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QUANTIFYING ACOUSTIC AND TEMPORAL CHARACTERISTICS OF VOCALIZATIONS FOR A GROUP OF CAPTIVE AFRICAN ELEPHANTS *LOXODONTA AFRICANA*

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ABSTRACT

In order to increase understanding of African elephant vocal communication and to standardise the terminology used to describe vocalisations, this study examined acoustic and temporal characteristics of 983 vocalisations from 2 male and 6 female captive African elephants. Recording collars were used to monitor vocalisations and videotape to simultaneously record behaviour, allowing for unambiguous attribution of sounds to individuals, even in close proximity. Eight acoustically distinct categories of calls were defined in terms of structural characteristics; two of these categories are described for the first time. Low-frequency vocalisations containing infrasonic components were predominant in this localised communication context and showed a gradation of variation in acoustic structure and duration. Most calls were part of temporally closed exchanges between individuals and coincided with short-distance interactions. In addition, male-female choruses and non-musth rumbles from males were documented, suggesting that the African elephant vocal repertoire may be more complex than previously reported.

Keywords: African elephant, vocal repertoire, infrasound, vocal strategies

INTRODUCTION

The African elephant *Loxodonta africana* is a long-lived mammal with a complex social structure. Elephants use a wide variety of sensory channels to communicate: tactile, visual, olfactory and vocal, which may lead to the use of complementary or redundant signals (Langbauer

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2000). Behaviour of elephants has been studied for decades (Douglas-Hamilton & Douglas-Hamilton 1975; Laws et al. 1975; Moss & Poole 1983) and new advances have been made in understanding the role of olfactory communication (Rasmussen 1988; Rasmussen & Schulte 1998; Rasmussen et al. 1996). However, there is currently no standard format for classifying African elephant vocalisations, based either on structural features or behavioural context (Langbauer 2000). In order to understand more fully the interplay of multiple sensory channels in African elephant communication, a greater understanding of vocal communication is needed, specifically acoustic and temporal patterns of production and sex-based differences in vocal strategies.

Vocal categories

Although several studies have examined elephant vocal behaviour, the extent of the acoustic repertoire of the African elephant is relatively unknown. Berg and colleagues first described African elephant vocalisations (Adams & Berg 1980; Berg 1983), and further studies resulted in the description of a total of 31 different call types (Berg 1983; Langbauer et al. 1991; McComb et al. 2000; Poole et al. 1988). However, of the vocalisations that have been described to date, the distinction between use of functional and structural characteristics to define call types is not always clear. Langbauer (2000) grouped the 31 call types by general and narrow behavioural context, but notes that the acoustic structure has been given for only 16 of these calls and many are acoustically similar.

Berg (1983) provided the first information on the physical characteristics of 10 sound types that comprised the vocal repertoire of a group of captive African elephants (1 male: 8 females). Vocalisations were categorised based on visual inspection of sonograms, although the structural characteristics used to determine categories were not given. Once categorised, corresponding structural properties of each category were determined and behavioural context was described. Berg (1983) found that high-frequency (fundamental frequency range 322-570 Hz) and low-frequency (fundamental frequency range 18-28 Hz) vocalisations each made up about 50% of recorded vocalisations. She also found that trumpets occurred primarily in high excitement settings, while low-frequency rumbles or growls were observed most often during low levels of excitement.

Berg suggested that because low-frequency vocalisations occurred during low levels of excitement, their function may be to reinforce group cohesion and coordinate social dynamics. Further studies examining low-frequency vocalisations have shown that these calls contain infrasonic components that have the potential to transmit information over very long distances (Poole et al. 1988). Subsequent studies have suggested that low-frequency vocalisations may be used more than 50% of the time (Langbauer 2000; Poole 1994; Poole et al. 1988), and that recordings made in much closer proximity to the sound source (as can be accomplished by recording collars) are necessary in order to ensure the lowest frequency vocalisations are adequately represented (Charif 1993; Langbauer 2000). Studies focusing on responses to low-frequency vocalisations produced in very specific behavioural contexts have lent insight to vocal strategies related to these calls (Langbauer et al. 1991; McComb et al. 2000; Poole et al.1988; Poole 1999); however, the prevalence of low-frequency vocalisations with respect to the total range of vocalisations given by African elephants has not been re-examined (Langbauer 2000).

There is currently no standard schema for classification of African elephant vocalisations that would allow for this type of re-examination. The first essential step in this process is the formal definition of specific high-frequency and low-frequency vocalisation categories based on acoustic properties and independent of behavioural context. Given the acoustic similarity of calls produced in a variety of contexts (Berg 1983; Poole 1994; Poole et al. 1988), subsequent investigation of acoustic distinctions within each of these categories also is needed.

Female and male vocal strategies

Elephants live in highly organised social units headed by a matriarch. These stable family units may interact with other groups of elephants in varying degrees depending on ecological conditions (Douglas-Hamilton & Douglas-Hamilton1975; Moss & Poole 1983; Poole et al. 1988). Males leave their family unit once they reach puberty and mature bulls experience periods of heightened sexual aggression known as musth. During this time, males may move over long distances in short spaces of time to contact cows in oestrus and may also try to avoid other large musth males (Hall-Martin 1987; Poole 1994). Given that the low frequency "rumbles" are the most frequent vocalisation (Poole 1994), infrasonic communication may be a means for elephants to maintain long distance social coordination in the contexts of group and individual avoidance. Low-frequency vocalisations may also facilitate social interactions necessary for reproduction in a species where oestrous females and musth males are widely separated in space (Poole et al. 1988).

In addition to the contrasting social lifestyles of adult male and female African elephants, many studies have observed differences in vocal patterns. Highly social females often chorus (overlap their vocalisations in time) with one another and with juveniles (Langbauer 2000; Poole 1994; Poole et al. 1988; C. O'Connell-Rodwell, pers. comm.). Once males reach adulthood, they vocalise infrequently and produce a distinctive musth rumble, not shared with females (Langbauer 2000; Poole 1987, 1989a, 1989b; Poole et al. 1988). Nothing has thus far been published on non-musth rumbles of adult males. These results have led to the suggestion that the vocal strategies of male and female African elephants should be markedly different, reflecting the differences in patterns of association of the two sexes (Langbauer 2000; Poole 1994). For many other species of mammals, the effects of sexual selection on shaping the evolution of acoustic signals has been well established (Andersson 1994; Clutton-Brock & Albon 1979); however, this phenomenon has not been studied explicitly in African elephants.

This study was designed to augment the existing information on the acoustic properties of African elephant vocalisations and to standardise the terminology used to describe vocalisations. We present information on vocalisations 1) based on both acoustic and temporal patterns of production and 2) with respect to spatially defined behavioural contexts for a group of captive African elephants. In addition, we compare the vocalisations of males and females in order to better understand sex-based differences in vocal strategies used by African elephants.

METHODS

Study animals

Subjects were two adult male (age 18 and 22 yrs.) and six adult nulliparous female African elephants (age range 19-30 yrs; all sexually mature) housed at Disney's Animal Kingdom, Florida, USA. All subjects were wild born but raised in captivity from an early age (3-5 years old) and are presumed to be unrelated.

Subjects were housed in individual stalls inside a barn at night and released daily into one of two large naturalistic outdoor enclosures ("main yard," 2.29 ha and "small yard," 0.55 ha) or a smaller outdoor yard attached to the barn ("barn yard," 0.04 ha) from approximately 0800-1700 h. Animals in the main yard and small yard were separated physically but not visually. Animals in the barn yard were physically and visually separated from animals in the main yard. All three yards were in vocal contact. Group composition of the elephant herd varied to achieve various animal management objectives, thus we limited our analysis to observation days with one male and four female elephants housed together in the main yard.

Vocal data collection

Elephant vocalisations were monitored via transmitters mounted in collars worn by the elephants. Collars were designed, built and packaged by Walt Disney World Co. Instrumentation Support Division of Ride and Show Engineering, modifying the original design of Dr. William Langbauer Jr. and Steven Powell. Each collar contained: (1) a Radio Shack 270-090C condenser microphone element (20/12 kHz flat to 30 Hz with 10 dB loss at 20 Hz); (2) a Jobcom 100, 150 to 160 MHz Ritron Handheld Radio with a custom cut and tuned antenna; and (3) a battery pack: 2EA Gel Cell, Royal Battery BC-632, 6 volt/3.2 amp-hour.

Each collar transmitted sounds on a unique frequency to an Antenna Specialties ASP-655 Temporary Base Station half-wave antenna, 136 to 174 MHz and a Hamtronics R-144/R226 VHF/FM receiver 150 to 160 MHz in the elephant barn. Each of these receivers was in turn connected to a separate channel of a Tascam DA-38 8-channel DAT recorder where they were recorded on separate tracks of a Sony DARS-60MP Digital Audio Tape. One one-hour tape was recorded each day that the collars were worn. Collars were put on each elephant in the morning and removed in the evening to charge batteries. All elephants but one male and one female regularly wore collars. The non-collared elephants were housed in the small yard or barn yard on observation days. On average, a collar was worn for 12 hours each observation day.

Behaviour data collection

Behaviour was documented by three to four observers for each observation session using Panasonic mini-digital video cameras (PV-DV910). All video cameras were time synchronised to each other and to the audio recording with ± 1 second margin of error. At the start of each session, the field observers positioned themselves at specific viewing locations around the elephant enclosure, then filmed continuously for the complete hour. An additional person in the elephant barn recorded the audio signals from the collars onto audio tape and coordinated field observers. Observers communicated via radio in order to identify elephants onscreen and in their view. Only animals filmed in the main yard were included in video analysis.

Observers filmed the elephants for 10-minute focal periods (Altmann 1974); attempts were made to observe each individual present for at least one complete 10-minute period each observation session. On average, two 10-minute periods were recorded per observation per elephant. Some focal periods were split between cameras as the elephants moved throughout the yard, this was possible through constant radio contact and the fifth observer coordinating from the elephant barn. To preserve information on social interactions and spacing among the elephants, animals that were nearby the focal individual were included in the camera view, as long as the focal animal did not become smaller than one third of the screen size. This allowed the preservation of social information such as proximity, while still recording an image of the animals at a screen size large enough to later analyse the behaviour of the focal animal.

After each observational session, the video signals from all four field video cameras were routed through an analogue quad-splitter (Panasonic Quad System WJ-MS424) to simultaneously re-record each video tape onto one quadrant of a VHS tape. During this procedure, time code (in VITC, Vertical Interval Time Code) was added to the dubbed tape. This resulted in one VHS tape with four windows, each containing the signal from one of the mini digital video cameras, synchronised in time, with the accompanying audio information from radio transmissions. One hour of observation was recorded weekly from November 1999 to December 2000, for a total of 53 hours of 8-channel audio and quad-split video recordings. Observations began between 1000 and 1300 h due to staffing availability and because elephant behaviour related to entering and leaving the barn was noted as markedly different from interactions throughout the rest of the day.

ANALYSIS

Vocalisation detection

Vocalisations were located on each channel of the tape using Real-Time Spectrogram (RTS) software (version 2.0, Engineering Design). The gain for each channel was adjusted through a Mackie 1202-VLZ Audio Mixer and filtered to avoid aliasing with a Tunable Active Filter Instrument (Frequency Devices model 900C/9L8B 8-Pole Butterworth Low-Pass Filter). RTS was set to a sample rate of 1200 Hz to visually locate vocalisations that contained infrasonic components; audible vocalisations were located by ear. Once located, vocalisations were saved as computer files at a sample rate of 7500 Hz to ensure adequate headroom. Collars were sensitive enough to record vocalisations of nearby elephants as well as the elephant wearing the collar; identity of the vocaliser was determined by relative strength and timing of signals recorded on all channels. In some instances the identity of the vocaliser could not be determined.

Vocalisation files were accessed through SIGNAL Digital Signal Analysis Language software (version 3.0, Engineering Design), printed as spectrograms and added to a library of vocalisations for further analysis. Vocalisation rates were also calculated for each individual for each recording session. Rates were only included for analysis if the collar had sent a clean signal for at least 60% of the entire observation session.

SPSS (version 9.0, SPSS, Inc.) and SYSTAT (version 9.0, SPSS, Inc.) were used for all statistical analyses.

Behaviour scoring

Behavioural context was scored from the video tapes using Observer software (version 4.0, Noldus Information Technology). For each observation, each elephant was monitored for time onscreen as well as five spatially defined behavioural contexts: 1) *Next to*: one elephant stands within 2 body lengths (8m) of one or more elephants, all must be stationary; 2) *Approach*: one elephant decreases its distance to one or more stationary elephants within a radius of 2 body lengths (8m), then stops; 3) *Leave*: an elephant that has been next to one or more stationary elephants increases its distance beyond a radius of 2 body lengths; 4) *Follow*: one elephant walks behind another elephant for more than 5 steps and within a distance of 2 body lengths (between 2 animals only), both animals are moving in same direction; 5) *Pass by*: one elephant walks within 2 body lengths on either side of one or more stationary elephants without stopping. Actor and recipient of each behaviour were recorded. All behavioural contexts occurred within very close-range of another elephant (within 2 body lengths, or 8 m), thus were considered to be group contexts. Animals greater than 2 body lengths from all other individuals were considered to be solo. Instantaneous behaviour (± 5 seconds to account for scoring reliability) was matched with vocalisations for which 1) the identity of the elephant vocalising was known and 2) the elephant was onscreen.

RESULTS

Acoustic and temporal patterns of vocal production

Standardisation of acoustic categories

In an attempt to standardise terminology, categories of vocalisations were defined by acoustic properties alone, based on sound quality and spectrographic characteristics. After listening to over 700 vocalisations, differences in approximate bandwidth, sound quality, approximate fundamental frequency, presence of infrasonic components, and duration were used to define eight mutually exclusive categories of calls: *trumpet*, *snort*, *croak*, *rev*, *chuff*, *noisy rumble*, *loud rumble*, *rumble* (Table 1, Figure 1). All vocalisations recorded in this study (N=983) fall into the above eight categories. An attempt was made to utilise established nomenclature where possible, based on qualitative descriptions and limited acoustic information. Two of the eight call types observed in this study, *croak* and *rev*, did not resemble any previously named vocalisations. These calls were sufficiently acoustically distinct and were recorded from more than one individual, necessitating the creation of the two new terms:

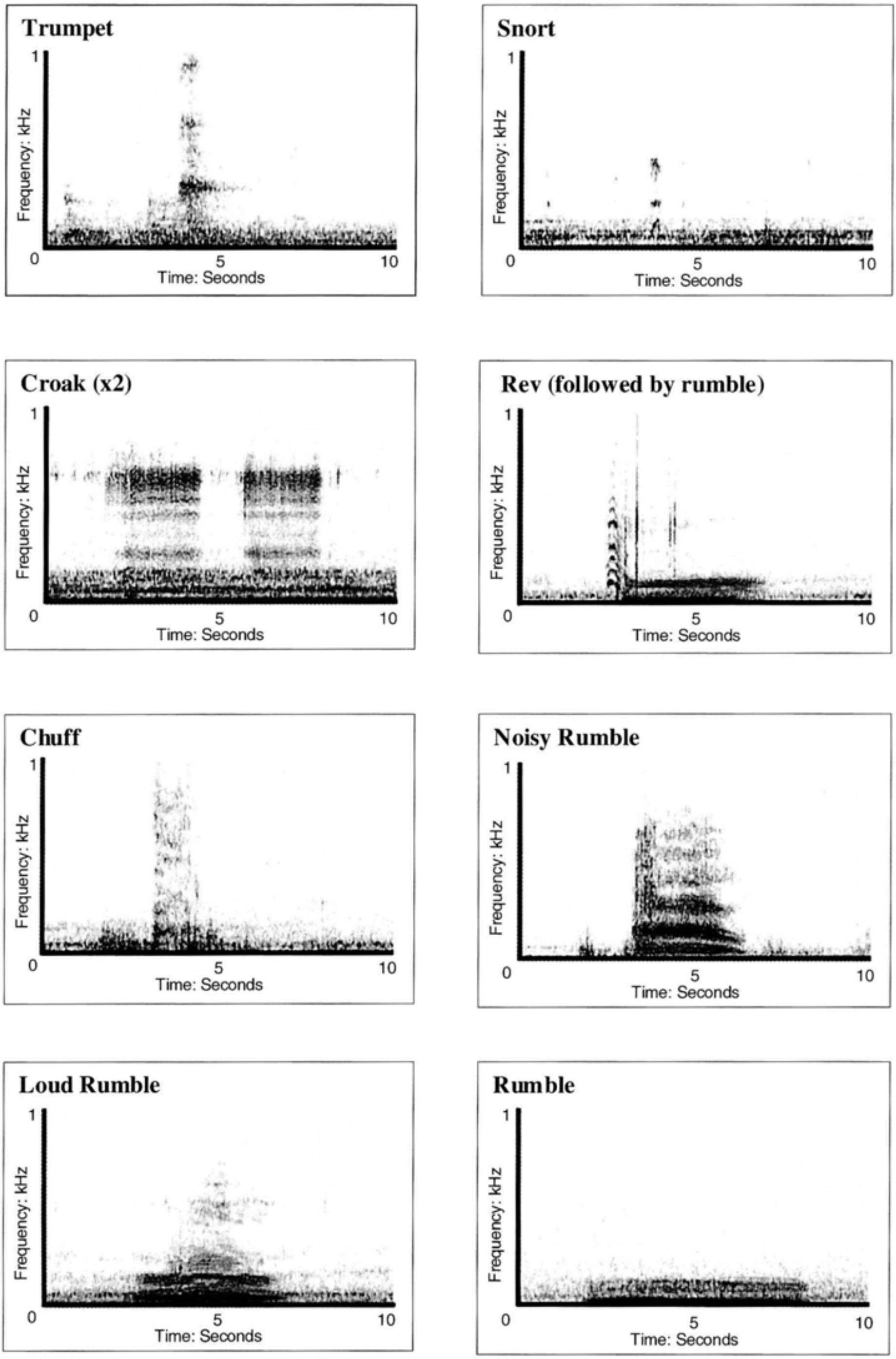

Figure 1. Representative spectrograms of the eight call types observed in this study.

TABLE 1

Acoustic parameters used to classify vocalisations into acoustic categories for analysis.

Call Type	Approximate bandwidth	Sound quality	Approximate fundamental frequency	Contains infrasonic components	Approximate range of duration
Trumpet	300-3000 Hz	Tonal harmonic	300 Hz	No	1-5 sec
Snort	200-1000 Hz	Tonal harmonic/ noisy	200 Hz when present	No	1 second
Croak	300-1000 Hz	Pulsatile	n/a	No	1-10 sec
Rev	75-800 Hz	Tonal harmonic	75 Hz	No	1 second
Chuff	20-1500 Hz	Noisy	n/a	No	1-5 sec
Noisy Rumble	18-800 Hz	Tonal harmonic with noisy components	18 Hz	Yes	1-10 sec
Loud Rumble	12-600 Hz	Tonal harmonic	12 Hz	Yes	1-10 sec
Rumble	12-200 Hz	Tonal harmonic	12 Hz	Yes	1-10 sec

(a) *Croak*: a total of 71 *croaks* was recorded from three different females and one male, with four additional *croaks* recorded from unidentified individuals. *Croaks* usually occurred in a repeated series of two or three *croaks* and were often associated with sucking water/odours into trunk.

(b) *Rev*: a total of 14 *revs* was recorded from four different females, with three additional *revs* recorded from unidentified individuals. All *revs* were extremely short vocalisations, less than one second, and were almost always followed immediately by a *rumble*, either from the same or different elephant. This vocalisation was rarely captured on video, although it may be associated with the elephant being startled, as the few that were videotaped coincided with the elephant raising its head suddenly, coming into visual contact with another individual from around a visual barrier, or being physically pushed from behind.

Distribution of acoustic categories

The eight acoustic categories of vocalisations were distributed significantly differently than would be expected by chance, i.e. equal numbers across all categories. ($\chi 2$=2107.1, df=6, p<0.001. Table 2). *Rumbles* alone accounted for 62.1% of all vocalisations, and 87% of all calls were low-frequency vocalisations containing infrasonic components (*noisy rumbles*, *loud rumbles*, and *rumbles*).

TABLE 2

Relationship between temporal category and acoustic category for all recorded vocalisations. High-frequency vocalisations (*Trumpet*, *Snort*, *Croak*) were most often adjacent (0–30 sec) to another call, low-frequency vocalisations with infrasonic components (*Noisy Rumble*, *Loud Rumble*, *Rumble*) occurred in all temporal categories but were more often less than 30 seconds (overlapping and adjacent) from another vocalisation.

Call type	Temporal Category				Total
	Over-lapping	Adjacent	Inter-mittent	Single	
Trumpet	2	20	1	1	24
Snort	0	6	2	4	12
Croak	1	63	6	5	75
Rev	6	10	1	0	17
Chuff	2	0	0	1	3
Noisy Rumble	8	3	1	0	12
Loud Rumble	69	61	50	51	231
Rumble	183	181	130	115	609
Total	271	344	191	177	983

Variation in acoustic categories

Within each category, vocalisations showed a high degree of variation in both frequency modulation and duration. Because the majority of vocalisations recorded were rumbles, SIGNAL software was used to perform preliminary spectral cross-correlation analysis on the fundamental frequency contour of 60 pseudo-random rumbles. SIGNAL will accept a maximum of only 63 spectral contours for cross-correlation, therefore twelve rumbles of good acoustic quality were chosen using a random number generator for each of the five females who regularly wore collars. Fundamental frequency contours were extracted using PEAK and smoothed twice. The CORMAT function was then used to create a matrix of cross-correlation similarity scores.

Examination of the cross-correlation additive tree structure revealed three major nodes and three sub-nodes, separating the rumbles into five types (Figure 2). Two vocalisations appeared to belong to a fourth major node but were not included in analysis because of the limitation in sample size. When these cross-correlation scores were subjected to Multi-dimensional Scaling in SYSTAT, the distances between the five types were shown to be so small that no distinct clusters of vocalisations were present (Figure 3). Overall, the rumbles appear to be acoustically graded. Vocalisations from individuals were evenly distributed throughout each of the five types and also did not show any clustering.

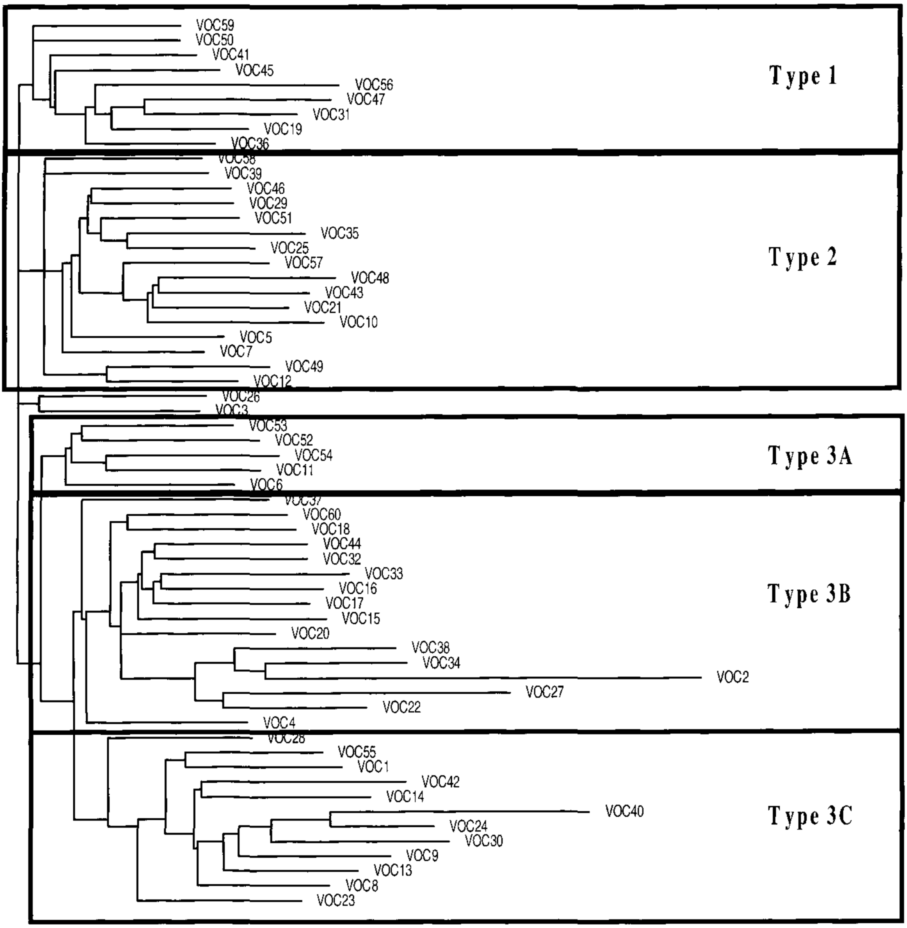

Figure 2. Additive tree for spectral cross-correlation similarity scores of fundamental frequency contour, calculated by SIGNAL for 60 pseudo-random rumbles. Major branches of the additive tree structure were used to divide rumbles into 5 types: types 1, 2, and 3 were differentiated by the first major node, types 3A, 3B, and 3C by sub-node. Vocalisations 3 and 26 were not considered in analysis due to small sample size.

In order to further examine distinctions between the five types of rumbles, average fundamental frequency, fundamental frequency range, maximum fundamental frequency, minimum fundamental frequency, duration, location of maximum frequency and location of minimum frequency were then measured for the fundamental frequency contour of each rumble. Amplitude was not measured as the collars were modified a number of times due to wear and tear and could not be calibrated reliably between modifications. Of the parameters measured, frequency modulation and duration appeared as the strongest acoustic

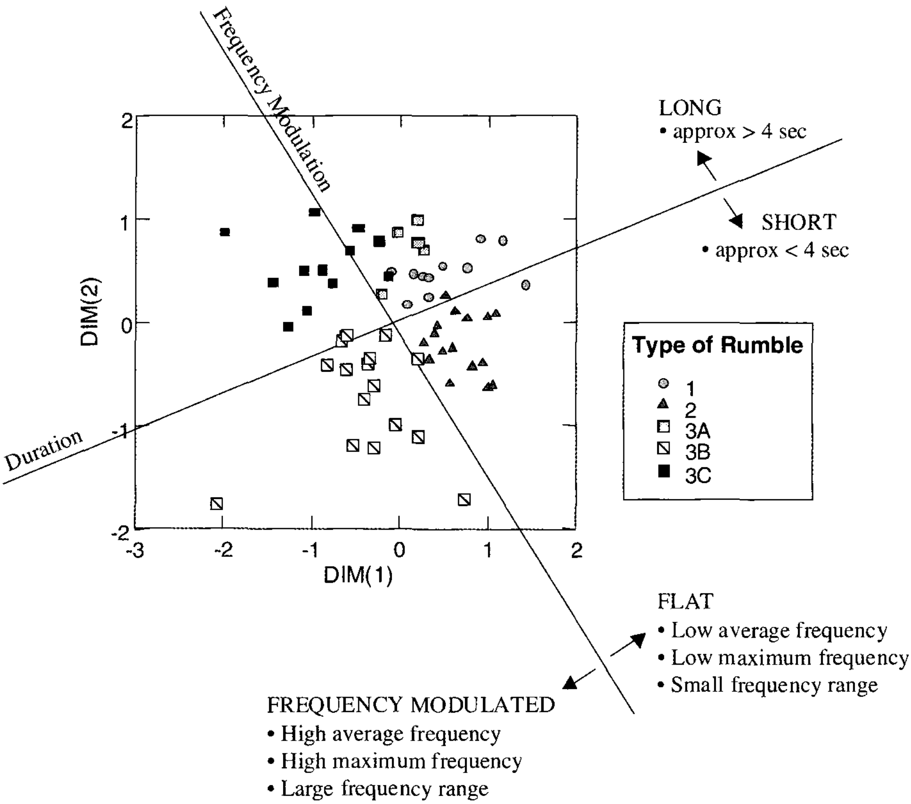

Figure 3. Multi-dimensional scaling of fundamental frequency similarity scores for 60 pseudo-random rumbles, shown with respect to two dimensions. The type of rumble was determined from additive tree branching. Frequency modulation and duration axes, as determined by comparison of fundamental frequency measurements, are overlaid to show specific acoustic properties important in distinguishing the 5 types.

characteristics defining the five types (Table 3). These parameters are overlaid in Figure 3 but did not correlate with the spatial behavioural contexts scored.

Definition of temporal categories

To examine patterns of vocal exchanges between individuals, calls were also categorised based on temporal relations among sequential vocalisations. Six-hundred and fifty-two intervals between calls were measured to determine appropriate boundaries for temporal category definition. An interval was defined as the total elapsed seconds between the end time of the reference call and the start time of the subsequent

TABLE 3

Acoustic measurements of fundamental frequency contour (Mean ± SD and indication of above/below overall average) for 5 types of rumbles. Rumble types were determined through cross-correlation scores for 60 pseudo-random rumbles using SIGNAL software. Frequency measures all seem to be related to frequency modulation

Rumble type	Rumble type description	Fundamental frequency	Fundamental frequency range	Maximum fundamental frequency	Minimum fundamental frequency	Duration
1	Lower frequency, flat, long	12.94 ± 0.98 Hz (below)	1.98 ± 0.87 Hz (below)	13.77 ± 1.26 Hz (below)	11.79 ± 0.88 Hz (above)	4.62 ± 0.38 sec (above)
2	Lower frequency, flat, short	12.67 ± 0.72 Hz (below)	1.77±0.72 Hz (below)	13.32 ± 0.90 Hz (below)	11.56 ± 0.95 Hz (below)	3.43 ± 0.55 sec (below)
3A	Very low frequency, flat, long	12.66 ± 0.53 Hz (below)	2.53 ± 0.62 Hz (below)	13.46 ± 0.69 Hz (below)	10.94 ± 0.33 Hz (below)	5.72 ± 0.56 sec (above)
3B	Higher frequency, frequency modulated, short	14.75 ± 1.12 Hz (above)	4.97 ± 1.02 Hz (above)	16.75 ± 1.56 Hz (above)	11.78 ± 0.97 Hz (above)	4.15 ± 1.24 sec (below)
3C	Higher frequency, frequency modulated, long	14.05 ± 1.37 Hz (above)	5.02 ± 1.92 Hz (above)	16.46 ± 2.39 Hz (above)	11.45 ± 0.78 Hz (below)	5.19 ± 1.07 sec (above)
Overall average		13.55 ± 1.33 Hz	3.38 ± 1.90 Hz	14.96 ± 2.17 Hz	11.58 ± 0.88 Hz	4.38 ± 1.13

call. Calls that overlapped in time were given negative scores and considered to be part of a chorus. Intervals showed the following distribution: 1st quartile: 1.5 seconds, median: 30 seconds, 3rd quartile: 118 seconds. These time periods were rounded and the following temporal categories were created: overlapping (<0 sec), adjacent (0-30 sec), intermittent (>30-120 sec) and single (>120 sec). Once temporal boundaries were defined, all vocalisations (N=983) were categorised with respect to the nearest vocalisation in time, either before or after the reference vocalisation. This ensured that even the first call in a chorus was scored as an overlapping call. By definition, overlapping calls were produced by different individuals. Adjacent and intermittent calls were noted as being produced by the same or different individuals.

Distribution of temporal categories

An analysis of temporal category showed that, overall, calls were not distributed equally across the four categories ($\chi 2=73.3$, df=3, $p<0.001$, Table 2). The majority (62.6%) of all calls occurred within 30 seconds of another vocalisation (overlapping and adjacent), and 82% of all calls occurred within 2 minutes of another vocalisation (overlapping, adjacent, intermittent). Of these, 63.69% were exchanges produced by different animals. Most overlapping sequences (77.6%, N=90) contained two vocalisations only; the largest choruses contained five vocalisations and were rarely observed (2.6%, N=3). A total of 80.2% of higher frequency calls (*trumpet*, *snort*, *croak*) were adjacent (0-30 sec) to another call. Low-frequency calls containing infrasonic components (*noisy rumbles*, *loud rumbles* and *rumbles*) occurred in all temporal categories and were also distributed significantly differently than would be expected by chance ($\chi 2=30.4$, df=3, $p<0.001$). Of these, 59.3% occurred within 30 seconds of another call.

Vocal strategies

Proportion of vocalisations used in very close-range behavioural contexts

Four-hundred vocalisations were recorded from the animals in the main yard for which the identity of the vocaliser was known and the elephant was onscreen. Of these, 354 calls contained infrasonic components. Significantly more of these low-frequency calls (67.5%) occurred when the vocaliser was within two body lengths of at least one other individual ($\chi 2=18.99$, df=1, $p<0.001$). Only 46 vocalisations did not contain infrasonic components. These occurred equally in solo and group contexts. Most call types occurred in more than one close-range behavioural context, with loud rumbles and rumbles occurring in all five group contexts.

Male vocalisations

Male rates of vocalisation were significantly lower than those of females, (Mann-Whitney $U=1297.5$, $p<0.01$). No musth rumbles were observed during the course of this study (again, the two bulls in this study were 18 and 22 years of age and neither had experienced musth prior to or during this study). Instead, 17 loud rumbles and 16 rumbles which were not associated with musth were recorded from the younger male. Two non-musth rumbles were also recorded opportunistically when the two males were introduced to each other for the first time. One of these was clearly produced by the older male. In addition, the younger male was occasionally observed chorusing (i.e. overlapping calls) with reproductively cycling females. No choruses were observed between the younger male and non-cycling females.

DISCUSSION

This study is the first to systematically formulate acoustic criteria for describing the major categories of African elephant vocalisations. Acoustic categories were defined for calls similar to those previously observed by other researchers (Berg 1983, Poole 1994, Poole et al. 1988), and two new categories were described (*croak* and *rev*). Upon discussion with our colleagues, the *croak* has now been observed in elephants in Amboseli National Park in Kenya (J. Poole, pers. comm.), and the *rev* at the Western Plains Zoo in Dubbo, NSW, Australia (L. Gardiner, pers. comm.). The 31 vocalisations previously described, for which consistent acoustic descriptions are lacking, seem to fit into the above eight categories with only a few exceptions. This system of nomenclature thus appears adequate to objectively describe major acoustic differences in elephant vocalisations. By developing a common language for these basic acoustic distinctions, we can begin to more systematically address some of the variation in acoustic structure and behavioural context observed within these categories.

Although each major acoustic category described is clearly distinct, considerable variation was observed within each call category. It is likely that within-category variation accounts for most of the differences in the 31 vocalisations previously described. Variation among rumbles shows a gradation of acoustic features that fall along a continuum. This type of complex system is typically more difficult to classify, and it is not always obvious which acoustic classification methods should be chosen to most adequately reflect meaning to the species in question (Clark 1982; Clark et al. 1987; Nowicki & Nelson 1990). Additional complications arise in describing behavioural contexts to which these acoustic categories are compared. Given the complexity and variation observed among calls, further analysis investigating the relationship between more detailed acoustic parameters and behavioural and reproductive context within each call category is needed to adequately describe the vocal repertoire in full detail.

Some within-category variation may also be due to individual differences. Not only do elephants have a complex social system in which dominant or submissive animals may use different vocal strategies (Langbauer 2000; McComb et al. 2000; Poole 1999), but also the elephants in this study have different individual histories. They may have originated in different parts of Africa and have been housed in different institutions for varying numbers of years, both of which may influence the types of vocalisations they produce. Since these individuals have been housed in captivity most of their lives, their vocal activity may also differ from that of their wild counterparts. In addition to more detailed information on behavioural and reproductive contexts, comparisons with vocal patterns of wild herds in geographically distinct locations in Africa will be necessary in order to investigate this supposition.

Almost all of the vocalisations recorded in this study occurred within 2 minutes of another vocalisation. Many of these were exchanges between different animals involved in close-proximity behavioural contexts, suggesting an important interaction between vocal signals and communication through other sensory modalities. In addition, over half of the vocalisations recorded in this study occurred within 30 seconds of another vocalisation, with 27.6% overlapping in time. Most of these overlapping bouts involved only two individuals. An individual may overlap its calls to indicate that it is paying close attention and is responsive to another individual, as in territorial songbirds where overlapping songs are known to signal arousal or readiness to escalate contests (Dabelsteen et al. 1997; Naguib & Todt 1997; Naguib et al. 1998). Little work has been done to examine this phenomenon for social mammalian species, and the function of overlapping vocalisations in this context is as yet unclear. However, it has been suggested that elephants may use chorused vocalisations in relation to social bonding (Poole 2000). Examination of elephant social interactions in more detail may provide insight into the role of temporal and acoustic properties of vocalisations in mediating social interactions, forming alliances and maintaining dominance hierarchies.

Although low-frequency vocalisations have been recorded from African elephants since the 1980s, this study is the first to document the proportion of vocalisations containing infrasonic components used by a stable herd in captivity where all calls and call types could be sampled exhaustively. The over-representation of rumbles used by this herd is significant given that all vocalisations recorded in this study were given in the context of short-range communication (less than 0.5 km) whereas in the past, the long-distance functions of low-frequency vocalisations have been emphasised.

The majority of low-frequency calls recorded in this study occurred when elephants were in very close proximity (8 m) to one another, and many corresponded simultaneously with active social interactions. The fact that most low-frequency vocalisations observed in this study coincide with very close-range behavioural contexts suggests a proximate function of low-frequency calls in mediating close-range interactions. However, because elephant physiology allows them to produce vocalisations reaching into the infrasonic range, even distant individuals would be able to gain valuable information.

Adult male and female elephants reportedly use different vocal strategies: females produce a broader range of rumbles and often chorus, while males rarely call and produce the distinctive musth rumble (Langbauer 2000; Payne 1989; Poole 1994). Results from this study support the lower calling rate of males vs. females but show more variety in adult male vocalisations than was previously reported. Field studies may record predominantly musth rumbles from males because musth males are more likely to be found in association with groups of females than non-musth males (Poole & Moss 1981; Poole 1994). During the course of this study, no musth rumbles were recorded, nor was either bull observed to experience musth. This suggests that males may switch vocal strategies as they come in and out of musth condition.

Female reproductive condition may also affect vocal strategies. A distinctive sequence of post-copulatory vocalisations, termed the "oestrous call," has been described previously (Poole et al. 1988), suggesting that females may advertise their reproductive condition to distant males. However, acoustic parameters that distinguish the oestrous call from other rumbles have not been adequately described. Although copulations were observed in this study, no sequences of vocalisations resembling the oestrous sequence were recorded. On the other hand, chorusing between an adult male and cycling female was observed, albeit rarely. Male-female choruses also may be related to female reproductive condition. Both male and female vocal strategies should be investigated in more detail with respect to the conditions of musth and oestrous, which may temporarily affect social status.

This study highlights the importance of low-frequency vocalisations in short-range vocal exchanges between African elephants and is a first step in standardising the terminology used to describe the vocal repertoire. While this study was able to quantify some characteristics of captive elephant vocalisations, studies monitoring vocalisations throughout a 24-hour period or in wild herds with varied social composition will likely reveal additional vocal types. Clearly, African elephant vocal communication is still a rich area for future investigation. Additional work examining within-category variation with respect to more detailed acoustic parameters, more specific social interactions, individual identity and the effect of male and female reproductive condition are necessary to provide a more complete understanding of African elephant vocal communication and its implications for both "in-situ" and "ex-situ" management.

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