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California State University, Dominguez Hills

Vocalizations and Associated Behaviors of the African Elephant (*Loxodonta africana*) in Captivity

By JUDITH KAY BERG

With 5 figures

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Abstract and Summary

This analysis presents the physical characteristics of the vocalizations of the African elephant and describes the associated behavioral contexts of the elephant's communicative system. One male and 8 female African elephants were systematically observed in a relatively large captive environment. Their repertoire of sounds constitutes 10 distinct vocalizations which are emitted during 11 behavioral categories. Although all but one of the sounds is emitted in more than one context, many of the sounds are more characteristic of a specific behavior than others. An interesting finding is that the fundamental frequency of the emitted sound is significantly correlated to the level of excitement of the individual. In general, sounds with a low fundamental frequency are emitted when the animals are in a low level of excitement and are important in those behaviors which promote group cohesion and the orderly interactions of individuals. In contrast, the higher fundamental frequency sounds predominate when the animals are in a high level of excitement and are emitted most often during aggressive type behaviors. The elephants' vocalizations and associated behaviors in captivity are discussed in comparison to those of their free-living relatives and to those of other animals showing similarities across some of the sounds and behaviors.

Introduction

The African elephant (*Loxodonta africana*) is a gregarious mammal which develops complex social behavior patterns and has a well-organized society (SIKES 1971; MOSS 1981). However, in order to understand how it organizes its orderly social interactions and group cohesiveness, it is necessary to understand its communicative systems. Yet, except for one study on optical transmission of information within the species (KÜHME 1962), no detailed analysis

has been performed on its communication. This void provided the motivation for the current study.

The elephant has acute hearing (ROBERTS 1951) and its vocal-auditory system is considered to be an important mechanism for information transfer (WILSON 1977). But, before one can demonstrate that information is being transmitted by this modality, it is first necessary to know the animal's sound repertoire and associated behavioral contexts. Although there have been references to vocal sounds made by elephants (ADAMS and BERG 1980; DOUGLAS-HAMILTON and DOUGLAS-HAMILTON 1975; MOSS 1975; SEBEOK 1968; SIKES 1971; and WILSON 1977), I present here the first systematic, quantitative analysis of vocalizations of the African elephant and the behaviors which elicit them.

Methods

The study was performed on a group of captive African elephants, 8 females and one male, located at the San Diego Wild Animal Park, San Pasqual, San Diego County, California. Their ages ranged from 5 to 30 years (Fig. 1). They were observed in their outdoor daytime enclosure, which was an oval shaped area, 190.6 m long by 68.6 m wide, surrounded by a moat. At night they were chained along with the Asian elephants (*Elephas maximus*) in a barn adjacent to this enclosure.

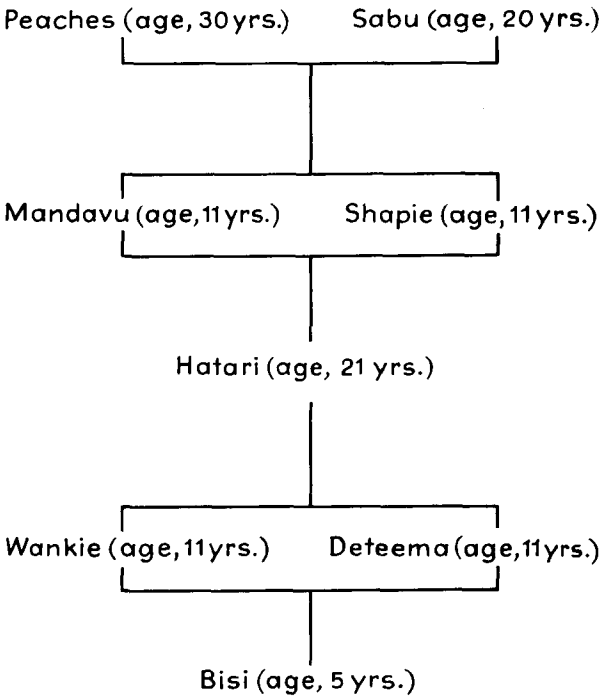

Fig. 1: The hierarchical structure of the African elephants at the San Diego Wild Animal Park. The elephants on a horizontal plane are considered equal in the hierarchy. Chico, the male, is not considered part of the hierarchy since by his age (18) in the wild, he would be a part of a male group

Observation began upon the elephants' morning release from the barn and ended upon their evening return. The study was conducted during 9 3-day observation periods from August 1980 through January 1981 for a total of 194 h.

Recording Procedure

Vocalizations of the elephants were recorded with a Sony EMC-220 Electret condenser cardioid microphone on one track of a Superscope CD-330 battery-powered stereo cassette recorder which ran continuously during the hours of observation. A second (lapel) microphone was used by the observer to systematically document the overt behaviors of the signaler and the behavioral responses of the receiver(s) on the second track of the recorder, synchronously with the vocalizations. In addition, the behaviors were periodically filmed for more detailed analysis.

The vocalizations were plotted with a Kay Elemetric 7029A Sonograph sound spectrograph analyzer. The sonograms in the text were made using a narrow-band analysis with 1000, 2000 or 4000 Hz as the maximum frequency.

Analysis

Each recorded sound of a known individual was sonographed. Taking individual variation into consideration, the sonograms were visually inspected and put into a category of sound depending on the structural appearance most often displayed. Then, each sonogram was cross-referenced with its behavioral category and filed by sound type.

The definition of elephant vocalizations used in this project is: sounds "... produced through the trunk or from the larynx or by means of a combination of both methods" (EISENBERG et al. 1971, p. 199). The terminology for the vocalization analysis came basically from DAVIS (1964) with the addition of the following:

1) *Dominant frequency* — the frequency of highest intensity as manifested by the blackest part of the sonogram. The measurement was taken at the midpoint (LEHNER 1978). 2) *Fundamental frequency* — the lowest frequency of the sound (DAVIS 1964). This frequency is determined by measuring the difference between the harmonics as displayed on the sonogram (M. J. BERG, pers. comm.). 3) *Peak frequency* — the highest frequency of a sound as displayed on the sonogram. 4) *Duration* — the measurement of time, in s, taken from the onset to the end of the sound as displayed on the sonogram. 5) *Intensity* — a subjective measurement of the amplitude of a sound, taking into consideration the distance the vocalizing elephant was from the microphone; classifications were low, medium and high intensity. 6) *Noise* — a sound or portion of a sound with no distinct harmonics or overtones and a side range of frequencies as displayed on the sonogram. 7) *Phrase* — a sequence of consecutive sounds of the same type emitted by the same individual with an interval shorter than that between individual sounds. 8) *Syllable* — an element of a phrase which, when plotted on a sonogram, manifests its own physical characteristics (i. e., duration, frequency, intensity etc.) displayed as a continuous trace on the sonogram.

To provide a framework for analysis, the behavioral categories were grouped under levels of excitement which are basically those of FOURIE (1977) with modifications for the species under study. The basic assumption of increases in the elephant's expressive components came from KÜHME (1962). The modifications and anticipated sound frequencies (low and high) were taken from the author's previous observations and a 40-h pilot study performed prior to this project:

Not excited — An elephant is lying down or standing still and resting. There is likely to be some normal ear flapping for cooling during the heat of the day and tail movements to ward off insects. The head will remain in the normal position with the trunk dangling from the head and the ears relaxed except when gently flapping. There is no vocal activity.

Low level of excitement — An elephant is either walking or standing while feeding, drinking, bathing, mudding, dusting, rubbing or manipulating objects. It is alerted to other elephants nearby or approaching, distant elephants and external stimuli. This alertness is

shown by raising the head above normal, moving the ears into various positions while listening and scenting. Vocal activity is primarily in the lower frequencies and not repeated by the emitter.

Medium level of excitement — There is an increase in excitement as demonstrated by an increase in the frequency and intensity of the elephant's head, ear, trunk, tail and body movements and/or short swift locomotions. There is an increase in vocalizations, primarily in the higher frequencies, and the sounds may be repeated by the emitter. There may be temporal gland secretions.

High level of excitement — An elephant will perform rapid locomotions for relatively long periods of time, covering long distances in their enclosure. There will be various head, ear, trunk, tail and body movements while in this highly aroused, exaggerated state. There will be many vocalizations with frequent reiteration of sounds. These sounds will be primarily in the higher frequencies. There will be temporal gland secretions.

Results

A. Physical Characteristics of the Vocalizations

10 sound types in the repertoire of the African elephant's vocal communication system were recorded (Table 1).

Growl. This is a deep, gurgling, guttural sound with uniform pitch throughout. Its fundamental frequency ranges from 18 to 28 Hz with peak frequencies reaching 700 Hz; its dominant frequency ranges from 90 to 161 Hz. It varies in intensity from low to medium but is primarily of low intensity. This sound is a complex of harmonics, overtones and noise with a duration which ranges from 1.1 to 4.4 s (Fig. 2 A).

Table 1: The duration, dominant frequency and fundamental frequency of representative elephant vocalizations

Vocalization	N	Duration (s)			[a] Dominant frequency (Hz)			[b] Fundamentals (Hz)		
		Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Low sounds										
Growl	26	2.16	1.03	1.2 - 4.4	132	17.47	90 - 161	All are approx. 18 - 28 Hz		
Rolling growl	57	3.0	1.07	1.1 - 6	133	11.04	105 - 161	All are approx. 18 - 28 Hz		
Snort	33	.65	.32	.2 - 1.3	[c] -		-	Unmeasurable		
Roar	8	3.8	1.5	2.2 - 6	574	79.92	500 - 714	Unmeasurable		
High sounds										
Trump	22	.6	1.54	.4 - .9	581	175.92	357 - 856	379	38.96	357 - 428
Trumpet	16	2.01	1.18	1 - 4.8	695	162.66	428 - 856	390	38.83	357 - 428
Pulsated trumpet	13	2.6	1.2	1 - 5.5	456	104.55	357 - 714	403	41.96	322 - 428
Trumpet phrase	8	4.34	1.71	1.85 - 5.6	576	160.26	428 - 784	395	38.31	357 - 428
Bark	16	.47	.15	.25 - .75	629	231.16	357 - 1000	Unmeasurable		
Gruff cry	2	1.15	-	1.1 - 1.2	857		857	Unmeasurable		
Cry	6	.53	.27	.35 - 1.1	518	-	450 - 570	518		450 - 570

[a] The midpoint of the darkest part of the sonogram (LEHNER 1978). See methods for description of measurements taken.

[b] The difference between the harmonics as measured from midpoint to midpoint. Some sounds were not conducive to accurate measurements.

[c] Dominant frequency was difficult to measure because it either persisted throughout sound or sporadically.

Rolling Growl. This is a deep rolling sound. The characteristic structure of this vocalization is a rise in pitch near the beginning or the middle, then a drop in pitch at the end. The rise varies by 18 Hz when compared to the lowest point of the dominant frequency. The fundamental frequency ranges

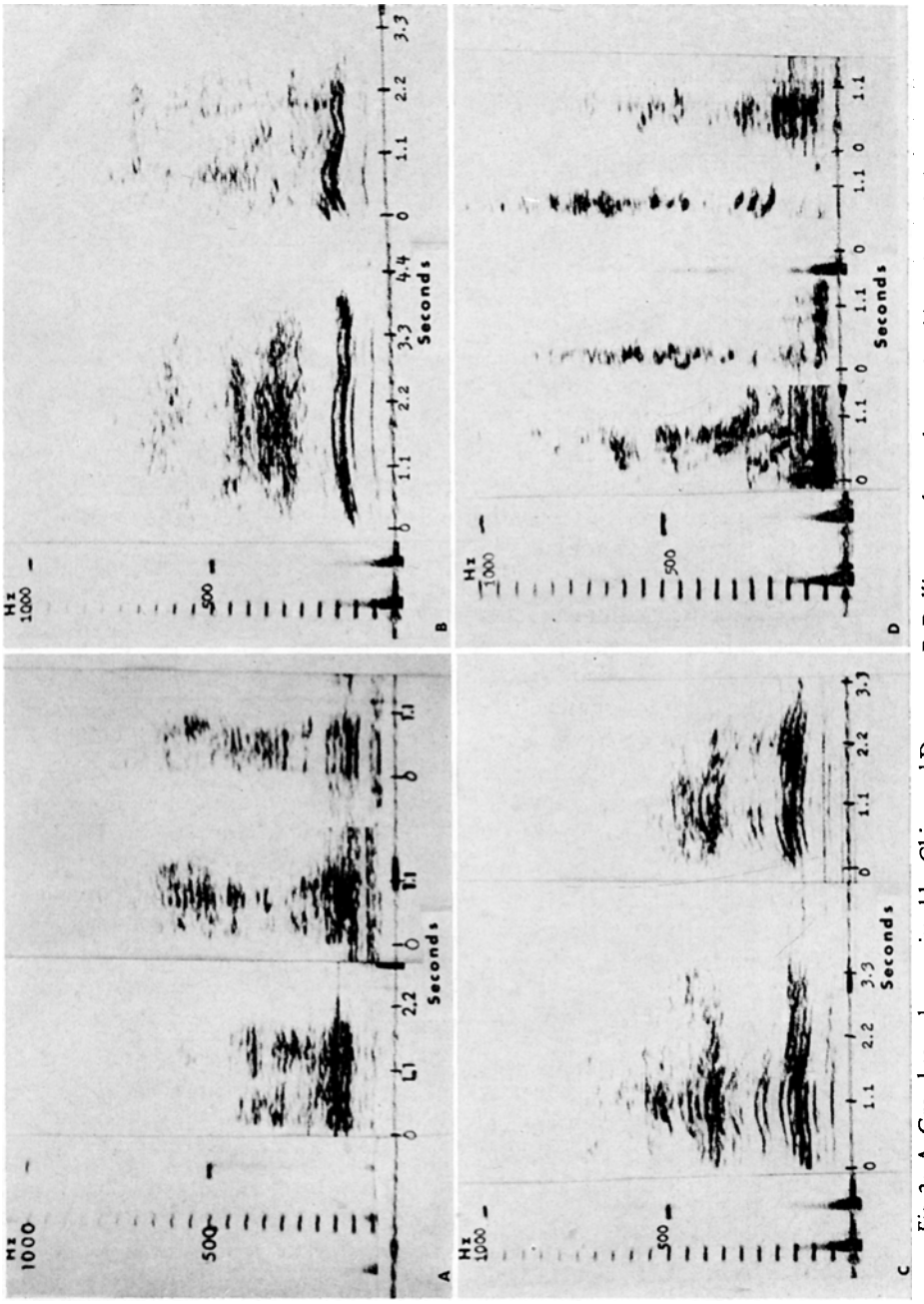

Fig. 2: A. Growl sounds as emitted by Chico and Deteema. B. Rolling growl sounds as emitted by Sabu and Shapie. C. Rolling growl sounds as emitted by Mandavu and Hatari. D. Snorts as emitted by Bisi, Sabu, Shapie and Mandavu

from 18 to 28 Hz with peak frequencies reaching 800 Hz. The dominant frequency ranges from 105 to 161 Hz; this is normally either a single harmonic or a complex of double or triple harmonics which is stressed throughout the sound. This sound varies in intensity from low to medium. This sound contains a complex of harmonics, overtones and noise. The duration ranges from 1.1 to 6.0 s (Fig. 2 B, C).

Snort. This sound is a noise whose peak frequencies reach 1500 Hz. The dominant frequency persists throughout the frequency range of the sound. It has a duration of 0.2 to 1.2 s (Fig. 2 D).

Roar. This sound begins as a low intensity growl then progresses into a high intensity scream then back to a low intensity growl. The peak frequency reaches 700 Hz during the growls, 1500 Hz during the scream. The scream is primarily a broad band of noise. The dominant frequency noted during the middle portion of the sound ranges from 500 to 714 Hz. The duration of the entire sound ranges from 2.2 to 6.0 s (Fig. 3 A).

Trump. This is a medium to high intensity short clear blast of air modulated through the trunk. This sound is a shortened version of the trumpet. Its peak frequency reaches 4000 Hz but its more distinct harmonics do not normally extend beyond 1500 Hz. This vocalization has a fundamental frequency range of 357 to 428 Hz with a dominant frequency range of 357 to 856 Hz. The dominant frequency of this sound is normally either the fundamental frequency or the second harmonic. The duration ranges from 0.4 to 0.9 s (Fig. 3 B).

Trumpet. This is a medium to high intensity sound modulated through the trunk. There is not a consistent structural appearance across all trumpets except that they are all frequency modulated. The number of harmonics can range from 1 to 10 within the same animal with noise in the higher frequencies reaching a peak of 8000 Hz; however, of the trumpets sonographically analyzed, most ranged from 1 to 3 in number and did not peak beyond 2000 Hz. The dominant frequency ranges from 428 to 856 Hz and is also the fundamental frequency or the second harmonic. The duration ranges from 1.0 to 4.8 s. There are subjective quality differences within this sound (Figs. 3 C, D).

Pulsated Trumpet. This is a low to medium intensity airy sound. Its structure shows intermittent intensity modulation which gives it a pulsated appearance. The peak frequency reaches 1500 Hz. The dominant frequency ranges between 357 and 728 Hz with emphasis on either the fundamental frequency or the second harmonic. The duration ranges between 1.0 and 5.5 s (Fig. 4 A).

Trumpet Phrase. This is a concatenated string of the trumpet sounds, consisting of 2 to 4 pulsated trumpets or a combination of 2 to 3 trumps and trumpets. The fundamental and dominant frequencies are the same as those of the trumpet sounds. The duration for the entire phrase ranges between 1.8 and 5.6 s (Fig. 4 B).

Bark. This is a short gruff burst of energy which ranges from low to medium intensity. The structural appearance of this sound ranges from a side

band of noise throughout its frequency range to a complex of harmonics and overtones. The dominant frequency ranges from 357 to 1000 Hz with a duration between 0.25 and 0.75 s (Fig. 4 C).

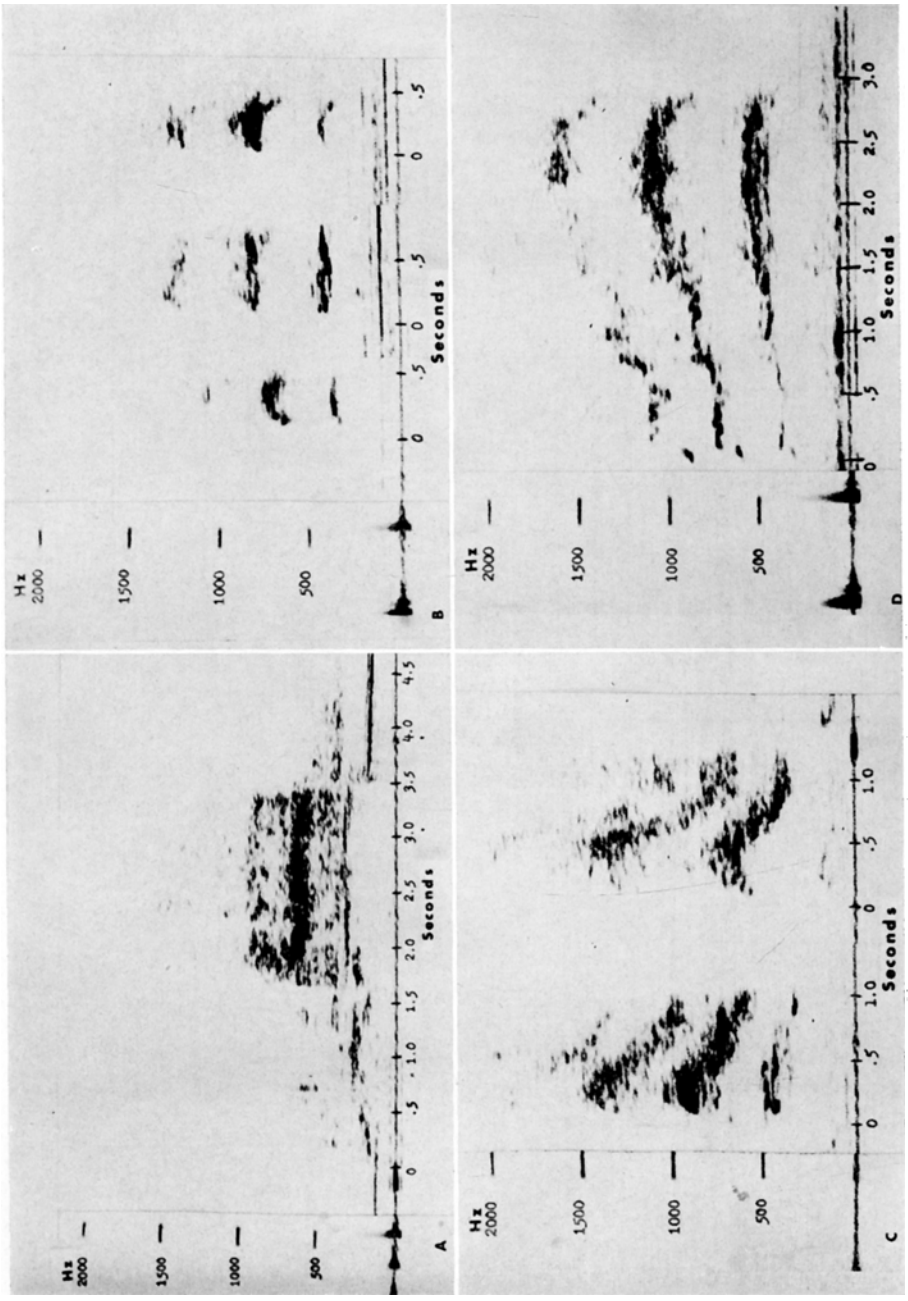

Fig. 3: A. Roar as emitted by Mandavu. B. Trumps as emitted by Shapie, Wankie and Shapie. C. Trumpets as emitted by Shapie and Wankie. D. Trumpet as emitted by Peaches

Cry. This is predominantly a clear tone with a characteristic stability in pitch. There is a variation which has a gruff vocal quality with harmonics. The dominant frequency of the clear tone, ranging from 450 to 570 Hz, is the

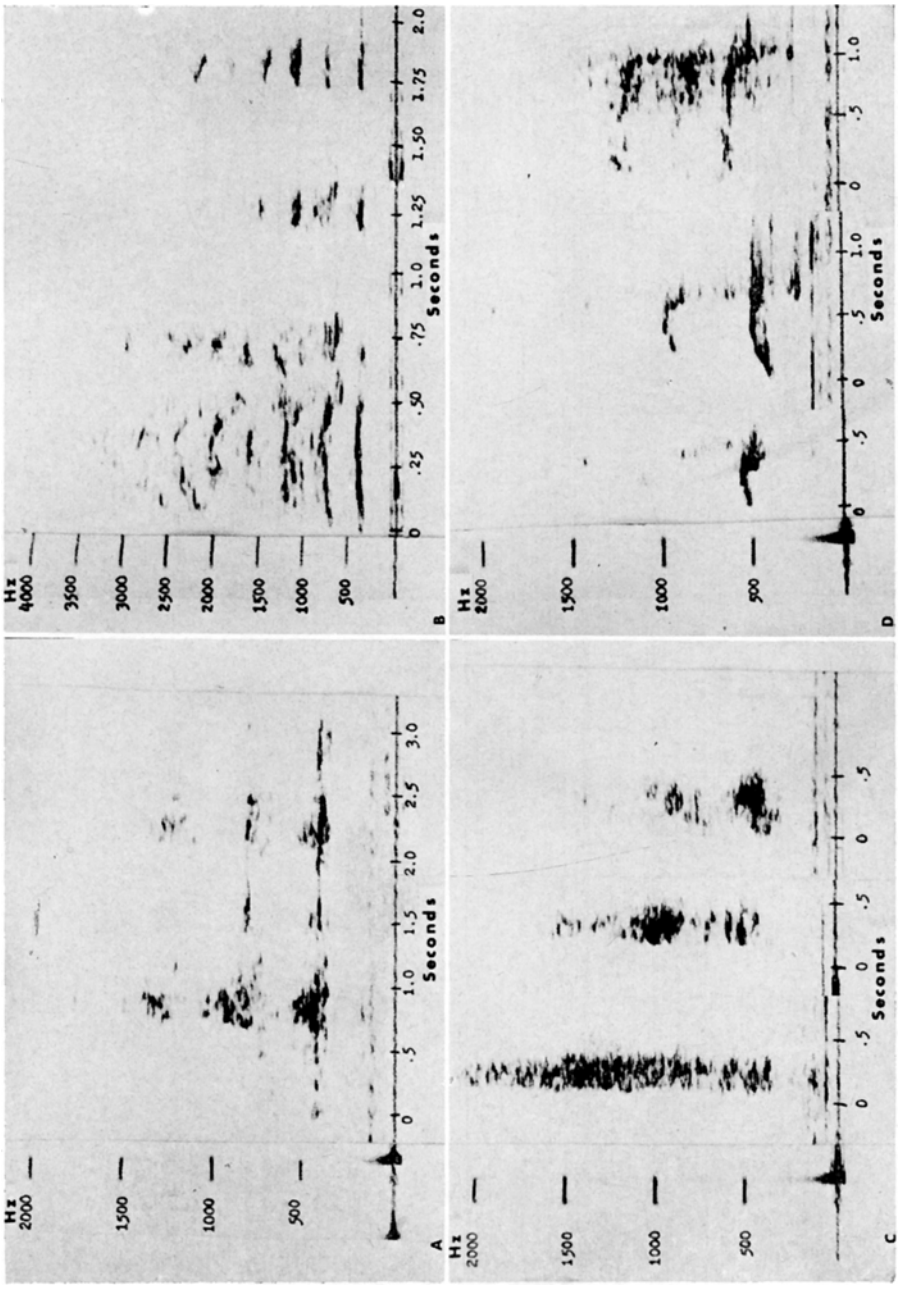

Fig. 4: A. Pulsated trumpet as emitted by Wankie. B. Trumpet phrase as emitted by Chico. C. Barks as emitted by Mandavu, Shapie and Wankie. D. Cries as emitted by Wankie and Mandavu; Gruff cry as emitted by Bisi

same as the fundamental and is the body of the sound. The dominant frequency of the gruff cry is 857 Hz. The duration of these sounds ranges from 0.4 to 1.2 s (Fig. 4 D).

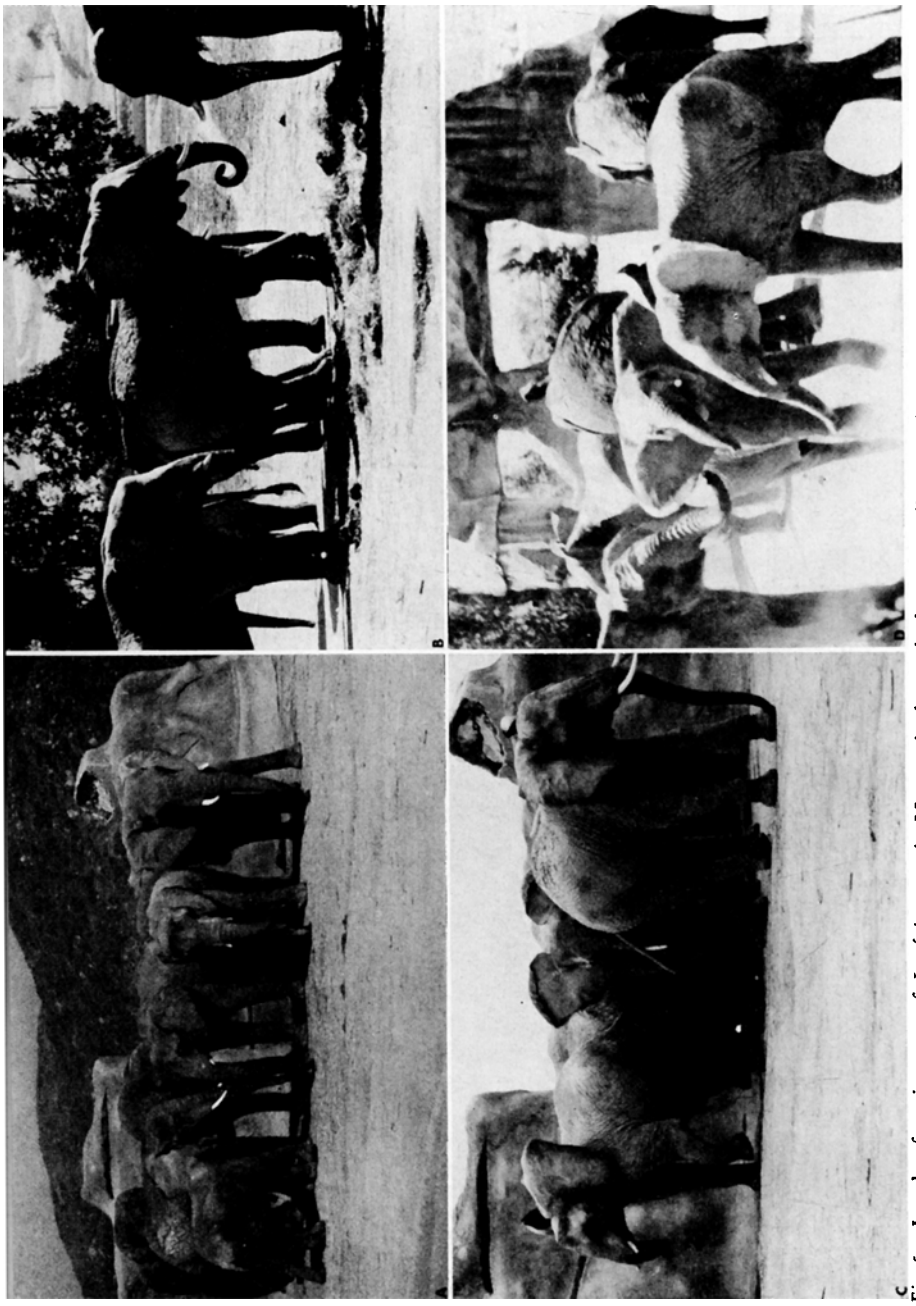

Fig. 5: Levels of excitement of *L. africana*. A. Not excited — elephants standing together and resting. B. Low level of excitement — greeting behavior as Peaches approached Sabu. C. Medium level of excitement — morning release from barn of Wankie, Hatari and Sabu. D. High level of excitement — behavior related to the mating pair. Deteema, Wankie and Bisi had been making long swift movements

Table 2 Number of sounds vocalized within each

Sounds	Total	Behavior Eliciting the Sounds			
		Low excitement			
		Greet.	Alert to external stimuli	Contact	R. to Asians
Low					
Growl	95	33	16	16	2
Rolling growl	91	19	22	34	2
Snort	69	35	15	5	5
Roar	9	-	-	1	-
[a]Unclass.	183	34	21	19	12
Total of low sounds	447	121	74	75	21
High					
Trump	104	10	-	-	2
Trumpet	249	8	1	1	7
Pulsated trumpet	94	1	-	1	-
Trumpet phrase	32	1	1	-	1
Bark	33	4	-	-	-
Cry	9	-	-	-	-
Total of high sounds	521	24	2	2	10
Total of all sounds	968	145	76	77	31
% of total sounds					
Low sounds		83 %	97 %	97 %	68 %
High sounds		17 %	3 %	3 %	32

[a] These sounds were unclassified due to poor recordings or because the amplitude was too low to be recorded.

B. Behavioral Context

11 behavioral categories were observed to be associated with the African elephant's vocalizations (Table 2). The descriptions of these behaviors follow.

Greeting-recognition. When one or two elephants are approached frontally, from the rear or from the side, by one or more elephants, either an approaching elephant or more often an elephant being approached will vocalize primarily a growl, snort or rolling growl (Fig. 5 B).

Alerting to external stimuli. When an elephant detects a familiar stimulus (one which occurs regularly, such as an approaching vehicle), it vocalizes a rolling growl, a growl or a snort. The recipients of this signal will respond either by a direct encounter with the signaler and/or by facing and scenting towards the external stimulus.

Seeking vocal contact. An elephant who is separated from one or more other elephants by being in the barn, the male's enclosure or a different part of the main enclosure, maintains vocal contact with the other elephants by emitting a growl or rolling growl, or on occasion, a snort. This sound normally elicits a responsive vocalization.

behavior category for three levels of excitement *Table 2*

Behavior Eliciting the Sounds							
Medium excitement				High excitement			Unknown
Startled	Mating	Morning release	Intraspec. aggress.	Inanimate aggress.	Active w / mating pr.	Active startled w / mating pr.	
1	3	12	5	-	4	-	3
2	-	6	2	-	4	-	-
-	-	3	1	-	3	1	1
5	-	1	-	-	1	1	-
1	-	30	2	-	61	2	1
9	3	52	10	-	73	4	5
2	-	39	2	11	26	9	3
2	-	74	-	33	83	38	2
-	-	4	-	42	25	21	-
1	-	7	-	4	4	13	-
-	-	13	-	3	9	4	-
-	-	-	9	-	-	-	-
5	-	137	11	93	147	85	5
14	3	189	21	93	220	89	10
62 %	100 %	29 %	50 %	0 %	33 %	4 %	
38 %	0 %	71 %	50 %	100 %	67 %	96 %	

Responding to Asian elephant sounds. The African elephants will occasionally respond to sounds emitted by the Asian elephants when the Asians are in their own enclosure, in the barn during the day, or on the path leading to the barn. Vocalizations emitted during this behavior are mainly trumpets or snorts.

Startled-frightened. When an elephant is alarmed by a novel stimulus or sudden movement by another elephant, it mainly vocalizes a roar.

Mating behavior. The male and oestrous female engage in increasing levels of tactile contact prior to the mount. Then the male restrains the female (sometimes preceded by a chase) by wrapping his trunk around one of her hind legs or grasping her tail with his trunk. He separates her legs and mounts while laying his trunk along her back while getting into position, then extends his penis into her vulva. A growl sound is occasionally detected during the mount. If penetration occurs, the pair immediately separates, each then engaging in low excitement behavior (usually feeding). If penetration does not occur, the interactions continue until the male is successful. Mating behavior may recur later in the day.

Morning release from the barn. When the elephants are released into their outdoor enclosure after being chained in the barn all night, they come together and vocalize. All sounds in the elephants' repertoire are vocalized during this behavior except the cry. The trumpets and trumps predominate (Fig. 5 C).

Intraspecific aggression. When one elephant pushes or hits another with its trunk, the recipient of the behavior emits primarily a cry or growl.

Interspecific and inanimate object aggression. The elephants become highly aroused, vocalizing pulsated trumpets and trumpets, while making long distance movements. During these movements, they chase peacocks or other birds from the enclosure, or bang against the gates creating loud noises, or scatter hay and/or droppings with their trunk and feet and/or make mock charges.

Active behavior related to the mating pair. During the chase and mating of the male and a female elephant in the main enclosure, the other females become highly aroused vocalizing primarily the trumpet type sounds, while remaining with the pair. Some of the other females also engage in inanimate object aggression and mock charges. This active behavior is initiated with the first mounting and subsequent chase of the pair (Fig. 5 D).

Active behavior related to the mating pair compounded by a low flying helicopter. The activities of this behavior are similar to the just described behavior except that a helicopter flew over the enclosure spreading grass seed. The group came together the first few times the helicopter flew near them, and became highly aroused after that. The trumpets and pulsated trumpets predominated.

Analysis

A log-linear analysis was performed on the data (biomedical computer programs P series — 1979; program BMDP 3F). The three-way interaction of

Table 3: Standardized residuals of the three-way interaction: 9 elephants, two levels of sound frequency (low and high) and three levels of excitement (low, medium and high)

Elephant	Frequency level of sound	Excitement level of behavior		
		low	medium	high
Peaches (P)	low	.5	- 1.2	- 3.0
	high	- 3.7	- 3.0	8.5
Sabu (S)	low	15.7	.5	- 2.9
	high	- 3.9	- 3.1	- 4.2
Mandavu (M)	low	7.5	1.7	- 2.6
	high	- 2.9	.2	- 2.2
Shapie (SH)	low	- 3.4	- 3.0	- 5.8
	high	- 4.0	10.3	5.3
Hatari (H)	low	11.9	- 1.8	- 2.8
	high	- 4.1	- 3.5	.7
Deteema (D)	low	7.2	2.2	- 1.6
	high	- 3.8	- 2.4	- .2
Wankie (W)	low	- 1.6	- 3.2	- 4.4
	high	- 3.9	1.9	9.1
Besi (B)	low	7.5	- 1.8	- 2.4
	high	- 2.7	1.5	- 1.2
Chico (C)	low	1.2	- .9	.4
	high	- 2.3	- 1.8	2.8

9 elephants, two levels of sound frequency (low and high), and three levels of excitement (low, medium and high) was significant, $G=33.01$, $df=16$, $p<.01$. The standardized residuals are given in Table 3. The values in this table indicate the deviation of actual observations from what would be expected if there were no interactions. The association of low frequency sounds with low excitement behaviors and high frequency sounds with high excitement behaviors is shown. The trend towards a decrease in the number of low frequency sounds as the level of excitement varied from low to medium to high, and the converse for high frequency sounds is also illustrated. Individual differences occurred in the pattern of vocalizing, with some animals being more vocal during low excitement behaviors with low frequency sounds (S, M, H, D and B) while other animals were more vocal during high excitement behaviors with high frequency sounds (P, Sh, and W). The sounds of the male (C) were more evenly distributed between the two levels of excitement and two levels of sound than those of the females.

Discussion

The context in which a vocalization (signal) was given seemed to be more important than the emission of a specific sound. This concept prevails in the free-living African elephant's growl (DOUGLAS-HAMILTON and DOUGLAS-HAMILTON 1975; MOSS 1975; SIKES 1971; WILSON 1977) and in sounds of other species such as the lion's (*Panthera leo*) roar (SCHALLER 1972) and the rock hyrax's (*Procavia capensis*) squeal (FOURIE 1977). Although each sound of the elephants in this study occurred in more than one context, some sounds were more characteristic of specific behaviors than others. In general, however, those sounds with a low fundamental frequency were emitted primarily during behaviors of a low arousal level, signaling non-agonistic intentions, with the converse for high fundamental frequency sounds. The medium level of excitement contained both levels of sounds. There was a trend for individuals to be more vocal during either low excitement behaviors with low fundamental frequency sounds, or high excitement behaviors with high fundamental frequency sounds. The predominating level of sound for each individual tended also to predominate during medium excitement behaviors.

Low Fundamental Frequency Sounds and their Associated Behaviors

WALTHER (1977), in reviewing the literature on artiodactyles, found that sounds used for contact between individuals also served an important function in group cohesion and individual recognition among the herds of gregarious species. A similar concept was found in the Asian elephant (EISENBERG and LOCKHART 1972). In the African elephant, the growl, rolling growl, and occasionally the snort, were used for vocal contact among individuals. They were also the predominant sounds used in alerting others to external stimuli and during the greeting-recognition behavior. These three sounds and these

three behaviors were the most important for group cohesion and the orderly interactions among individuals of this group.

The pictorial representation of the sounds shows more variation in the rolling growls as compared to the growls. In fact, the growl, with its lack of variation, and the snort, with its noise quality, lend themselves less to individualization than the rolling growl, and are emitted when the identity of the emitter can be otherwise determined. Such is the case during greetings, a behavior which all elephants performed and with which both sounds were most frequently vocalized; this is a behavior in which there is visual and/or chemical contact of the emitter and receiver.

The rolling growl, however, occurred most often during vocal contact, a behavior in which the emitter is separated from the group; thus, individualization may be one of its important characteristics. Seeking or retaining voice contact between conspecifics has been described in pigs (*Sus scrofa*), cattle (*Bos taurus*) and horses (*Equus caballus*) (KILEY 1972), Asian elephants (EISENBERG and LOCKHART 1972) and free-living African elephants (MOSS 1975; WILSON 1977). Elephants are a gregarious species with poor eyesight; therefore, it is important for members of the group to keep apprised of each other's location through voice contact. This is especially important in the wild, where groups may separate during the day or night for feeding purposes. Its significance has been retained in the captive elephant.

High Fundamental Frequency Sounds and their Associated Behaviors

Trumpets and trumps were the most frequently vocalized high fundamental frequency sounds. The emphasis on the fundamental frequency or second harmonic, or no particular emphasis on either, may reflect individual differences in producing these sounds. Interestingly, of the two most frequent known emitters of both sound types, Shapie emphasized her second harmonic and Wankie emphasized her fundamental frequency (Fig. 3 C).

Trumpets seem to be synonymous with elephants. In the free-living African elephant, the trumpet has been said to occur as a commanding call by the matriarch and during highly disturbing situations (DOUGLAS-HAMILTON and DOUGLAS-HAMILTON 1975; MOSS 1975; and SIKES 1971). In the current study, trumpets and trumps occurred most often during the morning barn release and while active with the mating pair. This latter behavior could have been considered a disturbing situation. The chase and mounting behavior of the mating pair created a high level of excitement in the other females, particularly the adolescents. The increase in excitement and vocalizing by the mating pair may have stimulated the increase in arousal of the others. KILEY (1972) has suggested a similar concept in ungulates. She found that the high excitement and accompanying vocalizations of one animal could initiate the same level of arousal in another, even if the other was not previously excited.

According to TEMBROCK (1963), excitement leads to shortness of breath; thus, the pulsated trumpet was vocalized during the high excitement of the elephants while they were moving swiftly over relatively long distances during

such behaviors as interspecific-inanimate object aggression. This behavior often began with the elephants chasing peacocks from the enclosure and continued even after the peacocks had flown away. Inanimate object aggression would often follow, with the signaler vocalizing its aggressive intentions repeatedly.

On occasion, an elephant would combine trumpets and trumps, or long and short pulsated trumpets in a sound sequence termed a "trumpet phrase". There did not appear to be a definite time interval between syllables of these sequences, except that it was a short interval of no more than 0.5 s. TEMBROCK (1963) has shown sound sequences to occur in a variety of mammalian species among the canids, felids, ungulates, and primates. Now we can add proboscidians.

Medium Excitement Behaviors and their Associated Sounds

Three sounds occurred most frequently during behaviors of this state: the roar, bark and cry.

The bark was a relatively short burst of energy whose acoustical quality was similar to the bark of a domestic dog. A variety of species are said to emit barks during medium to high arousal situations, such as the coyote (*Canis latrans*) (LEHNER 1978), the domestic pig (KILEY 1972) and the squirrel monkey (*Saimiri sciureus*) (SCHOTT 1975). This sound is of short duration in all these species, and in the elephant. During the current study it was most often emitted during the morning barn release. The elephants were released into their outdoor enclosure after being chained in the barn for about 15 h. Their state of arousal in this context was a response to the unnatural state of being restrained from locomotion and activities that would be experienced in their free-living state (DOUGLAS-HAMILTON and DOUGLAS-HAMILTON 1975) or in captivity when allowed to roam in a relatively large enclosure at night (KÜHME 1962).

The cry was a situation specific sound which occurred during intraspecific aggression, with the recipient of the behavior emitting the sound. This behavior occurred infrequently and involved pushes with the base of the trunk, or a slap with the end of the trunk by a superior directed toward an inferior.

The roar was emitted when something appeared to frighten or startle an animal. The emitter usually remained immobile, and the vocalized sound often caused the others to approach the emitter. This sound occurred most often during this behavior and may have functioned as a call for help.

During this study, mating behavior occurred during three observation periods. Three growl sounds were emitted by the male and oestrous female during their mounting behavior. The DOUGLAS-HAMILTONS (1975) documented a growl vocalized by a male during mounting in a pair of free-living elephants. In the current study, other low pitched, low intensity sounds were occasionally detected, but were too low to be recorded for analysis. According to COLLIAS (1960), sounds in some bird and mammal species during copulation may facilitate the behavior; this may also apply to elephants.

Zusammenfassung

10 charakteristische Lautäußerungen spielen eine bedeutende Rolle im Kommunikationssystem afrikanischer Elefanten. Obwohl 9 Vokalisationen in mehr als einem Kontext benutzt werden, haben viele einen besonderen Bezug zu spezifischem Verhalten. Die Hauptfrequenz der Laute korreliert signifikant mit dem Erregungsgrad des Elefanten: tiefe Frequenzen entsprechen geringem Erregungsgrad und spielen eine Rolle bei Gruppenzusammenhalt und normalem Zusammenleben. Höhere Frequenzen zeigen höhere Erregung an und treten meist während aggressiver Verhaltensweisen auf. Vokalisationen und die begleitenden Verhaltensweisen werden von gefangengehaltenen Tieren beschrieben und mit denen freilebender Elefanten und anderer Tiere verglichen, die ähnliche Verhaltensweisen und Vokalisationen haben.

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Author's address: Judith K. BERG, Research Associate, Zoological Society of San Diego, San Diego Wild Animal Park, Route 1, Box 725 E, Escondido, California 92025.