Call repertoire of infant African elephants: First insights into the early vocal ontogeny

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African savannah elephants (*Loxodonta africana*) have a complex acoustic communication system, but very little is known about their vocal ontogeny. A first approach in ontogenetic studies is to define the call repertoire of specific age groups. Twelve hundred calls of 11 infant elephants from neonatal to 18 months of age recorded at the Vienna Zoo in Austria and at the Daphne Sheldrick's orphanage at the Nairobi National Park, Kenya were analyzed. Six call types were structurally distinguished: the rumble, the bark, the grunt, the roar (subdivided into a noisy-, tonal-, and mixed-roar), the snort, and the trumpet. Generally, within-call-type variation was high in all individuals. In contrast to adult elephants, the infants showed no gender-dependent variation in the structure or in the number of call types produced. Male infants, however, were more vocally adamant in their suckle behavior than females. These results give a first insight to the early vocal ontogeny and should promote further ontogenetic studies on elephants. Due to their vocal learning ability in combination with the complex fission-fusion society, elephants could be an interesting model to study the role of imitation in the vocal ontogeny of a nonprimate terrestrial mammal.

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I. INTRODUCTION

African savannah elephants exhibit extraordinary vocal abilities and even proved to be capable of vocal learning (Poole *et al.*, 2005). Recent studies of elephant vocalizations indicate that their vocal repertoire is extensive and highly variable (Langbauer, 2000). However, all major repertoire papers have focused on adult individuals (Berg, 1983; Poole *et al.*, 1988; Leong *et al.*, 2003). For the first time, we provide data on the vocal repertoire of infant elephants from neonatal to 18 months of age. Our study aimed at (1) defining the structural and functional characteristics of infant calls, (2) standardizing call terminology, and (3) determining early sex- and age-dependent variations of call types.

Elephants produce structurally different sounds like low-frequency rumbles, trumpets, snorts, and a variety of higher frequency calls (Langbauer, 2000). In a review on elephant communication, Langbauer (2000) reports a classification into 31 call types, based on functional context. Berg (1983) and Leong *et al.* (2003) analyzed calls from captive groups of African elephants, whereas Berg (1983) distinguished ten, and Leong *et al.* (2003) eight, call types based on visual examination of spectrograms. The most commonly heard structural type of call is the rumble. Poole *et al.* (1988) characterized seven rumble subtypes by behavioral context, but there is no consensus about the number of rumble subtypes from a structural standpoint. Soltis *et al.* (2005) examined the acoustic structure of rumbles of a captive group and found a graded structure across this call type. Wood *et al.* (2006), in contrast, analyzed calls from one family group recorded at the Kruger National Park and documented three rumble subtypes based on acoustic parameters.

Elephants exhibit a pronounced sexual dimorphism in calling patterns, with males producing significantly fewer vocalizations and types of calls than females (Poole, 1994). Ontogenetically, the sexes do not only differ in growth (Lee and Moss, 1995), but also in early social development (Lee, 1986; Lee and Moss, 1986) and social interactions (Lee and Moss, 1999). This reflects the differences of associations between the sexes, pointing to an early sexual differentiation in vocal ontogeny.

To date, only few studies have dealt with the vocal behavior of calves or juveniles. In her thesis about the development of social behavior in translocated juvenile African elephants, Gerai (1997) presented some behavioral and acoustic aspects of vocalizations by 2- to 7-year-old individuals. We documented certain aspects of calls by a newborn African elephant in captivity (Horwath *et al.*, 2001; Horwath, 2002), but next to nothing is known about the call repertoire of different age classes and when elephants acquire the full adult vocal repertoire.

In this paper we provide acoustic details of infant elephant calls. Our recordings focused on two calves born in a zoo, which provided us with an opportunity to follow their vocal development over a longer period of time. Additionally, we observed a semi-captive group of orphaned elephants in Kenya to improve sample size and to compare calls at two distinct locations and environments.

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TABLE I. Acoustic features and parameters measured.

Main acoustic feature	Parameter measured
Manner features: [modified from Fant (1960)]: Via visual examination of the spectrogram	Feature 1: Tonal (frequency contours of the harmonics in tonal signals: straight, bent, left skewed, right skewed, bimodal, increasing, decreasing, multimodal)
	Feature 2: Noisy
	Feature 3: Transient
Duration	Signal duration
	Duration from signal onset to maximum frequency
Fundamental frequency: Automatically measured via Stx using simple inverse filter tracking method (one measurement/frame)	Minimum, maximum, mean, starting-, mid-, and ending frequency
First harmonic: Measured by cursor placement	Minimum, maximum, mean (calculated) starting-, mid-, and ending frequency
Amplitude difference	Difference in dB from the fundamental frequency to the second harmonic
Dominant frequency: The frequency of highest intensity	Mid-point of the dominant frequency
Bandwidth: Only high-quality calls that had been recorded in less than 10 m distance	Bandwidth at the mid-point of the call
First formant: Only low-frequency calls using LPC coef 60, for calls of up to 5-month-old elephants, 80 for those aged between 6 and 12 months, and 100 for calls of elephants older than 12 months	Minimum, maximum, mean, and mid point
Second formant	Minimum, maximum, mean, and mid point

II. MATERIAL AND METHODS

A. Study animals and housing

The studied animals were 11 infant elephants from neonatal to 18 months of age. We recorded a male (Abu) and a female (Mongu) calf at the Vienna Zoo in Austria from neonatal to 18 months, and five males aged 3 (Ndomot and Madiba), 11 (Taita), 13 (Tomboi), and 15 (Napasha) months, as well as four females aged 6 (Sunyei), 9 (Olmalo), 10 (Selengai), and 14 (Wendy) months at the Daphne Sheldrick orphanage in Nairobi National Park, Kenya. At the Vienna Zoo, the whole elephant group consisted of four adult females, the two calves, and an adult male, who was kept separately. Both calves are not related and had been raised by their mothers within the elephant group. The keepers have direct contact with the female group for approximately 1.5 h per day. The elephants spend the night unchained in the indoor stall (2100 m^2) within the family and are released into their outdoor enclosure (4700 m^2) for the day. At the Daphne Sheldrick orphanage, the elephants spend the night in small separated stables, accompanied by a keeper. At 6:00 a.m., the keepers and the elephants leave to the bush, return at midday for 1 h of public presentation, leave again to the bush and come back to the stables at 6:00 p.m. Approximately every 3 h, the orphans are fed a special milk formula compiled by Daphne Sheldrick, but otherwise move freely in the bush. Due to visitor- or shower-related noise, no recordings were made during public presentations.

B. Data collection

We recorded 1400 h at the Vienna Zoo from 2001 to 2004 and 300 h in January and February 2004 at the orphanage in Kenya. Recordings were made at 48 kHz sampling rate on a DA-P1 DAT recorder (frequency response: 100 Hz: −0.2 dB, 20 Hz: −0.26 dB, 15 Hz: −0.26 dB, 12 Hz: −0.3 dB, 8 Hz: −0.32 dB, and 4 Hz: −0.45 dB), with the condenser microphone AKG C 480 B and the omni directional condenser capsule AKG CK 62—ULS (frequency response: 100 Hz: 0 dB, 30 Hz: 0 dB, 20 Hz: −0.16 dB, 15 Hz: −0.23 dB, 10 Hz: −0.44 dB, and 8 Hz: −2.72 dB). Data recording took place only outdoors. At the zoo, recording distances ranged from 1 to 25 m. At the Sheldrick orphanage we were able to walk with the elephants in the bush during the day, yielding recording distances of approximately 0.5 to 30 m.

The following data were recorded for each call: identity of the caller (due to the short distance to the vocalizing animals, the caller could be identified by hearing), approximate distance to the vocalizing elephant, number and identity of individuals present, position of the other elephants in relation to the vocalizing animal within the group, presence or absence of the keepers, the behavioral context, and aperture angle of the mouth during vocalization, whereas two categories were distinguished: 1=almost closed, 2=opened.

C. Data analysis

We analyzed the signals with the computer program S_TOOLS-STx from the Acoustic Research Institute of the Austrian Academy of Sciences Vienna. For the frequency analyses in low-frequency calls, the signals have been downsampled to 8000 Hz. We analyzed 1200 calls of known infant individuals, taking 26 acoustic parameters (Table I). For measurements of the first and second formant we used the linear prediction coding method (LPC). Although we were sometimes able to define up to six formants, we considered only the first two; these were the most consistent ones.

D. Call type classification

Call types were defined from a structural point of view. Before the acoustic analyses, we developed two main call categories based on the way sound was produced: calls produced by the larynx (laryngeal calls) and sounds produced by a blast of air through the trunk (trunk calls).

We categorized putative call types and subtypes by ear and by visual inspection of the sound spectrograms based on manner features (Fant, 1960), e.g., a tonal versus a noisy production characteristic, as well as on structural differences in the frequency and time characteristics.

We tried to fit our calls into the established nomenclature where possible, based on qualitative descriptions and acoustic information. We additionally achieved an agreement on call terminology with the World's leading scientist on elephant vocal communication, Joyce Poole, from the Amboseli Elephant Research Project.

E. Statistical verification

For the statistical analyses we created balanced data sets by taking the same number of calls per individual for each putative call type/subtype. Discriminant function analysis (DFA) was used to test the validity of call type categories previously constructed by visual inspection. We performed one DFA for the laryngeal calls, and one separate DFA for the trunk calls. We used duration of the signal, start, mid, end, minimum, and maximum fundamental frequency and the dominant frequency. These were the parameters available for all call types, because especially in noisy signals, measurable acoustic features were limited to these parameters. Table IV provides acoustic details of the balanced data set of each call type. However, in the text we also give information about the total number of calls in the data set and the total number of individuals for which each call type has been recorded. We used "n_{ind}" to refer to the number of individuals and "n_{c}" to refer to the number of calls.

As the rumble dominates the acoustic repertoire of elephants, and to address the recent discussion on rumble subtypes, we analyzed this call in more detail. We used multidimensional scaling analyses (MDS) to examine the pattern of acoustic variation in rumbles without specifying prior subtypes. We randomly selected nine calls of each of the 11 individuals and entered them into MDS using 21 acoustic parameters (all acoustic parameter mentioned in Table I, excluding manner features and the second formant, because it was often absent in soft rumbles). We also performed MDS with calls from each infant individual to test whether the observed tendencies are consistent on the individual level, i.e., to exclude wrong results due to individual- or age-dependent variations. We used all available calls from each individual (at most 100). The Stress1 values were assessed after Kruskal: 0.20 poor, 0.10 fair, 0.05 good, and 0.02 excellent. We used a bivariate correlation coefficient to test for a correlation between the fundamental frequency and bandwidth in the rumbles.

F. Analyses of functional context

The functional contexts exhibited during the recording period were put into categories (Table II). We calculated the frequency of occurrence of behavioral categories for each call type. These descriptions are provisional and can serve as a basis for actual hypothesis testing later.

G. Analyses of age- and gender-dependent variations

To demonstrate age-dependent differences of the fundamental frequency in the rumble, we used rumbles recorded in reaction to abnormal suckle terminations, and took at least eight calls per individual at a specific age recorded solely in this context.

We used three male (Napasha, Taita, Tomboi) and three female (Olmalo, Selengai, Wendy) orphans between age 10 and 15 months to show a gender-dependent vocal activity in suckling situations. These six orphans were fed simultaneously each time. The keepers brought the milk bottles (two for each elephant) and each elephant was fed by one keeper. We analyzed the vocal activity of 18 such feeding situations by calculating the number of vocalizations of each individual. We used the chi-square test to show significant variations between gender and individuals.

III. RESULTS

A. Call repertoire

By visual examination of the spectrograms, we defined six putative call types: four laryngeal ones—the rumble, the bark, the grunt, and the roar, which we subdivided into the noisy roar, the tonal roar, and the mixed roar—and two trunk calls—the snort and the trumpet. We randomly selected 30 calls from each putative call type/subtype and performed DFA to test the validity of our previously constructed categorization. Laryngeal calls and trunk calls were tested separately. Table III shows the eigenvalues and variances explained by the first three functions for the laryngeal calls and the first function for the two trunk calls, and the correlation of variables. In the laryngeal calls, fundamental frequency parameters mainly separate call types in the first function, duration in the second function. Figure 1 shows the results of DFA for the laryngeal calls. In a leave-one-out classification, 100% of rumbles, 100% of barks, 96% of grunts, and 100% of roars were correctly classified. Within the roar, 100% of noisy roars, but only 73.3% of mixed roars and 60.6% of tonal roars were classified correctly. Six percent of tonal roars and 10% of mixed roars have been classified to noisy roars, otherwise tonal and mixed roars intermixed. In the trunk calls, dominant frequency is the most important factor separating snorts and trumpets. In the leave-one-out classification, 100% of trumpets and snorts were correctly classified. Table IV gives the duration, mean fundamental frequency, mean dominant frequency, and manner features for call types, and Fig. 2 spectrographically presents a typical example of each call type.

TABLE II. Description of the most important functional contexts.

Functional context	Explanation
Suckle intention	The calf repeatedly touches the mothers legs or teats (with mouth or trunk) attempting to make nipple contact. The orphans repeatedly touched the blankets (which have been fixed between two branches to facilitate feeding and to imitate the body of the mother)
Suckle start	The beginning of a suckle bout (one or more successful or unsuccessful nipple contacts separated by less than 60 s of time off the nipple (Lee and Moss, 1986)
Infant break	Calf removes its mouth from the nipple/bottle in between two nipple contacts
Abnormal suckle termination	Mother/keeper rejects, or anything that disturbed the calf during suckling, resulting in a compelled suckle break or termination, e.g., after receiving a push or "genital check" by another elephant during suckling
Trunk touch	The calf is being touched with the trunk by another elephant (e.g., at the genitals, mouth, temporal glands,…)
Begging	Repeatedly touching the keeper with the trunk begging for tidbits
Spatial separation	The calf does not see the mother or the other orphans because of bushes or other structures
Intraspecific agonistic behavior	The calf is being pushed, kicked, trunk slapped, or chased
Interspecific or object aggression	Making mock charges, chasing birds or warthogs, attacking machines, cars,…
Require care/help	E.g., the calf fell down and could not get up alone
Alerting to external stimuli	E.g., a sudden appearance of a rhino, or buffalo, or unfamiliar machine,…
Play behavior	play fights, pushing head/trunks, climbing on each other, object play,…

B. Description of call types and within-call type variation

1. Rumble

The rumble is conspicuous because of its very low fundamental frequency near the infrasonic range. In the infants, 53% of the total number of recorded calls were rumbles (n_c=795). We recorded rumbles in all 11 individuals ranging from neonatal to 18 months of age (Fig. 3). These rumbles are low-frequency tonal signals with formant formation. No infrasonic fundamental frequencies below 20 Hz were produced. Similar to adults (O'Connell-Rodwell *et al.*, 2001), the second harmonic has more energy than the fundamental one; on average, the mean difference ±SE was 15.90±5.304 dB (n_c=220, n_{ind}=11). Infant rumbles can be soft with a minimal documented bandwidth of 70 Hz, as well as very loud with extreme bandwidth values of up to 20 kHz; intermediate stages are also present. When producing rumbles with a bandwidth below 2000 Hz, the mouth was closed in 71.8% of cases. When producing rumbles with a bandwidth above 2000 Hz, the mouth was open in 68%.

TABLE III. Results of discriminant function analyses for laryngeal and trunk calls. Eigenvalues, variances explained, and structure matrix giving the correlation of variables.

Laryngeal calls				**Trunk calls**
	Function 1	Function 2	Function 3	Function 1
Eigenvalue	11.772	2.349	1.280	8.398
% Variance	75.9	15.2	8.3	100
Variables		**Correlation**		
Maximum F0	**0.916**[a]	0.170	−0.030	0.537
F0 mid	0.898	0.153	−0.037	0.493
F0 end	0.819	0.030	−0.377	0.496
Minimum F0	0.814	−0.053	−0.398	0.491
F0 start	0.790	−0.033	−0.270	0.462
Duration	−0.016	**0.966**[a]	0.040	0.211
Dominant frequency	0.231	−0.016	**0.823**[a]	**0.812**[a]

[a] The strongest factor loading of the variables on each discriminant function is shown in bold (F0=fundamental frequency).

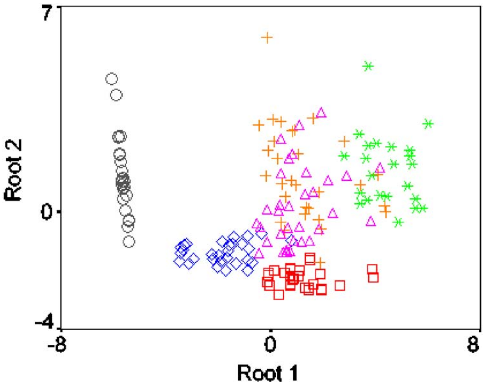

FIG. 1. (Color online) Scatter plot of laryngeal calls representing the results of function (root) 1 and function (root) 2 of discriminant analyses. Rumbles (circles), grunts (rhombus), barks (squares), and roars (triangles, stars, and crosses) separate well in these two functions. Noisy roars (stars) also separate from the other two roar subtypes, however tonal roars (triangles) and mixed roars (crosses) are intermixed.

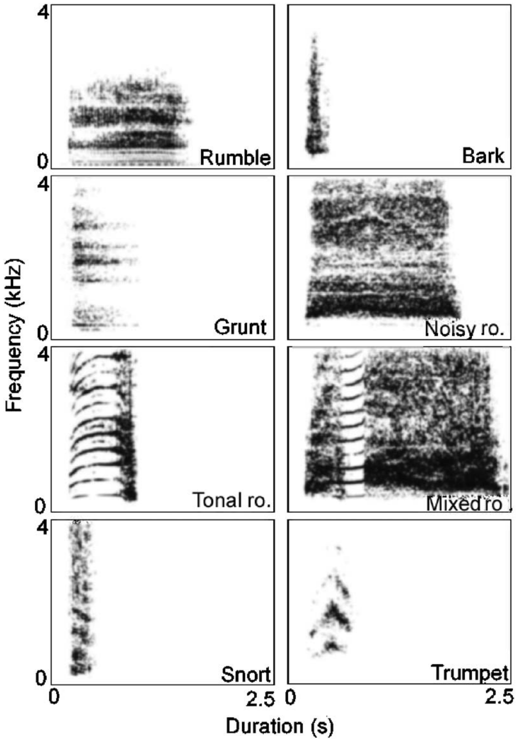

FIG. 2. Spectrograms giving a typical example of each call type (256-point fast Fourier transform, overlap 75%, Hanning window). Call types vary in manner features and structural differences in the frequency and time characteristics. (ro.=roar).

There is a weak positive correlation between the mean fundamental frequency and bandwidth ($r=0.249$, $n_c=220$, $p=0.000$). Loud rumbles with a bandwidth above 2000 Hz tended to have higher fundamental frequencies ($\bar{X}\pm\mathrm{SE}=29.82\pm5.139$ Hz, $n_c=100$) than soft rumbles with a bandwidth below 2000 Hz ($\bar{X}\pm\mathrm{SE}=25.27\pm2.634$ Hz, $N_c=100$). The correlation coefficient was stronger on the individual level (e.g., Madiba from the Nairobi orphanage: $r=0.695$, $p=0.000$, $n_c=80$). The rumbles had a harmonic structure in the lower frequencies but, when they were loud, often had noisy components in the upper frequency range.

a. Are there acoustically distinctive rumble subtypes? The infant rumbles showed a high degree of variation in the measured acoustic features. We applied MDS to test for distinctive subtypes in infant rumbles using 99 calls ($n_{\mathrm{ind}}=11$) and 21 acoustic parameters. No separation into discrete subtypes was obvious within the infant rumbles [Fig. 4(a)]. These MDS results were constant on the individual level [Figs. 4(b)–4(d)]. Whether different frequency contours represent further subdivisions remains unclear and needs to be investigated in more detail. The most common frequency contour, with 26.9%, was "straight," followed by "bent" and "left skewed," both with 15.5%, "right skewed" (13.3%), and "decreasing" (8.9%).

2. Bark

The bark is a transient and mainly noisy call. It differs from the other calls due to its short duration. We recorded a total of 80 barks in all individuals from the age of 3 weeks to 18 months. It consists of a single excitation of the vocal

TABLE IV. Basic acoustic features of each call type and subtype. D=duration of the signal, Mean F0=mean fundamental frequency, Do. Freq.=mid position of dominant frequency.

Call type	n_{ind}	n_c/Individual	D (s) $\bar{X}\pm$SE	Mean F0 (Hz) $\bar{X}\pm$SE	Do. Freq. (Hz) $\bar{X}\pm$SE	Manner features
Laryngeal calls						
Rumbles	11	20	1.6±0.5	28.1±5.0	53.32±8.6	Tonal
Barks	8	7	0.3±0.2	340.2±106.8	710.0±255.2	Transient
Grunts	2	40	0.5±0.3	250.2±102.4	405.9±67.0	Noisy
Roars						
Noisy roars	7	8	1.4±0.4	561.6±53.1	730.0±109.5	Noisy
Tonal roars	7	6	1.1±0.5	341.4±66.7	1093.3±310.7	Mainly tonal end noisy
Mixed roars	6	8	1.6±0.5	409.1±95.0	986.8±364.3	Multiple switching from noisy to tonal
Trunk calls						
Snorts	6	6	0.6±0.3	185.0±79.2	413.5±164.4	Noisy
Trumpets	4	9	1.16±0.7	586.43±156.4	1306.53±219.1	Tonal

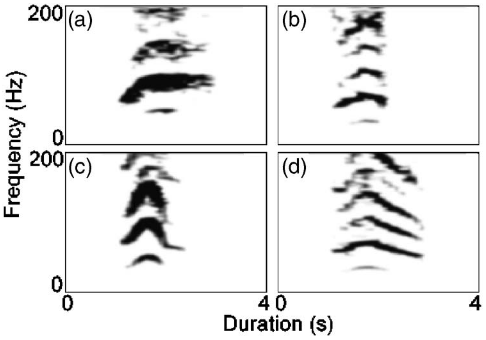

FIG. 3. Spectrograms giving the first 200 Hz of loud rumbles of one individual (Mongu, Vienna) at different ages: (a) 2 h after birth, (b) 2 months of age, (c) 5 months of age, and (d) 10 months of age (4096-point fast Fourier transform, overlap 75%, Hanning window).

cavities caused by the release of an overpressure. When uttering barks, the mouth of the elephants was wide open (posture 2). The short duration and the transient production characteristic are consistent; the call does vary to some extent in fundamental and dominant frequency (Table IV). Often, the bark is immediately followed by a rumble without an inhalation period (bark-rumble).

3. Grunt

The grunt ($n_{\mathrm{c}}=93$) did not resemble any previously named vocalization. Such calls were sufficiently acoustically distinct and were recorded in both individuals at the zoo, necessitating the classification into a new call type. We chose the term grunt because it is a nonfunctional name and has not yet been applied to elephant calls. Grunts were stereotyped in structure, being noisy with merely first indications of harmonics. Most grunt recordings stemmed from Mongu and Abu within the first few days of their lives. They stopped producing grunts at approximately 2 months of age. Grunts were very soft and barely audible when we were more than 20 m away. The mouth seems to be almost closed during most grunting vocalizations. The grunt was never produced in combination with rumbles or any other call.

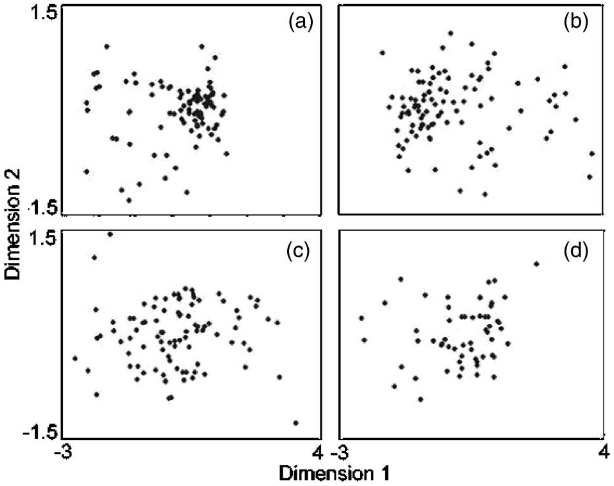

FIG. 4. Results from MDS analyses of infant rumbles using 21 acoustic parameters. (a) MDS results of 99 calls from 11 individuals (stress=0.0785, RSQ=0.989); (b) 100 randomly selected rumbles of Madiba (3 months old) recorded in January 2004 (stress=0.0843, RSQ=0.984); (c) 100 randomly selected rumbles from Mongu recorded from May to August 2003 (from neonatal to 3 months of age; stress=0.0633, RSQ=0.991); and (d) 70 rumbles from Ndomot (3 months old), recorded in January 2004 (stress =0.0718, RSQ=0.992). Results of each MDS analysis show no clustering into discrete subtypes, but point towards a graded variation of infant rumbles.

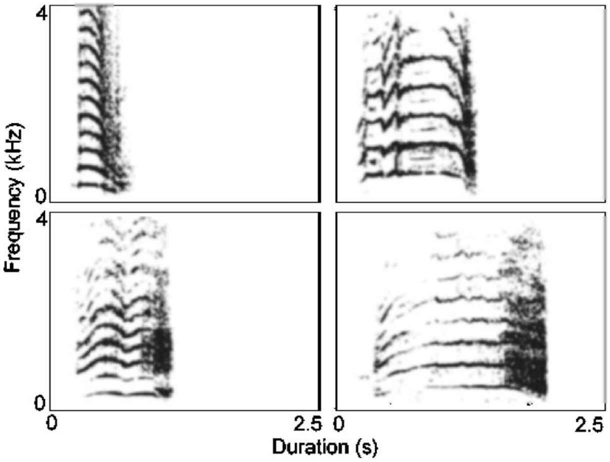

FIG. 5. Spectrograms (256-point fast Fourier transform, overlap 75%, Hanning window) presenting examples of tonal roars of four different individuals demonstrating structural variation within this roar subtype. Tonal roars vary in overall duration, and in the duration of the tonal and noisy segments. Furthermore, the tonal segments show different grades of modulation.

4. Roar

We recorded various roars ($n_{\mathrm{c}}=203$) of all 11 individuals from neonatal to 18 months of age. When uttering roars, the mouth of the infants was usually wide open. Based on manner features, we grouped the roars into three subtypes. Eighty roars were totally noisy with no tonal segments and are termed noisy roars. We recorded the noisy roars of ten individuals (6♂, 4♀). Noisy roars varied in fundamental frequency, but were highly stereotyped in their noisy acoustic structure characteristic (Table IV).

We characterized calls as tonal roars ($n_{\mathrm{c}}=60$; $n_{\mathrm{ind}}=6$♂, 3♀, age 0–18 months) when they were tonal for the main part of the call, sometimes with an abrupt and noisy ending. This call was not highly stereotyped (Fig. 5). The main variation involves the appearance and duration of the noisy ending (86% of calls had a noisy ending). The mean duration of the tonal part ±SE was 0.72±0.67 s; the mean duration of the noisy ending (if present) ±SE was 0.21±0.19. In contrast to the noisy roar, this call sounds very clear.

We further recorded calls characterized by multiple switching from tonal to noisy segments, termed mixed roars ($n_{\mathrm{c}}=63$). We recorded these calls in ten individuals (6♂,4♀) between the ages of 2 weeks and 18 months. Mixed roars were also not stereotyped in structure (Fig. 6); 44.4% switch from a noisy beginning to a tonal mid-part and to a noisy ending. The tonal segments varied in temporal placing, frequency contours of the harmonics, and duration. We documented a maximum of seven switches in one call. The error rates of approximately 30% (mixed roars) and 40% (tonal roars) in the leave-one-out classification show that solely duration and frequency parameters are inadequate to separate these subtypes. Manner features was the most im-

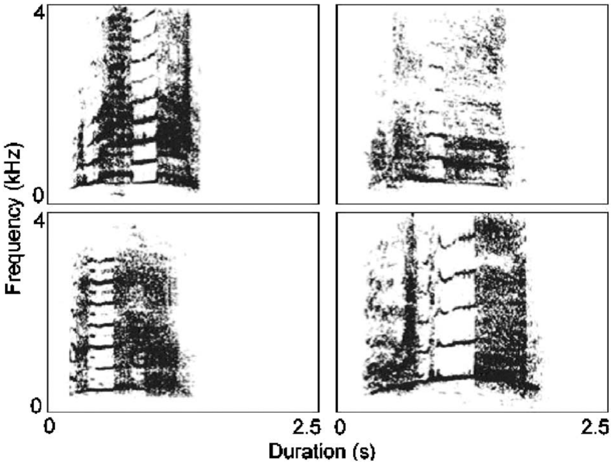

FIG. 6. Spectrograms (256-point fast Fourier transform, overlap 75%, Hanning window) presenting examples of mixed roars of four different individuals demonstrating structural variation within this subtype. Mixed roars vary in the number of tonal and noisy segments. The tonal segments vary in temporal placing, frequency contours of the harmonics, and duration.

portant factor enabling us to distinguish between tonal and mixed roars. All roar subtypes were often uttered in combination with rumbles, either before or after the rumble, without an inhalation period (rumble-roar, roar-rumble, rumble-roar-rumble, or roar-rumble-roar).

5. Snort

The snort ($n_c=68$) is a strong blast of air through the trunk without producing a tonal signal and a proper sound. The structure of this sound is very consistent, yet with some variations in frequency features (Table IV). It was recorded in eight individuals (5♂, 3♀), whereas 79.8% of all snorts were recorded in calves younger than 4 months.

6. Trumpet

We recorded trumpets ($n=72$) in seven (4♂, 3♀) individuals aged from 3 to 18 months. Infant trumpets are mainly tonal sounds, but harmonics are overlaid with noise. They appear in several forms, vary in duration, and can have a pulsated structure when the elephant is running while producing the call. The most common call structures were "increasing" (27.8%), "straight" (25%), and "multimodal" (12.5%).

C. Functional context

Although all calls were emitted in more than one context, we were able to determine predominant functions for all call types. The most common functional contexts of specific calls are given in Table V.

Rumbles in infant elephants were used in a variety of contexts. Generally, excited calves tended to produce calls with more harmonics than less excited calves. Soft rumbles were often answered by the mother or other elephants, indicating also a vocal contact function, whereas louder rumbles were mainly used as a protest or distress call. The bark was often produced after being pushed or kicked during walking or feeding, when the affected calf did not expect such an interaction. Grunts backed up suckle intention behavior; however, often they were immediately answered by a soft rumble of the mother, again indicating a vocal contact function. Most noisy roars where recorded when the animals required immediate care or were separated from the group. In contrast, the tonal and the mixed roars were most often produced as a reaction to abnormal suckle terminations. Many of our recorded snorts had no apparent communicational function; they probably represented a strong blast of air through the trunk for cleaning purposes. However, calves younger than 3 months sometimes snorted when producing

TABLE V. Functional contexts of specific call types and subtypes (%=frequency of occurrence of behavioral categories for each call type/subtype). The most common context is shown in bold.

Call type	Functional contexts
Rumble	
Soft rumbles (bw<2 kHz)	**Suckle contexts** (43%: suckle intention, suckle start, infant break); trunk touch (20%), begging (7.3%)
Loud rumbles (bw>2 kHz)	**Abnormal suckle termination** (39%); trunk touch (18%), begging (8%)
Grunt	**Suckle intention** (46%); play behavior (22%);
Bark	**Intraspecific agonistic behavior** (33.9%), begging (17.9%); trunk touch (14.3%)
Roar	
Mixed roar	**Abnormal suckle termination** (61.1%); requiring care/help (9.3%), intraspecific agonistic behavior (7.4%)
Noisy roar	**Requiring care/help** (28.5%); abnormal suckle termination (18%); intraspecific agonistic behavior (14%); spatial separation (10%);
Tonal roar	**Abnormal suckle termination** (54.9%); begging (11.8%); intraspecific agonistic behavior (7.8%)
Snort	**No communicative function** (59.9%); interspecific or object aggression (mock charges, 13.9%)
Trumpet	**Interspecific or object aggression** (mock charges, 57.9%), external stimuli (13.6%)

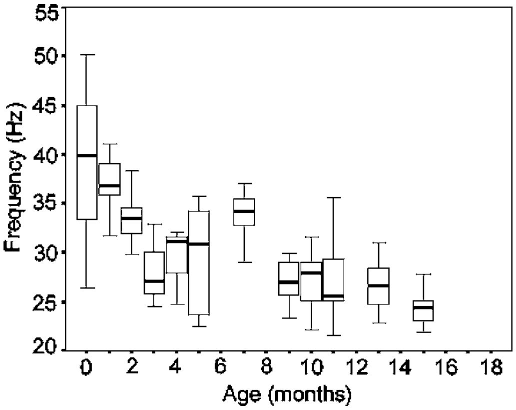

FIG. 7. Box plot presentation of the age-dependent fundamental frequency development in rumbles uttered after abnormal termination of suckling. Mongu 0–5 months (Vienna); 7, 9, and 10 months (females, Nairobi); and 11, 13, and 15 months (males, Nairobi).

mock charges. Most trumpets involved interspecific or object aggression. In infants, however, it is difficult to determine whether there is some aggressive intention when mock charging birds or warthogs, or if mere play is involved.

D. Age- and gender-dependent variations

We clearly documented age-dependent variation in the appearance of two call types, the grunt and the trumpet. We never recorded grunts in an individual older than 2 months. In contrast, although we intensively recorded the two zoo elephants from birth on, neither produced trumpets until they were 3 months old.

We documented age-dependent variation, particularly in the low-frequency rumble. As expected, older individuals tended to have lower fundamental frequencies in the rumble than younger individuals (Fig. 7), and there was a tendency for rumble duration to slightly increase with age.

We observed no gender-dependent variation in the acoustic structure of any call type. Furthermore, there was no difference in the number of call types produced by male and females calves at this ontogenetic level. We documented each call type in both genders.

In the feeding situations at the orphanage, male infants vocalized more frequently than females. Usually, when one bottle of milk was finished, the keepers had to remove the bottle from the mouth, creating abnormal breaks or terminations of suckling for the infants. We also observed a lot of pushing and barging between the infants, again resulting in abnormal suckle breaks. In 18 such feeding situations, the three male infants vocalized significantly more than the females (chi-square test: $1=54.6$, $p<0.001$). Although there are individual differences, each male vocalized significantly more than each single female (chi-square test: all $p<0.05$; Fig. 8). The calls were mainly loud rumbles and roars as well as combinations of both call types.

IV. DISCUSSION

This study is the first to describe the acoustic structure and the basic functional contexts of infant elephant calls. Due to the considerable gradation of the acoustic parameters, we did not distinguish more than six call types. Based on our acoustic analyses, the rumble in infants seems to be graded with no distinctive subtypes. A similar result was reported by Soltis *et al.* (2005), who analyzed rumbles produced by six adult females. Gerai (1997) distinguished a “low-rumble” and a “growl” in juvenile African elephants. She defines the “low-rumble” as a soft, low, monotone rolling sound, with the mouth appearing closed. The “growl” is a more guttural, rolling, periodic, and slightly louder sound than the “low-rumble,” whereby the mouth is generally open. In the parameter described, however, her “low-rumble” and her “growl” differ in mean duration and frequency, but the ranges overlap and it is unclear weather they are discrete call types. Her general descriptions agree with our observations of soft and loud rumbles, but, in contrast to Gerai (1997), we did not separate them as discrete call types or subtypes. Gerai (1997) further reported higher-frequency calls she termed “cries,” “bellows,” and “squeals,” but because of too small sample size, she was unable to adequately differentiate and structurally define the various loud sounds. Based on her general description and the given spectrograms, those high-frequency calls seem to fit into our roar categories. Note, however, that Gerai (1997) recorded 2- to 7-year-old juvenile African elephants, whose vocal behavior might differ from that of infants.

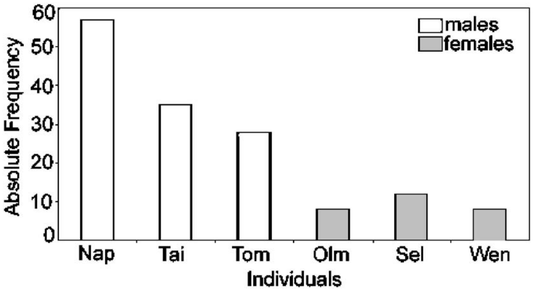

FIG. 8. Histogram demonstrating the frequency of vocalization of each individual (males: Napasha, Taita, Tomboi; females: Olmalo, Selengai, Wendy) in 18 suckle situations. Although there are individual differences, each male vocalized significantly more than each female (chi-square test, all $P<0.05$).

Elephants typically exhibit a very flexible and open communication system (Poole *et al.*, 2005), and gradation of acoustic features seems to be characteristic for elephants, complicating the classification of calls. Even a few calls in our data could not be clearly classified to a specific call category. We, for example, recorded few trunk sounds that differ from trumpets and snorts. The infants forced air out of the trunk pressing the trunk tips together, producing a squelching sound. Each call had a unique structure, and these sounds are probably idiosyncratic sounds with no communicative function. Our observed within-call type variation might also reflect individual characteristics of sound production and the different origins of the elephants. We recorded two unrelated infants in Vienna, whose parents originally come from different parts of Africa, and nine randomly joined infants, who originated from South Africa and different parts of Kenya. Considering that elephants are able to recognize one another based on their calls (McComb *et al.*, 2003), it is supposable that elephants—similar to other species capable of vocal learning and living in complex societies (e.g., Tyack, 2003)—use family-, bond group-, or population-specific dialects. Although elephant calves probably have to learn these dialect-specific call features by imitating calls of their mothers and other family members, genetically preprogrammed call type variation between distinct elephant populations may play a role.

The infants used their vocalizations to announce their needs and emotions to their mother, keeper, or closest individuals. Because of their milk dependency, we recorded many calls in the suckle context. Talking about the functional use of calls, we have to consider that there are situations in the wild that do not exist in captivity or at the orphanage. However, infants living in the wild, in the zoo, or in the orphanage share the same needs and similar "problems," go out on a limb, and require help and reassurance. Infant vocalizations are mainly associated with the satisfaction of needs and are therefore not strongly influenced by external conditions.

The fundamental frequency in the rumble decreased with age as the elephants grew and the mass of their vocal cords increased. In mammals, this growth is negatively correlated to voice pitch (Fitch, 1997). The louder rumble of very young infants (up to approximately 3–4 months old) sounded very harsh and subjectively differed from the rumbles of the older ones. Based on acoustic parameters and call structure, however, we did not to distinguish it as a discrete call type from rumbles produced by older infants. In the two zoo elephants observed for a longer period of time, they gradually sounded more like a rumble of older individuals as fundamental frequency decreased with age.

Grunts seem to be characteristic for new-born elephants. The calves stopped producing grunts at around 2 months of age. Nothing similar has yet been documented in a juvenile or adult African elephant. This call was very soft, which might explain why it has not been previously recorded, even in infants. In contrast, no trumpets were recorded in individuals younger than 3 months. Instead of the trumpet, they produced snorts during play behavior and when exhibiting mock charges. These are situations in which older elephants produce trumpets. More control of the trunk muscles and more power of the respiratory muscles may be needed to produce a proper sound when pressing air through the trunk. The complex coordination of the trunk must be practiced by infants (Moss, 1988). Therefore it would have been surprising if an elephant was able to trumpet from birth on.

We did not observe gender-dependent variations in the number of call types, in call structure, or in their general usage. Future studies targeting different ontogenetic levels will be necessary to determine the onset of the vocal sexual dimorphism. Male elephants require a second distinct phase of socialization (Bradshaw *et al.*, 2005) in which they leave their natal family to join the floating community of adult, reproductive males (Poole, 1994). This might be the ontogenetic level at which the pronounced sexual dimorphism in vocal behavior of elephants develops. In both genders, however, infancy starts with similar communicating, i.e., with the mother and closely allied individuals. We even observed that males were more vocally adamant in their suckle behavior than the females. Lee and Moss (1986) found that more suckle attempts are initiated by male infants, and that females appear to be less demanding as well as less persistent. Our observations confirm this.

Our results should promote further studies on the vocal ontogeny of elephants. Besides studying the call repertoire of different age groups, it would be important to examine the extent to which learning influences vocal development. Determining the role of learning in vocal ontogeny and the alignment of group-specific call characteristics in calves will be one of our main future research interests. Due to their vocal learning ability (Poole *et al.*, 2005) in combination with the complex fission-fusion society (Moss and Poole, 1983; Wittemayer *et al.*, 2005), elephants could be an interesting model to study the role of imitation in the vocal ontogeny and the social system of a nonprimate terrestrial mammal.

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