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Gary F. McCracken

Gary F. McCracken, Major Professor

We have read this thesis
and recommend its acceptance:

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Vice Provost and
Dean of the Graduate School

INDIVIDUAL VARIATION IN THE STRUCTURE OF PUP ISOLATION CALLS IN MEXICAN FREE-TAILED BATS (*TADARIDA BRASILIENSIS MEXICANA*)

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Deborah L. Gelfand

March 1985

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Date March 6, 1985

DEDICATION

This thesis is dedicated to Mary Sue Luker, friend and editor, without whose skill, patience and forbearance the writing of this thesis may have stretched on interminably. Not only was she willing to put in long hours of work under intense deadline pressures, but she endured this writer's crankiness and self-doubts while remaining an unflagging source of emotional support.

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ABSTRACT

This study investigated the presence of pup vocal signatures and the ability of adult females to recognize individual pup vocalizations in Mexican free-tailed bats, Tadarida brasiliensis mexicana. Female-pup nursing pairs and pregnant females were captured from large maternity colonies in central Texas. Vocalizations of 20 pups were recorded and nine call parameters were measured spectrographically or with a spectrum analyzer. Recordings of fourteen of the pups were played back to females to determine whether females discriminate among pup calls. Univariate and multivariate analyses of the call parameters showed that pup calls are structurally distinct, suggesting that the pups have individual vocal signatures. Calls also possess qualities that suggest they are attractive in nature and easy to locate. Regression analyses show that several call parameters increase in frequency as pups age. G-tests on the vocal responses of adult females to the playbacks of pup calls showed that females did not respond differentially to their own pup's call versus another pup's call or blank tape. Possible explanations for these latter findings are discussed.

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CHAPTER I

INTRODUCTION

Mexican free-tailed bats (Tadarida brasiliensis mexicana) are considered to be the most gregarious bat species. Their summertime maternity colonies frequently contain millions of bats in a single cave; approximately 95% of these bats are pregnant females, the remaining 5% are males and nonparous females. Most pregnant females give birth to a single pup which they deposit, after the first nursing, on a separate area of the cave wall where other pups are clustered. Twice a day each mother returns to a "nursery creche" to nurse a pup.

A previous study (Davis et al., 1962) concluded that the nursing of Mexican free-tailed pups is indiscriminant. It may be that the benefits derived from the utilization of creches, such as protection from predators, heat conservation, or socialization, counter the costs of not being able to locate an individual pup. However, nursing a pup other than her own, when lactation is so energetically expensive (Millar, 1977, 1978), does not seem to be evolutionarily adaptive for a female. She should be directing her reproductive efforts into pups who share some of her genes. A more recent study (McCracken, 1984), using allozyme genetic markers, found that nursing is not random but is, in fact, selective (although not exclusive) relative to the female-pup nursing-pair genotypes. That is, of 167 female-pup nursing pairs examined, only seven nonparental

genotype pairs were observed when 42.5 pairs would be expected if nursing were random.

According to W. D. Hamilton's (1963) currently accepted "inclusive fitness" hypothesis, individuals should behave to enhance the survival of others in proportion to the genetic relatedness between them. Thus, in order to enhance her inclusive fitness, a mother should nurse only her own pup or closely related pups. For such nepotism to exist, however, the females must recognize related individuals.

It is well established that a wide range of animals employ some system of mother-infant recognition which enables selective parental care (e.g., Kulzer, 1961, 1962; Jones, 1967; Thompson and Emlen, 1968; Beer, 1969, 1979; Kolb, 1977; Brown, 1976; Brown et al., 1983; Beecher et al., 1981; for an extensive review on parent recognition, see Colgan, 1983). The possible cues employed by mothers include vision (e.g., Bucklery and Buckley, 1972), spatial memory (e.g., Gould, 1971; Nelson, 1964, Brown, 1976; Barclay et al., 1979), olfaction (see Halpin, 1980 for examples) and audition (e.g., Espmark, 1971; Petrinovich, 1974; Kaplan et al., 1978; Cheney and Seyfarth, 1980, 1982). Marler (1967) and Scott (1968) point out that the animal's habitat and lifestyle restrict the choice of the sensory modality providing the mechanism for communication. As a nocturnal species, bats should have little use for visual signals, but chemical and auditory signals, as well as spatial memory, could be quite useful. There is a great deal of evidence to show that the sense of hearing

is highly developed in bats (e.g., Bodenhamer et al., 1980; Pollak, 1980; Suga and O'Neill, 1980) and is, therefore, likely to be a sensory modality used in communication.

Pups of many bat species vocalize when separated from their mothers. Such vocalizations have been termed "isolation calls" (i-calls), and they are known to elicit searching by females (e.g., Pteropus spp., Nelson, 1964; Desmodus rotundus, Schmidt, 1972; Antrozous pallidus, Brown, 1976; Corollia perspicillata, Porter, 1979; Rhinolophus ferrumequinum nippon, Matsumura, 1979; and Myotis lucifugus, Thompson, 1980). In most species, the mother bat emits a call which is closely associated with the i-call. This is either a direct response to the pup's call or a vocal exchange initiated by the mother herself that may facilitate reunion with the infant. The mother's call is referred to as a "directive" (Brown, 1976) or a search call (Gould et al., 1973; Nelson, 1964; Brown et al., 1983; Matsumura, 1979; Thompson, 1980; Schmidt, 1972). The antiphonal calling between the mother and the pup is an indication that communication is taking place.

Beecher (1982) points out that for individual recognition to occur, some sort of signature system must be employed by the signaler. A signature system is "a specific complex of phenotypic traits which is (to some degree) individually distinctive" (Beecher, 1982, p. 478). Marler (1959) and Emlen (1972) claim vocal signatures are best obtained when a call is highly complex. However, Beecher proposes a model showing how very complex calls are not required for individual recognition.

Marler, Emlen, and Beecher were all concerned with the structure of bird songs, the complexity of which lies in the variability in the ordering of phrases, syllables within phrases, notes within syllables, number of notes, syllables and phrases, and time length of notes, syllables and phrases. T. brasiliensis isolation and search calls are simple in contrast to this definition of complexity (Thompson et al., unpublished). They consist of only one type of note, but it is flexible enough in frequency, intensity, and pattern of frequency modulations that variation in information could be present (Sebeok, 1967). Because the hearing of bats is so sensitive, it is not unreasonable to assume that bats can be highly discriminating along these parameters (Griffin, 1977).

One difficulty associated with vocal recognition in T. brasiliensis, stems from the fact that the population in the caves is immense. Beecher does allow, however, that given the availability of several graded variables, the size of the population matters little, if at all. Several studies indicate that vocal signatures are found in other species of bats: Myotis lucifugus appear to have individual differences in intercall intervals (between i-call and search call; Turner et al., 1972); and there are individual differences in call durations among Antrozous (Brown, 1976) and Myotis infants (Turner et al., 1972). Differences in i-calls have not been found in other cases (e.g., Porter, 1979; Matsumura, 1979).

Other investigations are under way to determine if T. brasiliensis mothers recognize pups by spatial or olfactory cues.

The primary goal of this research was to determine if T. brasiliensis mothers recognize pups by auditory cues. McCracken's (1984) data demonstrate that kin recognition does occur, although the extent of its existence is unclear. While general behaviors regarding the range of cues employed to effect recognition between mothers and infants were observed both in the caves and in captivity, the focus of this study was to examine whether auditory cues aid in individual recognition. The predictions were (1) pups have vocal signatures and (2) mothers discriminate among pups' calls.

The Study Animal

Tadarida brasiliensis mexicana is a member of the suborder Microchiroptera and the family Molossidae. Adult females weigh 14.6 g on average in October and 11.5 g on average in April (Twente, 1956); this difference in weight parallels the availability of insects in summer and winter. Their average forearm length (the standard size determinant in bats) is about 45 mm (McCracken, pers. comm.). Tadarida brasiliensis are moth eaters (Barbour and Davis, 1969) and are found from the southwestern United States to as far south as Chile and Argentina (see Figure 1). The subspecies Tadarida brasiliensis mexicana is migratory. Males and females winter together (November through February) in the southern parts of their range, although some scattered groups winter in Arizona, California, New Mexico, and Texas as well (Villa and Cockrum, 1962). Females migrate northward each spring. T. brasiliensis become lethargic when roosting

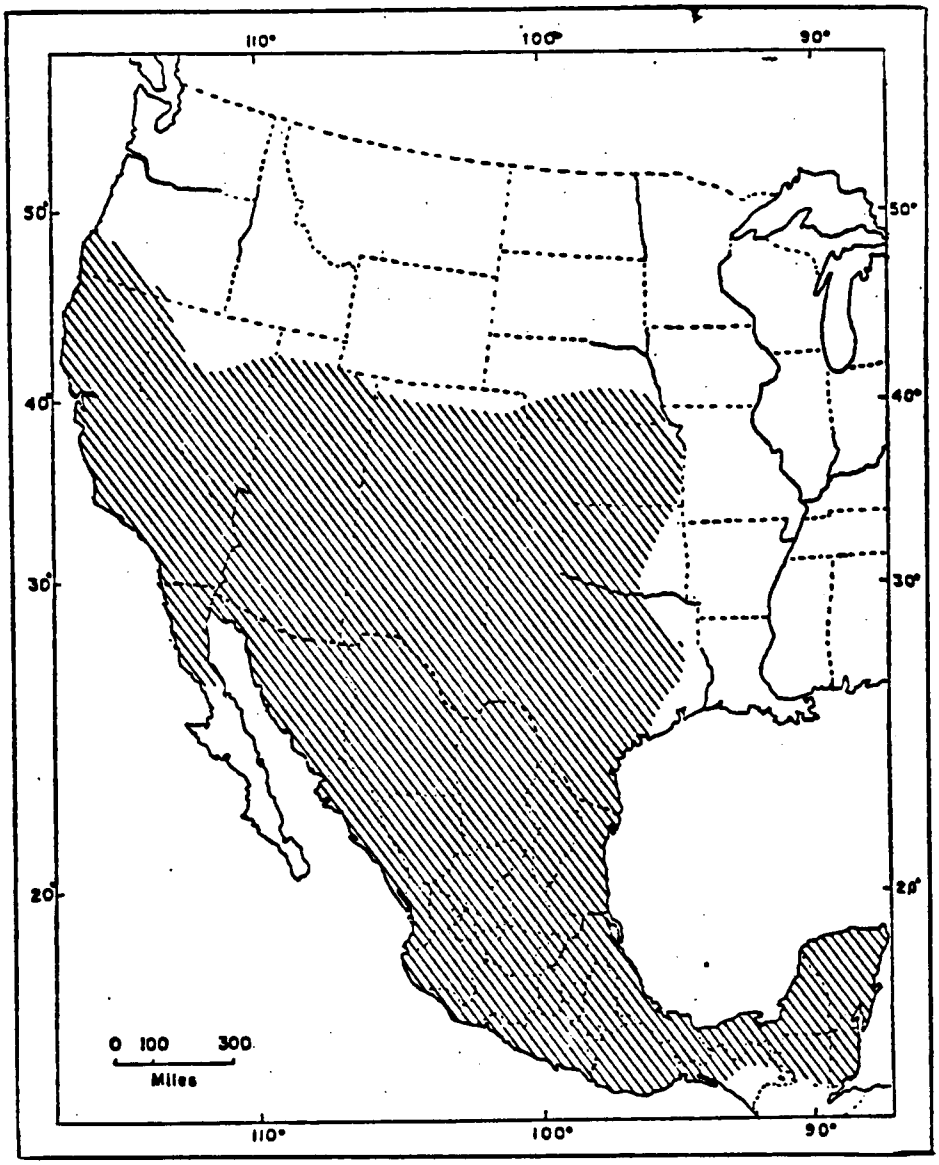

Figure 1. Geographic distribution of Tadarida brasiliensis mexicana in North America.

(From Villa and Cockrum, 1962.)

in cool places but there is no evidence that they hibernate (Davis et al., 1962; Constantine, 1967). Migrants first appear in Texas during late February and increase in numbers through April. By May, the population is stable and remains so until the pups are weaned in July or August. Females roost together in large maternity colonies (some up to 40 million adults) and males that have migrated north roost in small, separate summer colonies.

Male T. brasiliensis are sexually potent between January and early March (Davis et al., 1962). Breeding takes place in February and March before migration; ovulation and fertilization occur in late March. The gestation period is approximately 11 weeks, and each adult female goes through one gestation cycle a year and most give birth to only a single pup (twins are rare). During the peak birthing period, which is in June, 90% of the pups in the Texas colonies are born over a 15-day span (Barbour and Davis, 1969).

The average body weight at birth is 2.4 g for females and 2.66 g for males (Short, 1961). The average length of the forearm at birth is 17.6 mm for females and 18.6 mm for males (Short, 1961). They are pink, furless and capable of active crawling. Their skin color becomes darker, changing to dark blue-gray before the fur begins to grow at about 2-1/2 to 3 weeks of age. Their eyes are almost totally open at birth, and, unlike several other bat species (Brown, 1976), the tragus does not appear to block the opening to the middle ear. The close synchrony of pup and adult calling immediately after birth indicates that the newborns are capable of hearing (personal

observations). They begin to fly at about five weeks of age, and they attain full size after about 60 days (Barbour and Davis, 1969; Nowack and Paradiso, 1983).

During parturition, which normally takes place in the early afternoon, mothers hang from the cave wall or ceiling amidst clusters of other adults. Immediately after birth the pup crawls to one of its mother's teats to nurse. A few hours later the mother deposits the baby in a creche (Davis et al., 1962). Creches can exceed 54 m^2 in area and contain up to 3300 pups/m^2 (Henshaw, 1960). After leaving the pup in the creche, the mother goes to another area of the cave where she roosts until foraging time. This roosting area may contain 1100-1600 adult bats/m^2 (Twente, 1956; Henshaw, 1960). In the early evening (usually before dusk) the mothers fly to the creche to nurse their young. They then leave the young behind and emerge from the cave to forage. There is another nursing peak in the early morning.

Studies of captive and wild populations of T. brasiliensis by Herreid (1963a,b) indicate that coloniality is essential to their temperature regulation. He found that the clustering of bats kept T. brasiliensis adult and pup body temperatures between 32°C and 42°C and that individuals at the edge of a cluster of bats were several degrees cooler than those deep within the group. Herreid also found that there was an inverse relationship between the number of bats in a cluster and the metabolic rate of an individual bat. Twente (1956)

discovered that a T. brasiliensis roosting alone has a body temperature identical to the ambient temperature, whereas clustering bats have body temperatures considerably higher than the ambient temperature.

CHAPTER II

METHODS

Subjects

There were two types of subjects for this study: 1) pregnant females, in captivity for approximately 6 weeks, and 2) female-pup nursing pairs, in captivity for only 2-3 days. Pregnant females were collected May 30, 1983, approximately two weeks prior to the period of peak parturition, from the James River Cave in Mason County, Texas. Two clusters of roosting bats were captured from separate regions within the cave, using a 10 cm diameter bucket (as described by McCracken and Bradbury, 1981). Twenty pregnant females were taken from each of these clusters and transported to the captivity setup in Blanco County, Texas.

The female-pup nursing pairs were collected between June 23, 1983 and July 9, 1983, during the period of peak parturition and nursing, from either the James River (Mason County, Texas) or Davis Blowout (Blanco County, Texas) Caves. Three to six female-pup nursing pairs were removed at three to five day intervals from one of the caves. Since mothers nurse for several hours after birth and then deposit the pups in a creche separate from where adults roost, any pups found among the females were probably newborns attached to their own mothers and nursing for the first time. Therefore, to be as certain as possible of the true relatedness of

the females and pups, co-workers and I attempted to capture newborns attached to females within the adult roosting areas. This proved feasible only early in the birthing period. Later in the birthing period, as fewer pups were born each day, it became more difficult to find pups among the females. This means, that the female-pup nursing pairs used in this study, we cannot be certain all of the pups were the true offspring of the females; however genetic analyses (McCracken, 1984) indicate that this is highly probable.

Housing

Each cluster of 20 pregnant females was housed in a 10 cm x 10 cm x 20 cm cage for the first two days of their captivity. Prior experience has shown that it is difficult to train *T. brasiliensis* to eat in captivity; therefore, they were force-fed using a one cc syringe at approximately 7:30 a.m. and 7:30 p.m. for three days. They were fed a pureed mixture of three teaspoons cod liver oil, approximately 75 mealworms, one medium sized banana, and 1/4 kg cottage cheese. On the third day of captivity, each female was marked by placing an uniquely colored plastic band on the left forearm. Each group was then placed in a 45 cm x 45 cm x 45 cm wire cage and force-fed one more day. At this point, food was placed in the cages at the regular feeding times, and it was hoped that the captive bats would eat on their own. One day later each group of females was placed into a captivity roost. The captive environment was modeled after that of Thompson et al. (unpublished) and

consisted of two wire cages surrounding ferrocement roosting enclosures connected to a common light-proof observation chamber (Figure 2). The bats normally clung to the interior of the ferrocement roost which was separated from and accessible to the observation chamber by hinged plexiglass doors. The bottom of each roost was open, allowing the bats access to the wire cage. There was a shelf 3.75 cm below the opening of each roost to serve as a light buffer and food shelf. The observation chamber was lighted with a red light bulb and the bats were observed through the plexiglass window. In order to match temperatures in the caves (which are around 29.5-42.2°C in the summer) a heater in the observation room heated the roosts to a minimum of 32.2°C. A fan, used only during observation periods, created negative air flow so that the observer's odor would not disturb the bats. Plywood doors covered the cages on all sides at night to preserve warmth within the captivity roosts. The plywood doors were opened during the day for air circulation and to let daylight in. General observations of mother-pup behavior among the captive bats were recorded. The pregnant females housed in the captivity roosts were also used for observational study (McCracken and Gustin, unpublished).

Each female-pup nursing pair was housed in a pint-sized ice cream container with screen on the top, bottom, and interior walls of the container. This allowed for circulating air and a surface from which to hang. Neither females nor pups were marked with

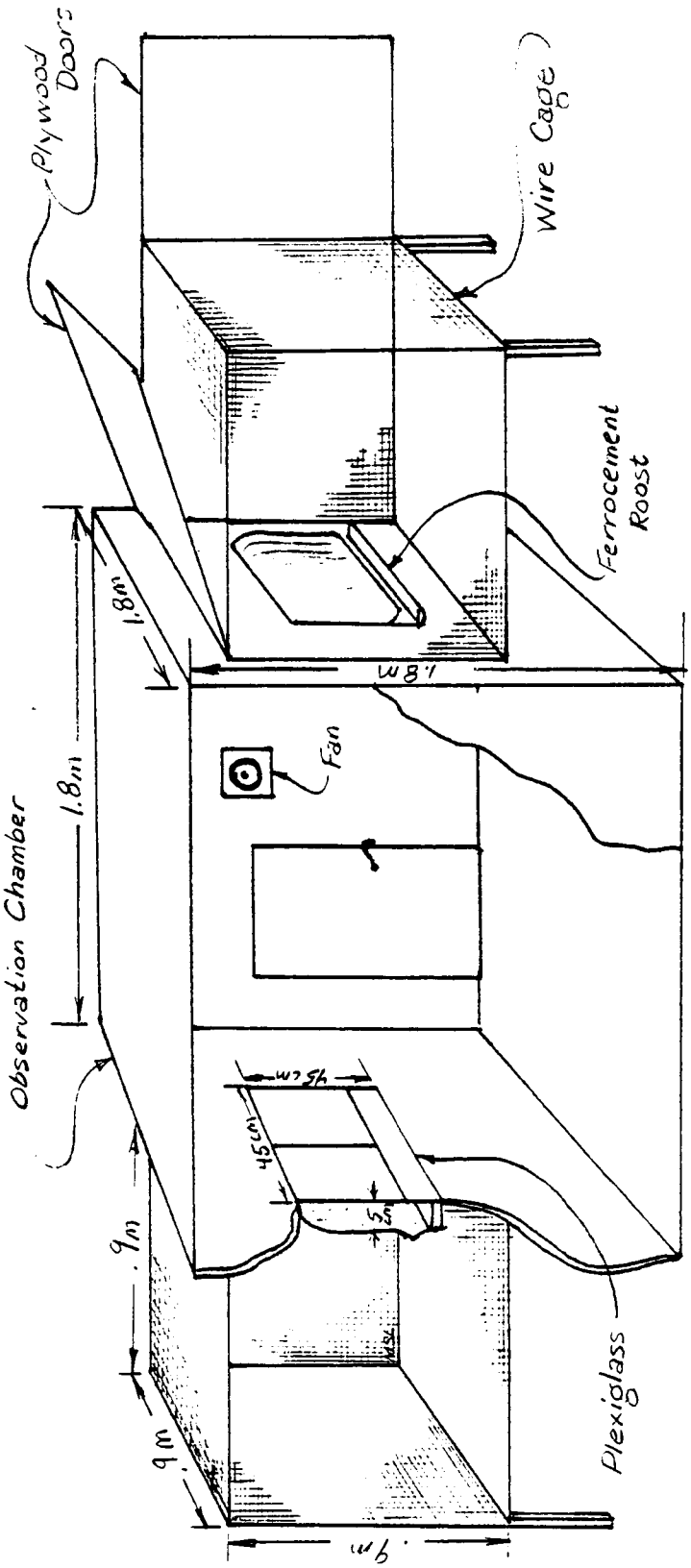

Figure 2. Enclosures for captive bat study.

Dimensions are given; see text for further explanation.

plastic bands; their containers, however, were marked with identifying numbers. The first three female-pup nursing pairs captured were designated as 1, 2 and 3; the second group of pairs captured were 21, 22, and 23; the third group captured were 31, 32, and 33, and so on. Each pair was kept from two to three days while pup vocalizations were recorded and playback experiments were conducted. During this period, each pair was given water and the food described earlier in small dishes. To keep disturbances at a minimum, they were not force-fed. When vocalizations were not being recorded and playbacks were not being conducted, the female-pup nursing pairs were kept in their marked ice cream containers, in the captivity roost observation chamber.

Vocal Signatures

Vocalizations were recorded using a Racal (Lockheed) Store 4D tape recorder (76 cm/s) through a QMC model SM1 PSM1 microphone and a custom made (Carleton University) microamplifier (see Simmons et al., 1979 for specifications). The output from the microphone was monitored using a Tektronix 212 oscilloscope to avoid signal saturation.

Individual pup vocalizations were recorded by separating the pups from the females, placing each in its own container, and removing them from the room which housed the females. At first an attempt was made to record pup vocalizations within the captivity roost's dark observation room; however, this room proved to be too

humid for the recording equipment to function properly. Since no other room was available, recordings were made outside, but in the shade. The microphone was placed approximately 15 cm from the ice cream container and a cloth was draped over both to reduce disturbances to the pup within. The pups were recorded whenever they were vocally active, generally, between 3:00 and 6:00 a.m. and 7:00 and 11:00 p.m. I attempted to record five minutes of calls from each pup. Two pups born to females in the captive colony also were recorded. These recordings were made while pups were in the ferrocement roosts or wire cages and with their mothers in close proximity.

Playbacks

To determine whether females recognize their pup's isolation calls, I played taped isolation calls to them. The females were presented with three types of "recordings": (1) their own pup's vocalization, (2) an unfamiliar pup's vocalization, and (3) tape with nothing recorded on it. Subsequently, these three recordings will be referred to as pup, nonpup, and blank, respectively. Each playback recording lasted approximately 10 to 15 seconds. The playback experiments were first conducted in a 5 cm x 30 cm x 45 cm arena, but the bats were too disturbed to allow assessment of behavioral reactions. Even with a five minute acclimation period, many bats were still disturbed; some hung perfectly still throughout the playbacks, while others moved around wildly the entire time. At this point it was decided that the females would remain minimally

disturbed if they were retained in the ice cream containers (although still separated from the pups) while the playbacks were conducted. Vocal response from the adult was chosen as the behavior to measure because its presence or absence can be clearly determined (see below). Behaviors such as head orientation or wing flapping, which may also be of consequence, lend themselves less well than vocal responses to objective assessment. Playbacks were also conducted outside, but in the shade and with a dark cloth draped over the speaker, microphone, and ice cream container. Playbacks consisted of three consecutive presentations of each of the three recordings. At the end of each presentation, a timer was turned on and vocal responses were noted. The time lapse prior to vocalization (rspl) and the number of vocalizations (nmrsp) were noted over a 90 second period. Because adult bat vocalizations often are inaudible to humans, responses were determined by observing an oscilloscope attached to a microphone facing the tested females. The tape was then rewound and after another 30 seconds, the same recording was presented and responses were recorded for 90 seconds. This continued until there were three trials for each of the three recording tapes. Between each of the three recording types the bat was left in quiet for five minutes. This procedure was followed for each female.

The order in which the females were tested and the order in which the recording types were presented were randomized by tossing a coin. Playbacks were conducted between 9:00 a.m. and 5:00 p.m. Due to equipment failures only 14 adults whose baby's calls were

recorded were completely tested on the first day and only nine on the following day. In each series of playbacks, one of two nonpup recordings was presented. Fifty-seven percent of the pup/nonpup playbacks were blind, that is, the observer did not know whether the pup or nonpup playback was being presented.

Recorded vocalizations that were presented to females were amplified by a Dyanaco preamplifier and a Realistic amplifier through a Kef T57 speaker. The signal was flat from 1 to 40 kHz. This output was also monitored by a Tektronix 212 oscilloscope to avoid signal saturation.

Sonagram Production

Samples of the pup isolation calls were transformed into sonagrams by a Kay 6061A sound spectrograph, using a narrow filter bandwidth at a frequency range of 80-8000 Hz, with the recorder played at 1/8 original speed. Measurements obtained from the sonagrams were used to determine whether pups have calls that are structurally different, thereby suggesting the existence of individual vocal signatures. These measurements include minimum frequency of the fundamental (mff), maximum frequency of the fundamental (mxff), frequency modulation of the fundamental (fml), frequency modulation of the second harmonic (fm2), dominant frequency (frequency with the largest amplitude, df), call duration (cd), intercall interval (ii), and minimum frequency of the

second harmonic (msh) (See Figure 3 and Table 1). Characteristics of harmonics above the second were not measured because high frequency sounds are attenuated over short distances and, therefore, the sonagrams may have been distorted from reality at higher frequencies. Because of other problems or distortions from the sonagrams, three of the above measurements (ii, df, and cd) were also obtained by other potentially more accurate means. Dominant frequencies were determined by running the taped isolation calls through a Fast Fourier spectrum analyzer (Figure 3b). Initial frequency (iff) was also obtained by this method. Intercall interval and call duration were obtained by film strips of Dual trace oscilloscope readings. Calls on one channel were produced by interrupting the flow of the recorded signal to the oscilloscope with a period meter (see Simmons et al., 1979 for specifications). The second trace was a 5 cycle per second signal produced by a signal generator. The two traces were filmed by a Kymograph camera with a film speed of 25 mm/s and a recorder speed of 37.5 cm/s.

Measurements of ii, cd, and df

A Paired t-test was used to analyze the degree of similarity between the two methods of measurement for ii, cd, and df. For 21 cases in which ii was measured for the same call by each method, there were no significant differences in the average readings or standard deviations obtained from either of the two methods (Table 2). The correlation between the two methods also was high ($r = .84$,

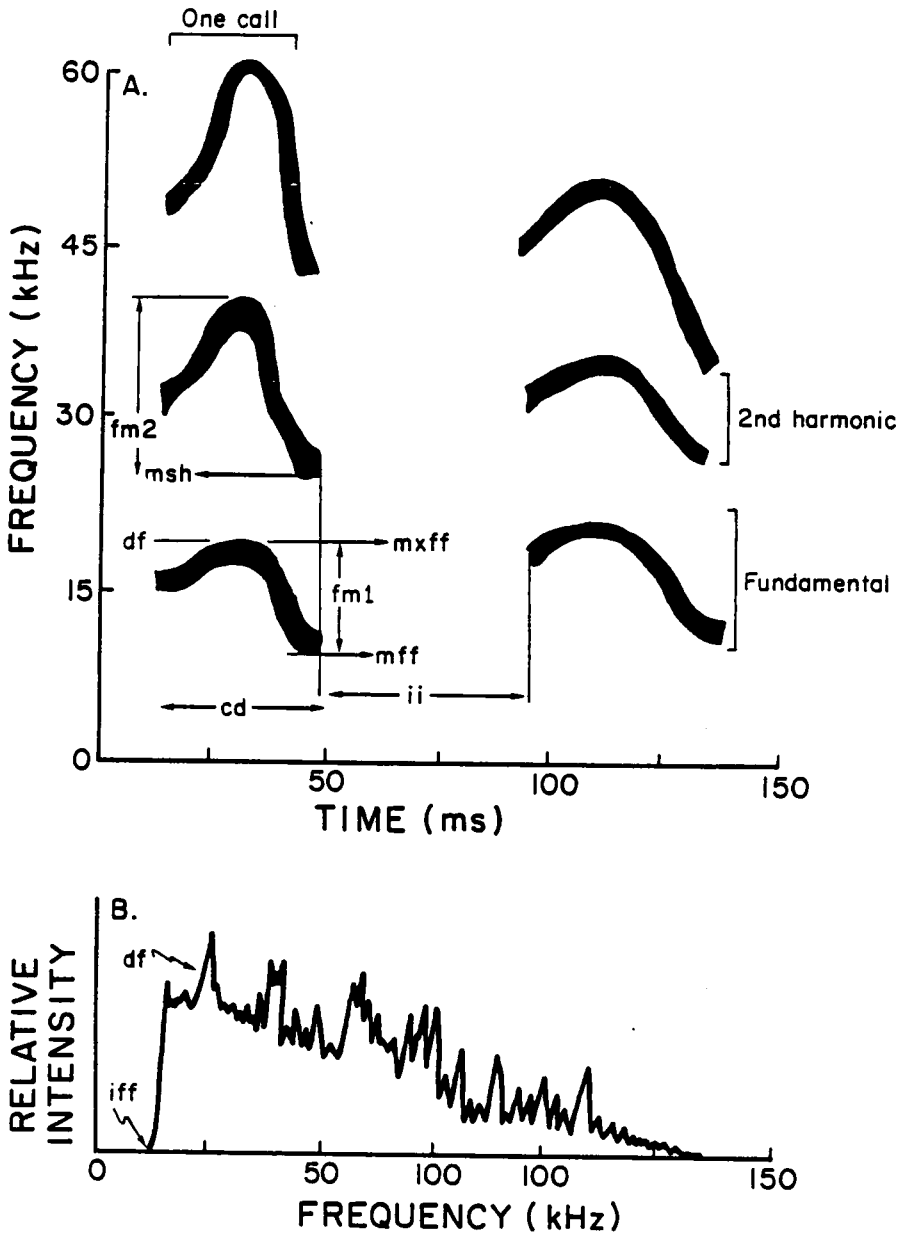

Figure 3. Examples of pup vocalizations illustrating the nine call parameters that were measured in this study.

(A) A sample sonagram produced by a sound spectrograph. mff = minimum frequency of the fundamental; mxff = maximum frequency of the fundamental; fml = frequency modulation of the first harmonic; fm2 = frequency modulation of the second harmonic; msh = minimum frequency of the second harmonic; cd = call duration; ii = intercall interval; iff = initial frequency; df = dominant frequency. (B) A sample display from a spectrum analyzer. if = initial frequency; df = dominant frequency.

Table 1. Abbreviations of call parameters used in this paper.

Call Parameter	Abbreviation
Minimum Frequency of Fundamental	mff
Maximum Frequency of Fundamental	mxff
Frequency Modulation of 1st Harmonic	fm1
Frequency Modulation of 2nd Harmonic	fm2
Dominant Frequency	df
Call Duration	cd
Intercall Interval	ii
Minimum Frequency of 2nd Harmonic	msh
Initial Frequency	iff

Table 2. Similarities between measurements of ii[a], cd[b], and df[c], as obtained by two methods.[d]

	ii	cd	df
Mean			
Method 1	1015.4ms	228.76ms	18.48kHz
Method 2	1066.8ms	253.72ms	21.04kHz
t[e]	.76	-2.21	-3.28
Probability	.4565	.0321	.0017
Standard Deviation			
Method 1	313.61	78.35	2.82
Method 2	264	95.39	7.92
F[f]	1.41	1.48	7.93
Probability	.4484	.1855	.0001

[a]Intercall Interval.

[b]Call Duration.

[c]Dominant Frequency.

[d]Measurements from the two methods are interchangeable for ii and cd, but not for df.

[e]t-Statistic from Paired t-test.

[f]F-statistic from F test.

$p<.0001$), indicating that, within the range of measurements taken, the two methods agreed on average, and the individual measurements from the two methods concured. These results indicate that the two methods are convergently valid (Campbell and Fiske, 1959), and are essentially interchangeable. Because many more measurements were obtained from the sonagrams (iil) than the filmstrips (ii2), the data from iil were used in further analyses.

Of 47 cases in which cd was measured by two methods, there was a significant difference between the means of the measurements from each method (Table 2). Further investigation into this bias showed that it depended on which pup was being measured. A closer look at cd2 (filmstrips) showed that the differences between pups were, in fact, caused by a blurring of the filmstrips of specific pups. This does not indicate that cdl (sonagrams) was a better method than cd2; it only implies that cd2 could not be measured properly in some cases. Despite this problem, the standard deviations of the measurements from each method were not significantly different (see Table 2) and the correlation was high ($r = .72$, $p<.0001$). Again, because of the apparent interchangeability of the data and the number of measurements gathered, the data from cdl were used in further analyses.

Significant differences in both means and standard deviations were detected between the two methods used to measure df (Table 2). There was also no correlation between the two methods ($r = .16$, $p = 1876$). It was, therefore, concluded that the two methods were

not interchangeable. The df1 measurements obtained from the sonagrams were based on judgement as to the darkest areas, which indicated the frequencies with the highest amplitudes. Some of the sonagrams were very easy to read in that the contrast between light and dark areas was high. However, some had no "darkest area"; in these cases, the dominant frequency was simply assumed to be the middle frequency of the fundamental. Df2 measurements were obtained by utilization of the Fast Fourier spectrum analyzer. This method produced clear, precise readings which indicated exact amplitudes. Of these two methods, the subjective readings of df1 had a potentially higher margin for error than the more objective and exact readings of df2. For this reason, df2 was the more preferable set of data. However, because only a small sample of df2 measurements were obtained, this variable was not used in the discriminant analysis.

Statistical Analysis

To assess if differences in isolation calls exist between pups, the variables fm1, fm2, iff, cd and msh were used in a discriminant analysis (Nie et al., 1975) a variance component analysis (SAS Institute, Inc., 1982) and a general linear model analysis (Neter and Wasserman, 1974). Intercall interval was not used in the discriminant analysis because it could not be assigned as belonging to a particular call. Mff and mxff were also not used in the discriminant analysis because preliminary tests

indicated that each are highly correlated with several of the other six variables and they added no additional information to the discriminant functions; therefore, for simplicity's sake, they were excluded.

Effects on playback responses of recording types, blindness of the observer, trial number, order of presentation of the recordings, and day of playback were examined with the G-test (Sokal and Rohlf, 1981). The G-test was also used to assess the relationship between age of pups and response of females to the playbacks.

Regression Analyses (Draper and Smith, 1981) were done to determine whether changes in any of the variables occurred as the pups got older. R^2, the percent of total variation explained by the regression model, was used as a measure of the effectiveness of the model. However, according to Draper and Smith (1981), the R^2 should be modified because repeated measurements for different levels of the independent variable produce within-pup error. That is, variations within each pup cannot be explained by age, and these unexplainable variations are the within-pup error. Because the within-pup error cannot be explained, no matter what model is fitted to the data, R^2 cannot equal one. Thus, the maximum R^2 attainable or explainable is

$$R^2 \text{ maximum} = \frac{\text{Total Sum of Squares - Within-Pup Sum of Squares}}{\text{Total Sum of Squares}}$$

Because of this, the actual R^2 for the model is

$$R^2 \text{ actual} = \frac{R^2 \text{ model}}{R^2 \text{ maximum}}$$

rather than

$$\frac{R^2 \text{ model}}{1}$$

In other words, R^2 actual is the percent of the variation due to differences between pups explained by the model. Note that since pups were kept for only two to three days, I considered maturational changes to be differences between older and younger pups. Because several studies in pups have found that forearm length increases with age (e.g. Short, 1961; Brown, 1976; Brown et al., 1983), approximate age was estimated by the pup's forearm length. Forearm lengths were obtained for only 13 of the 20 pups.

CHAPTER III

RESULTS

Description of Calls

Isolation calls of 18 pups collected from the caves and two pups born in captivity were recorded. Pups in the captivity roosts called at various times throughout the day, often with no apparent stimulation. The bats in the ice cream containers, however, were observed to call only when separated from their mothers between 7:00 p.m. and 7:00 a.m. There were 1-5 minutes of calling recorded from each of the 20 pups. An average of 18.35 calls per pup (range 9-36) was used to measure the nine call parameters (see Appendix I for number of calls analyzed for each pup).

Most pup vocalizations were variations of sinusoidal waves with the major sound energy in the fundamental (Figures 4-6). Calls contained varying proportions of both CF (constant frequency) and FM (frequency modulated) components with different portions emphasized or deleted. Calls also varied as to whether they began with a descending or ascending FM, but there were never more than two ascensions or descensions in any one call. Some pups produced calls that were almost purely CF (e.g., Figure 6A), and some pups produced stacatto bursts of FM pulses (e.g., Figure 6F). The pup calls can be described acoustically as clear peeps rather than buzzes, clicks, or squawks. Appendix I shows the mean, standard deviation, and range

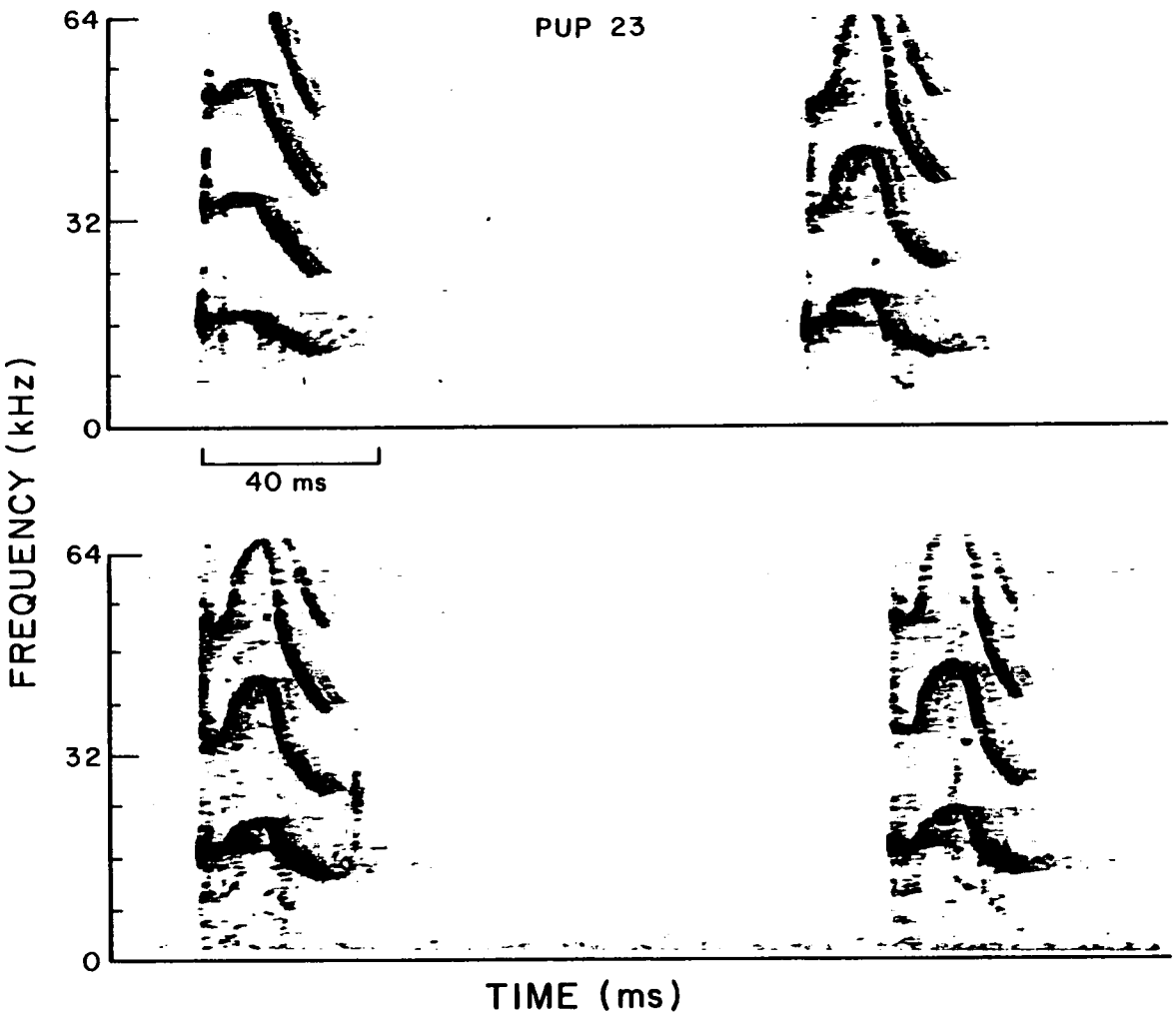

Figure 4. Sample calls that illustrate small within-individual variation. Four consecutive calls emitted by pup 23 are shown.

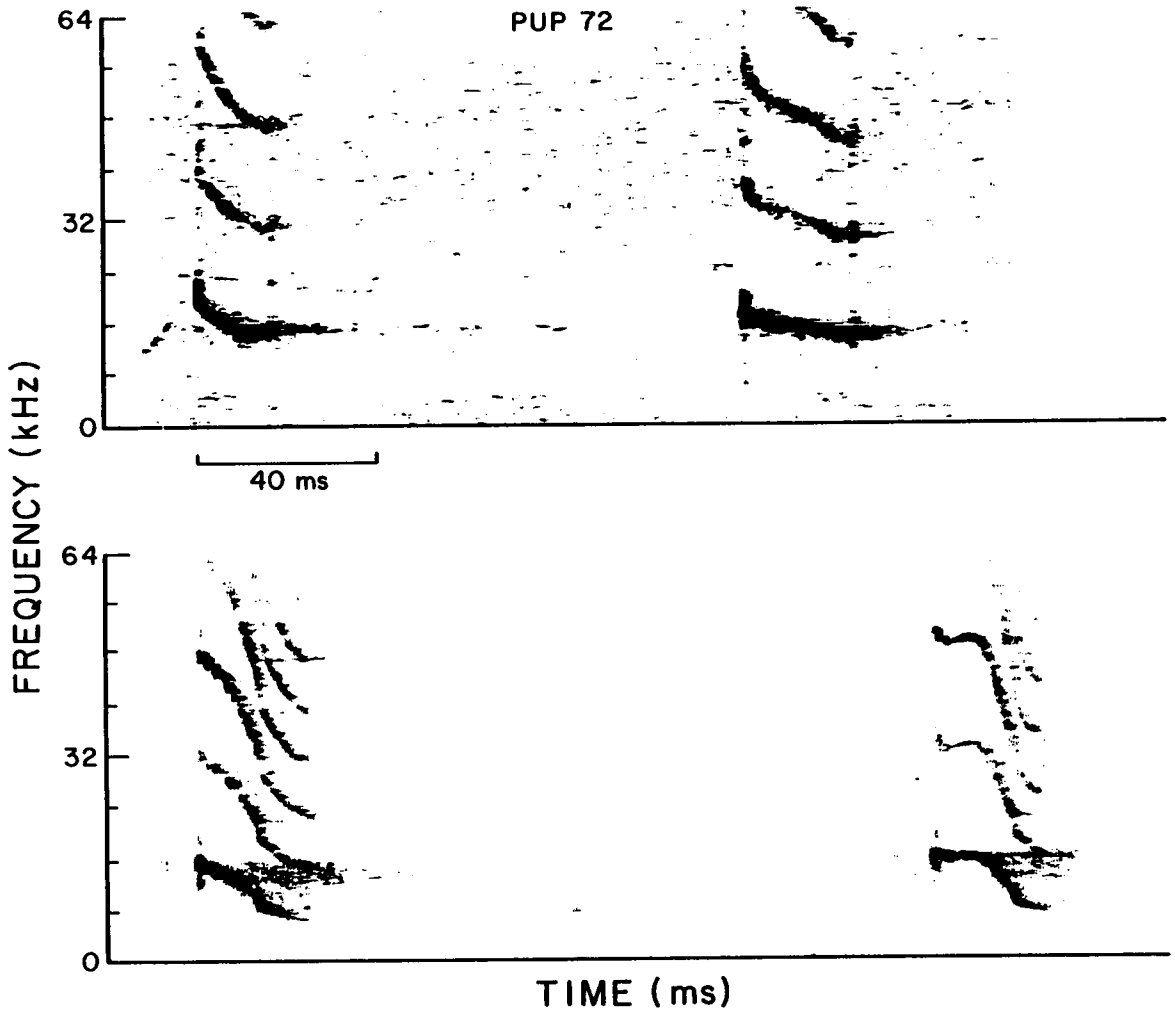

Figure 5. Sample calls that illustrate large within-individual variation. Two examples of sonagrams of two consecutive calls emitted by pup 72 are shown.

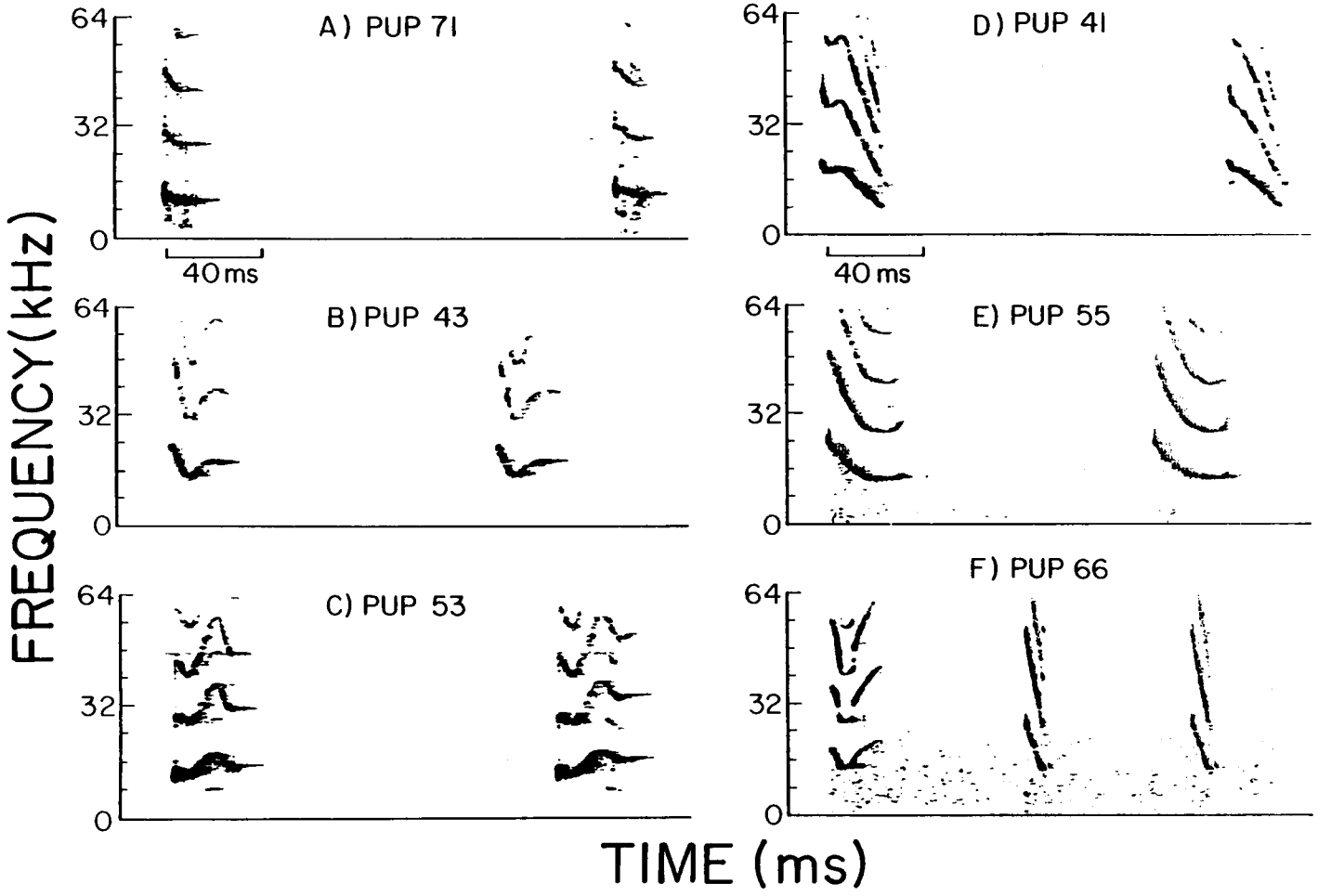

Figure 6. Sonagrams of calls by six different pups that illustrate large between-individual variation.

for each pup for each variable. The frequencies of the fundamental ranged from 8 kHz to 54 kHz, with a mean initial frequency of 18.3 kHz and a mean frequency modulation of 10.2 kHz. The mean minimum frequency of the second harmonic was 26.7 kHz and the average oscillation of the second harmonic was 16.8 kHz. The mean call duration was 25.5 ms (ranging from .9 ms to 55 ms) and the average time between calls was 130.8 ms.

Examples of pup calls are illustrated in Figures 4, 5, and 6. Figure 4 shows calls, given by pup 23, illustrating a large amount of within-individual consistency. Figure 5, on the other hand, demonstrates the ability of one pup to produce calls with various shapes, durations, frequency modulations, etc. In Figure 6 variety among calls of six different pups is exemplified. Clearly, the shapes of the calls reflect much individual variation, however these differences were not statistically analyzed. Pup 71's calls tended to show short call durations, low initial frequencies, and small frequency modulation in both harmonics. That is, the mean call duration of pup 71 was 17.0 ms as compared to pup 53 ($\bar{x}$=20.1 ms), pup 41 ($\bar{x}$=23.7 ms), and pup 43 ($\bar{x}$=30.1 ms); the mean initial frequency of pup 71 was 14.4 kHz as compared to pup 55 ($\bar{x}$=23.1 kHz), pup 43 ($\bar{x}$= 21.7 kHz), and pup 41 ($\bar{x}$=20.9 kHz); and mean fm1 and fm2 for pup 71 was 7.8 kHz and 8.1 kHz, respectively, as compared to pup 41 (fm1 $\bar{x}$=16.9 kHz, fm2 $\bar{x}$=27.5 kHz) and pup 55 (fm1 $\bar{x}$=16.0 kHz, fm2 $\bar{x}$=24.9 kHz). One also can see a contrast between the very low minimum second harmonic of pup 41 ($\bar{x}$=19.4 kHz) and the quite high msh of pup 43 ($\bar{x}$=30.9 kHz).

Age-Related Changes

Regression analyses were done to ascertain whether call qualities (dependent variables) were different in pups of different age (independent variable). Table 3 shows the maximum amount of variation (maximum R^2) and the actual amount of variation (actual R^2) that a linear model and a quadratic model explains for each variable. It also shows the model R^2 for age and the model R^2 for age with age^2 included in each model. It can be seen by this table that the actual R^2's for mff, mxff, msh, and iff were high. This means that most of the variation between pup vocalizations for these variables was accounted for by differences in the ages of the pups. Furthermore, because more variation was accounted for by including age^2 in the model, there was a quadratic relationship between age and each of these variables. Thus, as the pups got older, the maximum frequency of the fundamental (mxff) increased; and in older pups, the increase in mxff was accelerated (Figure 7A). Although the linear models were statistically significant for all the variables, I arbitrarily considered cases in which one third or less of the variation was explained to be of no practical significance. That is, the statistical significance of the model means merely that the variation present was significantly different from zero; however, models that accounted for less than one-third of the maximum variation were essentially useless since they explained only a small portion of the total explainable variation. Thus, models explaining more than one-third of the total

Table 3. Age-related changes in vocalizations.[a]

R^2	mff	mxff	cd	msh	iff	df2	fml	fm2	ii
Age (Linear Model)	.137	.311	.036	.140	.172	.033	.148	.146	.031
Age + Age^2 (Quadratic Model)	.377	.471	.059	.473	.343	.083	.152	.164	.122
Maximum	.524	.598	.384	.627	.498	.170	.469	.599	.362
Actual Age[b]	.26	.52	.09	.223	.346	.195	.317	.245	.086
Actual Age + Age^2[c]	.72[d]	.78[d]	.15	.754[d]	.688[d]	.495[d]	.325	.274	.339[d]
p[e]	.0001	.0001	.0116	.0001	.0001	.1035	.2775	.0224	.0005

[a]The values are the percent of variation (R^2) in each dependent variable (mff, mxff, etc.) that is explained by age (the independent variables). In all cases the quadratic relationship accounts for a greater percentage of the variation than the linear one. See text for further explanation.

[b]R^2 actual = R^2 age ÷ R^2 maximum.

[c]R^2 actual = (R^2 age + age^2) ÷ R^2 maximum.

[d]Models with over 33% of R^2 explained are arbitrarily considered to be of practical significance. (See text.)

[e]All linear models, except for df2, were significant at $p<.0005$. This p is the significance of including Age^2 in the model.

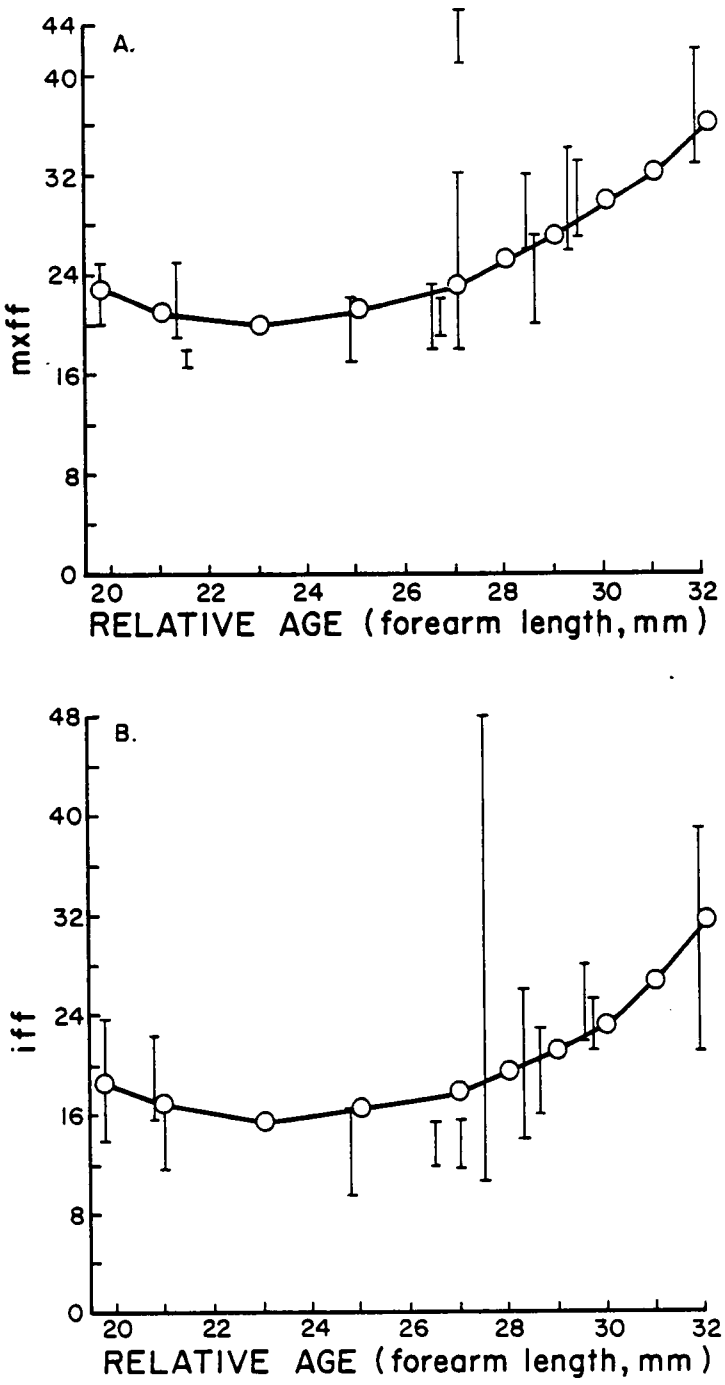

Figure 7. Examples of quadratic relationships between call parameters and pup age (as determined by forearm length).

Vertical bars indicate the range of observations at each age. (A) The relationship between maximum frequency of the fundamental and age. (B) The relationship between initial frequency of the fundamental and age.

variation are useful in that they explain enough variation to connote a relationship between age and the variable. For example, the linear regression equation explained only 24.5% of the variation between age and fm2. The inclusion of age in the model explained only 3% more of the variation. Both of these models were statistically significant, but the small amount of variation that was accounted for in each, 24.5% and 27.4%, were less than one-third of the total variation. This implies that there was basically no meaningful relationship between age and fm2 for the ages used in this study.

It is important to note that a direct causal relationship between each variable and age cannot be determined, due to high correlations between the descriptive variables. As stated by Leger et al. (1980, p. 234), "Strongly correlated variables are equally capable of yielding significant differences between two or more groups simply because they account for the same portion of total variance." For example, because mxff is highly correlated to fml, the causal relationship may be between fml and age; and the observed relationship between mxff and age may be a result of the relationship between fml and age.

Vocal Signatures

Univariate Results

To determine whether pups have individually distinct calls, univariate and multivariate analyses were conducted. Using an analysis of variance (ANOVA), it was found that there was significant

variation in vocalizations between the pups for each variable (Table 4), and with the exception of df2 (for which p=.038), p-values were always less than .0001. A variance component estimation procedure was used to examine the relative significance of the between-pup and within-pup variances. As can be seen in Table 5, the between-pup variance was approximately twice as large as the within-pup variance for variables fm1, fm2, and msh. In other words, about two-thirds of the variation in the observed measurements (of fm1, fm2, and msh) was due to differences between the pup's vocalizations while only one-third of the variation in the measurements was due to differences in the vocalizations from the same pup. By looking at the maturational results (Table 3), one can see that 75.4% (actual R^2) of the between-pup variation in msh was due to differences in the ages of the pups, while only 32% and 27.4% of the between-pup variation on fm1 and fm2, respectively, was due to age. The rest of the variation between pups must have been due to other factors, such as physiological, genetic, motivational, or contextual differences. Although the ANOVA indicated significant variation between the pups for cd1, df2 and ii1, the variance component procedure indicated that the within-pup variance was larger than the between-pup variance for these variables; thus, the between-pup variation that did occur was different from zero but not large enough to distinguish among pups.

Multivariate Results

A discriminant function analysis using measurements from 325 calls showed that pups could be distinguished when msh, fm1, fm2,

Table 4. Results of analyses of variance of pup vocalizations.[a]

Source of Variation	n	df	F
msh	362	19,343	25.25**
mff	365	19,346	20.61**
mxff	362	19,343	31.27**
fm1	362	19,343	24.79**
fm2	355	19,336	42.69**
iff	361	19,342	19.81**
cd1	354	19,335	14.79**
df2	62	6,56	2.42*
ii1	170	19,151	4.35**

[a]These results show that the variation among pups (independent variable) is significantly different from zero for each call parameter (dependent variables).

*Significant at .05.

**Significant at .001.

Table 5. Estimates of between-pup and within-pup variance in vocalizations.[a]

	msh[b]	mff	mxff	fm1[b]	fm2[b]	iff	cd1[c]	df2[c]	ii1[c]
Between-pup Variance	27.27	4.96	14.75	12.04	30.07	13.13	1354.74	8.03	27308.26
Within-pup Variance	15.47	5.00	11.14	7.05	13.58	13.08	2535.08	56.19	54550.52

[a]These estimates were obtained by Variance Component Procedures.

[b]Between-pup variance is considerably larger than within-pup variance.

[c]Within-pup variance is considerably larger than between-pup variance.

iff, and cd were linearly combined (Wilks' Lambda = .0116, $p<.001$; Table 6). The Eigenvalues (relative between-pup variability that is explained by each function) indicated that the first three discriminant functions explained over 90% of the total variability (Table 6). Because of this, further examples will be discussed only in terms of these three functions.

In Figures 8A and B, four randomly selected pups provide an example of how the first three discriminant functions can be used to distinguish pup's vocalizations. The circles represent the area within which there is a 95% probability that the calls emitted by a particular pup will lie. Figure 8A shows that pup 1 has little overlap with pups 23, 31, and 32 on the first canonical function (CAN1). Pup 31 has little overlap with pups 1, 23, and 32 by CAN2. In Figure 8B, CAN2 separates pup 31 from 1, 23, and 32; CAN3 separates pup 1 from 23, and pup 23 from pups 31 and 32. The degree of overlap among the pup calls in Figures 8A and B reflects the discriminability of the pups from one another. In other words, the calls of pups 1 and 31 are distinguished well by CAN1, CAN2 and CAN3 but the calls of pups 23 and 32 are not distinguished well.

The relative contributions of each of the five discriminating variables to the first three functions is represented by the standardized discriminant function coefficients shown in Table 7. Msh, cd, and iff are the most important variables to the first function; fm2 is most important to the second function; and fm2, fm1, and iff are most important to the third function.

Table 6. Results of the discriminant analysis.[a]

Discriminant Function	Canonical Correlation	Eigen-value	Relative Percentage of Variation	Cumulative Variance	F Statistic	DF	Prob
1	.912714188	4.9897	52.09542	52.1 %	23.1241	95	0.0000
2	.860599130	2.8555	29.81311	81.8 %	15.9725	72	0.0000
3	.694182973	.9301	9.71079	91.6 %	9.7825	51	0.0000
4	.616003847	.6115	6.38442	98.0 %	7.3244	32	0.0000
5	.400627482	.1912	1.99624	100 %	3.8875	15	0.0000

	Value	F	DF	Prob
Wilks' Lambda	.01168753	23.1241	95	0

[a]These results show that all five canonical functions can significantly discriminate among pup's vocalizations, yet the first three functions account for over 90% of the variation among pups.

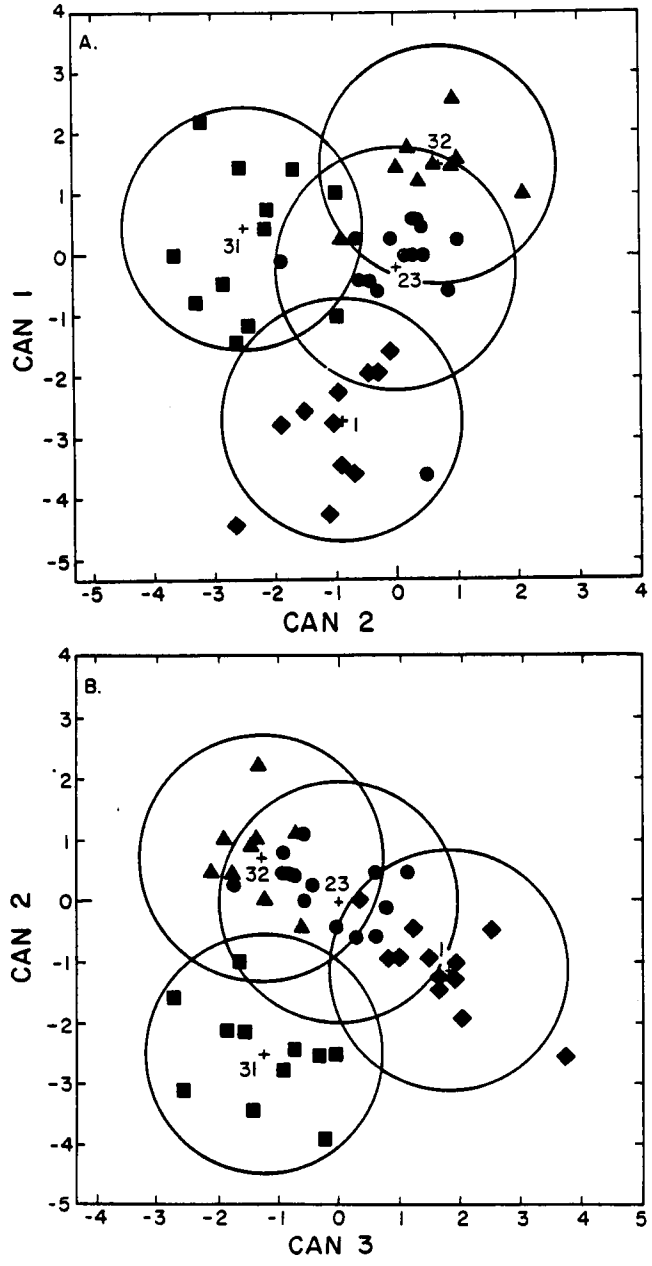

Figure 8. The calls of four randomly selected pups plotted relative to three canonical functions.

The "+" plotted within each circle indicates the centroid for each pup. The circles represent the area within which there is a pup. The circles represent the area within which there is a 95% probability that a call will belong to a particular pup based on its location in relation to the two canonical functions. (A) Plotted relative to the first two canonical functions. (B) Plotted relative to the second and third canonical functions.

Table 7. The standardized canonical coefficients of the first three canonical functions for the five variables used in the discriminant analysis.

	CAN1	CAN2	CAN3
msh	1.1724	-.9818	-.6650
fml	.2176	.0283	1.0665
fm2	.6677	1.3522	-1.3998
iff	1.1161	-.0760	.9543
cd	1.0949	.0431	-.6419

Discriminant analysis was also used to predict what calls were given by which individual. To make these predictions, the data (n= 337) were randomly split. Fifty-five percent (n=183) of all measured calls was used to produce the discriminant functions. These functions then were used to classify the remaining 45% (n=154) of the calls (Morrison, 1969). The classification results are given in Table 8. Entries on the main diagonal are calls that were correctly classified. All other entries are misclassifications. Overall, 60.4% (n=93) of the second set of calls were correctly classified. That is, the discriminative functions matched each call with the correct pup about 60% of the time. Because there were 20 pups, the prior probability of properly classifying any call by an individual pup was 5% (Morrison, 1969). The overlap among the vocal characteristics of pups seen in Figures 8A and B illustrates that the calls of pups are not always totally distinct. This overlap is what prevents the number of correct classifications from being higher than it is.

A closer look at Table 8 reveals a nonrandom pattern of misclassification. The boxed areas in the table are examples of clumped, misclassified calls. Note that of seventeen calls emitted by pup 51, seven were misclassified; however, instead of misclassifications being spread evenly among the nineteen other pups, the calls were assigned to only two other pups, three calls to pup 43 and four to pup 55.

TABLE 8. Number and percent of calls that were assigned to each pup according to the discriminant functions.[a]

From Pup	Predicted Pup 1	3	21	22	23	31	32	33	41	42	43	51	52	53	54	55	61	66	71	72	Total
1	1 20.00	1 20.00	0 0.00	1 20.00	1 20.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	1 20.00	5 100.00
3	0 0.00	3 100.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	3 100.00
21	2 50.00	0 0.00	1 25.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	1 25.00	0 0.00	4 100.00
22	0 0.00	0 0.00	0 0.00	7 100.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	7 100.00
23	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	2 50.00	2 50.00	0 0.00	0 0.00	4 100.00
31	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	3 50.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	3 50.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	6 100.00
32	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	3 75.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	1 25.00	0 0.00	0 0.00	4 100.00
33	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	2 50.00	0 0.00	0 0.00	1 25.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	1 25.00	0 0.00	0 0.00	0 0.00	4 100.00
41	0 0.00	1 8.33	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	11 91.67	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	12 100.00
42	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	7 87.50	0 0.00	0 0.00	0 0.00	1 12.50	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	8 100.00
43	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	2 25.00	0 0.00	0 0.00	4 50.00	2 25.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	8 100.00
51	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	3 17.65	10 58.82	0 0.00	0 0.00	0 0.00	4 23.53	0 0.00	0 0.00	0 0.00	0 0.00	17 100.00
52	0 0.00	0 0.00	0 0.00	0 0.00	1 20.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	4 80.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	5 100.00
53	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	1 16.67	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	3 50.00	2 33.33	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	6 100.00
54	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	4 80.00	0 0.00	0 0.00	0 0.00	0 0.00	1 20.00	5 100.00
55	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	2 40.00	0 0.00	0 0.00	0 0.00	3 60.00	0 0.00	0 0.00	0 0.00	0 0.00	5 100.00
61	0 0.00	0 0.00	0 0.00	0 0.00	3 16.67	0 0.00	3 16.67	0 0.00	0 0.00	0 0.00	0 0.00	1 5.56	0 0.00	0 0.00	0 0.00	0 0.00	8 44.44	3 16.67	0 0.00	0 0.00	18 100.00
66	0 0.00	0 0.00	1 10.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	2 20.00	3 30.00	0 0.00	0 0.00	0 0.00	0 0.00	2 20.00	0 0.00	1 10.00	1 10.00	0 0.00	0 0.00	10 100.00
71	0 0.00	0 0.00	0 0.00	1 20.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	4 80.00	0 0.00	5 100.00
72	0 0.00	4 66.67	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00	2 33.33	6 100.00
Total	3	9	2	9	5	4	6	4	13	10	8	15	4	7	8	7	12	7	5	4	142
Percent	2.11	6.34	1.41	6.34	3.52	2.82	4.23	2.82	9.15	7.04	5.63	10.56	2.82	4.93	5.63	4.93	8.45	4.93	3.52	2.82	100.00
Priors	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	0.0500	

[a]The vertical column indicates which pup emitted the call and the horizontal row indicates which pup the call was predicted to be emitted from. Entries on the main diagonal are correct classifications; all others are incorrect.

Playbacks

Recordings of pups were played to fourteen females to determine whether adult females discriminate among pups. Only nine of these females were tested on a second day. With three trials per recording, and three recording types, this resulted in a total of 207 playback trials.

The G-test was used to examine the relationship between the responses of the females to the playbacks (number of responses (nmrsp) and latency until first response (rspl)) and the playback treatment situations (recording (pup, nonpup and blank), order, trial, day, and blindness). Each type of female response was divided into two or three categories: rspl as fast (0-5 seconds), medium (6-20 seconds), and slow (21-45 seconds) and nmrsp as few (0-5) and many (6-10). The tests revealed that, regardless of whether the observer was blind or not, there were no relationships between any of the variables. Appendix II-A shows the overall G-test probabilities for each possible relationship. In some cases additional G-tests were performed to determine the effect of additional variables. Again, as seen in Appendix II-B, no relationships were found. Appendix II-B shows that the females responded similarly to all three recordings, and in both cases the blindness of the observer made no difference in the test results. Appendix II-C illustrates that there was no apparent habituation of adult females to the recordings from one day to the next and from one trial to the next. That is, the responses of the females did not change with repeated presentations of the playback recordings.

The G-test was also used to assess the relationship between the ages of the pups and the vocal responses of the mothers in the playbacks. Rspl and nmrsp were each divided into the categories described above. Age was categorized so that 3-4 pups were in each group: youngest = 19-22 mm; older = 25-28 mm; and oldest = 28.1-33 mm. Of the fourteen pups with calls used for playbacks, forearm lengths of only eleven were obtained. The G-test did not reveal a significant relationship between rspl and age ($df=4$, $G=3.19$, $p<.05$) but did find a relationship between nmrsp and age ($df=2$, $G=6.667$, $p=.0357$). This significant relationship indicated that females responded more (6-10 times) to younger pups (19-22 mm) than to older pups (25-33 mm). However, the significance of this test should be considered with caution because there was a 100% chance of finding at least one significant test (at $p=.05$) in 20 tests, and 28 tests were done.

CHAPTER IV

DISCUSSION

Call Quality

Morton (1977) and Nelson (1964) suggest that clear, high frequency calls, such as the ones that these pups emit, often are used to attract conspecifics. This is in contrast to harsh (wide bandwidth), low frequency calls which generally signal aggression. There are also characteristics in these calls which facilitate the identification of the senders location by another individual: first, they are short, repetitive signals which start and end sharply (see Figure 6, page 29), and second, they occur at a range of high (ultrasonic) frequencies (Marler, 1959).

Age-Related Changes in Calls

Maturational changes in structure of vocalizations have been found frequently in bat pups (e.g., Gould, 1971; Turner et al., 1972; Konstantinov, 1973; Brown, 1976; Matsumura, 1979). In T. brasiliensis at least five of the variables measured (mff, mxff, msh, iff, and df) change with pup age, all of which indicate that pup calls increase in pitch as the pups get older. This might be expected if the isolation call is a precursor of an echolocating call. However, it also is possible that the isolation call of T. brasiliensis is a precursor of an adult communicatory call. Adults in captivity emitted a variety of apparently communicatory calls such as irritation buzzes, trills,

and directives. Which call, if any, the T. brasiliensis i-call is a precursor of cannot be determined here.

Age at Which Recognition Occurs

Many studies (e.g., Davies and Carrick, 1962; Beer, 1979; Beecher et al., 1981; Thompson and Emlen, 1968; and Holmes and Sherman, 1982) have pointed out that parental recognition is influenced by the age of the offspring. For example, Davies and Carrick (1962) found that when they cross-fostered eggs and chicks in crested tern nests, parents accepted all eggs, but parents were suspicious of foreign one-day old chicks. Two to three-day old chicks were almost always rejected by alien adults yet were accepted by their own parents. Apparently crested tern parents do not fully recognize their young until the chicks are 2-3 days old. Presumably there is no need for recognition until chicks are mobile enough to wander away from the nest and intermingle with other young (Colgan, 1983). In other words, the crucial age at which recognition in any species must occur, if it occurs at all, is when offspring from different parents intermingle.

In the case of T. brasiliensis, the means of recognition must be established during the first nursing period, before the mobile newborns are placed in creches with thousands of other infants. During the first nursing period, the T. brasiliensis pup and mother vocalize frequently giving the mother opportunity to learn her pup's call, or vice versa. This close contact also allows the mother to learn the scent of the pup, or possibly even to mark it with her

facial sebaceous glands. It is also possible that this first nursing period permits the mother to establish a phenotypic template of her pup based on vocalizations, scent, or any combination of cues. Then, when she searches for her pup during later nursing periods, she could compare this model phenotype to those of pups she checks within the creche. If phenotypic similarity is correlated with genetic similarity, then the search for a similar phenotype could result in a mother nursing at least a related pup, if not her own. It also is possible that phenotype matching in I. brasiliensis is effected by means of inherent knowledge possessed because of a recognition allele or alleles. Since a pup's call changes as it matures, the mother must change her phenotypic template (if indeed, she has one) to compensate for these changes in order to continue recognizing the pup until it is weaned. If the mother changes her phenotypic template over time, it is more likely that she learns the phenotype than that she has an inherent phenotypic template.

Discriminability of Pup Calls

Results of the univariate and multivariate analyses demonstrate that the calls of the I. brasiliensis pups recorded in these experiments are statistically discriminable and suggest that each pup has a distinct vocal signature. There are certain combinations of the variables measured that can account for most of this observed discriminability. The first three discriminant functions account for over 90% of the observed between-pup variation, and the largest

between-pup variances were found for the variables msh, fml and fm2. Leger et al. (1980, p. 241) predict that "those parameters exhibiting the greatest between-class variation would be best suited for conveying information." From this, it might be expected that msh, fml and fm2 would be important variables in the canonical functions; as they are. Msh is one of the primary variables in CAN1, fm2 is the primary variable in CAN2, and fml is the secondary variable in CAN3. T. brasiliensis emit frequency modulated signals to echolocate (Simmons et al., 1975; Simmons et al., 1978), and clearly are capable of obtaining information using FM signals. It seems likely that they also have the ability to decipher information from the FM components of the pup calls. If the frequency modulation of the lower harmonics and middle range frequencies (such as the minimum of the second harmonic) are not attenuated or distorted substantially by the high temperatures, humidity, and echo quality of caves, then these three variables may be parameters useful to mothers for discriminating among pups.

The discriminative functions correctly predicted which pup emitted a particular call 60.4% of the time. Although this 60% success in prediction does not, at first glance, appear overwhelming, it is a 1200% increase over the 5% prior probability. This implies that if a mother were to analyze pup calls by a method similar to this discriminant analysis, she would have about a 60%, instead of a 5%, chance of choosing the correct pup in a group of twenty. In addition to the 60% correct prediction rate, there was a nonrandom pattern of misclassification. This clumping of misclassified calls indicates

that calls of some pups are more similar to one another than they are to the calls of other pups. This may mean that a mother is not equally likely to nurse any pup, but is more likely to nurse among subsets of pups with similar calls. Thus, if females use calls to identify pups, the reduction in choices combined with the high probability of making a correct choice results in very high odds that a female can find a particular pup or one of a particular set of pups. This idea is contrary to the suggestion of Davis et al. (1962) that finding one's own pup seems mathematically improbable since there are so many pups, because the pups do not stay in one location, and because several pups may attempt to nurse from each female. More recent findings show that, in fact, pups appear to move limited distances between milk meals, females move across the creches at a speed which enables only a few pups the chance to attempt to nurse, and mothers kick or shove aside most attempted milk stealers (McCracken, pers. comm.).

Possible Causes for Playback Results

Methodological Problems

Even though the pups' calls are statistically discriminable and structured so as to be easily located, the results of the playback experiments provide no evidence that the females do discriminate among calls of different pups. There are, however, other explanations for these negative results. Several of these explanations concern methodological problems. First, the females may not have reacted

in their usual fashion because of the abnormalities of the captive environment. Second, because the microphone distorted frequencies above 40 kHz, the pup calls may not have been reproduced adequately. Third, the females may not have responded because the pup captured along with each of them may have been a pup who, in the confusion caused by our approach, simply attached itself to the nearest female. That is, the female may not have chosen the pup attached to her. Finally, the playback tests were performed between 9:00 a.m. and 5:00 p.m.; these hours are not at the peak feeding periods during which T. brasiliensis mothers search for their pups. Thus, the mothers may not have responded differentially to pup calls in the playbacks because (1) they were disturbed by the captive environment, (2) the calls were not adequately reproduced, (3) they had no interest in communicating with the pups at that time, or (4) because of a combination of these or other factors. Because it seems likely that the females responses to the pup and nonpup recordings should have been different from their responses to the blank tape, it is likely that one or more of these methodological problems had a detrimental effect on the results of the playback experiments.

Other Sensory Modalities

The lack of discriminability by the females in the playback experiments also may have occurred because mothers actually do not use calls to locate pups. Gustin (unpublished) has found that a T. brasiliensis mother will approach, sniff, and rest quietly next to a

cotton swab containing the scent of her own pup more frequently than one with the scent of a randomly selected pup. It seems apparent that adult T. brasiliensis females discriminate among the odors of pups and probably use scent as a proximal cue. But it seems likely that odor would not work except over short distances. The use of spatial memory as a cue in the location of their pups is also highly probable. Since females have been shown to land an average of about 45 cm, and as far as 1 m, from the pup they nurse (McCracken, pers. comm.), a mid-range distance cue, such as vocalizations, seems necessary as well. Given the large amount of between-pup variation that occurs in these vocalizations, it seems reasonable to assume that mothers would use vocal recognition as a means of discriminability. Also, because bats can process and analyze subtle differences in sound, it would be surprising if these abilities were not utilized for discriminating call structures that facilitate recognition of a specific pup.

Selective Pressures and Recognition

It is also possible that pups recognize their mothers (e.g., Hansen, 1976; Beer, 1969, 1979; Turner et al., 1972). By being able to recognize their mothers, pups can obtain milk not only from their own mothers, but they can retain an individual attachment that provides essential socialization. Beer (1979) and Harper (1970) suggest that a consistent attachment, between an offspring and its mother may be crucial to the social development of the offspring (see also Gubernick, 1981; Swartz and Rosenblum, 1981). The ultimate

result of socialization through attachment to a particular individual is "an appropriately functioning adult who is capable of interacting in a species-typical and predictable fashion with other members of its species" (Swartz and Rosenblum, 1981, p. 418). While it would be advantageous for the pup to recognize its mother in order to obtain vital social skills, it may also be advantageous for the pup to attempt to nurse from any lactating female. This could result in the more aggressive pups being stronger and selectively favored. Although it is clear that milk stealing is frequently attempted, and sometimes successful, it is not clear whether recognition plays a part in this behavior. The pups may recognize who their mothers are and also attempt to steal milk from others, or they may not recognize their mothers at all and, therefore, attempt to nurse any lactating female possible. It would seem to be in the pup's best interest to recognize its mother, to retain an attachment to her, and to steal milk from other mothers as well.

Selective pressures, such as the high cost of lactation and the need for reproductive success, result in its being highly adaptive for mothers to be able to recognize and selectively nurse their own or related pups. Although further investigations are necessary, it seems that the mother's best interest should be served by recognizing her pup, especially since pups attempt to steal milk. It seems apparent that mothers normally choose whom they nurse. McCracken (pers. comm.) has observed mothers moving through a creche in search of their pups, kicking or shoving aside pups who attempt to nurse,

yet choosing one particular pup and nudging it under her wing. He suggests that milk stealing is more likely to be successful when the mother is taken by surprise, as in some disturbance in the cave.

CHAPTER V

SUGGESTIONS FOR FUTURE WORK AND CONCLUSIONS

Future investigations are necessary to further determine the age at which recognition is established, who (mother and/or pup) does the recognizing and the sensory modalities by which recognition is determined. To ascertain when and if vocal signatures are learned (either by pup or parent), a future investigation may entail performing Caesarian sections on anesthetized pregnant females (as in Adams and Baer, 1966) and cross-fostering the pups at various ages in conjunction with vocal recording playback tests. In order to know which generation (if either or both) is individually recognizable, this investigation should involve observing the willingness of mothers to nurse nonpups and their ability to recognize their own pups. It should also involve the playing back of adult calls to pups to test for pup discrimination abilities, and to determine the existence of adult vocal signatures. Female responses to pup calls could also be checked by using actual pup vocalizations rather than playbacks of recordings, as used in this study.

Although this study has not conclusively proved that adult free-tailed bats discriminate among pups, it is highly probable that this is the case because (1) pup vocalizations are statistically discriminable, (2) recognition mechanisms are necessary for the adult bats to nurse nonrandomly and (3) these bats are equipped with suitable ears and brains to effect such subtle auditory discrimination.

This study has clearly demonstrated that the vocalizations of T. brasiliensis (1) increase in frequency as the pups get older, (2) are structured so as to be attractive in nature and easy to locate, and (3) are statistically discriminable, suggesting that each pup has a distinct vocal signature.

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APPENDIXES

APPENDIX I

THE MEANS, STANDARD DEVIATIONS, AND RANGES OF EACH VARIABLE FOR EACH PUP'S VOCALIZATION
(n = number of calls analyzed from each pup.)

A. MEANS

Pup	n	mff	mxff	fm1	fm2	iff	df2	msh	cdl	iil
1	12	12.2500	20.9167	8.7500	11.1667	17.5833		23.7500	21.4583	149.375
3	11	10.0909	19.0909	9.000	16.0000	15.5455		18.7273	25.5556	152.500
21	11	12.1818	23.0909	10.9091	17.4545	19.4545		25.7273	20.4545	159.500
22	12	13.2500	17.6667	4.4167	5.6667	14.5000		26.3333	22.2917	151.042
23	16	12.8750	22.3125	9.4375	17.6875	18.6875	27.5429	25.4000	19.8906	144.781
31	13	15.6154	21.2308	5.3846	9.7692	16.6364		31.2727	37.1154	105.586
32	9	13.8889	25.2222	11.3333	22.1111	18.1111		27.5556	34.5833	127.500
33	17	13.6250	24.2500	10.6250	17.7500	19.7059		27.7500	32.5000	119.888
41	33	10.5455	26.8438	16.9063	27.5357	20.8788	23.7000	19.4516	23.7500	100.735
42	18	11.9444	20.2222	8.3889	15.6111	11.2222		23.9412	31.3333	113.906
43	21	15.7143	27.3810	11.6667	19.3333	21.6667	22.6857	30.9474	30.0595	115.694
51	36	14.1667	29.0556	15.3611	24.3333	23.9444		28.4706	31.4236	125.221
52	19	21.0526	35.0000	12.1176	14.7143	26.2941		44.7059	24.7794	125.972
53	18	13.4444	20.5556	7.1111	14.1667	13.5556	15.4400	27.0000	20.0556	123.357
54	11	11.7273	20.0000	8.2727	16.2727	14.0909		23.1818	30.4545	115.833
55	11	13.6364	29.6364	16.0000	24.9091	23.9091	22.0778	27.6667	9.8864	126.350
61	30	12.3667	23.0000	10.5000	21.1667	19.7333		24.7333	30.5000	169.205
66	33	12.9394	23.6667	10.7576	19.7879	17.8788	21.1917	25.7931	18.8030	99.528
71	12	13.5000	21.3333	7.8333	8.0833	17.4167		29.2500	17.0000	154.750
72	24	12.2917	21.5833	9.2917	14.0833	16.5000	17.7200	24.0000	27.6705	136.818

B. STANDARD DEVIATIONS

Pup	n	mff	mxff	fml	fm2	iff	df2	msh	cdl	iil
1	12	0.96531	1.88092	1.95982	3.35297	1.44338		1.05529	4.3247	27.4175
3	11	1.44600	2.21154	2.00000	3.54965	1.63485		1.61808	4.1510	22.5970
21	11	1.16775	2.30020	2.34327	5.24144	2.76997		2.14900	3.6773	33.8032
22	12	0.96531	0.49237	0.90034	1.43548	1.38170		1.49747	3.0073	36.0158
23	16	0.50000	1.62147	1.63172	2.98259	1.95683	10.6394	2.58567	14.5194	33.5329
31	13	0.96077	1.48064	1.60927	2.89119	1.62928		2.24013	8.9470	24.8418
32	9	0.78174	0.66667	1.11803	2.52212	1.05409		2.12786	2.9974	19.5256
33	17	1.02470	1.84391	1.58640	2.40832	2.31205		3.71484	3.8998	38.4682
41	33	4.13892	7.67530	5.49110	4.17650	7.60657	7.6368	6.90333	5.6510	40.6155
42	18	1.66176	1.59247	1.71974	2.83131	1.95706		4.37993	6.4860	15.1692
43	21	0.78376	1.24403	1.01653	2.76285	2.90402	1.6283	1.61499	3.3184	25.2883
51	36	1.50238	1.81965	2.23163	1.97122	1.43317		2.47699	5.0458	21.6020
52	19	5.19052	2.12132	3.31441	2.61441	4.44079		8.97750	5.9986	38.5163
53	18	0.70479	0.98352	1.18266	1.75734	0.98352	0.7589	1.36626	17.9092	13.8590
54	11	1.10371	1.41421	1.73729	3.28910	0.83121		2.18358	1.7023	17.7600
55	11	0.67420	1.91169	1.89737	2.30020	2.91392	4.1874	1.22474	12.4188	24.6827
61	30	1.09807	1.48556	2.17747	2.40808	1.83704		1.36289	2.8542	15.9420
66	33	1.27327	4.37798	3.79992	5.98309	6.47475	12.9799	2.87078	16.3079	38.4867
71	12	2.54058	2.05971	3.53768	2.90637	2.06522		1.54479	1.8819	17.9278
72	24	3.04287	2.71736	3.95055	6.02831	1.53226	0.9247	5.27889	2.8425	33.9041

C. RANGES

Pup	n	mff	mxff	fm1	fm2	iff	df2	msh	cdl	iil
1	12	11-14	19-26	6-14	2-15	15-21		22-26	12.500-27.50	116.25-193.75
3	11	8-12	14-22	5-12	9-20	13-18		16-21	20.000-32.50	128.75-187.50
21	11	10-14	20-25	7-14	11-26	14-23		22-29	12.500-25.00	112.50-196.25
22	12	12-15	17-18	3-6	4-8	12-17		24-28	18.750-27.50	121.25-218.75
23	16	12-14	19-25	6-12	11-23	16-22	17.2-40.0	17-28	3.750-37.50	100.50-193.75
31	13	14-18	19-24	3-8	5-14	14-20		28-36	25.000-55.00	68.75-135.00
32	9	13-15	24-26	9-13	17-26	16-20		23-30	27.500-38.75	105.00-140.00
33	17	12-16	21-28	9-15	12-21	15-24		25-41	22.500-37.50	85.00-187.50
41	33	8-28	20-54	9-36	20-36	15-48	18.4-42.4	14-50	6.250-32.50	30.00-176.25
42	18	8-14	17-22	5-13	12-24	9-15		14-29	12.500-37.50	88.75-132.50
43	21	15-18	25-30	10-14	14-25	15-26	20.4-24.8	29-36	25.000-36.25	71.25-166.25
51	36	12-18	26-34	12-21	20-28	22-28		25-34	22.500-38.75	80.00-171.25
52	19	7-26	33-42	8-20	9-18	21-39		23-54	7.500-30.00	88.75-186.25
53	18	12-14	19-22	5-10	11-17	11-15	14.0-16.4	24-29	3.750-50.00	105.00-146.00
54	11	10-13	18-23	5-10	10-20	12-15		19-26	27.500-33.75	97.50-146.25
55	11	12-14	27-33	14-19	22-28	21-32	11.5-24.8	25-29	8.875-35.00	96.00-184.00
61	30	10-14	20-27	8-17	16-25	16-23		23-28	25.000-37.50	188.75-192.50
66	33	11-16	17-32	6-17	11-31	11-31	12.8-60.1	22-36	0.875-45.00	46.00-167.50
71	12	8-17	18-25	5-16	4-13	15-22		27-32	12.5000-18.75	126.25-175.00
72	24	8-17	18-28	2-15	2-23	14-20	16.0-19.2	18-31	23.750-32.50	97.50-193.75

APPENDIX II

RESULTS OF G-TESTS AMONG TREATMENT SITUATIONS IN THE PLAYBACK EXPERIMENTS (BLINDNESS OF OBSERVER, RECORDING TAPE, ORDER, DAY, TRIAL) AND THE RESPONSES OF FEMALES TO THE PLAYBACKS (nmrsp AND rspl)

		df	G	
A.	Blind x nmrsp	1	1.069	.25<p<.5
	Blind x rspl	2	1.410	.25<p<.5
	Recording x nmrsp	2	3.550	.10<p<.25
	Recording x rspl	4	7.771	.10<p<.25
	Order x nmrsp	2	2.130	.25<p<.50
	Order x rspl	4	5.583	.10<p<.25
	Trial x nmrsp	2	.503	.25<p<.50
	Trial x rspl	4	6.021	.10<p<.25
	Day x nmrsp	1	.068	.75<p<.90
	Day x rspl	2	3.315	.10<p<.25
B.	Blank tape x Blind x nmrsp	1	.258	.50 <p<.75
	Pup tape x Blind x nmrsp	1	1.820	.10<p<.25
	Nonpup tape x Blind x nmrsp	1	.120	.50<p<.75
	Blank tape x Blind x rspl	2	.325	.75<p<.90
	Pup tape x Blind x rspl	2	1.050	.50<p<.75
	Nonpup tape x Blind x rspl	2	3.978	.10<p<.25

		df	G	
B.	(Continued)			
	Blank tape x Day x nmrsp	1	.377	.50<p<.75
	Pup tape x Day x nmrsp	1	.000	.990<p<.995
	Nonpup tape x Day x nmrsp	1	.957	.25<p<.50
	Blank tape x Day x rspl	2	2.042	.25<p<.50
	Pup tape x Day x rspl	2	.955	.50<p<.75
	Nonpup tape x Day x rspl	2	2.808	.10<p<.25
	Pup tape x Trial x nmrsp	2	1.084	.50<p<.75
	Blank tape x Trial x rspl	4	4.614	.25<p<.50
	Pup tape x Trial x rspl	4	6.194	.10<p<.25
	Nonpup tape x Trial x rspl	4	.692	.95<p<.975
C.	Age x nmrsp	4	3.190	.50<p<.75
	Age x rspl	2	6.667	.025<p<.05*

*Significant at p<.05.

VITA

Deborah Lori Gelfand was born in Los Angeles, California on July 22, 1957. She attended elementary schools in that city and was graduated from Palisades High School in June 1975. The following September she entered The University of California, Davis. While pursuing a Bachelor's degree in Animal Behavior, she participated in research projects on tamarin and squirrel monkeys, pikas, and California ground squirrels.

After receiving her Bachelor of Science degree in December 1979, she worked as a research assistant in a study of Belding and Arctic ground squirrels at The University of California, Berkeley from April to August 1980. She became co-author in 1980 of an article published in Zeitschrift für Tierpsychologie concerning single-note vocalizations produced by California ground squirrels.

In September 1980 she entered The University of Tennessee, Knoxville and began study toward a Master's degree in Life Sciences. During this pursuit she was a teaching assistant in Psychology and she instructed classes in General Biology. Her Master of Science degree was awarded in March 1985.

Ms. Gelfand will seek employment as a teacher of General Biology and Animal Behavior in California.