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ROOST AND FORAGING ASSOCIATIONS AMONG MEXICAN FREE-TAILED BATS (*Tadarida brasiliensis mexicana*)

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Maria A. Okoniewski

August 1986

ACKNOWLEDGEMENTS

There are many who deserve credit for helping me with my thesis research. First and foremost, I'd like to thank my major professor, Gary McCracken for countless hours spent guiding me through my graduate degree. His criticisms, advice, and support are greatly appreciated. He has stimulated and encouraged me, opening numerous opportunities to enhance my graduate studies. I am also indebted to my committee members, Gorden Burghardt and Susan Riechert, for their suggestions and criticisms. I thank Anna and Clinton Schulze and Billy and Gould Davis for allowing me access to their caves. They were most helpful to me while in the field, and certainly made my stay in Texas a richer experience. Much gratitude is due Hugh Britten for his hard work and insightful suggestions as my field assistant. I couldn't have asked for a better person to work with! I would also like to extend my thanks to Kitty Gustin for technical and logistical help prior to, and while in the field. I thank Dean Urban for writing the computer program used in my analyses. He went beyond the call of friendship, putting in long hours to help me with that aspect of my thesis. Finally, I extend many thanks to my colleagues Leslie, Carol, Doug, Nicholas, and John, who have edited early documents, and offered continuous support, encouragement, stimulation, and friendship. Without them, graduate school could never have been quite the same!

ABSTRACT

Radiotelemetry was used to tag groups of lactating adult Mexican free-tailed bats (Tadarida brasiliensis mexicana) in Texas nursery colonies. The existence of stable roosting and foraging associations was investigated. The presence of such groups was used to further explore how natural selection is operating to maintain communal nursing among adults in these caves.

Although individuals seem to show some roost site fidelity, there is no evidence that stable roosting groups exist. Nor is there any evidence of stable foraging associations among these bats.

Environmental variables were measured, and correlated with both the time and compass direction of the bat column as they depart for their evening foraging flight. While no significant correlations were found with departure direction, a number of variables were significantly correlated with the time bats leave the cave. Column departure time seems to be cued by lunar changes, the amount of cloud cover, and the windspeed.

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CHAPTER 1

INTRODUCTION

Grouping can be an important strategy by which individuals increase their inclusive fitness (Alexander 1974, Vehrencamp 1979). If some individuals of a group clump relative to one another in space and/or time, natural selection may operate differently than it would if no such pattern of association were present (Maynard Smith 1964, Vehrencamp 1979). Therefore, studies of the structure and stability of animal assemblages are essential to understanding the selective forces that may act in natural populations. Bats are well suited to such investigations since they often form large groups and show great diversity in their social organizations (Bradbury 1977).

Theoretical Background

Benefits of Grouping

The interests of an individual in a group rarely are identical to the interests of the other individuals in the group. Therefore, when attempting to understand the evolution of social groups, it is necessary to specify the conflicting pressures which shape group formation (Alexander 1974). The net benefits or costs of group living result from a combination of the benefits and costs of all the attributes of group life (Pulliam and Caraco 1984). Numerous benefits can be gained by an individual in a group, including more adequate thermoregulation, lower predation mortality, and enhanced foraging

opportunities (Brown and Orians 1970, Alexander 1974, Vehrencamp 1979). In many bat species, including the study animal, Tadarida brasiliensis mexicana, clustering elevates and helps stabilize body temperatures and metabolic rates (Twente 1956, Herreid 1963a,b,c, 1967, Constantine 1967, McNab 1969). Based on current evidence, it seems as if individuals in colonies of T. b. mexicana gain a net benefit from grouping with regard to increased thermoregulatory efficiency (Twente 1956, Herreid 1963a,b,c, 1967). It has also been speculated by several authors that grouping may act to decrease per capita mortality from predation (Sprunt 1950, Twente 1955a, 1956, Herreid 1962; see review in Pulliam and Caraco 1984). Finally, grouping by bats is reported to enhance foraging in several ways (Bradbury and Vehrencamp 1976, 1977a,b, Bradbury 1977, McCracken and Bradbury 1981). Existence of foraging benefits in T. b. mexicana has not been investigated. However, Davis et al. (1962) and McCracken (personal communication) have observed distinct pulses of small groups during the dense flights which occur as these bats exit and return to the cave before and after foraging. These groups are most apparent at the beginning and end of these flights, when the density of individuals entering or leaving the cave is low. This behavior suggests that individuals may enter the cave, leave the cave, and perhaps forage in groups.

Natural Selection Theory

Four mechanisms can be proposed for the maintenance of behaviors which represent a cost to the performer and a benefit to the

recipient: mutualism, reciprocal altruism, kin selection, and group selection. Although selection can operate in theory on groups of unrelated individuals, there is no clear evidence for adaptations that have evolved to assist the group as a whole at the expense of the individuals involved (Vehrencamp 1979, Trivers 1985). Furthermore, if group selection were to occur, it is necessary that there be small effective population sizes, genetic variance among groups attributable to genetic drift, low migration rates, and high group extinction rates (Maynard Smith 1964). These conditions are unlikely to be met in T. b. mexicana for at least two reasons. First, colonies of T. b. mexicana are enormous, and several studies have shown that adult females frequently move between caves prior to giving birth (Davis et al. 1962, Villa and Cockrum 1962, Cockrum 1969). These potentially violate the small effective population size and/or low migration rate criteria. Second, electrophoretic studies have shown that the among-group genetic variance required by group selection theory is not present among populations of T. b. mexicana (McCracken 1984).

Mutualism occurs when each individual involved in an interaction gains immediate fitness benefits, and these benefits exceed any costs incurred from the interaction (Vehrencamp 1979). Reciprocity differs from mutualism in that a time delay occurs between an individual's giving and receiving of benefits. Here, one individual incurs a cost while benefiting another individual. At some point in the future, the cost-benefit roles will be reversed, and the second individual will incur a cost while benefiting the first individual. Reciprocity can

only evolve when: 1) the benefit to the recipient is greater than the cost incurred by the actor, 2) there is sufficient time and sufficiently close proximity of cooperating individuals for reversal of the cost-benefit roles to occur, and 3) costs and benefits are constant for successive acts (Trivers 1971, 1985, Vehrencamp 1979).

Alternatively, kin selection operates when genetically related individuals engage in a cooperative interaction. A behavior is selectively favored if the total benefit received by a relative, when weighted by the relatedness between interacting individuals, is greater than the cost in personal fitness to the individual performing the act (Hamilton 1964, Maynard Smith 1964).

Unlike mutualism, both reciprocity and kin selection are enhanced by social stability. That is, kin selection and many forms of reciprocity require that cooperation only occur among individuals of a stable group (Maynard Smith 1964, Vehrencamp 1979). Consequently, detailed information on the stability of associations among individuals can lend insight into the selective mechanisms which may be acting on those individuals.

The Study Animal

The Mexican freetail bat, (*T. b. mexicana*), has a body weight of 11 - 15 grams (Twente 1956) and a diet that consists mainly of moths (Storer 1926). It lives in Mexico most of the year, and adult females migrate north each spring forming large groups in caves throughout the American Southwest (Twente 1956, Davis et al. 1962, Villa and Cockrum 1962). Females give birth in these caves, and deposit their young in

nursery creches. Mothers roost in groups away from the creche, returning to their offspring twice each day to give them a milk meal. Females give birth to a single young, but occasionally are seen nursing more than one pup (Davis et al. 1962, McCracken 1984). McCracken (1984) has shown that mothers apparently actively search out their own pup to feed, although other pups may take milk in the process. Gelfand and McCracken (1986) have presented data suggesting that each pup has a vocal signature, which is used by an adult female to recognize a particular pup. Furthermore, Gustin and McCracken (in press) have shown that mothers are able to identify their own pup solely on the basis of scent cues. The existence of these recognition cues suggests that selection favors females which consistently find and nurse a particular pup. However, creching may make it difficult for females to do this, and it is known that pups occasionally take milk from females which cannot be their mother (McCracken 1984). The selective mechanisms permitting this "non-parental" nursing are of interest because the energetic costs of lactation (Millar 1977, 1978) and the possible reduced survivorship of a female's own offspring may substantially decrease a female's success in rearing a pup to weaning.

McCracken (1984) has shown that an apparently random distribution of genotypes exists within the cave roosting assemblages of adult females. The genetic tests performed were admittedly imprecise, however, and may not have been sensitive enough to detect a mosaic of small kin groups within the roost. Nevertheless, since there is no evidence that related individuals do roost adjacently, it seems

unlikely that stable groups of related adult females are present in T. b. mexicana nursery colonies. Thus, it seems unlikely that kin selection is operating among adult females. McCracken (1984) also reports that pups typically move about in the creche independently of other pups suggesting a lack of group stability among pups in the creche. Consequently, it seems unlikely that reciprocity is occurring with regard to nursing since it does not seem feasible for stable groups of unrelated adults to consistently nurse a group of pups if these pups do not remain together. Thus, McCracken (1984) concluded that the mutual benefits resulting from thermoregulation served as the most likely factor acting to offset the cost involved in maintaining communal nursing.

The goal of this study was to examine individual associations among lactating adult females roosting in the cave, and exiting the cave to forage. Information on these associations should provide insight into how selection is operating with regard to "non-parental" nursing, as well as other behaviors exhibited by adults in these colonies. If the same adult females cluster either in the roost or in foraging associations, selective mechanisms other than mutualism may be operating. To resolve this issue, two questions were addressed by this investigation: 1) is there roost site stability among adult females, and 2) do small groups of individuals leave for and return from foraging together, and do these groups consist of the same individuals?

Hypotheses

Three hypotheses were formulated and tested sequentially in this investigation (Table 1). If reciprocity is occurring in these bats, then social stability should exist either with regard to roosting associations, foraging associations, or both. Based on where group stability is found, reciprocity may exist with regard to foraging enhancement, communal nursing, or some other, yet unspecified behavior. If it is shown that group stability does not exist, mutualism is the most likely force acting to shape the behavior of individuals found in the nursery colonies. The three hypotheses presented are designed to test systematically the possible alternatives.

For the purpose of this study, stable roosting groups were defined by determining the spatial distribution of individuals relative to one another over time. If an individual is located in the same roost site over the course of the sampling period, it shows roost site fidelity. If adjacent individuals consistently roost together, this will indicate that they are a stable roosting group. Similarly, a stable foraging group was defined as a group of individuals which consistently enter and leave the cave together.

The first hypothesis, (H1), predicts that bats in stable roosting groups also leave for and return from foraging together. If the data support this hypothesis, reciprocity may be operating with regard to foraging enhancement. However, if H1 is rejected, it still may be the

Table 1. Hypotheses to be tested measuring adult female group stability and foraging associations in T. b. mexicana nursery colonies.

Hypotheses	Test
H1: Stable groups of adults are present in the roost and in foraging associations.	Observe behavior of a roosting cluster of females with respect to roost dispersion in the cave over time and movement relative to one another as they leave for and return from foraging.
H2: Stable groups of adults are present in the roost, but not in foraging associations.	
H3: Stable roosting groups do not exist, but there are stable foraging associations.	Observe behavior of the individuals of a foraging cluster of adult females as they leave for and return from foraging.

case that roost site stability exists among the adult females. This alternative is represented by H2, which states that groups roosting together are stable even though these groups do not remain together when leaving for and returning from foraging. If this were the case, reciprocity could still be acting with regard to a behavior other than foraging enhancement.

The third hypothesis (H3) to be tested postulates that stable foraging groups may exist, despite the absence of stable roosting groups. McCracken and Bradbury (1981), have argued that roosting group stability may not be necessary for foraging enhancement to exist. That is, selective pressures may result in the formation of stable foraging groups, but selection may not favor stable roosting associations. As an example, individuals may utilize a particular foraging beat each night, and those occupying adjacent areas may engage in cooperative interactions, perhaps with regard to locating or herding insects. Consequently, they may leave for and/or return from foraging together, but not roost together within the cave because there is no net advantage to such roosting associations. It may be impractical for individuals to find one another from among the mass of bats within the cave prior to foraging flights. Therefore, individuals may leave the cave independently, but engage in cooperative interactions once feeding begins. If H1 and H2 are both rejected (that is, no apparent roost nor foraging group stability exists), H3 will be tested by monitoring when tagged individuals enter and leave the cave relative to one another, and the direction in which

they go to forage. If the third hypothesis is not supported by the data mutualism may sufficiently explain the advantage of group living in this species.

CHAPTER 2

METHODS AND MATERIALS

Study Site

Data were collected between 17 June and 17 July 1985, primarily from the James River Cave in Mason, Texas. Davis Cave, located approximately 50 miles east southeast of Mason, also was used as a study site. Much of the available information on T. b. mexicana nursery colonies has been collected from these caves, and both were utilized in the studies of Davis et al. (1962) and McCracken (1984). Population numbers of adult females have been estimated at 6-7 million in James River Cave, and 3-4 million in Davis Cave (Davis et al., 1962). James River Cave also houses perhaps a thousand Myotis velifer. M. velifer roost in a separate area of the cave, and no interactions between the two species were observed during the sampling period.

The cave was mapped (Figure 1), and reference stakes were placed throughout it. The maximum width of the cave is approximately 45m, and the maximum length about 40m. Since the floor and ceiling are both sloped, and the wall surface irregular, the distance measurements are approximate and only indicate the relative postions of bats.

Capture Methods

Five groups of bats (n=2-5, $\bar{X}$=3 bats per group, total = 15) were observed during this study. All subjects were lactating females. The forearm length of the sampled bats averaged 42.7 mm (range = 41.9 -

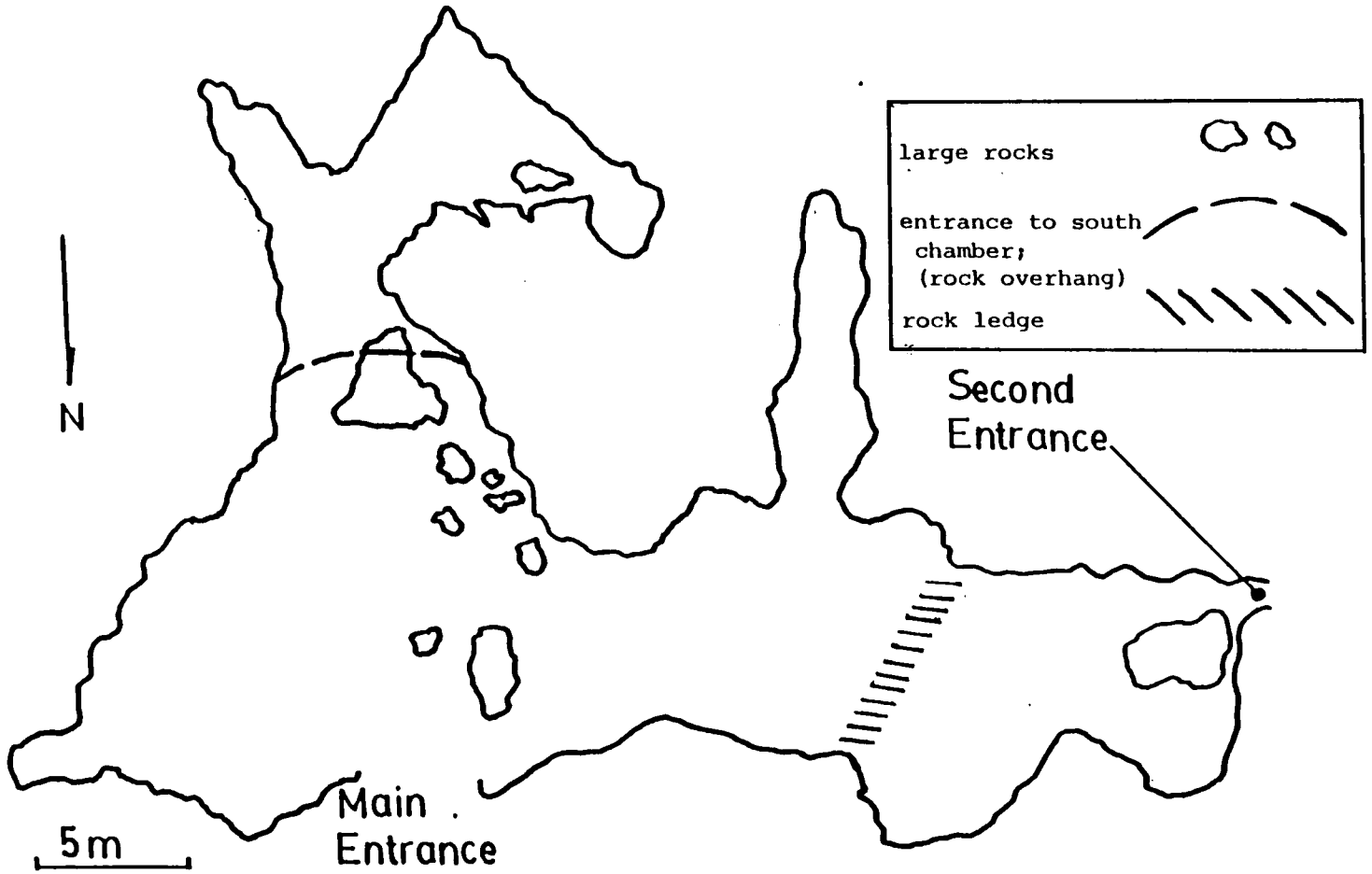

Figure 1. James River Cave floor plan.

44.5 mm). Each group of bats was monitored for up to 7 days (n= 2-7, $\bar{X}$=3.5). Three different methods were used to capture groups of bats; however, all five groups of bats were subject to the same analyses, regardless of the sampling technique used. Groups 1 (n=2) and 2 (n=3) were sampled by picking individuals by hand from their roost site. Bats roosting adjacently were considered to be a group. After sampling these two groups, I decided to discontinue using this method because of the possible effect of disturbance on roosting patterns. I then captured bats at night after they left the cave, by setting up mist-nets across local rivers. Four bats were caught in this manner on three different nights, and in three different locations. On the first two nights, nets were strung across the James River (a different location was used each night) and a single bat was caught per night. On the third night, two bats were caught in nets strung across the Llano River. This method was abandoned because 1) it was difficult to catch a group of bats, and 2) even if more than one bat was caught in a given location, it was not clear that the bats were actually flying as a group. Although this set of mist-netted bats is termed the third "group", data collected from them are considered to represent a control condition. Finally, bats were caught by raising a mist-net on poles across the mouth of the cave as "pulses" of bats returned in the morning after foraging. Individuals caught in the same pulse constituted a group. The remaining two groups (4 and 5, n=3 each) were captured in this manner. Table 2 lists all individuals which were observed during this study.

Table 2. Bats radio-tagged, James River Cave.

Bat Identification	Date	# days Radio-tagged
Group 1		
1.1	17 June	3
1.2	17 June	4
Group 2		
2.1	20 June	5?
2.2	20 June	4
2.3	20 June	4
Group 3		
3.1	24 June	8
3.2	26 June	12?
3.3	27 June	7
3.4	27 June	11
Group 4		
4.1	3 July	10
4.2	3 July	9
4.3	3 July	9
Group 5		
5.1	12 July	5*
5.2	12 July	4*
5.3	12 July	5*

? = Radios fell off bats in the cave and were retrieved from the guano. I estimate the number of days the radio was carried based on the last day the bat was known to leave the cave to forage.

* = These bats left the cave before the radios were recovered, and the exact number of days the radios were carried is unknown. The number of days data were obtained on these bats is given.

Marking Methods

Radiotelemetry was used to mark individuals. Bats of the first group were tagged using radios built in our lab (see specifications in Wilkinson and Bradbury, in press; average weight = 1.5g, battery life = 3-4 days). All other radios were purchased from Holohil Electronics (RR #2, Woodlawn, Ontario KOA3MO; average weight = 0.94g, battery life = 2-3 weeks). The commercial radios weighed less than 10% of the bat's body weight, which has been suggested as the upper allowable load limit (Bradbury et al. 1979). Because the commercially made radios have a long battery life, and because the bats were only followed for a small portion of that time, some radios were used to tag a second bat. All radios emitted signals in the 148.0 - 148.275 MHz range, which could be picked up on one of 12 channels using a CE-12 portable telemetry receiver (Custom Electronics, 2009 Silver Ct. W., Urbana, IL 61801). Hand-held, collapsible 3 element Yagi directional antennaes also were used.

Radios were attached to the center of the bat's back with Skin Bond Cement (UNITED division of Howmedica, Inc., 11775 Starkey Rd., Largo, FL 33543). Most radios remained on the bats for 7 or more days when pelage was not clipped prior to attachment (groups 3, 4, and 5), as compared to 4-5 days when fur was clipped (groups 1 and 2). Radios that were still attached after the completion of observations were removed using Uni-Solve adhesive remover. All radios also had a piece of reflective red Scotch-Lite glued to them to facilitate visual sighting of tagged bats in the cave. Bats were released at the site

of capture within an hour after capture. Due to possible effects of the disturbance of being captured, and to allow time for the bats to habituate to carrying the radios, no data collected on bats within the first 24 hours after marking were incorporated into the analyses.

Roosting Data

The in-cave position of tagged individuals was recorded daily by measuring the distance and compass direction to the nearest reference stake. Individuals were located using the radio signal, with the Scotch-Lite tag aiding in pinpointing the bat's precise location on the cave ceiling or wall. These measurements were taken between 1030h and 1330h, with most taken between 1100h and 1130h. The position of each bat was plotted on a map. Composite maps were created for each individual, and for all individuals in the group over the entire sampling period.

On one occasion, the locations of radio-tagged roosting bats were monitored at 2-hour intervals throughout the day to determine the degree to which the shifting of roost site occurred throughout the day.

Foraging Data

The approximate time and compass direction of departure of each bat were recorded as it left the cave to forage each evening. After the initial data were taken, I walked approximately 100m up to the top of a small hill and continued to monitor the direction in which the bat was flying every 1-3 minutes until the signal could no longer be

received. The last signal recorded is referred to as the vanishing direction of the bat. Compass directions were obtained using a SUUNTO optical reading compass. I also recorded the time at which the stream of bats began to leave the cave, and the direction in which the column flew as the bats left the cave. Tagged bats left the cave with the column, then generally broke away from the column and began heading off in other directions. All readings taken after the bat broke from the column were collapsed into a single data point by computing the mean flight direction (Zar 1984). This mean represents the straight line course of the bat if it were actually flying directly for a particular site. Analyses were done using both the mean and vanishing directions of each bat.

To determine if particular environmental factors influence the departure time or flight direction of the bat column, information on air temperature, amount of cloud cover, wind speed and direction, sunrise and sunset time, moonrise and moonset time, and phase of the moon were recorded daily. Most information was recorded from the cave area prior to the evening exodus. Sun times and data on the moon were obtained through the National Climatic Data Center (Asheville, N.C.) and were recorded at a weather station in San Antonio, Texas.

On 6 days (5 at James River, 1 at Davis Cave) I counted the number of individuals per group entering the cave. To facilitate accurate counts, this measurement was taken near the end of the return flight as the density of bats decreased, and the pulses were more distinct. To quantify the existence of discrete groups, on one

morning I recorded the length of time between pulses of entering bats, and the time duration of each pulse. These data were collected at Davis cave.

Data Analysis

Roosting Data

Two types of analyses were performed on the roosting data. First, to determine roosting locational stability of individuals, the mean and variance of a) distance moved between days, and b) distance moved from day 1 to the day in question were computed. For bats which were collected in the roost (groups 1 and 2), the position of the sampling area was used as the bat's position on day 1. Second, the size of the area within which a bat moved was calculated using the minimum area method (Southwood 1971). Density estimates (McCracken, unpublished) were used to determine the approximate number of bats found within that area. Roost site fidelity among individuals within a group was assessed using these area estimates.

Foraging Data

Plots were made of 1) the mean direction, and 2) the vanishing direction of a) individuals over time, and b) the position of all bats of a particular group on each day. A computer generated simulation was used to determine the probability that a particular pattern of points would occur due to chance alone (see Appendix for FORTRAN program). The distribution of points was considered clumped if $P < .05$, when compared to the expectations of this random model.

Data on the time of departure from the cave for evening foraging flights were analyzed in two ways. First, to determine if an individual bat left the cave at about the same time each night, the range and mean of its departure times for all sampling nights were computed and plotted. Second, to determine if bats of the same group left the cave together on any single sampling night, the departure times of each bat in the group were compared for each night, and a mean and range of times computed. Two further analyses were performed on this latter measure. First a Mann-Whitney U test was run to determine whether bats which were captured together left the cave closer together than bats which were not captured together. Second, the number of individuals which exited from the cave between radio-tagged bats was estimated. This estimate was based on the total number of adults in the cave, and the duration of the exodus.

Column Data

Statgraphics statistical graphics system (version 1.0, by Statistical Graphics Corporation; 1985, STSC, Inc., USA) was used to run a Kendall's Rank Correlation test among all nine of the environmental variables measured with both the time and direction of column departure.

CHAPTER 3

RESULTS

Roosting Data

Figures 2 and 3A show maps of roost site locations for all individuals of each group. Although each bat seemed to roost primarily in a particular section of the cave, most bats also roosted in different areas of the cave on one or more days. Table 3 presents data on the distance roost sites are moved between days, and the distance moved between the first sampling day and each subsequent observation. Any roost site which was two or more standard deviations from the closest roost site for an individual bat was defined as an outlier roost site. Bats 1.1 (Fig. 2A) and 4.3 (Fig. 2D) were the only two bats which did not have any such outlier roosts. Note that although individuals prefer roosting in certain sections of the cave (Figs. 2 and 3), there is a great deal of movement of roost sites within those sections (Table 3). Some individuals (eg., 3.2 and 3.3, Fig. 2C) show no apparant roost site stability, while others (eg., 3.4 and 4.2, Figs. 2C and D, respectively) seem to roost in two separate areas of the cave. This latter pattern is one which was also seen in bat 5.3 (Fig. 3B) when observed at two hour intervals throughout one day. Estimates of the size of an area in which bats were found roosting on successive days (Table 4) indicate that, on the average, bats roosted in an area encompassing approximately $6.2m^2$. (Outlier roost sites were excluded from these area estimates.) The

Figure 2. Roost location of bats on consecutive sampling days. Group 1 bats are shown in A, group 2 bats in B, group 3 bats in C, and group 4 bats in D. Symbols represent individual bats, numbers represent the sampling day that an individual was found at a particular location. Sampling days for each group are numbered separately. S in A and B is the sampling area.

Bat Identification:

1.1	●	3.2	★
1.2	▲	3.3	△
2.1	◒	3.4	○
2.2	◪	4.1	■
2.3	◬	4.2	X
3.1	□	4.3	☆

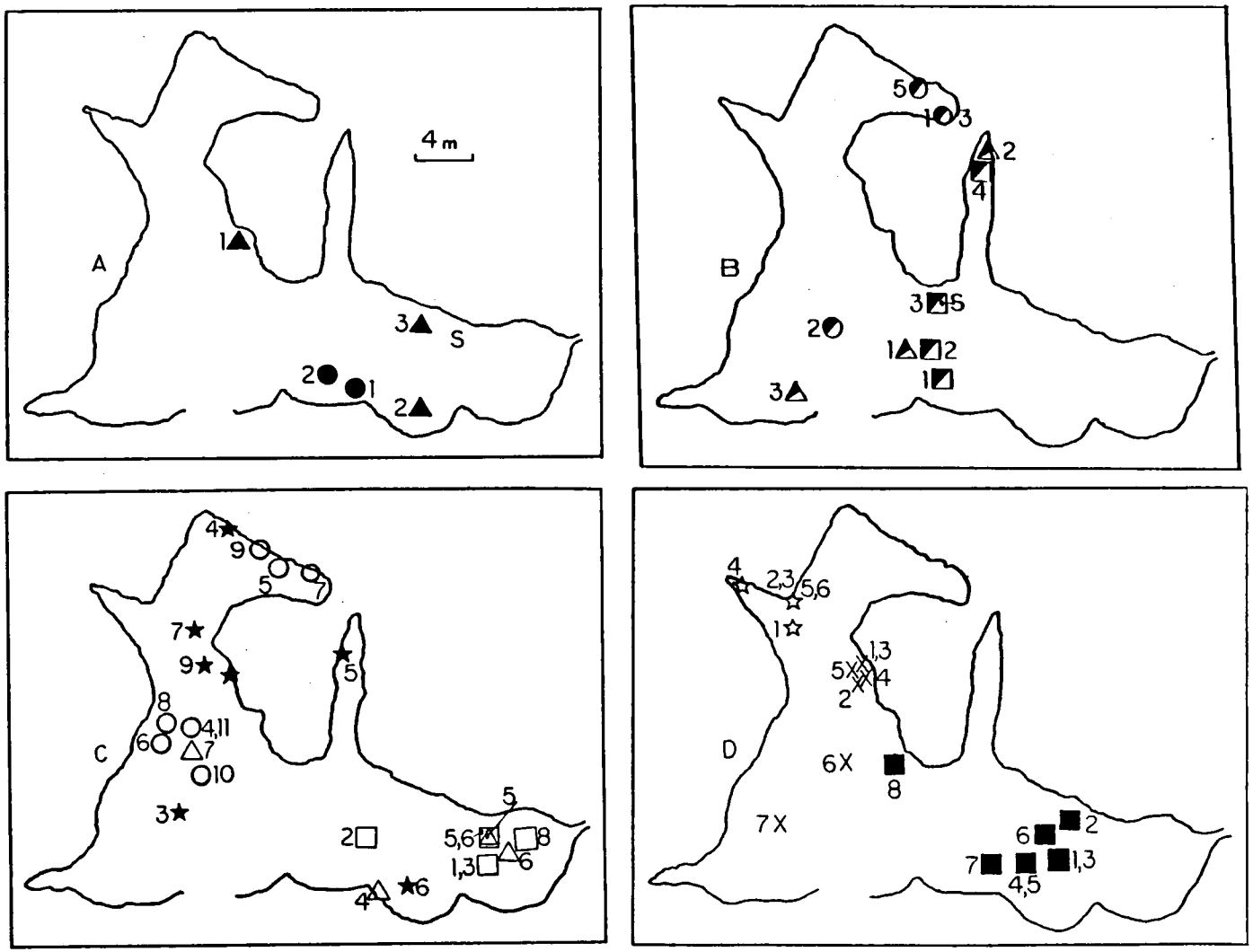

Figure 2

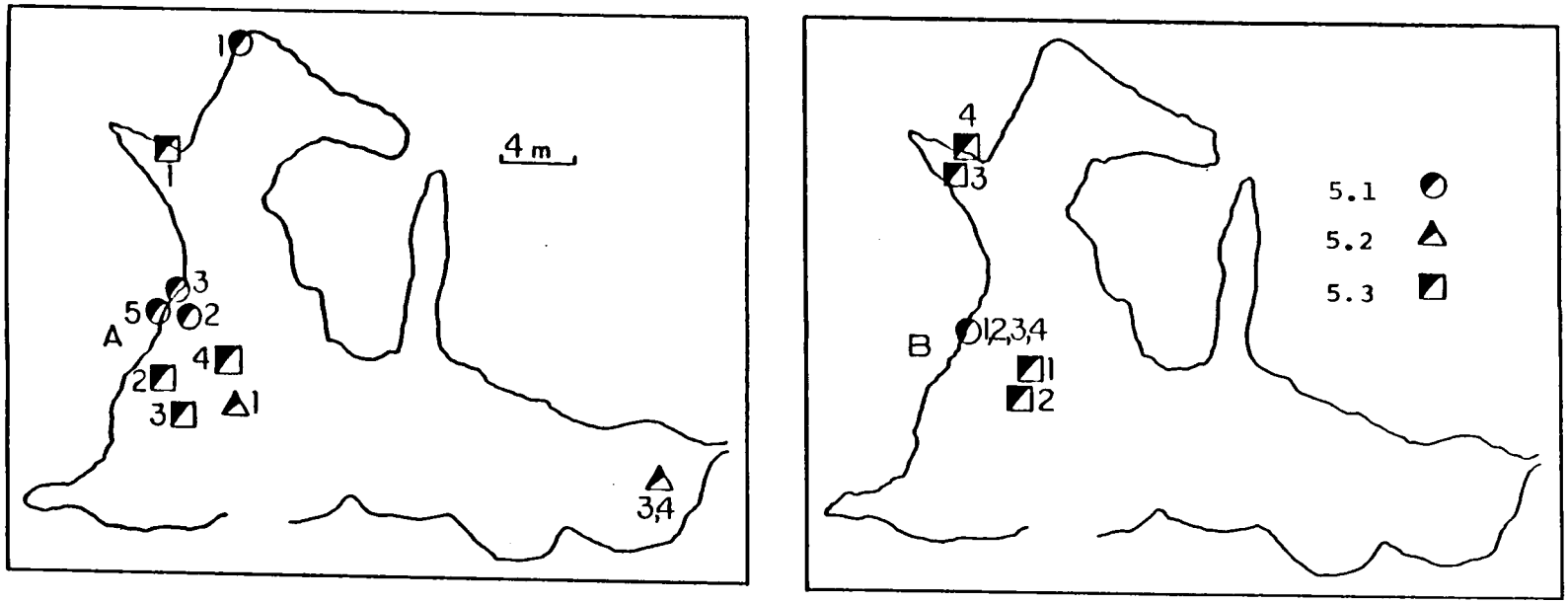

Figure 3. Roost location of group 5 bats. A is the location of individuals on consecutive sampling days (1-5). B is the location of 2 of those individuals on one day at 2-hour intervals. The numbers (1-4) in B represent consecutive sampling periods. Symbols in both A and B represent individual bats.

Table 3. Mean ($\bar{X}$) and standard deviation (s) of distance (in meters) that bats moved their roost site between n successive sampling days and from the first sampling day.

		Distance Moved			
		Between sampling days		From first sampling day	
Bat	n	$\bar{X}$	s	$\bar{X}$	s
1.1	2	7.15	5.87	12.25	1.34
1.2	3	18.70	9.31	11.77	10.34
2.1	4	22.23	22.95	9.00	14.46
2.2	4	7.53	5.01	6.88	5.80
2.3	3	19.73	12.66	12.60	5.41
3.1	6	5.00	6.47	3.65	4.57
3.2	6	22.37	15.76	21.10	5.91
3.3	3	15.40	15.96	16.60	5.74
3.4	7	20.91	4.00	10.00	10.20
4.1	7	4.07	4.33	4.40	5.88
4.2	6	3.77	3.84	5.28	6.96
4.3	5	2.78	2.68	3.00	1.92
5.1	3	8.10	11.87	21.67	0.71
5.2	2	17.05	23.55	33.75	0.07
5.3	3	9.20	9.6	19.60	2.10

Table 4. Roost site area and density estimates. N roost site locations were connected to form a minimal polygon, the size of which is given in square meters. Outliers (points more than 2 standard deviations from the mean) were excluded from the polygon measurements. Density estimates are based on 1800 bats per square meter (McCracken, unpublished).

Bat	n	# outliers	size of polygon	# bats in area
1.1	3*	0	15.0	27000
1.2	3*	1	16.5	29700
2.1	4	1	1.5	2700
2.2	4*	1	7.5	13500
2.3	3*	1	21.5	38700
3.1	6	1	1.25	2250
3.2	3	4	4.25	7650
3.3	3	1	4.00	7200
3.4a	5	3**	6.00	10800
3.4b	3	5**	1.25	2250
4.1	7	1	7.5	13500
4.2	5	2	1.0	1800
4.3	6	0	5.5	9900
5.1	3	1	1.0	1800
5.2	2	1	1.0	1800
5.3	3	1	5.0	9000

* includes sampling area as day 1
** bimodal distribution

mean density of adults roosting in this cave is estimated at 1800 bats per m^2 (McCracken, unpublished); therefore, it is calculated that approximately 11,222 bats roost, on average, within an area of 6.2m^2. This implies that there are at least 11,222 different roost sites within the average roosting areas measured for individual bats.

Foraging Data

Direction of Departure

Table 5 shows the results of a computer generated simulation which provides the probability that n points span a particular arc on a circle. Of the 14 individuals observed for more than 1 night, 6 showed a significantly clustered distribution ($P < .05$) in their mean angle of departure from the cave (Table 6); those same 6 bats, and an additional one (3.4), also showed significantly clustered distributions in their vanishing direction (Table 7). Bat 3.4 had a significantly clustered distribution of its vanishing directions, although the distribution of its mean directions was not significant ($P=.10$). When the distribution of mean and vanishing directions of bats over time are compared to the computer model, a significantly clustered distribution ($P < .05$) is shown on 2 of 15 days with regard to mean angle (Table 8) and on 0 of 15 days with regard to vanishing direction (Table 9). On 2 days, the distribution of mean angles is significantly overdispersed (Table 8) as is the distribution of vanishing directions on 1 day (Table 9).

Table 5. Computer generated probabilities of spanning arc for a set of n points on a circle. Numbers represent the size of an arc (in degrees) in which the distribution is significantly overdispersed or clustered.

Group size (n)	Probability			
	Overdispersed		Clustered	
	99%	95%	5%	1%
2	178	171	9	2
3	228	213	44	18
4	249	236	83	46
5	264	252	113	74
6	276	265	139	104
7	284	274	159	120

Table 6. Range of values and spanning arc (in degrees) of mean angles for each bat leaving the cave to forage on n nights.

Bat	n	Range	Spanning arc	Significance level
1.1	2	44 - 107	63	NS*
1.2	4	10 - 54	44	.01
2.1	3	30 - 201	171	NS
2.3	2	26 - 124	98	NS
3.1	2	126 - 223	97	NS
3.2	2	119 - 138	19	NS
3.3	2	93 - 140	47	NS
3.4	5	161 - 298	137	NS
4.1	7	234 - 336	102	.01
4.2	4	3 - 322	51	.05
4.3	4	271 - 352	81	.05
5.1	4	29 - 42	13	.01
5.2	3	98 - 257	159	NS
5.3	3	220 - 228	8	.01

* NS = not significant

Table 7. Range of values and spanning arc (in degrees) of vanishing direction for each bat leaving the cave to forage on n nights.

Bat	n	Range	Spanning arc	Significance level
1.1	2	44 - 118	74	NS*
1.2	4	10 - 45	35	.01
2.1	3	141 - 299	202	NS
2.3	2	22 - 136	114	NS
3.1	2	102 - 341	121	NS
3.2	2	86 - 128	42	NS
3.3	2	111 - 184	73	NS
3.4	5	208 - 311	103	.05
4.1	7	263 - 335	72	.01
4.2	4	11 - 338	33	.01
4.3	4	1 - 282	79	.05
5.1	4	8 - 28	20	.01
5.2	3	116 - 295	179	NS
5.3	3	220 - 260	40	.05

* NS = not significant

Table 8. Range of values and spanning arc (in degrees) of mean angles for n bats from the same group as they leave the cave to forage on particular nights.

Date	Group	n	Range	Spanning arc	Significance level
18 June	1	2	35 - 107	72	NS*
19 June	1	2	10 - 44	34	NS
21 June	2	2	26 - 201	175	.05**
23 June	2	2	30 - 124	94	NS
28 June	3	3	138 - 161	23	.05
30 June	3	3	43 - 298	181	NS
4 July	4	3	10 - 286	84	NS
5 July	4	2	7 - 235	132	NS
6 July	4	3	281 - 322	41	.05
7 July	4	3	13 - 304	69	NS
10 July	4	2	271 - 336	65	NS
14 July	5	3	29 - 228	161	NS
15 July	5	3	30 - 221	191	NS
17 July	5	2	42 - 220	178	.01**

* NS = not significant
** points are significantly overdispersed

Table 9. Range of values and spanning arc (in degrees) of vanishing directions for n bats from the same group as they leave the cave to forage on particular nights.

Date	Group	n	Range	Spanning arc	Significance level
18 June	1	2	35 - 118	83	NS*
19 June	1	2	10 - 44	34	NS
21 June	2	2	26 - 299	87	NS
23 June	2	2	71 - 136	65	NS
28 June	3	3	128 - 272	144	NS
30 June	3	3	111 - 311	170	NS
4 July	4	3	4 - 294	70	NS
5 July	4	2	301 - 356	55	NS
6 July	4	3	242 - 315	73	NS
7 July	4	3	11 - 310	61	NS
10 July	4	2	282 - 335	53	NS
14 July	5	3	28 - 235	153	NS
15 July	5	3	8 - 223	215	.05**
17 July	5	2	22 - 220	162	NS

* NS = not significant
** points are significantly overdispersed

Time of Departure

When all the departure times of each individual bat were compared, it was shown that, on the average, a bat left the cave to forage within 47 minutes of the time it left the cave on previous nights (s=31 min., s^2 =936, Table 10). Given that the entire evening exodus takes 2 - 3 hours, it does not seem as if an individual leaves the cave at the same time each night. When the departure times of bats of the same group were compared on a single night, a similar pattern emerged. These bats left within 27.46 minutes of each other (s=20.74 min., s^2 =429.98; Table 11). Bats radiotagged as different groups were observed on four of the same nights. These data are also presented in Table 11. The times between departures of those bats which were not captured together (those of different groups and group 3 bats) were significantly greater than the times between departures of those bats belonging to the same group (Mann-Whitney U test; U=1, P <.001; Siegel, 1956). Finally, Table 11 gives an estimate of the number of bats which left the cave between the departure of radiotagged bats each night (flow rate). A conservative estimate, (based on a cave population of 6 million bats leaving the cave in 3 hours), is that 33,333 bats exit the cave each minute during the exodus. However, this assumes that bats exit at a constant rate, when in fact the density of bats visibly fluctuates during the course of the exodus. The numbers given in Table 11, then, are merely crude estimates.

Table 10. Difference (in minutes) between all the departure times of an individual bat on n successive sampling nights. The time difference represents the number of minutes within which a bat left the cave to forage, relative to when it left on previous nights.

Bat	n	Time difference
1.1	2	19
1.2	4	93
2.1	3	65
2.3	3	68
3.1	2	5
3.2	2	82
3.3	2	35
3.4	5	97
4.1	8	42
4.2	5	46
4.3	4	60
5.1	4	28
5.2	3	11
5.3	3	10

Table 11. Difference (in minutes) between departure times of n bats from the same group on each sampling night. Time differences represent the number of minutes which passed from the time the first bat of a group left the cave. Numbers in parenthesis represent data for bats of different groups observed together. Flow rate is an estimate of the number of bats which exit the cave during the number of minutes specified.

Group	Date	n	Time difference	Flow rate
1	18 June	2	23	766,659
	19 June	2	7	233,331
2	20 June	2	19	633,327
		3	(94)	(3,133,302)
	21 June	2	3	99,999
	23 June	2	16	533,328
3	28 June	3	56	1,866,648
	30 June	3	43	1,433,319
4	4 July	3	20	666,660
		4	(63)	(2,099,979)
	5 July	2	3	99,999
		3	(60)	(1,999,980)
	6 July	3	5	166,665
	7 July	3	48	1,599,984
	10 July	3	24	799,992
5	14 July	3	39	1,299,987
	15 July	3	16	533,328
	17 July	2	17	566,661

Pulse Data

Pulses of bats returning from foraging took approximately 6.27 seconds to enter the cave (n=91, s=7, range = 0.9-40). The interval between pulses averaged 19.47 seconds (n=91, s=22, range = 0.9-106). The average number of individuals counted in groups returning to Davis Cave was 4.4, while the average number of individuals counted in groups returning to James River Cave was 11.3. However, very large groups (>20) could not be accurately counted. Twenty was assigned to these groups, and was used in computing the mean, although the groups may have actually been larger. This was more of a problem at the James River Cave, and the mean for that cave is therefore an underestimate of actual group size. The frequency of each group of a particular size (n=1-20) was calculated for both caves. These frequencies were standardized by converting each score to a percent of the total number of groups observed in each cave. As Figure 4 shows, most groups were ≤ 5 or ≥ 20, with differences between the two caves apparent. Of the 129 groups counted entering Davis Cave on 19 July, only 5 consisted of 20 or more individuals (3.9%), while 94 consisted of 5 or fewer bats (72.9%). In contrast, of the 376 groups counted over 5 days at James River Cave, 166 consisted of 20 or more individuals (44.1%), whereas 112 consisted of 5 or fewer bats (29.8%).

Time and Direction of Column Departure

The correlation coefficients between nine environmental variables and both the a) time and b) compass direction of column departure are given in Table 12 and 13, respectively. None of the environmental

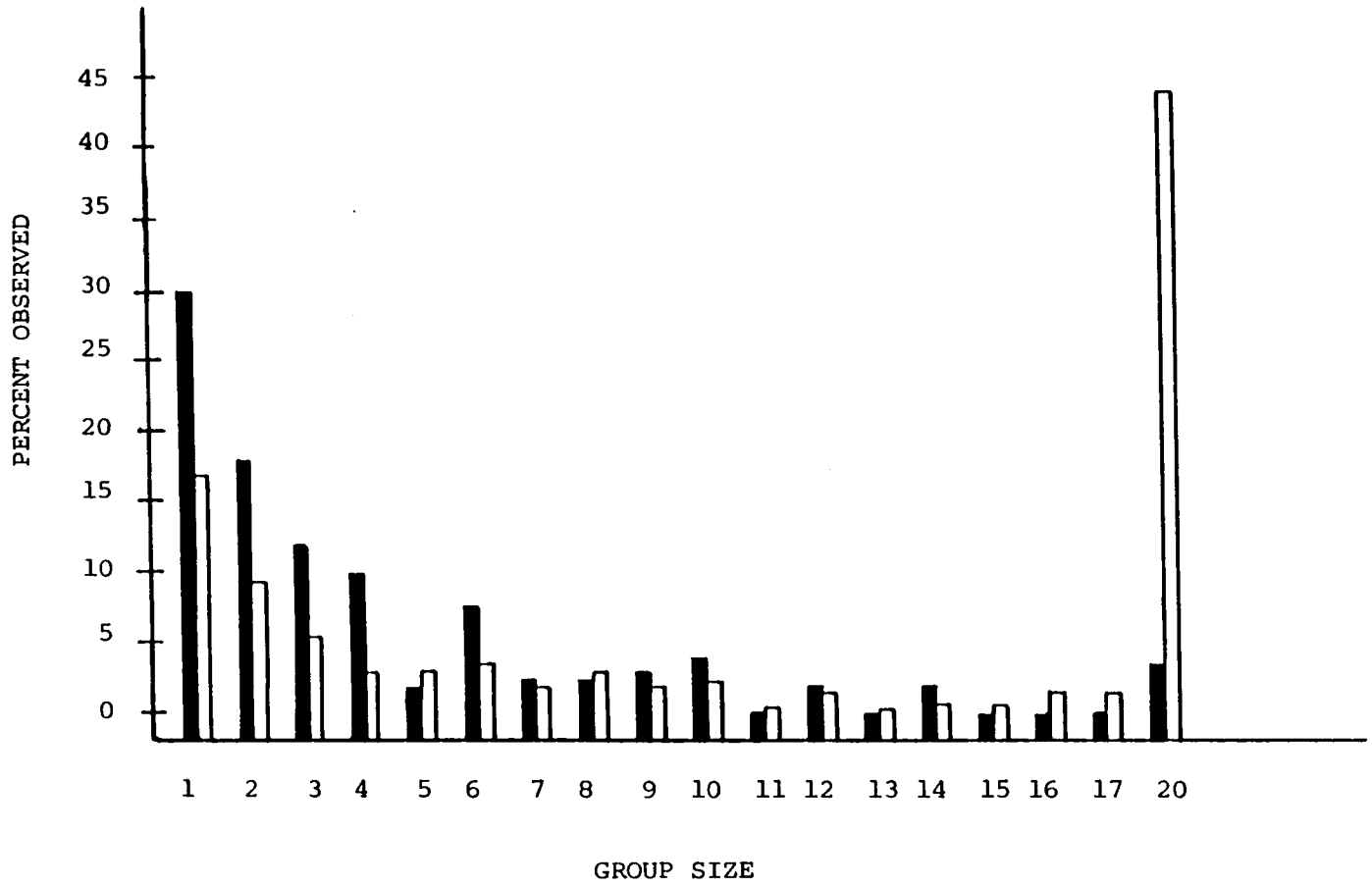

Figure 4. Frequency of groups of a particular size entering both the James River and Davis Caves during the morning return flight. Frequency is expressed as percent of total number of groups observed at each cave. Davis Cave (n=129) is the solid bar and James River Cave (n=376) is the open bar.

Table 12. Results of Kendall Rank Correlation test for time of column departure and environmental variables.

Departure time	n	Correlation coefficient	z value	Significance level
Temperature	15	.059	0.32	.37
Cloud cover	21	-.284	-2.08	.02*
Wind speed	24	.352	2.74	.003*
Wind direction	18	.060	0.36	.36
Sunset	25	-.365	-2.80	.003*
Sunrise	25	.200	1.49	.07
Moonrise	25	-.518	-3.70	.0001*
Moonset	25	-.066	-0.46	.32
Moon phase	25	-.228	-1.65	.05*

* denotes significant correlation

Table 13. Results of Kendall Rank Correlation test for direction of column departure and environmental variables.

Departure direction	n	Correlation coefficient	z value	Significance level
Temperature	15	-.127	-0.690	.25
Cloud cover	21	-.039	-0.281	.39
Wind speed	23	.034	0.253	.40
Wind direction	18	.147	0.882	.19
Sunset	23	.110	0.801	.21
Sunrise	23	.223	1.573	.06
Moonrise	23	.116	0.788	.22
Moonset	23	-.145	-0.959	.17
Moon phase	23	.225	1.549	.06

variables showed a significant correlation with the direction of column departure (Table 13). However, several variables showed a significant correlation with the time of column departure. The strongest correlation was with moonrise time ($P < .0001$) while sunset time ($P < .003$), windspeed ($P < .003$), cloud cover ($P < .02$), and phase of the moon ($P < .05$) were also significantly correlated with the time of column departure (Table 12).

CHAPTER 4

DISCUSSION

Do Stable Roosting Groups Exist?

Although individuals roost in particular areas of the cave (Figs. 2 and 3, p. 21 and 23; Table 3, p. 24) at least two lines of evidence suggest that roost site stability is not precise in location. First, the area in which an individual roosts is quite large, and contains several thousand roost sites (Table 4, p. 25). Second, although individuals roost in a certain area of the cave most of the time, they also roost in outlier sites (Figs. 2 and 3, p. 21 and 23). These outliers may represent roosts which bats utilize secondarily to their primary roosting area. This idea is supported by bat 5.3 (Fig. 3A, p. 23) which roosted in one area of the cave throughout most of the sampling period; however, on one occasion it roosted elsewhere. When monitored at 2-hour intervals throughout the day (Fig. 3B, p. 23), that "outlier" area was used as a roost site by bat 5.3 during half of my observations. Bat 3.2 (Fig. 2C, p. 21) also showed a preference for roosting in two areas of the cave. It is possible that other bats also have secondary roost sites, but that 3.2 and 5.3 utilized these "outlier" areas more often, thereby showing a bimodal roost pattern. To more accurately determine the nature of these outlier roost positions, it is necessary to monitor bats for longer periods of time and/or several times each day.

These two lines of evidence suggest that roost site fidelity

is only present in these bats in a general sense. Furthermore, it is clear that no two bats from the same group consistently moved their roost site synchronously from day to day (Figs. 2 and 3, p. 21 and 23). There is no evidence from this study to suggest that stable roosting groups exist. Consequently, both the first and second hypotheses (which state that such associations exist) must be rejected (Table 1, p. 8).

Do Stable Foraging Groups Exist?

Although half of the individuals observed leaving the cave to forage had a significantly clustered distribution of mean and vanishing directions over time (Tables 6 and 7, p. 28 and 29), there is no evidence to suggest that individuals captured together leave the cave to forage in the same direction (Tables 8 and 9, p. 30 and 31). However, individuals captured together do leave the cave closer together in time than individuals not captured together (Mann-Whitney U test, $P < .001$). This tendency in itself is not sufficient to demonstrate the existence of stable foraging groups for two reasons. First, several minutes (3-76) pass between the departure times of bats of the same group. During this timespan hundreds of thousands of bats exit the cave (Table 11, p. 34). So, even though these bats leave the cave closer to one another in time than bats tagged in different groups, they do not really leave "together". Second, among those bats which do leave the cave within a few minutes of each other (Table 11, p. 34), only rarely do they fly off in the same direction after departing from the cave (Tables 8 and 9, p. 30 and 31). Consequently,

it is unlikely that stable foraging groups exist, although it is possible that bats form stable groups once they reach the foraging grounds. Further study is necessary before the third hypothesis can be rejected (Table 1, p. 8).

The question of why group members leave the cave relatively close together remains unanswered. It is possible that certain sections of the cave "empty-out" first, so that bats roosting near one another would be leaving the cave closer together temporally than with bats roosting elsewhere. However, bats of the same group found departing close to one another in time (Table 11, p. 34) do not necessarily roost near one another in the cave (Figs. 2 and 3, p. 21 and 23), which does not support this possibility. A second possibility is that each individual bat has its own circadian activity cycle, which differs slightly from that of the other bats present. Bats which were captured together when returning from foraging may be more likely to leave closer together since they may have a more similar circadian rhythm (group 4 and 5 bats). Each individual may have some minimal amount of time it forages each evening so that it gets enough food. If each individual cues in to some internal mechanism determining the length of time needed, it will leave the cave and return to it again based on these cues. If some individuals are on similar schedules, they then may be leaving the cave close together in time. The presence of an endogenous activity cycle which helps determine cave departure time has been demonstrated in a variety of bat species (Voute et al. 1974, Erkert 1978, Marimuthu et al. 1981). This

circadian rhythm may be fine-tuned by the activity of other bats in the cave (Marimuthu et al. 1981), by sunset times (Erkert 1978), or by light levels outside the cave (Subbaraj and Chandrashekaran 1977). Bats appear to assess light levels changing outside the cave by "light-sampling", wherein an individual flies towards the entrance of the cave, then back in to the cave again in a circular pattern. These circles become larger and larger on each pass as the bat flies further out of the cave until it is several meters outside the cave entrance, and eventually departs for the night. Bats presumably exit the cave when light levels fall below some threshold (Twente 1955b). This light-sampling behavior seems to occur in T. b. mexicana (Twente 1955b, 1956). If the bats are performing the behavior to help "set" a biological activity clock, this may partially explain the close departure times of some of the bats. While this idea could support findings for group 4 and 5 bats (Table 11, p. 34) group 2 bats do not fit the explanation. These bats also show close synchrony of departure times (Table 11, p. 34) even though they were not captured while leaving for or returning from foraging (Table 2, p. 14).

A second question which remains unanswered is why some individuals tend to exit the cave in the same direction on several consecutive sampling nights (Tables 6 and 7, p. 28 and 29). One possibility is that these bats are cueing in to a locally abundant food supply which is present over the course of several days. Individuals may fly to where food was abundant the previous night, moving from one location to the next as the insect supply varies.

Given this scenario, it would be necessary to monitor foraging flights for longer periods of time to determine whether periodic shifts in foraging locations do occur among these bats.

What Determines the Time and Direction of Column Departure?

None of the environmental variables measured showed a significant correlation with the direction of column departure (Table 13, p. 38). Williams and Williams (1969) have shown that T. b. mexicana fly at high altitudes once they leave the cave (1500 - 10000 feet), and they suggest that the direction of departure from the cave may be related to the wind direction at these altitudes. Measurements of wind speed and direction at these altitudes may prove to be a better predictor of column behavior than those measures taken at ground level.

The time which the evening exodus begins seems to be influenced by a combination of environmental factors (Table 12, p. 37). Several of the variables measured which deal with lunar or solar cycles showed a significant correlation with the time of column departure. However, the exact relationship among the variables is difficult to determine. Sunset time shows a significant negative correlation ($P < .003$) with the time of column departure; this means that the later the sun sets, the earlier the bats leave the cave to forage, while the earlier the sun sets, the later the bats leave the cave. This seems counter-intuitive, although closer examination of the data set provides some insight. During the four week period that data were collected, sunset time only varied by four minutes. Erkert (1978), who noted a relationship between sunset time and cave departure time, observed bat

activity patterns seasonally where sunset times fluctuated much more. It is likely that longer term monitoring of this cave is necessary to extract any existing relationship between departure time and sunset time.

Measurements of the moonrise time and phase of the moon yield intuitively more meaningful results. Bats leave the cave earlier as the moon rises later ($P < .0001$) and as the moon becomes larger and more visible ($P < .05$) A rising moon and a larger moon both mean an increase in the brightness of the night. Since the bats seem to move out of synchrony with these two measures, it is possible that the total length of the dark period is an important determinant of when the evening exodus begins. If this is the case, one also would expect a significant negative correlation between column departure time and the amount of cloud cover. The data support this expectation ($P < .02$). It has been suggested that light is the most important factor regulating bat activity patterns (Erkert 1982). Many bat species are known to decrease their activity levels when the moon is most bright, a behavior known as lunar phobia (Crespo et al. 1972, Hirshfeld et al. 1977, Fenton et al. 1977a, Morrison 1978, Haussler and Erkert 1978, Usman et al. 1980). Lunar phobia may occur in response to predation by nocturnal birds of prey (Fenton et al. 1977b, Morrison 1978). Alternatively, bright nights may decrease insect activity, which consequently decreases the activity of bats which prey upon these insects (Anthony et al. 1981).

One other variable, wind speed, showed a significant correlation

with column departure time ($P < .003$; Table 12, p. 37). The stronger the wind, the later the bats exit the cave. The implication is that high winds curb flight activity, perhaps because it makes manuvering and hunting more difficult.

To summarize, although some environmental correlates have been found with the time of column departure, a clear pattern is elusive. It seems as if there is a combination of factors operating on column departure time, both biotic and abiotic. Among the abiotic factors, the sun and moon seem to have an influence. Since lunar changes occur on a monthly basis, rather than on an annual basis as do solar changes, any observed relationship between the time of column departure is more likely to be real since data were collected over a month's time. This may explain the seemingly paradoxical correlation between sunset and column departure time. Other abiotic factors such as the amount of cloud cover and windspeed are also involved. Finally, variables which were not measured such as relative humidity may also play a role, perhaps by influencing insect abundance. One would expect that the amount of food consumed the previous night, and perhaps the amount of energy expended within the past twenty-four hours would be important determinants of departure time as well. Further study is necessary before the relationship among all the variables can be precisely determined.

Conclusions

The evidence presented in this study does not suggest that adult females in Tadarida brasiliensis mexicana nursery colonies form stable groups either with regard to roosting or foraging associations. In the absence of such groups, both kin selection and reciprocity seem unlikely, and mutualism may sufficiently explain how evolution is operating in these caves. As concluded by McCracken (1984), it seems as if increased thermoregulatory efficiency may be the primary benefit obtained from mutualistic interactions among individuals, although the potential effect of predatory pressure cannot be ignored (Twente 1956, Pulliam and Caraco 1984). Hawks (Buteo spp.) were seen preying upon bats leaving the cave on several occasions. Mammals such as racoons (Procyon lotor), opossums (Didelphis virginiana), and feral pigs (Sus scrofa) have been seen in the caves at night, sometimes removing bats from the cave walls (McCracken et al., in press). Systematic study of predation mortality on these bats is necessary before its influence as a selective mechanism can be inferred.

Finally, further study on the precise nature of foraging behavior in these bats is imperative to a clearer understanding of the spatial and temporal distribution of individual bats. Questions on where the bats go, what kinds of insects they take, and whether they forage alone or with other individuals all remain. The answers to these and other related questions may help explain why the nursery colonies form in specific caves throughout the American Southwest, and lend further insight into how natural selection is operating on these bats.

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APPENDIX

FORTRAN CODE FOR COMPUTER SIMULATION

Code Used When n=2

```
      INTEGER X1, X2, TEMP, CT, SPAN, GAPF, GAPR
      OPEN(UNIT=21,DEVICE=DSK,FILE='CIRCLE.DAT')

C     Our sample size will be 10,000
C     KREP is the Kth replicate
      DO 10 KREP=1,10000

      X1=360.0*RAN(0)
      X2=360.0*RAN(0)
      IF (X1.LE.X2) GO TO 20
      TEMP=X1
      X1=X2
      X2=TEMP
   20 CONTINUE

      CT=X1
      X1=0
      X2=X2-CT

C     GAPF = "gap forward"
      GAPF=X2
C     GAPR = "gap reverse"
      GAPR=360-X2
C     SPAN = minimum gap

      IF (GAPF.LE.GAPR) SPAN=GAPF
      IF (GAPF.GT.GAPR) SPAN=GAPR
      WRITE (21,1001) SPAN
 1001 FORMAT(I5)
   10 CONTINUE

      CLOSE(UNIT=21,DEVICE=DSK,FILE='CIRCLE.DAT')
      STOP
      END
```

Code Used When n=3-8

```
      INTEGER X(8), G(8), TEMP, GMAX, CT, SPAN
      OPEN(UNIT=21,DEVICE=DSK,FILE='CIRCLE.DAT')
C     Specify group size for this run
      N=8
C     Our sample size will be 10,000
      DO 10 KREP=1,10000
```

```
C     Do these repetitions for each member of the group
      DO 20 K=1,N
C     Generate a random direction [X(K)] between 0 and 360
      X(K)=360.0*RAN(0)
   20 CONTINUE

C     Bubblesort, which will bring the smallest numbers to top
      NN=N-1
   29 DO 30 I=1,NN
      M=I+1
      IF (X(I).LE.X(M)) GO TO 30
      TEMP=X(I)
      X(I)=X(M)
      X(M)=TEMP

C     Back-up for bubblesort
      II=I-1
      DO 40 J=1,II
      JJ=I-J
      MM=JJ+1
      IF (X(JJ).LE.X(MM)) GO TO 40
      TEMP=X(JJ)
      X(JJ)=X(MM)
      X(MM)=TEMP
   40 CONTINUE
   30 CONTINUE

C     Check rank, double check the bubblesort
      DO 31 K=1,NN
      KK=K+1
      IF (X(KK).LT.X(K)) GO TO 29
   31 CONTINUE

C     Rotate points on the circle so X1=0
      CT=X(1)
      DO 50 KX=1,N
      X(KX)=X(KX)-CT
   50 CONTINUE

C     Generates G for gap of 1 - (N-1)
C     GMAX is the maximum gap
      GMAX=0
      M=N-1
      DO 60 L1=1,M
      L2=L1+1
      G(L1)=X(L2)-X(L1)
      IF (G(L1).GE.GMAX) GMAX=G(L1)
   60 CONTINUE
```

```
C     Generates G for the last gap
      G(N)=360-X(N)
      IF (G(N).GE.GMAX) GMAX=G(N)

C     Generates minimum spanning arc
C     SPAN is 360 - biggest gap, which is the spanning
C       arc for that replicate
      SPAN=360-GMAX
      IF (SPAN.GT.0) GO TO 80

C     Illegal value check
      DO 70 KX=1,N
      WRITE(5,999) X(KX), G(KX)
  999 FORMAT(5X,'X:',I5,5X,'GAP:',I5)
   70 CONTINUE
      WRITE(5,998) GMAX, SPAN
  998 FORMAT(/5X,'MAX GAP:',I5,5X,'SPAN:',I5/)

C     Output to data file for SAS
   80 WRITE(21,1001) SPAN
 1001 FORMAT(I5)
   10 CONTINUE
      CLOSE(UNIT=21,DEVICE=DSK,FILE='CIRCLE.DAT')
      STOP
      END
```

VITA

Maria Adele Okoniewski was born in Buffalo, New York on August 11, 1962. She attended elementary schools in that city and was graduated from Holy Angels Academy in June 1980. The following September she entered Canisius College in Buffalo, receiving a Bachelor of Arts degree in Psychology in May 1984. In the Fall of 1984 she accepted a teaching assistantship at The University of Tennessee, Knoxville and began study toward a Master's degree. This degree was awarded in August 1986.