Roosting behavior of the Mexican free-tailed bat (\emph{Tadarida brasiliensis}) in a highway overpass

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ROOSTING BEHAVIOR OF THE MEXICAN FREE-TAILED BAT (TADARIDA BRASILIENSIS) IN A HIGHWAY OVERPASS

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ABSTRACT.—A colony of Mexican free-tailed bats (Tadarida brasiliensis) roosting in an interstate highway overpass in Belton, Bell County, Texas, was studied weekly from 28 June to 21 November 1996 (except for the week of 4 July). We examined 2 aspects of roosting behavior: site-specific fidelity to locations within the roost and gender-related segregation within the roost. Colony estimates based on guano production showed a marked decrease in the number of bats from 19 to 26 July; many of these departing bats were adult females. No female bats sampled after this interval were pregnant. Male bats outnumbered females on nearly all sampling occasions. Throughout the study, one section of the roost was dominated by males, ranging from 83% to 100% of total bats. The majority of bats recaptured at least once were faithful to specific locations within the roost, and more than 70% of bats recaptured multiple times were faithful to specific roost locations.

Key words: Tadarida brasiliensis, roosting ecology, roost fidelity, intraroost fidelity, sexual segregation.

Roosts are important features in the life histories of bat species (Kunz 1982). Whether in natural or anthropogenic structures, roosts provide refuge from predators and inclement weather. They also are locations where breeding may occur and where young are born and reared. In this study we investigated intraroost segregation and intraroost site fidelity of Mexican free-tailed bats, Tadarida brasiliensis, within a man-made structure (a highway overpass). Tadarida brasiliensis, a relatively common species throughout the southern United States (Barbour and Davis 1969), is the most common species of bat in Texas (Schmidly et al. 1977, Schmidly 1991). A highly social species, T. brasiliensis uses a wide variety of roosts including caves, attics, culverts, bridges, and highway overpasses (Cockrum 1969, Fraze and Wilkins 1990, Adam and Hayes 2000).

Previous studies of roosting habits in this species have demonstrated segregation within a site on the basis of age and sex (see references in Wilkins 1989). For example, Krutzsch (1955) reported segregation of young from adult bats after parturition in an attic roost, with young bats occupying the center and adults confined to the ends of the room. Distinct segregation of adults by sex was shown for an attic-roosting colony of T. b. cynocephala in Florida, with females roosting in the main section of the attic and males restricted to an alcove in the northeastern corner of the attic (Hermanson and Wilkins 1986).

McCracken (1984) demonstrated that female Tadarida brasiliensis in large maternity colonies relocate and nurse their own young approximately 83% of the time, a remarkable feat considering the millions of young present in these caves. This suggests a spatial awareness in the bats. However, little is known about intraroost positioning of individuals within a site, and site-specific fidelity (return of an individual to the same location within a roost after one or more departures from the roost) is not well documented. The purpose of this study was to examine roosting patterns of T. brasiliensis in the expansion joint of a highway overpass to determine if (1) spatial segregation based on gender and (2) site-specific fidelity occur within the roost.

METHODS AND MATERIALS

Site Description

The roost that we studied is located in the highway overpass at the intersection of Interstate 35 and Farm-to-Market Road (FM) 436, in Belton, Bell County, central Texas (31°02′ N, 97°28′ W). Bats occupied the only expansion joint in this structure; the joint spans the full

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length of the underside of the overpass (Fig. 1). The expansion joint is 3.1 cm wide by 49.0 cm deep by 66.5 m long and is divided into 100 individual compartments separated by metal bolts (Fraze 1989). Concrete embankments are present at both the north and south ends of the overpass. The overpass is divided into 4 sections by 3 series of concrete support columns oriented in an east-west direction. One set of columns is located in the median of FM 436, a 4-lane divided roadway. The other 2 sets of columns are situated at the base of the north and south embankments.

We designated 21 sampling sites along the expansion joint (Fig. 1). Seven sites, positioned at 1-m intervals from the top of the embankment, were sampled above the north embankment of the overpass. Six sampling sites were similarly designated above the south embankment. We selected 4 sampling sites above the westbound lanes of FM 436 (north roadway), 2 over the sidewalk and 2 directly over traffic lanes. Similarly, we established 4 sampling sites above the eastbound lanes of FM 436 (south roadway), 2 over the sidewalk and 2 directly over traffic lanes. Accessibility was a primary determinant of specific locations of sampling sites. We could reach the sites above the concrete embankments by standing on the embankments. Sites above roadways were reached by a hydraulic boom-arm lift and bucket from locations where the vehicle could be parked safely.

### Sampling and Handling of Bats

We sampled the colony weekly (except for the week of 4 July) during a 21-week period from 28 June through 21 November 1996. On each sampling day we removed up to 5 bats per sampling site from the roost and placed them into cloth sample bags marked to denote sample site. Bats were removed from the roost by gently nudging them with a dowel to the edge of the crevice. We grasped them delicately with long forceps and then placed them into holding sacks. All sampling was conducted between 0900 and 1100 hours.

Within 2 hours of capture, all bats were individually examined in the field. Females were assigned to 1 of 3 reproductive categories (pregnant, lactating, or nonreproductive) following Kunz et al. (1995) and Sgro (1997). Bats were weighed to the nearest 0.1 g by using an Ohaus C305-S portable electronic balance. We examined both canine wear (Twente 1955, Davis et al. 1962) and development of the metacarpal-phalangeal joint of the fourth digit (Davis and Hitchcock 1965, Kunz and Anthony 1982) to determine age. Bats were then placed into 2 categories of relative age: those with conspicuously dull or blunt canines were classified as adults, whereas individuals with conspicuously sharp or pointed canines were classified as juveniles. Bats were banded with uniquely numbered plastic split rings (size XB, A.C. Hughes Ltd., Hampton Hill, Middlesex, England); use of bands of different colors allowed visual determination of sex without having to handle the bat subsequently.

### Population Estimates

The amount of guano produced at the site was used to estimate the population of the roost (Fraze 1989, Fraze and Wilkins 1990, Sgro 1997).
We collected guano at the end of the following sampling days: 19, 26 July; 1, 8, 15, 22 August; 5, 12 September; 10, 17, 31 October; 14, 21 November. Rain and heavy winds removed guano accumulations during the 8 other weekly sampling sessions and prevented collection. Any remaining guano was swept up and discarded on days when weather prevented collection, allowing a new 1-week guano sample to be deposited at the site.

We swept guano along a 2.0-m-wide strip directly beneath the expansion joint. Though most of the guano that fell from the roost accumulated on this strip, some was blown by prevailing light winds beyond the collection zone, resulting in conservative estimates of colony size. Because some sections of the expansion joint were directly over heavily trafficked roadways, we could not sweep the entire distance along the expansion joint. However, we were able to sweep 49.4 m of the length, or 74.3% of the full length of the roost (Fraze 1989). Guano was placed into a plastic bag and the date of collection recorded on the bag. Drying time and subsequent dry weight of collected guano were calculated after returning to the laboratory. We initially weighed a 250-mL sample of guano to the nearest 0.1 g by using an Ohaus C305-S electronic balance. This sample was then heat-dried by volume at 70°C and weighed every 30 minutes to the nearest 0.1 g. Once an asymptotic weight was reached, we used the time recorded for drying all weekly samples. Guano samples were heat-dried at 70°C for 3 hours and dry mass recorded to the nearest 0.1 g. We then calculated average daily guano production at the roost by dividing the total amount collected in a given sampling period by the number of days between collections.

Individual bats were collected from the roost for the purpose of determining the amount of guano produced by a single bat over a 12-hour interval. We collected 30 bats on the following days: 15 August, 6 bats; 17 October, 4 bats; 14 November, 6 bats; 21 November, 14 bats. Bats were captured and placed into individual cloth sample bags. After 12 hours of captivity, they were released and guano was collected from each sample bag. This 12-hour interval approximates the time bats spend in the day roost depositing guano.

Guano produced by individual bats was dried and then weighed to the nearest 0.0001 g using a Fisher Scientific XA analytical balance. From those figures we calculated an average of individual bat guano production over a 12-hour interval. Average daily guano production at the site was divided by average per capita guano production over a 12-hour interval. This provided a means for estimating the number of bats at the roost during each guano-sampling period. Such estimates were divided by 0.743 to correct for the 25.7% of the distance beneath the roost that could not be swept.

Our use of guano production as an indicator of population size assumes that similar amounts of guano are produced by active individuals, independent of sex, reproductive condition, age (other than neonates), or season. There is evidence, however, that feeding rates in female Tadarida brasiliensis vary with reproductive condition, the intake of food nearly doubling from pregnancy into lactation and again from early lactation to mid-lactation (Kunz et al. 1995). Increased food intake likely would increase volume of guano produced. If so, then our estimates of colony size during the intervals of pregnancy and lactation are perhaps overestimates.

**Data Analyses**

We performed analysis of the data using the Statistical Analysis System (1990). To test for sex-biased segregation, chi-square tests of independence and Fisher’s exact tests were run on frequencies of sex categories for the 4 sections (north embankment, north roadway, south roadway, south embankment). Fisher’s exact test can be used when sample sizes are relatively small (Hays 1994). Site-specific fidelity was tested by calculating the likelihood of a bat randomly returning to any 1 of 21 sampling sites and the likelihood of bats returning one or more times to a sampling site. A binomial probability and associated P-value were then determined. Alpha levels were set at 0.05.

**RESULTS**

**Population Estimates**

Thirty individual bats were captured to determine per capita guano production. The amount of guano produced daily per individual bat ranged from 0.0064 g to 0.5558 g ($\bar{x} = 0.0646$ g, $s = 0.0985$ g). The amount collected weekly by sweeping ranged from 574.9 g on
Population estimates based on guano production at the site ranged from 10,729 bats on 19 July to 1711 bats on 15 August (Fig. 2). A sharp decrease in the estimated population occurred between 19 and 26 July (from 10,729 bats to 2118 bats). After this date the population fluctuated between approximately 1700 and 5000 bats for the duration of the study, with notable increases on 1 August (from 2118 bats to 4661 bats) and 17 October (from 3221 bats to 5048 bats).

Similar numbers of bats were sampled from the northern and southern halves of the overpass roost, with 632 bats (50.2%) from the northern half and 627 (49.8%) from the southern half. Overall, bats seemed to prefer roosting over roadway segments of the site (29% over southern roadway, 31.1% over northern roadway) to roosting over embankment sites (19.1% over northern embankment, 20.8% over southern embankment). And, during population ebbs, relatively few bats roosted over embankments.

Sex-related Patterns

The 1259 bats sampled included 806 males (64% of the sample) and 453 females (36% of the sample). Reproductive condition was determined for 430 (95%) of these females. No pregnant bats were captured after 12 July. Lactating females were found in samples from 12 July to 22 August, with the highest weekly percentage lactating (87%) on 1 August. The percentage of nonreproductive females was erratic from 28 June to 26 July, but it steadily increased throughout August. From 29 August onward, no females were pregnant or lactating (Fig. 3).

Male bats outnumbered females during all but 3 weeks (Fig. 4): On 1 August, equal numbers of males and females were handled. Females represented 52% of the sample on 19 July and 63% on 29 August, a date when the south roadway could not be sampled. The vast majority of bats (83% to 100%) roosting in the south roadway section throughout the study were males. In contrast, the proportions of females in the other 3 sections of the overpass were greater than the proportion of females in the south roadway section. A drastic drop in the percentage of females occurred in all 4 sections of the overpass between 19 and 26 July (north embankment, from 57% to 11%; north roadway, from 60% to 11%; south roadway, from 15% to 5%; south embankment, from 71% to 46%), the same time as the large population decrease. Analyses for differences in sex-class frequencies between the 4 sections of the roost indicated significant P-values for chi-square and Fisher’s exact tests on all sampling dates.
Fig. 3. Reproductive status (pregnant, lactating, or nonreproductive) of female Tadarida brasiliensis sampled at the Belton overpass roost during 1996. From 29 August until sampling was completed on 21 November, no females were pregnant or lactating.

except 15 August (no bats present over the north embankment), 29 August (south roadway was not sampled), and 19 September (no bats over south embankment).

Site-specific Fidelity

Initial banding of bats occurred on 12 July. After being banded and released, most bats quickly returned to the roost. The majority of bats that returned immediately to the roost rarely went to the same location from which they had been captured. The sample of 103 recaptures was analyzed to evaluate site-specific fidelity. The first recaptured bat was caught on 19 July. We recaptured 86 bats: 72 bats recaptured only 1 time, 11 bats recaptured twice, and 3 bats recaptured 3 times. Of the 14 bats recaptured multiple times, 11 (7 females and 4 males) returned to the same roost location at least once. In 56 different instances, bats were recaptured in the same location where they had been banded, representing 54% site-specific fidelity. Calculating this percentage only for bats recaptured within 1 m from where they were banded resulted in 62% site-specific fidelity. On 67 occasions bats were recaptured within 2 m of their original capture location, representing 65% site-specific fidelity. Nine bats were recaptured in corresponding locations at the opposite end of the overpass from where they were initially captured and banded.

The likelihood of a single bat returning to any 1 of 21 sampling sites by random chance was 0.04762. Of the 86 bats recaptured, 46 (22 female, 24 male) returned to the same location 1 or more times. Therefore, the proportion of bats returning 1 or more times to the same location was 0.53488. The cumulative binomial probability for bats returning 1 or more times to the same location was >0.99999 (P < 0.00001). A cumulative binomial probability was then calculated for bats recaptured 2 or more times. There were 31 multiple recaptures (i.e., individuals with 2 or more recaptures); for 23 of these, bats were found in the same location where they had been banded each time they were recaptured. Therefore, the proportion of recaptures at the same location to 2 or more total recaptures for a bat was 0.70968. The cumulative binomial probability for bats recaptured 2 or more times returning to the same location was >0.99999 (P < 0.00001).

DISCUSSION

Population Estimates

Examination of population estimates at the Belton roost indicates that a large number of
bats left the roost during the week following the 19 July sample, the date with the highest population estimate. The rapid decrease in percentages of female bats in all 4 sections of the overpass roost from 19 July to 26 July was coincident with the rapid decrease in number and percentage of adult bats documented at the site. Both phenomena occurred when female bats sampled were no longer pregnant. These observations suggest that female bats giving birth early in the parturition period might have vacated the roost and moved to alternate site(s) once their young had attained adult size and volancy. Fraze (1989) documented movement of bats between the Belton roost and a culvert roost 11.3 km to the south in Salado. His study showed that at approximately this same time, 26 July, the bat population at Salado reached its highest density, with most (89%) being female. Fraze also documented movement of banded bats between the Belton and Salado sites. This offers indirect evidence that some of those females vacating the Belton roost after their young became independent might have moved to the Salado roost. Fraze and Wilkins (1990) suggested that the Salado site acts as a "spillover" roost. However, it is evident from the data that those females giving birth late in the season were still lactating and suckling young beyond 26 July at the Belton roost.

Reasons for females vacating the Belton roost once their young became volant might be related to physiological stress of roost overcrowding. Glass (1982), for example, associated the onset of the autumn exodus from nursery caves in Oklahoma with the need for relief from overcrowding. At the population peak in Belton (19 July), bats were seen hanging, many completely exposed, from the protruding bolts and along the exterior bevel of the expansion joint.

Population estimates at the Belton roost fluctuated between approximately 2000 and 5000 bats from 5 September to 21 November 1996. *Tadarida brasiliensis* from the Great Plains region begin their southward migration in late August and early September. This migration continues through October, and by November the population is concentrated from central Texas southward (Glass 1982). One possible explanation for the fluctuations in population estimates at the Belton roost during this time may be the presence and subsequent departure of bats that are migrating south for the winter. Davis and Cockrum (1963) found that transient bats often use artificial roosts. Fraze (1989) suggested that the Belton roost serves as a stopover site during spring migration northward. This might suggest that the Belton roost also serves as a stopover site for bats migrating southward during autumn.

**Sex-related Patterns**

Bats segregate within the Belton roost based upon sex. Eighty-six percent of all sampling

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**Fig. 4.** Weekly percentages of male and female *Tadarida brasiliensis* sampled at the Belton overpass roost during 1996.
dates show that sex-related segregation occurs between the 4 main sections of the overpass roost. The only dates not indicating such segregation were days on which complete samples could not be obtained.

The vast majority of males occupied the south roadway section throughout the study, the percentage of females roosting in this section never exceeding 17%. Although the sex ratio for the entire roost still favored males, females in the other 3 sections of the overpass (north and south embankments, north roadway) were relatively more abundant than females in the south roadway. Similar sex-biased segregation within an attic colony of Tadarida brasiliensis was documented in Florida (Hermananson and Wilkins 1986). These investigators found that males congregated in an alcove in the northeastern corner while females roosted in the main section of the attic. A study of Myotis lucifugus documented similar sex-biased segregation within another attic colony (Davis and Hitchcock 1965). They found that adult males roosted in crevices beneath sloping regions of the roof while females congregated at the roof peak. Both studies were in artificial sites, and both reveal similar patterns of segregation of the sexes.

Site-specific Fidelity

The recapture data clearly show that over 70% of the bats sampled more than once exhibited fidelity to specific locations within the Belton roost. Based upon recaptures, minimal residence times within the roost ranged from 1 week to over 4 months. This suggests that the site is a long-term, summer day-roost for at least a portion of the population. The findings demonstrate that many bats return to the same locations within the Belton roost and remain faithful to these positions during at least part of their residency at the site. The data also suggest that male and female bats exhibit similar degrees of fidelity to a specific site. Fidelity to certain sites may be associated with proximity to food sources (Kunz 1982), defense of territory (McWilliam 1987), availability and structure of roosts (Brigham 1991), or reproductive advantages (Brigham and Fenton 1986).

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