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AN ECOLOGICAL STUDY OF A RESIDENT POPULATION OF *TADARIDA BRASILIENSIS* IN EASTERN TEXAS

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The literature concerning free-tailed bats of the species *Tadarida brasiliensis* in the United States was summarized by Barbour and Davis (1969). Additional details on the ecology and movements of this species in Texas were given by a number of authors, especially Short *et al.* (1960) and Davis *et al.* (1962).

Both *Tadarida brasiliensis cynocephala* and *Tadarida brasiliensis mexicana* occur in Texas, but it is not known if their ranges overlap. Barbour and Davis (1969) suggested the two may be reproductively isolated and thus might not interbreed even if sympatric. Davis (1966) considered the two to be distinct species, but most recent authors have preferred to consider them as subspecies of *T. brasiliensis* as proposed by Schwartz (1955).

T. b. mexicana is a migratory cave bat, which is thought to be absent from Texas between late December and late February except for a few individuals in the extreme south, and is believed to be scarce but present during most of early December and March (Davis *et al.*, 1962). During the remainder of the year *T. b. mexicana* is abundant, especially in the guano bat caves of the Edward's Plateau of central Texas. During migration they commonly occur in buildings along the flight path. In the autumn, migrants from Oklahoma also are present in Texas (Glass, 1959).

T. b. cynocephala is apparently a nonmigratory subspecies roosting primarily in man-made structures, but apparently never in caves (Barbour and Davis, 1969).

The *Tadarida* colony we studied in College Station is situated near the eastern edge of the distributional limits of *T. b. mexicana* as shown

on the range map of Davis (1966), approximately 137 kilometers northeast of the eastern limit of the Edward's Plateau, the region where *mexicana* is known to be abundant (Davis *et al.*, 1962). However, College Station is also less than 80 kilometers west of the western edge of the east Texas pine-hardwood forest region where *T. b. cynocephala* occurs.

A series of 18 specimens collected by LaVal at a colony in Houston, Texas (137 kilometers southeast of College Station) was identified as *T. b. cynocephala* by Dillard C. Carter (personal communication), whereas 46 specimens from the College Station colony were identified by Carter as *T. b. mexicana*. Most of these specimens were collected during the winter.

In the research effort described herein we hoped to band a large percentage of the population that occupies or uses the College Station roost and thus be able to study monthly population fluctuations and temporal and seasonal occurrence of individual bats in the colony. Finally, from these data, we hoped to be able to make some statement relating the College Station colony to other populations of *Tadarida brasiliensis* in Texas.

MATERIALS AND METHODS

The *Tadarida* colony was sampled at least once monthly during an 18-month period. Mist nets were set across one entrance of the structure occupied by the colony; other entrances were closed during netting. A total of 1063 bats was banded with No. 2 bat bands furnished by the U.S. Fish and Wildlife Service. Of these, 668 were males and 395 females. Initially, captured bats were banded and released about 200 meters from the site of capture. In the autumn of 1970, captured individuals were banded at the site of capture and immediately released so that data on elapsed time away from the roost could be recorded. Netting was initiated at sunset and terminated at midnight on a majority of nights. In the autumn of 1970, we netted twice from dusk to dawn and once from midnight to dawn.

During portions of January and February 1971, temperature data were obtained with thermistors inserted into the crevices utilized by the bats. Recordings were made with a Polypoint Sequential Compiler designed and built by James Albert of the Texas A&M Wildlife Electronics Laboratory. The system incorporated a Porto-Hygro-Therm (Model PHT) and a Rustrak single channel recorder (Model 288) for continuous monitoring. Other weather data were compiled from records of the Department of Meteorology, Texas A&M University.

Individuals prepared as museum specimens are deposited in The Museum, Texas Tech University or in the Texas Cooperative Wildlife Collection, Texas A&M University.

DESCRIPTION OF ROOST SITES

We know of two roost sites on the Texas A&M University campus. The larger and more heavily used site is located within the Animal Pavilion, a building housing a large, earthen-floored arena. The bats roost in crevices formed at the juncture of the walls and roof. Each crevice is approximately 5 centimeters deep, 30 wide, and 2.5 high. Several inaccessible intrawall spaces utilized by the bats appeared to be larger but could not be measured precisely. Each smaller crevice had a capacity of 15 to 25 bats.

The interior of the pavilion is not temperature-regulated at any time of the year. Numerous windows in the building are generally closed during the winter months and open throughout the summer. Three large doorways are normally open at all times. Laboratories situated beneath the grandstand seating area surrounding the arena supply only a minimal amount of heat to the interior in the winter.

During certain times of the year, primarily during the spring and autumn, the pavilion is occasionally used at night. At such times the interior of the building is lighted for periods ranging from one to six hours. The bats remain inside the building until the lights are turned out on such nights.

The second roost site is situated behind a metal gutter located on the west side of a building approximately 300 meters from the pavilion. This site seems to be poorly protected from environmental changes but is nevertheless occupied by bats except during periods of prolonged cold weather. We have been unable to collect individuals from this roost because of its inaccessibility.

POPULATION FLUCTUATIONS

Although we have no precise estimate of the total number of bats present at any given time in either of the two roosts known to us, differences in the number of bats caught per night at the accessible roost should reflect true differences in the total number of bats present in the roost. Although our data suggest that disturbance of the colony through banding activity affects the number of bats returning to the roost on a given night, there is no evidence that such disturbances have affected the number of bats utilizing the roost over extended periods of time. On 19 September, the first of the two all night netting periods, 89 individuals were recorded leaving the roost. Of these, only 14 re-

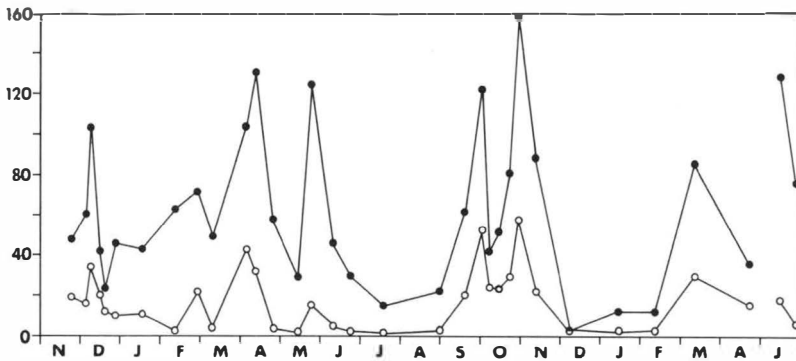


FIG. 1.—Fluctuations in a permanent population of *Tadarida brasiliensis* in College Station, Texas, from November 1969 to July 1971. Solid circles indicate total number of individuals caught per night; open circles indicate total number of females caught per night.

turned during the night. In addition, 33 bats not present in the roost the previous day entered the roost. The data for the second of the two all-night sessions, 15 October, revealed a similar pattern, with 53 bats leaving the roost, 15 of these returning, and 19 bats not present the previous day entering the roost.

Although our data indicate that many bats leaving the pavilion colony on nights of netting activity fly to another roost for the remainder of the night (probably to the other known roost on campus), we do not know how many bats would return to the pavilion roost on a night not netted. However, based on the two dusk-to-dawn netting efforts, and visual observations, we believe a much greater percentage of bats failed to return on the nights of netting activity.

That our banding activities did not lead to a decline in the number of bats utilizing the building is indicated by: 1) our observations of colony activity after netting was terminated each night; 2) by data from periods of unusually frequent netting activity (for example, see 7-29 October 1970, Fig. 1); and 3) by long-term population trends as indicated by numbers of bats captured (Fig. 1).

The total number of bats caught per night fluctuated substantially during the study period (Fig. 1), from a high of 159 (29 October 1970) to a low of three (8 December 1970). Year to year variation is well demonstrated by the catch of 61 bats on 5 December 1969.

Sexual composition of the colony fluctuated throughout the study period although males generally made up a greater percentage of the population (Fig. 2). Females were more abundant on only three occasions, one of which (8 December 1970) was represented by a sample size of only three bats.

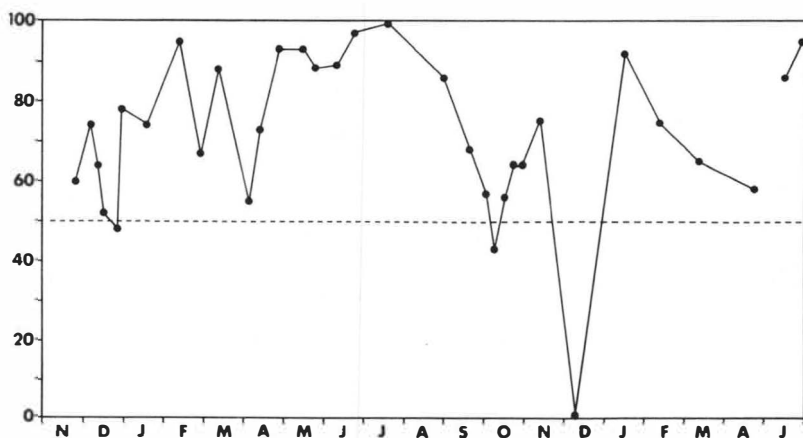


FIG. 2.—Sexual composition of the *Tadarida* colony from November 1969 to July 1971 expressed as percentage of males caught per night.

Our data reveal two principal periods during 1970 in which there were relatively large numbers of bats present in the roost (Fig. 1). These periods, spring and autumn, correspond to times when seasonal migrations of *Tadarida* to and from Oklahoma occur (Glass, 1959). The bimodal peak evident in spring 1970 (Figs. 1, 4) is probably a result of several factors. The high point in April can be attributed to: 1) high metabolic demands due to higher environmental temperatures, necessitating nightly feeding for all bats in the colony and 2) an influx of unbanded migrants of both sexes (Fig. 3). The peak in late May followed a low point during which migrant females had vacated the roost, leaving the males behind. A new influx of males, most of which were banded individuals, was added to the group of males already present, resulting in a second high. This pattern suggests differential migratory periods based on both age and sex. Notably, 63 per cent of the bats recaptured on 24 May had been banded prior to April; 70 per cent of these had been recaptured one or more times between their date of banding and April.

Although we cannot state conclusively that all or even most of these bats were permanent residents, our evidence strongly supports the hypothesis that a large number of bats are present throughout the winter, but that as individuals they do not emerge to feed on all favorable nights until warmer and more stable environmental conditions prevail (see section entitled "Overwintering and winter feeding activity").

A total of 94 females was banded during April 1970, but only four of these were recaptured on 24 May, suggesting that they were indi-

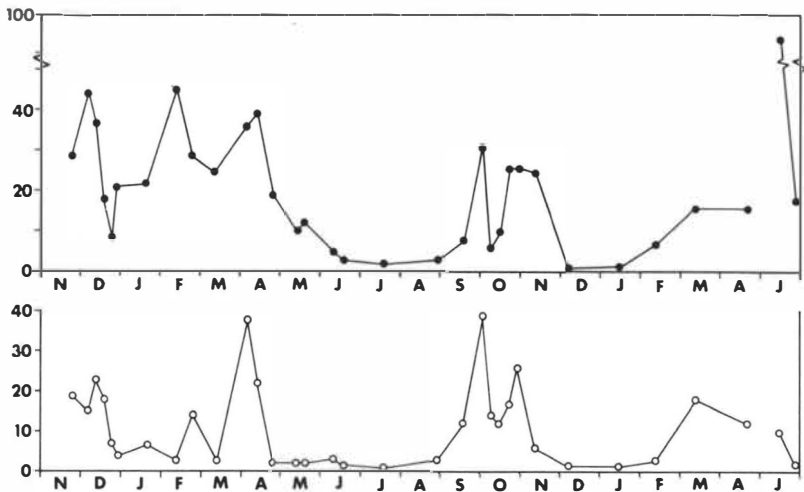


FIG. 3.—Number of unbanded bats caught per night throughout the study period. Solid circles indicate number of males; open circles indicate number of females.

viduals migrating to bat caves in Texas or Oklahoma. *Tadarida* begin arriving in Texas bat caves in late February (Davis *et al.*, 1962) and in Oklahoma caves in early April (Glass, 1958). It appears that at least some of the males may follow migratory patterns similar to those of the females, because approximately one-half of the males banded in April were not recaptured on 24 May.

Following May, the population of the pavilion colony dropped rapidly, remaining at the lowest levels for the year during summer (Fig. 1). Virtually all summering individuals were males. We have no evidence to indicate where the great majority of our banded bats spent the summer. It is conceivable that the few females resident in the winter migrate to the bat caves with the transient females. However, dissection showed that females caught in February, March, and April contained no embryos. Over-wintering females, early transient females, or both may be nonreproductive, and may not go to the nursery caves. The earliest date on which pregnant females were obtained was 14 May 1969. These individuals were unbanded when caught. Transient females netted in late May were usually pregnant.

From mid-September through early October 1970 there was a rapid increase in the number of bats utilizing the pavilion roost. Figs. 3 and 4 indicate that banded males constituted the largest percentage of the catch during this period, outnumbering banded females and unbanded individuals. In early October there was a relatively large

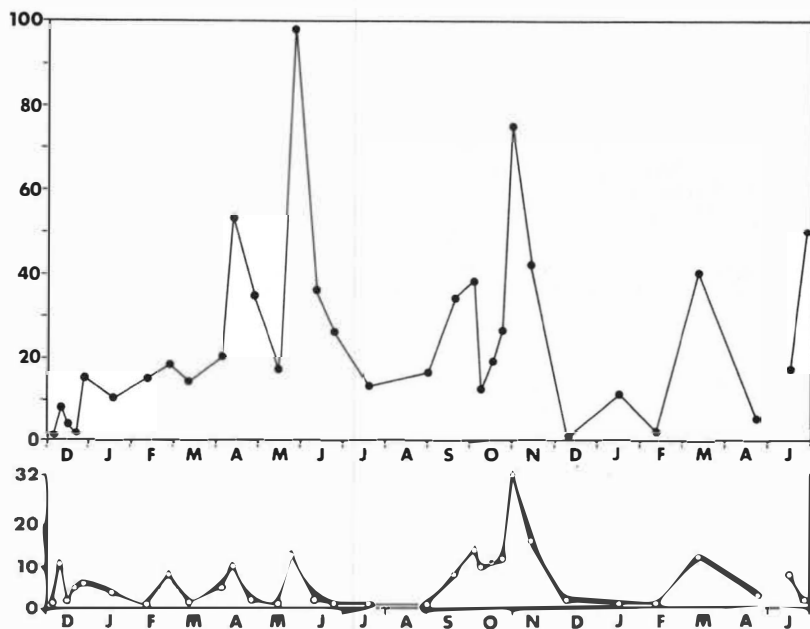


FIG. 4.—Number of recaptured bats per night throughout the study period. Symbols as in Fig. 3.

influx of unbanded bats, in which females slightly outnumbered males (Fig. 3). Many of these were young of the year, but no count was made by age group. By December 1970, there were few bats present in the colony. In contrast, there was a relatively large population present in the pavilion during December 1969.

The fall migration is somewhat similar to the spring migration in that the curve for the autumn is bimodal (Figs. 1, 3, 4). One of these peaks may result from an influx of bats migrating south from Oklahoma. The other may represent post-breeding season dispersal of the Texas cave population. We have little evidence to suggest which phenomenon (if either) is responsible for which peak, except that the Oklahoma caves are deserted by late October (Glass, 1958) and thus these bats are probably passing through Texas during that month.

Following the autumnal migration, the population of bats in the pavilion remained at a fairly low level, relative to the previous year's population, until March when there was an increase in both banded and unbanded bats. This increase occurred about one month earlier than in the preceding year. Banded individuals constituted 64 per cent (males accounting for 50 per cent, and females, 14 per cent) of the total caught on 11 March 1971.

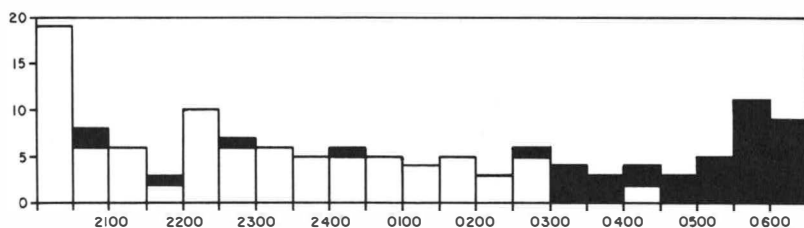


FIG. 5.—Flight activity at the *Tadarida* roost on 19 September 1970. Solid bars indicate number of bats returning to roost; open bars indicate number of bats leaving roost. Compare with Fig. 6 and see text for further explanation.

No netting was attempted during April, May, or June 1971, and the study was terminated in July after two nights of netting activity. The data for July reveal a very different situation from the preceding summer. On 15 July 1971, 104 of 129 bats caught were unbanded. Ninety-four of the 104 were males. All females were lactating. On 30 July 1971, of 74 bats captured, only 20 were unbanded. Nevertheless, only 12 of the banded bats captured on 30 July had been banded on 15 July, the remainder having been banded on many different dates scattered throughout the preceding 18 months. The four females caught, of which two were banded, were lactating.

We can only speculate as to the explanation for the large mid-summer population in 1971 as contrasted with 1970, when the number of bats was sometimes less than 20. The lack of disturbance in April, May, and June 1971 may have encouraged bats that had vacated the roost in summer 1970 to remain. A large summer male population may be the rule rather than the exception for the College Station roost. This would be a logical state of affairs in view of the need of roost space for males while females and young occupy the nursery caves. Generally, our data tend to support the observations of Davis *et al.* (1962) that males tend to appear before females in spring and that they tend to be erratic in numbers, time, and place of appearance.

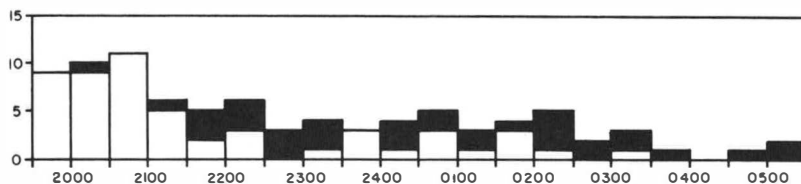


FIG. 6.—Flight activity at the *Tadarida* roost on 15 October 1970. Symbols as in Fig. 5. Compare with Fig. 5 and see text for further explanation.

NIGHTLY ACTIVITY PATTERNS

The results of two nights of continuous netting from dusk until dawn, 19 September 1970 and 15 October 1970, are contrasted in Figs. 5 and 6, respectively. The initial flight on 19 September was rather heavy but subsided quickly; another less intense flight followed about two hours later. On 15 October, fewer bats departed during the first two hours but the rate of exodus was more sustained relative to that of 19 September.

The early morning entrance flight evident in Fig. 5 is absent in Fig. 6. Bats returned to the roost at a slow but regular rate on 15 October, whereas on 19 September few bats entered the roost before 0500. A strong temperature-activity correlation is evinced by the following data: on 19 September the temperature dropped from 32° C at 1800 to 24.5° C at 0600 the following morning; on 15 October, the temperature at 1800 was 18° C and fell to 10° C by 0600. It is apparent that on the warmer night, 19 September, most bats remained out of the roost until dawn, whereas on 15 October, when the temperature dropped below 15.5° C after 2130, there was a fairly steady rate of bats returning to the roost. It is probable, therefore, that at ambient temperatures somewhat below 15° C, the bats were unable to find night roosts that afforded them sufficient protection from the lower temperature and chose to return to the pavilion. Conversely, on 19 September, when the ambient temperature failed to drop below 24.5° C, the bats were able to utilize night roosts. Our hypothesis is supported by data from 26 September 1970, when few bats returned to the roost until about 0330, at which time the temperature dropped below 15° C. After that hour the rate of returning bats soon rose to the morning's high.

Fig. 7 illustrates a flight pattern resulting from a thunderstorm that occurred in the immediate vicinity of the roost. At approximately 2030, light rain began falling and continued through 2100. During this period only five bats entered the pavilion. A somewhat heavier rain fell from 2100 to 2130, after which time it became a downpour. The greatest number of returning bats arrived between 2130 and 2200, coinciding with the beginning of the heavy rainfall. By 2230, all incoming activity had ceased. Rain continued to fall throughout the night, and, although netting was discontinued at about 2330, we presume that no bats left the roost during the remainder of the night. *Tadarida* are apparently able to cope with light to moderate rainfall in flight, but must seek shelter when the rate of precipitation is high.

Time spent away from the roost for individual bats during a single night varied from several minutes to several hours. For example, on

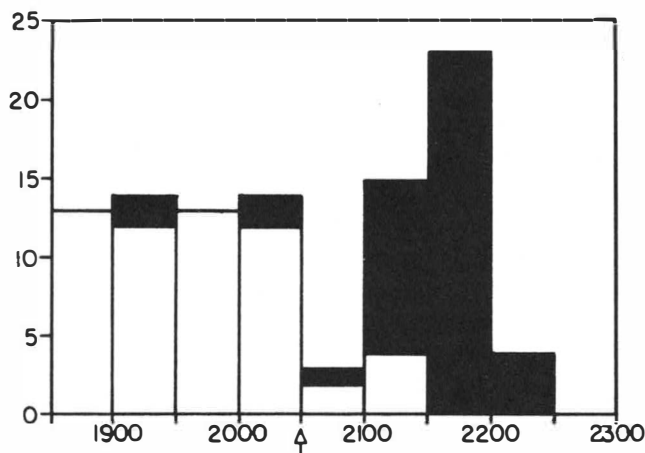


FIG. 7.—Flight activity at the *Tadarida* roost during a thunderstorm on 11 March 1971. Arrow indicates time of onset of rain. Other symbols as in Fig. 5.

15 October 1970, the shortest time spent away from the roost by an individual was eight minutes whereas the longest time was five hours. We think it highly probable that some of the bats were utilizing another roost or roosts for several hours before returning to the pavilion colony.

OVERWINTERING AND WINTER FEEDING ACTIVITY

Our data (Fig. 1) demonstrate conclusively that bats were not only present throughout the winter of 1969-70, but that numbers netted were nearly half those of peak populations in the spring and autumn. On all winter nights netted, temperatures were 10°C or above at dusk. Observations of the building entrance on evenings when temperatures at dusk were between 0°C and 10°C revealed no signs of activity. However, on any warm winter afternoon, bats could be heard vocalizing inside the building. As temperatures fell rapidly after dusk some bats returned to the building within one or two hours. These individuals invariably had remains of chewed insects in their mouths, although the stomach distension typical of bats feeding during the warmer seasons was rarely evident. Notably, fresh guano accumulated on the building floor throughout the winter.

The results of several studies summarized by Ross (1967) indicate that *T. brasiliensis* feeds primarily on moths. Moths are commonly observed flying in College Station when temperatures are above 10°C , but relatively few are seen at lower temperatures. The Texas A&M University Department of Entomology light traps yield moths

throughout the winter but no quantitative or temperature correlated data are available with respect to the traps. However, during the winter of 1969-70, the temperature was 10° C or above at sunset on 28 days in December, seven days in January, and 25 days in February. Weather records indicate that January 1970 was unusually cold. During the winter of 1970-71 fewer bats overwintered than in the previous year, even though the weather was much milder in January. A serious disturbance in the roost building on 3 December 1970 may have caused many of the bats that would normally have overwintered to migrate southward or move to another wintering colony. As an alternative hypothesis, the low population observed in the winter of 1970-71 may simply represent the type of erratic population fluctuation observed several times in our data and inexplicable within the scope of this study.

Davis *et al.* (1962) hypothesized that *Tadarida brasiliensis* would overwinter only in a favorable building (which they implied should be heated above ambient temperature) located in a favorable climate (which they defined as occurring along the Gulf Coast below Corpus Christi and in the lower Rio Grande Valley, an area where frosts are rare). Our building appears to meet the first qualification, in that the temperature in the bat crevices stayed well above freezing (range: 8-16° C) between 16 January and 13 February, the period monitored. It fails to meet the second criterion, as College Station is 200 miles north-northwest of Corpus Christi, and is subject to frequent frost during January and February. In reality, both temperature and the availability of food are probably limiting factors, and some *T. brasiliensis* may winter as far north as favorable roosting sites and dependable food supplies are available.

Although Davis *et al.* (1962) failed to find this species in mid-winter in caves or buildings within their vast study area, there is one report in the literature of a few overwintering *Tadarida* in Blow-out Cave, in central Texas (Krutzsch and Sulkin, 1958). Spennrath could locate no bats in that cave on 23 December 1970. However, bats of the same nominal species are known to winter in California, Oregon, and in the Southeast (see Barbour and Davis, 1969). We have established in the present study that at least some *T. brasiliensis* overwinter in this part of Texas, and we suspect that many other small wintering colonies remain to be discovered. This suggestion is supported by the fact that 120 of the 178 bats caught at the pavilion during January and February 1970 were unbanded, in spite of an intensive earlier effort that had resulted in the banding of 299 bats, representing all the individuals leaving the roost on six nights in late November and De-

TABLE 1.—*Bats recaptured between 24 November 1969 and 15 July 1971, inclusive, as percentage of bats banded from 24 November 1969 through 12 November 1970.*

Number of times recaptured	Per cent	
	Males	Females
Not recaptured	37.98	59.83
1 or more	62.02	40.17
2 or more	39.28	13.87
3 or more	24.81	4.04
4 or more	14.85	0.86
5 or more	8.27	—
6 or more	4.89	—
7 or more	1.88	—
8 or more	0.75	—
9	0.19	—

ember 1969. Thus it would appear that many bats banded during November and December left this roost, and that bats from other roosts had moved into the building, during January and February.

SIGNIFICANCE OF TIMES-RECAPTURED DATA

Because we had relatively few chances to recapture bats banded near the end of the study, we decided to analyze recapture data only for the 532 males and 352 females banded between November 1969 (the beginning of the study) and November 1970. Times-recaptured as percentages of bats banded are given in Table 1. Considering our large sample size, the difference between male and female times-recaptured is obviously real. A *Chi-square* test performed comparing the difference between males and females using the one or more times-recaptured data is significant at the .005 level of probability. It should be pointed out, however, that the number of times an individual bat might have used the roost in the absence of disturbance might be greater than the number of times bats returned after the experience of being caught and banded. Also, the banding experience might have a differential effect on the two sexes.

The times-recaptured data indicate that a majority of males used the same roost more than once, and that some males used the roost frequently, with a few caught as many as eight, nine, or 10 times. By contrast, relatively few females were ever recaptured, and no females were caught more than five times. This discrepancy is partially a product of the seasonal change in sex ratios (Fig. 2). A large majority of

the bats netted in the summer and winter were males, and some individual males were being recovered at various times throughout the year, suggesting permanent residence. Females banded in the spring or autumn were, by contrast, rarely recovered until the following spring or autumn, and were very rarely captured more than once in a single season. Thus the times-recaptured data strongly support the hypothesis that the roost is occupied by males, many of which are permanent residents in the College Station area (with a few being transients), and females that stop over only briefly during migratory flights. A sizable majority of bats of both sexes probably return habitually to this same roost, even though their presence may be only transitory. We feel confident in making this statement, because every time we netted, we recaptured bats never before recaptured, and indeed, most of the bats we netted were recaptures. Thus, with an extension of the netting study, the percentages shown in Table 1 would continue to rise until natural mortality factors had eliminated most of the bats banded during the November 1969-November 1970 period.

Only two individuals have been reported from localities other than the College Station site. A female banded on 10 June 1970 was reported from approximately 35 miles south of College Station on 18 June 1970. The only distant recapture was a female banded on 22 October 1970 and recovered in San Benito, Texas, on 23 November 1970, a distance of approximately 320 miles southwest of College Station. This recovery suggests that at least some of the bats banded at the pavilion colony fly south following the summer.

DISCUSSION

Due to the proximity of an apparent *T. b. cynocephala* colony (Houston) and the observed overwintering of bats thought to be *T. b. mexicana* in the College Station roost site, it appears possible that at least some individuals of the *T. b. cynocephala* population might be present in the College Station roost, and vice versa. The finding of individuals of undetermined subspecies at Navasota, one-third of the way from College Station to Houston, and in Prairie View, two-thirds of the way to Houston, supports this hypothesis. However, we feel that, with the exception of the overwintering behavior described herein, the population and activity patterns we observed are basically those of *T. b. mexicana* as recorded in the literature. This exception may prove to be significant, because the year-round presence of males of *T. b. mexicana* suggests the possibility of gene flow between populations of the two subspecies. The assumption made by Barbour and Davis (1969) in suggesting that reproductive isolation may exist

between the two is that copulation in the migratory *T. b. mexicana* occurs in México, whereas copulation in the nonmigratory *T. b. cynocephala* takes place in the southeastern United States. That their assumption may not be entirely valid is supported by our data. Further, no published study has established that all (or even most of) the individuals of the *T. b. cynocephala* population are non-migratory.

Although we cannot resolve finally the problem of specific or sub-specific recognition for *T. b. cynocephala* and *T. b. mexicana*, we feel the answer lies in the location and detailed study of additional colonies in the area between the Balcones Escarpment and the pine-hardwood forests of east Texas, which is the area where either intergradation or sympatry would occur.

ACKNOWLEDGMENTS

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