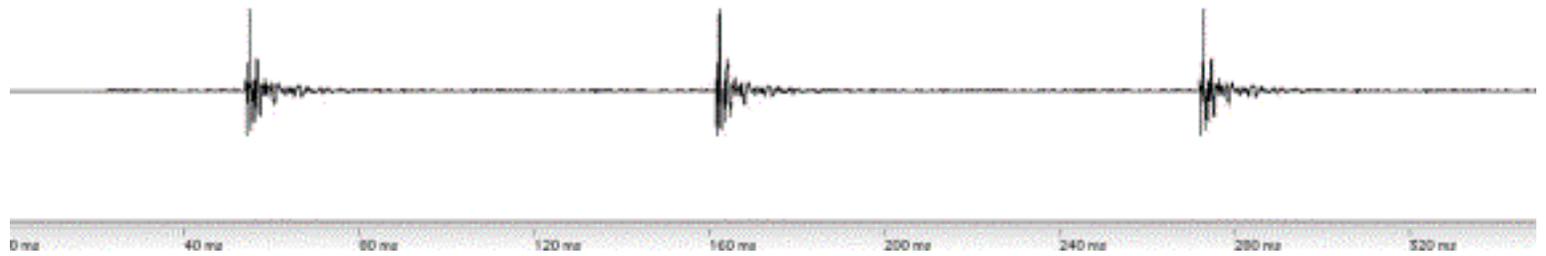


18. Alarm call—This call consisted of a series of loud clicks only emitted by a very limited number of bats, either male or female, when first received by the authors. The bat raised its body up by extending the elbows, opened its mouth wide and bared its teeth, jerking its entire body repeatedly while emitting these sharp clicks. The behavior appeared to be elicited in response to a perceived threat from unfamiliar handling attempts. Alarm calls ranged from 9 to 47 kilohertz. (Graph shows call slowed 8 times.)

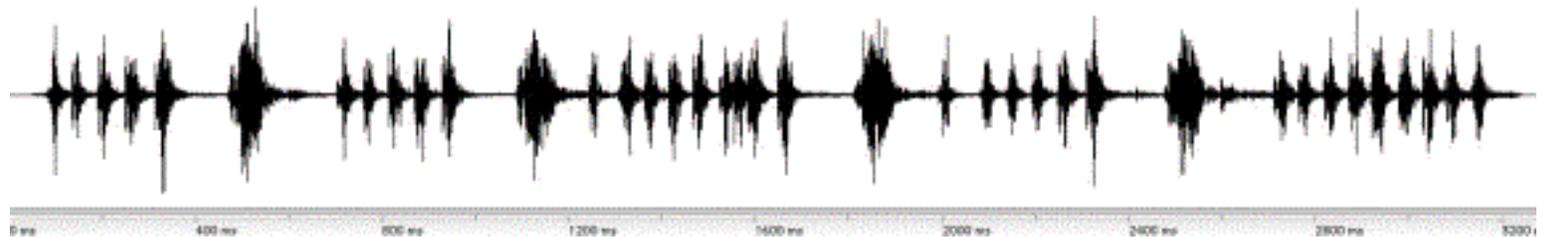


19. Anticipation click—This call consisted on a series of “sneeze-like” sounds emitted by bats in

the early evening just prior to the time when feeding activity took place. Bats also emitted these clicks again in the early morning when handlers entered flight cages for the purpose of hand feeding bats. Anticipation clicks were also emitted by some bats following hand-feeding sessions. Anticipation clicks ranged from 2 to 22 kilohertz. (Graph shows sound slowed 8 times.)



20. Food solicitation chirp; food solicitation buzz—The food solicitation call consisted of a series of chirps emitted by either males or females as they crawled toward the caretaker during hand-feeding sessions. When repeated rapidly, the chirps sounded like buzzes. Bats often emitted these buzzes while hanging on a roosting pouch or cage wall and flapping their wings until handed a mealworm. After eating the mealworm, they repeated the call and wing flapping behavior until handed another one. Food solicitation calls ranged from 1 to 60 kilohertz. (Graph shows call slowed 8 times.)



Discussion

Twenty distinctive vocalizations were recorded in both colonies. Irritation buzzes were emitted by both males and females while butting heads in the roost. These calls were also emitted whenever bats were physically disturbed in the roost by the authors for the purpose of hand feeding, roosting pouch maintenance, or routine physical examination. Similar vocalizations were described in a wild colony of *Antrozous pallidus* by Orr (1954). Squabbling was associated with both males and females while they were in roosting pouches and appeared to be associated with disputes over roosting positions. Anticipation clicks were “sneeze-like” sounds emitted by both males and females when handlers entered caging areas for the purpose of hand feeding bats. Similar clicks have been heard by the authors in wild colonies of this species

just prior to their emergence from daytime roosts. Similar, nonvocal, explosive nasal sounds were documented in a wild colony of *Antrozous pallidus* by Orr (1954) and believed to be associated with a clearing of the nasal passages. An alarm call was emitted when a bat bared its teeth and raised up its body by extending its elbows. Some bats emitted the call when initially removed from glass containers used to transport them to the authors. These bats were always exposed in the container. Such behavior appeared to be a defensive response to a perceived threat. (The behavior was never observed by the authors when bats were delivered in fabric or wooden carriers containing cloths or other materials within which the bat could hide.)

Chittering was associated with both males and females in this study during periods of physical contact as bats rubbed their muzzles together and appeared to be associated with periods of relaxation or contentment. Similar sounds were also documented by Orr (1954) in a wild colony of *Antrozous pallidus*. An exaggerated chittering sound was emitted by bats as they hopped towards other bats and resembled a kind of play.

Territorial or announcement buzzes were emitted by reproductively active males and were often accompanied by wing flapping. These calls appeared to announce mating territories and were intended to both attract females and warn other males away. Warning calls were emitted in the roost when two males confronted one another and bobbed their heads in ritualistic displays associated with territorial disputes. Territorial disputes occasionally involved physical aggression as males locked jaws and emitted screeches. The authors have received injured males from the wild that had been observed in similar confrontations. These males had visibly enlarged gular glands. Distinctive vocalizations have also been associated with courtship, territorial defense, and copulation in other bat species (Nelson, 1964; Kleiman and Racey, 1969; Roer and Egsback, 1969; Khajuria, 1972; Bradbury and Emmons, 1974; Racey, 1974; Wickler and Seibt, 1976; Bradbury 1977a, 1977b; Barclay and Thomas, 1979; Porter, 1979; Miller and Degen, 1981; Gerell and Lundburg, 1985; von Helversen and von Helversen, 1994; Wilkinson, 1995). When females were removed from the pouches of territorial males, males often emitted territorial calls. Females sometimes responded to these calls with a series of quiet clicks (female response calls).

The dominance scold was emitted by reproductively active males when females approached the roosting pouch being occupied by the male. The male left his roosting pouch to meet the approaching female, jumped on her back and emitted this series of vocalizations while the female assumed a submissive posture against the cage wall. Females sometimes responded with the female response call. When the vocalization stopped, the female, then the male entered the roosting pouch. This vocalization appeared to function as a way for the male to display dominance over the female. Once inside roosting pouches, these males emitted a series of buzzes while appearing to "herd" the females into a small group. These same herding buzzes were emitted by non-territorial males after they caught reproductively-active females. Females caught by the non-territorial males emitted protest squeals, and often struggled free from the male's grasp. The courtship or marking call was emitted by territorial males while females were in their roosting pouches. A male raised his wings slightly and sometimes moved his ears up and down as he made this call as if in display. Males sometimes rubbed the gular gland on roosting

surfaces as he emitted this song-like call. As a note of interest, males appeared at times to dab their penises into the gular gland on their throats and then dip their chin in the gland. This activity was followed by the male flapping his wings as he emitted the territorial call. The wing flapping may serve to disperse an individual male's odor towards females in a manner similar to that exhibited by *Saccopteryx bilineata* (Voigt, 1999)

Directive calls were emitted by females during the birthing process and following birth. Females emitted this call intermittently as they approached their infants and as they nudged the infant's face and body with their muzzles. Isolation calls were emitted by infants immediately following birth and sporadically throughout the weeks they were still nursing whenever their stomachs were empty. The call therefore appears to be an attempt to solicit food. Mothers responded to these calls periodically with directive calls as they approached their infants to nurse them. Both directive calls and isolation calls have also been recorded in wild populations of the Mexican free-tailed bat and described as methods by which mothers and pups identify and locate one another in large colonies (Balcombe, 1990; Balcombe and McCracken, 1992).

The fact that mothers who did not give birth to viable young continued to give directive calls for up to four days following birth is of interest as some mothers who gave birth to stillborn infants were observed nursing and responding to the isolation calls of other young in colony A. One female in particular who did not give birth to a viable infant was subsequently observed nursing the infant of another female. Both females responded to the isolation call of this pup and continued to nurse the infant over a period of three weeks. The practice of calling after a pup has died could be a method by which these mothers are able to establish relationships that allow them to assist in raising other pups or to adopt pups who have lost mothers. Such behavior could account for the small percentage of nonparental nursing observed in wild colonies—McCracken, 1984). Practice flight calls were emitted by pups prior to the time they were able to fly, and were associated with a rapid flapping of the wings.

Bats, both male and female, emitted a series of chirps to solicit food during hand-feeding sessions. Some bats emitted the familiar series of chirps and then a series of buzzes to solicit food.

In summary, the authors have heard vocalizations in wild colonies of this species that were similar to those recorded from the two captive colonies, including the isolation call, directive call, warning call, irritation buzz, territorial announcement buzz, courtship or marking call, squabbling, screeching, anticipation click, chattering, exaggerated chattering, escape cries, and protest squeals. Some of these vocalizations have been recorded in wild colonies of the Mexican free-tailed bat (Balcombe, 1990; Balcombe and McCracken, 1992) and similar vocalizations have been described in wild colonies of other species (Orr, 1954). Behaviors associated with these vocalizations in the captive colonies in this study suggest that they are mainly associated with mating activity, territorial defense, the process of giving birth, individual recognition/location, food solicitation, and both passive and aggressive social interactions. Together these observations give us a cursory view of what appears to be a complex social communication system of a highly colonial bat species.

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