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Vocal communication in Asian elephant calves (*Elephas maximus*)

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1. Deutsche Zusammenfassung

Asiatische Elefanten (*Elephas maximus*) gelten laut der IUCN Artenschutzliste 2009 als gefährdet. Ihr natürlicher Lebensraum schwindet durch anthropogenen Einfluss. Auf der Suche nach Nahrung plündern sie häufig Anbauflächen der Menschen, welches oftmals zu tödlichen Zusammenstößen auf beiden Seiten führt. Um diesem entgegenzuwirken, könnten akustische Frühwarnsysteme in der Nähe von menschlichen Siedlungen eingesetzt werden, um Zusammenstöße zu verringern (Seneviratne *et al.*, 2004). Die Voraussetzungen zur Entwicklung solcher Frühwarnsysteme bedingt ein umfassendes Verständnis der sozialen Struktur, der akustischen Kommunikation und des Verhaltens Asiatischer Elefanten.

Ein Großteil der Elefantenforschung konzentrierte sich bisher auf Afrikanische Elefanten (*Loxodonta africana*) (Berg, 1983; Langbauer *et al.*, 1991; Garstang *et al.*, 1995; Lee and Moss, 1999; McComb *et al.*, 2003; Payne *et al.*, 2003; Soltis *et al.*, 2005a; b; O'Connell-Rodwell *et al.*, 2007). Unterschiede in der sozialen Struktur wie auch in der akustischen Kommunikation der beiden Arten (McKay, 1973; Fernando and Lande, 2000) zeigen, dass Studien an Afrikanischen Elefanten nicht einfach auf Asiatische übertragen werden können. Zum Beispiel werden die Lauttypen „Rumble“, „Roar“, „Trumpet“ und „Snort“ zwar von beiden Arten geäußert, der Lauttyp „Squeak“ ist jedoch nur bei Asiatischen Elefanten ausgeprägt. „Squeaks“ werden entweder einzeln, meistens aber mehrfach aufeinander folgend in einer Sequenz geäußert, welche von McKay (1973) „chirping“ genannt wurde.

Asiatische Elefanten leben in kleinen, stabilen Familiengruppen, die aus einer Matriachin und ihren Nachkommen unterschiedlichen Alters bestehen (McKay, 1973; Fernando and Lande, 2000). Dies indiziert, dass gerade die akustische Kommunikation zwischen Jungtieren und adulten Artgenossen von großer Bedeutung ist. Die bisher einzige Studie über vokale Ontogenie bei Elefanten bezieht sich auf Afrikanischen Elefanten (Stoeger-Horwath *et al.*, 2007).

Die Lautforschung bei Tieren beschränkte sich lange Zeit auf harmonische Laute und ließ Unregelmäßigkeiten in den Lautäußerungen (nichtlinearen Phänomene) außer Acht, obwohl diese sowohl bei Säugetieren (Riede *et al.*, 1997; Wilden *et al.*, 1998; Riede *et al.*, 2000; Tokuda *et al.*, 2002; Riede *et al.*, 2007) als auch bei Vögeln (Fee *et al.*, 1998; Fletcher, 2000) häufig vorkommen. Nichtlineare Phänomene spielen eine wichtige Rolle in der Erkennung von Individuen als auch Altersklassen wie beispielsweise die Mutter-Kind-Erkennung (Fitch *et al.*, 2002).

In der vorliegenden Studie wurden die Laute sowie das Verhalten von sechs Asiatischen Jungelefanten im Alter von sechs bis 27 Monaten in zwei europäischen Zoos (Köln, Deutschland und Emmen, Niederlande) aufgenommen und analysiert. Zoos bieten bei der Erforschung von Elefanten ideale Bedingungen. Besonders die akustische Kommunikation der Jungtiere ist stark von gruppeninternen Faktoren geprägt und bezieht sich meist auf die Erfüllung von Grundbedürfnissen, die in der freien Wildbahn und in menschlicher Obhut ähnlich sind. Weiters sind Asiatische Elefanten Waldbewohner, was die Aufnahme und Zuordnung der Laute sowie das Beobachten des Verhaltens in freier Natur erschwert.

Diese Studie präsentiert erstmals akustische Daten zur vokalen Ontogenie Asiatischer Elefantenkälber, beschreibt das häufige Vorkommen von nichtlinearen Phänomenen und gibt Aufschluss über das Verhalten im Zusammenhang mit dem Auftreten der vier häufigsten Lauttypen („Rumble“, „Roar“, „Trumpet“ und „Squeak“). Die vier Lauttypen unterscheiden sich in den Frequenzparameter signifikant von einander. Bei Jungtieren treten „Squeaks“ außerdem in Form von zwei Untergruppen auf: ein lang gezogener sowie ein kurzer, pulsierender „Squeak“. Jungtierlaute zeichneten sich im Vergleich zu adulten Tieren (Artelt, 2006) häufig durch eine höhere Grundschwindung aus, wobei kein Infraschall nachgewiesen werden konnte. Dies ist nicht überraschend, denn Jungtiere sind körperlich noch unausgereift und die Erzeugung von tiefen Frequenzen benötigt entweder lange Stimmfalten oder einen großen Larynx (Fitch, 2006). Weiters wird Infraschall von Elefanten u. a. zur Kommunikation über weite Distanzen verwendet (Payne *et al.*, 1986). Dies ist für Jungtiere, die sich ständig in der Nähe der Mütter und Geschwister aufhalten nicht von Bedeutung. Da Körpergröße mit der Länge und Elastizität der Stimmfalten korreliert (Garstang, 2004), könnten adulte Artgenossen die Jungtiere anhand höherer Frequenzen erkennen.

Acht Modulationen der Grundschwingung wurden in den vier Lauttypen nachgewiesen. Einzig in „Squeaks“ und „Roars“ wurden die verschieden Modulationen in einem ähnlichen Muster verwendet. Geschlechterabhängige Muster konnten nur bei „Rumbles“ festgestellt werden. In keinem der Lauttypen wurden altersabhängige Muster nachgewiesen.

Weiters hat sich gezeigt, dass nichtlineare Phänomene mit Ausnahme von harmonischen Schwingungen sehr häufig bei Asiatischen Elefantenkälbern vorkommen. „Roars“ bestanden meist aus deterministischem Chaos, während „Squeaks“ gleichermaßen deterministisches Chaos und Harmonien überlagert von deterministischem Chaos enthielten. „Trumpets“ waren meist harmonisch überlagert von deterministischem Chaos. Nur „Rumbles“ enthielten häufig harmonische Schwingungen. Die Lauttypen zeigten hinsichtlich des Auftretens nichtlinearer Phänomene signifikante Unterschiede. Die meisten Laute enthielten nur ein nichtlineares Phänomen, während in den anderen Kombinationen mehrerer Phänomene gefunden wurde. Die häufigsten Kombinationen fanden in „Roars“ statt, die wenigsten in „Trumpets“.

Frequenzsprünge kamen kaum vor, in „Rumbles“ überhaupt nicht. Nichtlineare Phänomene mit Ausnahme von harmonischen Schwingungen sind bei Afrikanischen Elefantenkälbern seltener vor als bei Asiatischen Kälbern (persönliche Kommunikation mit Stoeger-Horwath, 2009). Möglicherweise unterscheiden sich die beiden Arten in der Entwicklung ihrer Stimmproduktionsmechanismen.

Die Untersuchungen des Verhaltens während der Lautäußerungen zeigen, dass alle vier Lauttypen in den meisten Verhaltenskategorien verwendet wurden. Ausnahmen sind „Rumbles“ und „Roars“ welche nicht während des Spielens auftraten und „Trumpets“, welche nicht während Interaktionen mit Tierpflegern oder anderen Menschen vorkamen. „Squeak“ Sequenzen oder „Chirping“ wurden meistens während dem Spielen geäußert. Agonistisches Verhalten führte selten zu Lautäußerungen. Die Kälber im Alter von 6 bis 12 Monaten (Altersgruppe 1) produzierten gleich viele Laute während der Interaktion mit Müttern oder anderen adulten Elefanten sowie während Gruppenkoordinations- und Spielverhalten. Die Kälber im Alter von 24 und 27 Monaten (Altersgruppe 2) vokalisierten meist während des Spielens, gefolgt von Gruppenkoordinations- und Mutter-Kalb-Interaktionen. Signifikante Unterschiede wurden zwischen den beiden Altersgruppen in Bezug auf Interaktionen zu Menschen oder Artgenossen gefunden. Während die Kälber der Altersgruppe 1 fünf Mal mehr Laute während Interaktionen mit Artgenossen als bei Interaktionen mit Tierpflegern produzierten, passierte dies bei Individuen der Altersgruppe 2 etwa gleich häufig. Diese Ergebnisse entsprechen dem Umstand, dass die Kälber der Altersgruppe 1 noch von der Muttermilch abhängig sind und auch häufiger den Schutz von adulten Elefanten suchen, als die bereits etwas unabhängigeren Kälber der Altersgruppe 2.

Vorhergehende Studien haben gezeigt, dass die akustische Struktur der Laute Aufschluss über den emotionalen Zustand des Individuums geben kann (Soltis *et al.*, 2005b; Soltis *et al.*, 2009). Es konnte jedoch in der vorliegenden Studie kein Zusammenhang zwischen nichtlinearen Phänomenen und Verhalten entdeckt werden.

Während für die Unterscheidbarkeit von individuellen Unterschieden sowie für die Funktion der nichtlinearen Phänomene weitere Studien notwendig sind, konnte diese Studie zeigen, dass sich Laute Asiatischer Elefantenkälber von denen der adulten Artgenossen in Höhe der Grundschwingung sowie im häufigen Vorhandensein von nichtlinearen Phänomenen unterscheiden. In akustischen Frühwarnsystemen können diese Ergebnisse genutzt werden.

2. Abstract

Asian elephants (*Elephas maximus*) are highly endangered animals. Early acoustic warning systems could help protect humans and elephants from deadly encounters (Seneviratne *et al.*, 2004). Therefore, research on the social structure, vocal communication and behaviour in Asian elephants is needed. Up to now, the main research focus considering these aspects was on African elephants. But since differences in vocalisation between African and Asian elephants have been confirmed, more investigations of the latter are required to protect this endangered species. Due to the elephant's social system of mother-calf units, acoustic communication between adults and calves is of particular interest.

The present study provides the first acoustical data on vocal ontogeny of the most frequent call types (roar, rumble, squeak and trumpet) of Asian elephant calves. Vocalisation and associated behaviour of six calves were recorded in two European zoos.

The study revealed that Asian elephant calves use two subtypes of squeaks: a short squeak (uttered in a short and pulsated-way), and a long squeak (vocalised in a stretched way). It also showed that parameters of the fundamental frequency in the four call types are usually higher than those recorded in adults. A similar pattern of frequency contours could be found in squeaks and roars. Gender-dependent variations were only present in the rumbles of female calves.

Moreover, the study reveals that the majority of calls consist of nonlinear phenomena other than harmonics. Most roars consisted of deterministic chaos. Squeaks contained equally often harmonics overlaid with deterministic chaos and deterministic chaos. Trumpets consisted primarily of harmonics overlaid with deterministic chaos, while only rumbles contained mainly of harmonic features. Only one irregular phenomenon could be detected in most calls, while combinations of different phenomena were found less frequently. The latter were highest in roars and lowest in trumpets. I argue that higher frequencies and nonlinear phenomena in calls may therefore enable adults to distinguish calf from adult vocalisations.

No correlation was found in the usage of call types during different behaviours, therefore no safe conclusions can be drawn for behavioural categories from call type utterance. Furthermore, no relation was found between nonlinear phenomena and behavioural categories, which would indicate coherency with different levels of emotional states of the calves. However, differences in call frequency were detected regarding two age groups. I assume that this is caused by the milk dependency and the higher need of protection of the infants, while the individuals aged 24 and 27 months are less dependent.

To sum up, the study yielded that calls of Asian elephant calves are higher in fundamental frequency and obtain frequently nonlinear phenomena. These results help to discriminate adult from calf calls and can help to establish early acoustic warning systems.

3. Introduction

Elephants are highly endangered animals because their different habitats in Africa (savannahs, except the smaller, forest-living *Loxodonta cyclostis*) and Asia (forests) shrink through human impact. Encounters between humans and these strong and heavy animals often end lethally on both sides. To avoid such encounters, acoustic recordings of elephants near human settlements could help detect sex, age, and population size and could form the basis for the establishment of acoustic monitoring and early acoustic warning systems to help protect humans as well as animals. Therefore, a broad comprehension of social structure, vocal communication and behaviour in elephants has to be obtained.

Elephants are highly social mammals. Previous research on social structure, communication and behaviour in elephants was mostly focussed on African savannah elephants (*Loxodonta africana*) (Berg, 1983; Langbauer *et al.*, 1991; Garstang *et al.*, 1995; Lee and Moss, 1999; McComb *et al.*, 2003; Payne *et al.*, 2003; Soltis *et al.*, 2005a; b; O'Connell-Rodwell *et al.*, 2007). Only a few studies have dealt with communication and social structure of Asian elephants (*Elephas maximus*) and those revealed differences between the two species. Social structure involves the dispersal of males before puberty, whereas females stay with their mothers to live in complex and flexible societies (Douglas-Hamilton, 1972; Moss, 1988). African elephants congregate in complex multi-tiered social structures of mother-calf (or offspring) units, family units, bond (or kinship) groups and clans (Douglas-Hamilton, 1972; Moss, 1988). Fusions and fissions of lower and higher-tied units occur on a regular basis, while individuals remain stable within units independent of time and season (Wittemyer *et al.*, 2005). In contrast, female groups of Asian elephants seem to form only close family groups, which consist of a matriarch and several generations of her offspring, with no inter-group transfer observed (McKay, 1973; Fernando and Lande, 2000). Habitat differences may be the reason for these varieties between African savannah elephants and Asian elephants. Group size depends on benefits and costs of predator pressure and food availability (Krebs and Davies, 1996). Animals living in open habitats as savannahs have a higher predator pressure than forest-living animals and benefit from bigger groups, while forest-living animals should tend to small groups for less food competition (Barja and Rosellini, 2008).

Elephant calves mature in a rich society (Lee and Moss, 1999), which supports the development of high communication skills on various sensory modalities. Acoustical, chemical, visual, tactile and seismic communication skills have been observed in elephants, emphasising that long- and short distance communication are important for maintaining intra- and intergroup cohesion (Langbauer, 2000). Up-to-date, the acoustic repertoire of adult African elephants is not agreed upon (Soltis *et al.*, 2005b), as calls show high within-call type variations due to e. g. emotions (Soltis *et al.*, 2009). Call types of Asian as well as African elephants include rumbles, roars, trumpets and snorts. One call type that is unique to Asian elephants is chirping. Chirping consists of multiple short squeaks and has been assigned to wild elephants as agonistic behaviour (McKay, 1973). Only one African elephant bull in zoo Basel (Switzerland) is known to imitate the squeak after sharing the enclosure for 18 years with Asian elephants (Poole *et al.*, 2005).

As elephants form stable mother-calf units, the acoustic communication between adults and calves is of particular importance. Stoeger-Horwath *et al*. (2007) documented six call types of eleven infant African elephants, ranging from neonatal to 18 months of age. These very young elephants showed high variation within call types, indicating family-, bond group- or population-specific dialects. While no gender-dependent variation was found, age-dependent variation was discovered in at least three call types (grunt, rumble and trumpet). Grunts were only produced in the first two months of age and were classified as being noisy with traces of harmonics. Roars of the African elephant infants were divided in noisy, tonal and mixed roars, all of them showing at least some noisy features. Only rumbles, barks and trumpets were considered tonal or transient (Stoeger-Horwath *et al.*, 2007).

Research on mammal vocalisations has for a long time been reduced to tonal calls, discarding irregularities. Yet the vibrations of vocal folds show instabilities in the desynchronization of either both folds or in vertical and horizontal modes of a single fold and result in nonlinear phenomena (Wilden *et al.*, 1998). Non-linear phenomena (NLP) are due to interacting anatomical and neural factors and play an important role in individual and age-class related acoustic output and synchronous behaviours, e.g. mother-infant recognition (Fitch *et al.*, 2002). NLP include harmonics, subharmonics, deterministic chaos, biphonation and discrete frequency jumps. NLP seem to be widespread in mammals (Riede *et al.*, 1997; Wilden *et al.*, 1998; Riede *et al.*, 2000; Tokuda *et al.*, 2002; Riede *et al.*, 2007) and also occur in birds (Fee *et al.*, 1998; Fletcher, 2000). Subharmonics and frequency jumps often occur in human infants' cries and young children's non-cry vocalisations, whereas biphonation may indicate metabolic or neurological disease in neonatal cry, but also seems to be a common feature in normal developing children (Robb and Saxman, 1988). The functions of NLP in animal communication still need to be investigated. They may provide information about the vocaliser's identity, and/or fitness or increase the attention of listeners through their unpredictable occurrence, which prevents a habituation effect in the listeners (Fitch *et al.*, 2002; Riede *et al.*, 2004). To understand more about those functions the behavioural context in which the calls occur may have significant importance.

Asian elephants inhabit forests, making it difficult to observe them in their natural habitat. Therefore, crucial insights on elephant behaviour, anatomy, and physiology have been discovered by investigating captive animals (Schulte, 2000). Although external conditions are not as harsh as in the wild, elephants in captivity share similar needs. Especially infant's behaviour and vocalisation may reflect mainly the behaviour of their mothers and relatives. Furthermore recording usable elephant vocalisations is a challenge and zoos provide much better conditions than national parks. In contrast to the wild where a lot of unpredictable situations may affect efficient vocal data recording, zoos can be seen as already existing experimental set-ups in which vocalisation occurs within a well known social relationship among individuals.

The present study was designed to provide the first acoustical data on vocal ontogeny of the most frequent call types of Asian elephant calves. Vocal recordings were complemented by video taping to put vocalisation into behavioural and social context. Six Asian elephant calves (six to 27 months of age) were investigated in two European zoos. As instabilities in vocal expression occurred on a regular basis, the focus was laid on nonlinear phenomena.

4. Material and methods

4.1. Study objects and locations

Vocalisation and associated behaviour of six calves were recorded in two European zoos (Table 1).Three calves were located at the zoo in Cologne, Germany: Marlar (female, born March 30, 2006, orphan), Ming Yung (male, April 16, 2007) and Maha Kumari (female, May 9, 2007). Another three calves were investigated at the zoo in Emmen, Netherlands: Unt Bwe (male, born May 23, 2006), Swe Zin (female, August 8, 2007) and Ananda (male, February 25, 2008).

Table 1. Information on study animals and location.

name of calf	Abbrev.	gender	age at recording (months)	name of mother elephant	age of mother (years)	location
Ananda	ANA	m	6	Htoo Yin Aye	27	Emmen
Maha Kumari	KUM	f	11	Thi Ha Phyu	28	Cologne
Ming Yung	MIN	m	12	Tong Koon	20	Cologne
Swe Zin	SZI	f	12	Htoo Kin Aye	27	Emmen
Marlar	MAR	f	24	Khaing Lwin Htoo	†	Cologne
Unt Bwe	UNT	m	27	Swe San Htay	29	Emmen

The two zoos were selected due to the age (maximum 2.5 years of age) of juveniles, relatively large group size and species-appropriate husbandry. The elephant keepers in both zoos had no direct contact to elephants (’protected contact’), keeping human impact to a minimum. The elephant park in Cologne provided an area of approximately 13,200 m² for 13 elephants (Figure 1). The outdoor area could be separated into a 4,650 m² cow-enclosure, a 3,390 m² bull-enclosure and a mating enclosure of 2,370 m², whereas the indoor area was divided into a 2,000 m² cow- and a 750 m² bull-enclosure. While the indoor area was always strictly gender divided (calves of both sexes staying with the females), the outdoor area was flexibly varied on a half-day-basis. During 9.30 a.m. and 5 p.m. the elephants were kept in the outdoor area. During one half of the day (morning or afternoon) the older male was allowed to stay with the females and juveniles in the total outdoor area, while the younger male was kept in the indoor enclosure. During the other half of a day the younger male was kept in the mating and bull enclosure with some of the adult females, while calves, mothers and two to three female adults remained in the cow-enclosure. This arrangement was needed as the younger male and one of the mothers were not compliant. During the night, the adult males were separated from the females, although both genders could use their indoor and outdoor enclosures.

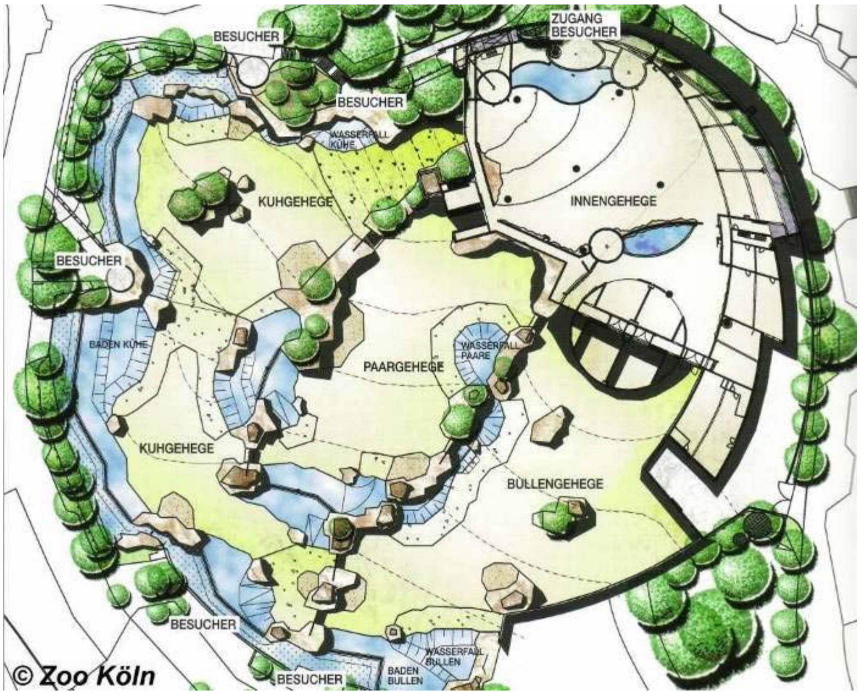


Figure 1. Indoor and outdoor enclosure of the elephant park at the zoo in Cologne, Germany.

The elephant park in Emmen also provided species-appropriate husbandry for 14 elephants on 4,535 m^2. The outdoor enclosure covered an area of 3,670 m^2, consisting of a separable bull and cow enclosure (Figure 3). Females, juveniles and the adult male were kept together all time. From 9.30 a.m. to 6 p.m. the elephants were kept in the outdoor area, in the night they stayed in the indoor enclosure (865 m^2, Figure 2).

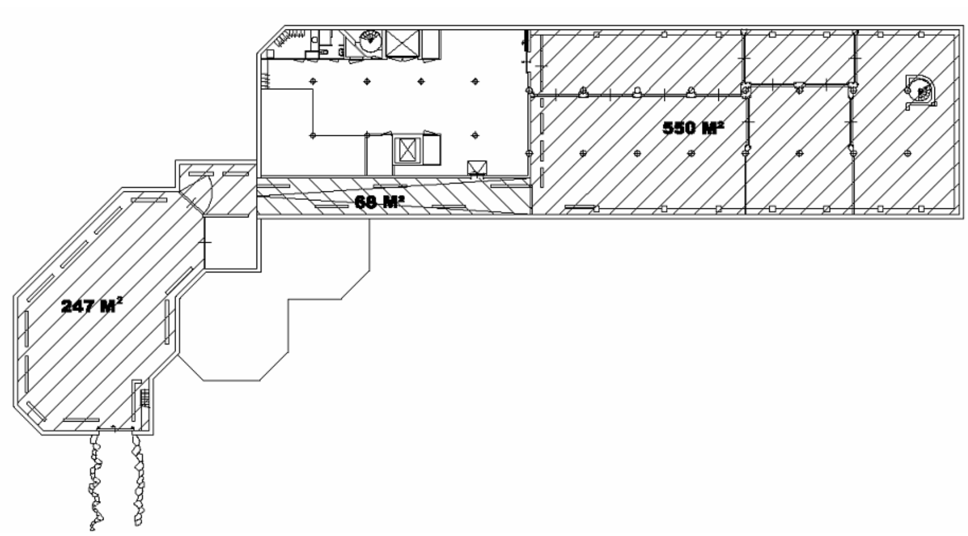


Figure 2. Indoor enclosure of the elephant park at the zoo in Emmen, Netherlands.

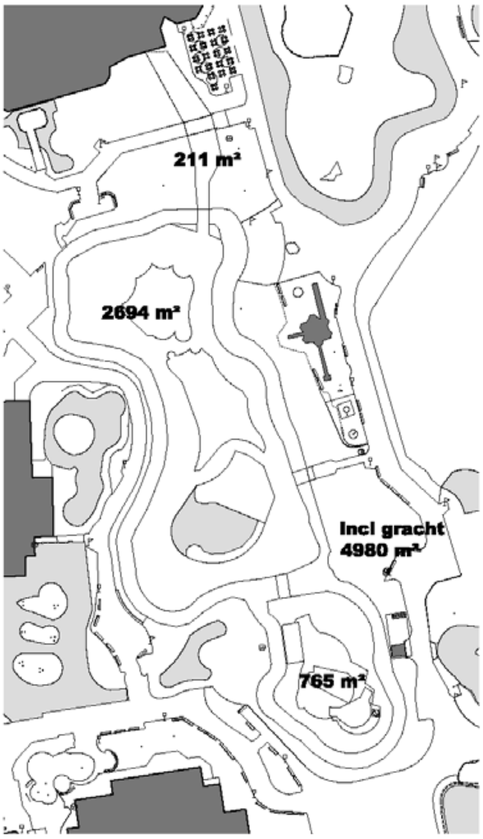


Figure 3. Outdoor enclosure of the elephant park at the zoo in Emmen, Netherlands.

4.2. Data collection

Data collection took place in April 2008 at the Cologne zoo (Koelner Zoo), Germany, and in August 2008 at the Emmen zoo (Noorder Dierenpark) in the Netherlands. Acoustic recordings of a total of 111 hours were made between Monday and Friday in the time between 9 a.m. and 7 p.m. (in Cologne one recording took place during the night, between 7 p.m. and 9 a.m.). Weekends were excluded because of increased background noise caused by zoo visitors. Recordings were carried out with a HD P2 Sound Devices 722 recorder and an AKG condenser microphone C480 B with the condenser capsule AKG CK 62 – ULS, at sampling rates of 48 kHz. Acoustic recordings were complemented, whenever possible, with video recordings by using a digital video camera Panasonic NV-GS60. Most data collection was performed outdoor and videotaped whenever possible (resulting in 57 hours of video recordings). During acoustic recordings the following data were additionally noted for each detected vocalisation: identity of caller, level of confidence of caller identification (A for certain, B probably/likely and C for unconfident/uncertain), behavioural context, position of the caller and the other elephants within the enclosure, mouth condition (closed, half open, wide open) and trunk position during the call, indoor or outdoor, as well as presence and absence of the animal keepers. Data of behaviours were collected with focal sampling and continuous recording. Only calls and behaviours with the confidence level A were used for the analyses.

4.3. Data analysis

4.3.1. Four acoustic call types of Asian elephants

Four call types that occurred in the repertoire of Asian elephants (McKay, 1973; Artelt, 2006) were selected for this study: the roar, rumble, squeak and trumpet. While roars, rumbles and trumpets also occur in the repertoire of African elephants, the squeak, however, is unique for Asian elephants. McKay (1973) defined the basic single sound as squeak and sequences or multiple short squeaks as chirping. To unify call terminology in Asian and African elephants the term ‘growl’ used by Artelt (2006) has been replaced by the term ‘rumble’ used for the similar call type in African elephants. Roars, rumbles and squeaks are produced with the larynx, whereas trumpets are generated with the trunk.

4.3.2. General data analysis

For the acoustic analyses of the recorded signals, the software (S_TOOLS-STX 3.8.2 (Acoustics Reseach Institute, Austrian Academy of Sciences, Vienna, Austria) was used. The following parameters were measured: call duration, intervals of calls within a sequence, parameters of the fundamental oscillation (five equally distributed points of measurement, as well as the mean, minimum and maximum frequency), dominant frequency, form of frequency contour, and call-structure features. Calls were structured according to the kind of nonlinear phenomena that occurred. These include the sum and duration of harmonic and subharmonic components, of deterministic chaos, biphonation, harmonic overlaid with deterministic chaos, and of harmonic windows as well as the sum of frequency jumps and bifurcations. For signals that showed no clear fundamental frequency, only the parameters call duration, intervals of calls within a sequence, dominant frequency and call-structure features were quantified. Sequences were defined as series of multiple calls of the same call type and intervals being less than a second between each call. A total of 327 calls were analysed (Table 2).

Table 2. Number of calls with and without data on fundamental frequency (f0). Calls without fundamental frequency lack information of 8 parameters, i.e. five equally distributed points of measurement, and mean, minimum and maximum of the fundamental oscillation.

	roar	rumble	squeak	trumpet	total
with f0 data	18	24	132	30	204
without f0 data	18	2	92	11	123
total	36	26	224	41	327

4.3.3. Call structure features (nonlinear phenomena)

Definitions of nonlinear phenomena (NLP) were adopted from Wilden *et al.* (1998) and Fitch *et al.* (2002). Harmonics are defined as periodic vibrations. Subharmonics result from period doubling in a time domain and can be perceived by frequencies that are half or a multiple of half of the fundamental frequency. One vocal fold has more tension than the other and goes through two periods while the other goes through one period (Fitch *et al.*, 2002). Deterministic chaos may appear similar to white or pink noise (irregular signal), but shows traces of harmonic or subharmonic phonation and therefore is not totally random (Wilden *et al.*, 1998). Biphonation occurs if there is a weak asymmetry in the two vocal folds, which results in them vibrating at independent frequencies (Wilden *et al.*, 1998). Harmonic windows are periodic vibrations within a call in between fractions of deterministic chaos. Frequency jumps are defined as sudden and abrupt leaps of the fundamental frequency. Bifurcations are transitions between any of the different nonlinear phenomena (Wilden *et al.*, 1998; Fitch *et al.*, 2002). In addition, the NLP 'harmonic overlaid with deterministic chaos' ('harmonic overlaid') was included when analysing the calls of the Asian elephant calves. It is defined as clearly visible periodic frequencies, which are surrounded and slightly overlaid by deterministic chaos.

4.3.4. Age groups

Three age groups were defined as follows: age group 1 contains all individuals from six to 12 months of age (Ananda, Maha Kumari, Ming Yung and Swe Zin), age group 2 comprises of individuals from 24 to 27 months of age (Marlar and Unt Bwe) and age group 'combined' includes all calves from Cologne (Maha Kumari, Ming Yung and Marlar, aged 11 to 24 months) (Table 3). Age group 'combined' includes calls that were certain to come from one of the Cologne calves, but could not be allocated to a certain individual. This age group was included to increase the amount of data for analyses and was not used for direct comparison of the age groups.

Table 3. Number of calls that could be confidentially allocated to individuals. Individuals are divided into 3 defined age groups. See Table 1 for abbreviations of calf names.

	Age group 1					Age group 2		Age group 'combined'	Total
Individuals	ANA	SZI	ANA or SZI	KUM	MIN	MAR	UNT	MAR, MIN OR KUM	
Roars	10	3	3	4	4	10	2		36
Rumbles	5	3		2	3	11	2		26
Squeaks			12	6	28	104	39	35	224
Trumpets	4			1	15	16	3	2	41
Total	19	6	15	13	50	141	46	37	327

4.4. Statistical analysis

4.4.1. Classification

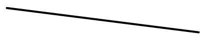
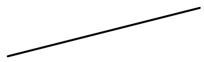
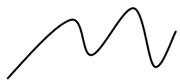
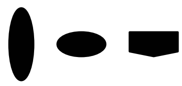
Calls were visually and acoustically divided into the four call types. To verify this classification of call types, a factor analysis was performed in SPSS 11.5 (SPSS Inc., Chicago IL) on 204 calls and the following ten variables: call duration, five points of the fundamental frequency (including start, mid and end), minimum, maximum and mean of the fundamental frequency and dominant frequency. A Kruskal-Wallis-Test was carried out to test for significant differences between the regression factor scores of the factor analysis of all four call types. Mann-Whitney U-tests were then used for pairwise significance tests of all call types.

Squeaks varied in their utterance. Therefore they were subjectively divided into two subtypes, a short squeak (uttered in a short and pulsated-way), and a long squeak (vocalised in a stretched way). A further factoral analysis was performed with the two subtypes of squeaks and a Mann-Whitney U-test was used to test for significance between the regression factor scores of the two subtypes.

4.4.2. Frequency contours

Various frequency contours were found in the calls of the four call types (Table 4). An average linkage hierarchical cluster analysis based on Pearson correlation distances was performed on the relative frequency (%) of the eight frequency contours and the four call types (n_{CALL}=327) to find similarities between call types. Four further average linkage hierarchical cluster analyses based on Pearson correlation distances investigated similarities of frequency contours between individuals (roars n_{CALL}=17, n_{IND}=6, rumbles n_{CALL}=25, n_{IND}=6, squeaks n_{CALL}=134, n_{IND}=4, trumpets n_{CALL}=33, n_{IND}=5). All cluster analyses were performed in SPSS 11.5.

Table 4. Eight frequency contours found in roars, rumbles, squeaks and trumpets.

frequency contours	form
straight	
bent downwards	
bent upwards’	
sloping to the right	
ascending to the right	
multiple ups and downs’	
single ups and downs (including variation)	
frequency clusters	

4.4.3. Nonlinear phenomena

A G-test of independence was performed to compare the frequency of each nonlinear phenomenon of all call types. All p-values are two-tailed and Williams' continuity corrected. The G-test was performed with an Excel spreadsheet by John H. McDonald (Dept. of Biological Sciences, University of Delaware, Newark). An average linkage hierarchical cluster analysis based on Pearson correlation distances investigated the relative frequency of call structures in the four call types (n_{CALL}=327).

4.4.4. Functional context

For the analysis of the functional context, calls were further included that could be certainly allocated to the individuals, but were of too poor quality for acoustical analysis. Moreover, call combinations were not considered and were treated as separate calls whereas sequences were treated as a single call. Sequences were defined as series of multiple calls of the same call type with intervals being less than a second between each call (e.g. squeaks, Figure 4). Call combinations were defined as series of multiple calls of at least two different call types with intervals being less than a second between each call (e.g. roar-rumble, Figure 7). Therefore squeaks consisted of 111 squeak sequences (or chirpings) and of 6 single uttered squeaks and trumpets consisted of 2 trumpet sequences and 45 singly produced trumpets (Table 5).

Table 5. Numbers of calls used for behavioural analysis include calls with and without data on fundamental frequency (f0). Calls without fundamental frequency lack information on 8 parameters: five equally distributed points of measurement, and mean, minimum and maximum of the fundamental oscillation.

roars	rumbles	squeak sequences	single squeaks	trumpet sequences	trumpet	total
37	26	111	6	2	45	227

Calves vocalised during specific behavioural contexts, which were split into six categories (Table 6).

Table 6. Behavioural contexts in which calf vocalisations occurred and their definition.

Category	Functional context	Description
Group coordination and cohesion:	Approaching passive	Elephant vocalizes, another/others start approaching him
	Approaching active	Elephant vocalizes and approaches another/other elephant/s
	Someone approaching	Elephant vocalizes while other elephant approaches
	Other species reaction	Elephants vocalize immediately (within 10 s) after another species (lion etc.) has vocalized
	Loud noise	Loud engine noise (low flying plane, close van or helicopter)
Calf –mother/other elephant	Contact protest	Calf vocalizes after being touched with trunk from mother or other elephant - e.g. after a genital check by another elephant
	Calf touch active	Calf touches an elephant with another body part than trunk and vocalizes
	Separated	Calf is separated from mother and searching for mother, allomother or other family members
	Requires assistance or care	Situation in which a calf needs help, e.g. it has fallen over, is stuck in some manner and vocalizes
	Reaction call	Elephant vocalizes after a call of another elephant
Calf play:	Calf running	Calf runs around and vocalizes or vocalizes and then runs playfully
	Bathing	Elephant vocalizes while bathing
	Object play	Elephant vocalizes while manipulating things e.g. sticks, stones, throwing sand around or chases other species (birds, mice)
	Play fights	Calf vocalizes during play fights, pushing head/trunks,
	Climbing	Calf vocalizes while climbing onto another elephant
	Auto play	Spins, turns, shakes itself or bends down playfully and vocalizes thereby
Agonistic behaviours:	Flight	Elephant vocalizes and flees after another elephant approaches
	Trunk mouth	Elephant vocalizes after another elephant placed his trunk into his mouth, which is considered to be a sign of dominance.
	Intraspecific agonistic behaviour active	Elephant that kicks or pushes calf away vocalizes
	Interspecific or object aggression	Calf is making mock charges; chasing birds, warthogs or other animals; attacking machines, cars etc
Keeper interaction:	Human interaction	Keeper or observer interacts in any way with the elephant and the elephant vocalizes. Elephant sees observer/keeper coming or walks up to him and vocalizes.
	Food	Elephant vocalizes before being fed
	Let in	Elephants will soon (within approx. 30 min) be let in, standing near gate, sometimes keeper give commands for them to come to the gate
	Begging	Crying for food by keeper without touching him
Unknown	Unknown	Elephant vocalizes without obvious reason
	Not seen	Behaviour was not observed

To examine differences between age group 1 and 2 in regard to the relative frequency of two behavioural categories (calf/mother or other elephant interactions, n_{CALL}=33 and keeper interactions, n_{CALL}=18) Fisher's exact test was performed using PAST 1.69.

5. Results

5.1. Classification of the four call types

The call types roar, rumble, squeak and trumpet were classified (Figure 4). To test whether this classification was correct, a factor analysis was performed including ten variables (duration, eight parameters of the fundamental oscillation and dominant frequency). The first two principal components (PC) explained more 93.8% of the total variance (PC1 86.5%, PC2 7.3%). The scores of component 1 of all four call types are depicted in boxplots (Figure 5). The average regression factor score differed significantly in all four call types, as revealed by a Kruskal-Wallis test (H= 125.919, df: 3, $p<0.001$). Mann-Whitney U-tests showed significant differences between any of the four call types (roar: n_{CALL}=18, rumble: n_{CALL}=24, squeak: n_{CALL}=132, trumpet: n_{CALL}=30; roar-rumble, Z=-4.956, $p<0.001$, roar-squeak, Z=-6.842, $p<0.001$, roar-trumpet, Z=-5.537, $p<0.001$, rumble-squeak, Z=-7.780, $p<0.001$, rumble-trumpet, Z=-6.267, $p<0.001$, squeak-trumpet, Z=-6.394, $p<0.001$).

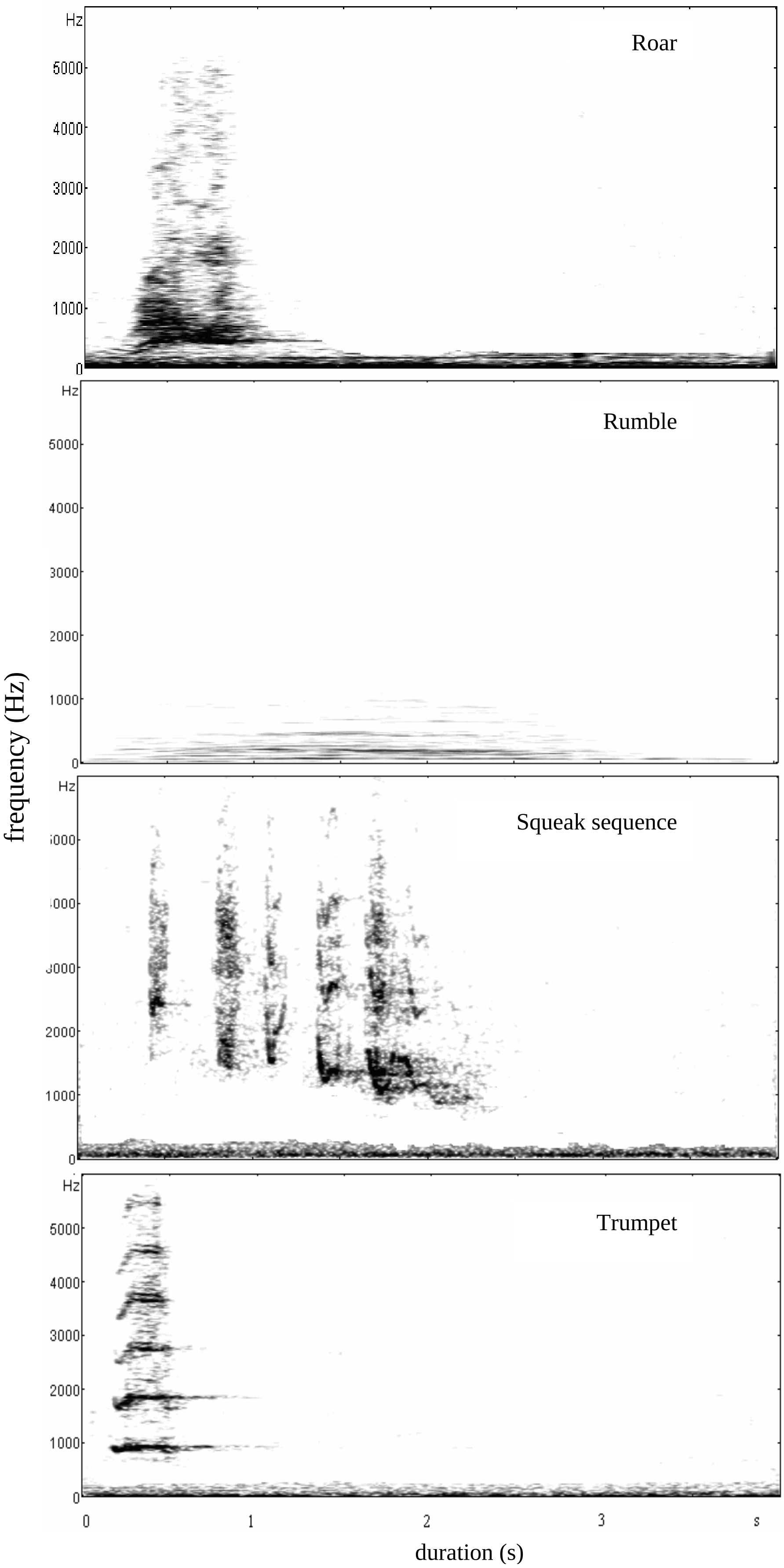


Figure 4. Spectrograms of the four call types roar, rumble, squeak and trumpet. The third spectrogram of the squeak consists of six squeaks (squeak sequence). The first five squeaks are short squeaks and the last one is a long squeak (see 5.1.1).

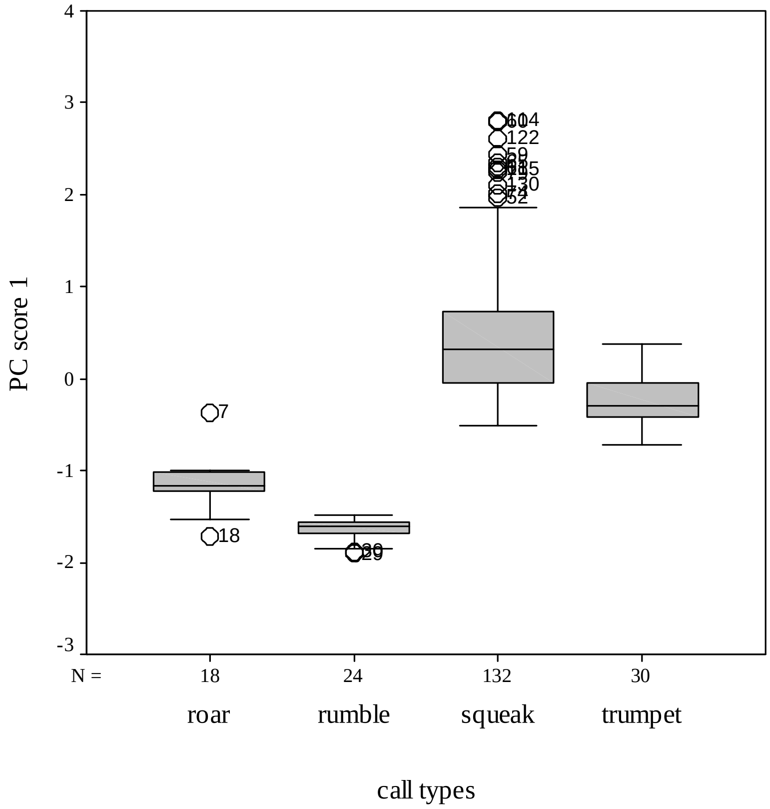


Figure 5. Box plot depicting the regression factor scores of a factor analysis performed on ten call variables of four different call types.

5.1.1. Variation within the call type squeak

Squeaks (n_{call}=224) varied in their structural appearance and were therefore subjectively divided into two subtypes, a short squeak (uttered in a short and pulsated-way), and long squeak (expressed in a stretched way) (Figure 4). To test the correctness of this classification, a factor analysis was performed (total number of squeaks with f0 data: n_{CALL}=132, thereof squeak short: n_{CALL}=102 and squeak long: n_{CALL}=30). The first two components of the ten variables (duration, eight parameters of the fundamental oscillation and dominant frequency) explained 88% of the variance (PC1 76.1, PC2 11.9%). The average regression factor scores of both PC factors were significantly different between the two subtypes (regression factor score 1: Mann-Whitney U, Z=1004.000, $p<0.001$; regression factor score 2: Mann-Whitney U, Z= 140.000, $p<0.001$). Figure 6 depicts the distribution of scores of both regression factors and squeak types. For further analyses only the four main call types were considered, the subtypes of squeaks were pooled.

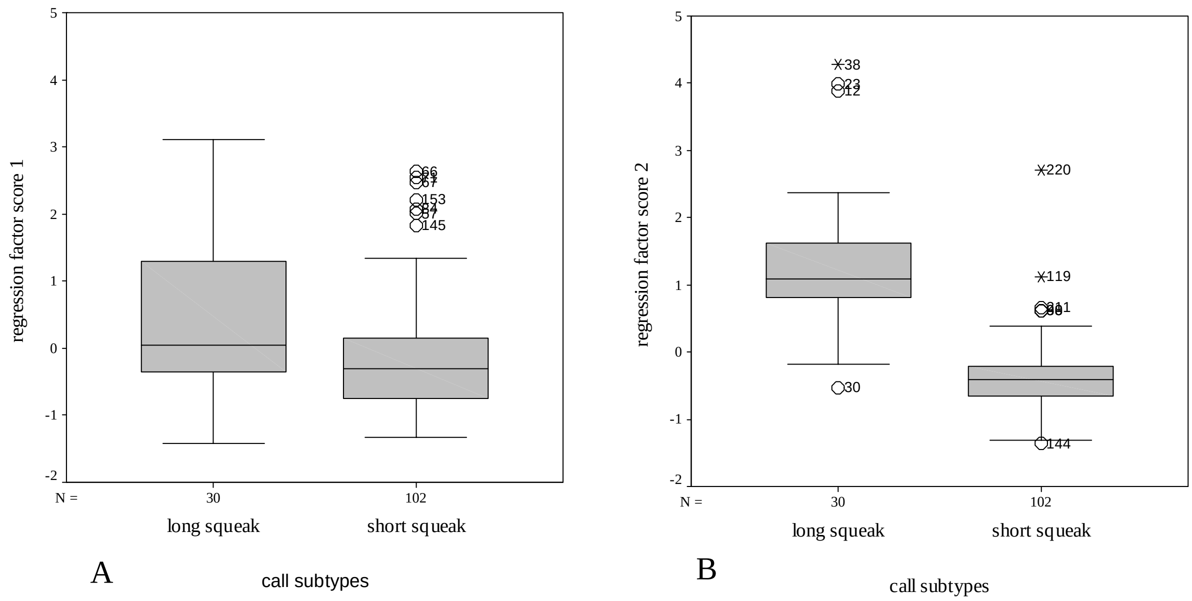


Figure 6. Boxplots depicting regression factor score 1 (A) and 2 (B) of a factor analysis on ten variables of short (pulsated, n_{CALL}=102) and long (stretched, n_{CALL}=30) squeaks.

5.2. Basic acoustic information on the four call types

A total of 36 roars (Figure 4) could be clearly allocated to individuals, i.e., 24 to the age group 1 and 12 to the age group 2. Roars were either uttered in a single vocalisation (18 times) or combined with rumbles (15 times as a roar-rumble (Figure 7), once as a rumble-roar-rumble and once as a roar-rumble-roar-rumble). In only 50 % of the roars the fundamental frequency could be used to measure f0 data (Table 7).

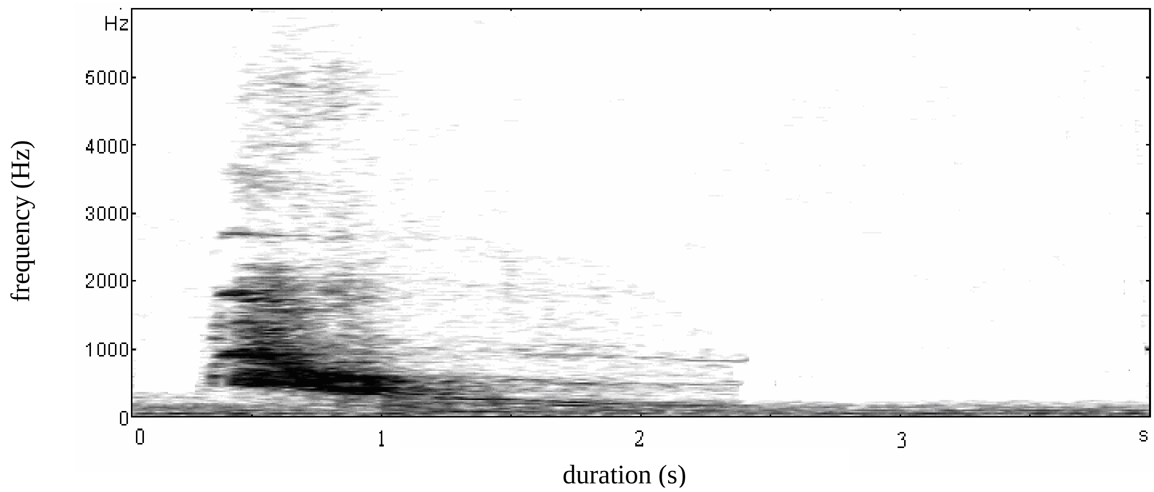


Figure 7. Spectrogram of the frequent call combination roar-rumble.

Table 7. Duration and frequency values of roars. Call duration and dominant frequency were analysed in all roars, whereas fundamental frequency data (mean, min and max) could be measured in only 62.5 % of roars for age group 1 (six to 12 months of age) and 8.3 % of roars for age group 2 (24 to 27 months of age).

	age group 1 n_{CALL} / n_{IND}	age group 2 n_{CALL} / n_{IND}	range	mean	SD
duration (s)	24/4	12/2	0.36 – 2.39	0.91	0.52
f0 mean (Hz)	15/4	3/2	62.40 – 780.80	325.75	151.66
f0 min (Hz)	15/4	3/2	44 - 747	298.28	149.48
f0 max (Hz)	15/4	3/2	80 - 799	360.56	153.49
dominant frequency (Hz)	24/4	12/2	236 - 804	439.86	120.76

A total of 26 rumbles (Figure 4 and Figure 8) could be clearly allocated to individuals, 13 of which belonged to each of the two age groups. Rumbles were very seldom uttered as a single call (5 times), but mostly in combination with roars (21 times; see roars, Figure 7). In 92.3 % of all rumbles the fundamental frequency could be clearly determined and measured. No infrasonic fundamental frequencies less than 20 Hz were uttered by the calves (Table 8).

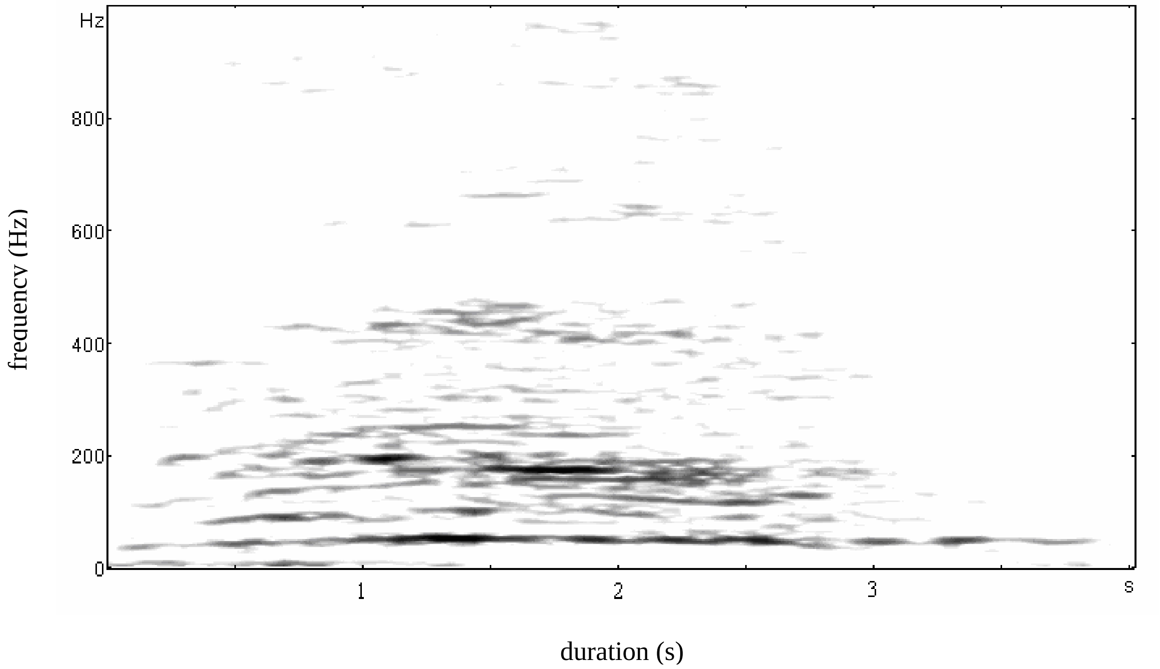


Figure 8. Spectrogram of the low-frequency call rumble.

Table 8. Acoustic parameter of rumbles. Call duration and dominant frequency were analysed in all rumbles, fundamental frequency data (mean, min and max) were measured in 92.3 % of rumbles of age group 1, and in only 7.7% of rumbles of age group 2.

	age group 1 n_{CALL} / n_{IND}	age group 2 n_{CALL} / n_{IND}	range	mean	SD
Call duration (s)	13/4	13/2	0.65 – 3.17	1.48	0.80
f0 mean (Hz)	12/4	12/2	34.80 – 136.00	57.83	22.04
f0 min (Hz)	12/4	12/2	30 – 133	53.70	23.53
f0 max (Hz)	12/4	12/2	33 - 139	69.30	25.42
dominant frequency (Hz)	13/4	13/2	41 - 550	209.96	143.75

A total of 224 squeaks could be clearly allocated to individuals, i.e., 46 to age group 1, 143 to age group 2 and 35 to age group 'combined'. Squeaks were mainly produced in sequences (chirpings) (Figure 4), 5 times (2.2 %) as a single call and three times (1.3 %) in combination with trumpets (one single squeak-trumpet and two squeak sequence-trumpets, always uttered by the 24 month old female). Intervals between single calls of a sequence lasted for up to 0.7 s (mean 0.18 s, SD 0.13 s). The fundamental frequency could be clearly identified and measured (Table 9) in 58.9 % of the squeaks.

Table 9. Acoustic parameters of the call type squeak. Call duration and dominant frequency were analysed in all squeaks, whereas fundamental frequency data (mean, min and max) could be measured in 73.9 % of squeaks of age group 1, 0.7 % of squeaks of age group 2 and 40 % of squeaks for age group 'combined'.

	age group 1 n_{CALL} / n_{IND}	age group 2 n_{CALL} / n_{IND}	age group 'combined' n_{CALL} / n_{IND}	range	mean	SD
duration (s)	46/2	143/2	35/3	0.05 – 2.54	0.27	0.29
f0 mean (Hz)	34/2	84/2	14/3	670.80 – 2781.60	1301.66	474.91
f0 min (Hz)	34/2	84/2	14/3	561 – 2349	1182.60	414.68
f0 max (Hz)	34/2	84/2	14/3	339 - 3214	1437.15	609
dominant frequency (Hz)	46/2	143/2	35/3	724 – 3709	1602.04	668.60

A total of 41 trumpets (Figure 4) could be clearly allocated to individuals, i.e., 20 to age group 1 and 19 to age group 2 and 2 to the age group 'combined'. Trumpets are mainly uttered in a single vocalisation (33 times) and only twice in a trumpet sequence by the individuals of age group two, twice combined with squeak sequences (chirping) and once combined with a single squeak. The fundamental frequency could be clearly identified and measured in 73.1 % of all trumpets (Table 10).

Table 10. Acoustic parameters of the call type trumpet. Call duration and dominant frequency was analysed in all trumpets, whereas fundamental frequency data (mean, min and max) contain only 75 % of trumpets of age group 1, 5.3% of trumpets of age group 2 and 100% of age group 'combined'.

	age group 1 n_{CALL} / n_{IND}	age group 2 n_{CALL} / n_{IND}	age group 'combined' n_{CALL} / n_{IND}	range	mean	SD
duration (s)	20/4	19/2	2/3	0.17 – 1.46	0.57	0.29
f0 mean (Hz)	15/3	13/2	2/3	557.80 – 1263.00	856.11	174.53
f0 min (Hz)	15/3	13/2	2/3	533 - 1213	803.43	155.45
f0 max (Hz)	15/3	13/2	2/3	597 - 1433	915.70	209.90
dominant frequency (Hz)	20/4	19/2	2/3	739 – 2225	1065.28	318.85

5.3. Frequency contours of the four call types

The most common frequency contour in all four call types was 'straight'. 'Bent upwards' and 'sloping to the right' was also identified in each call type. 'Multiple ups and downs' were only produced in squeaks and trumpets, 'single ups and downs' and 'bent downwards' in squeaks only. Frequency clusters were never found in rumbles, but mostly in roars followed by squeaks and trumpets. 'Ascending to the right' was rare in rumbles, squeaks and trumpets (Figure 9).

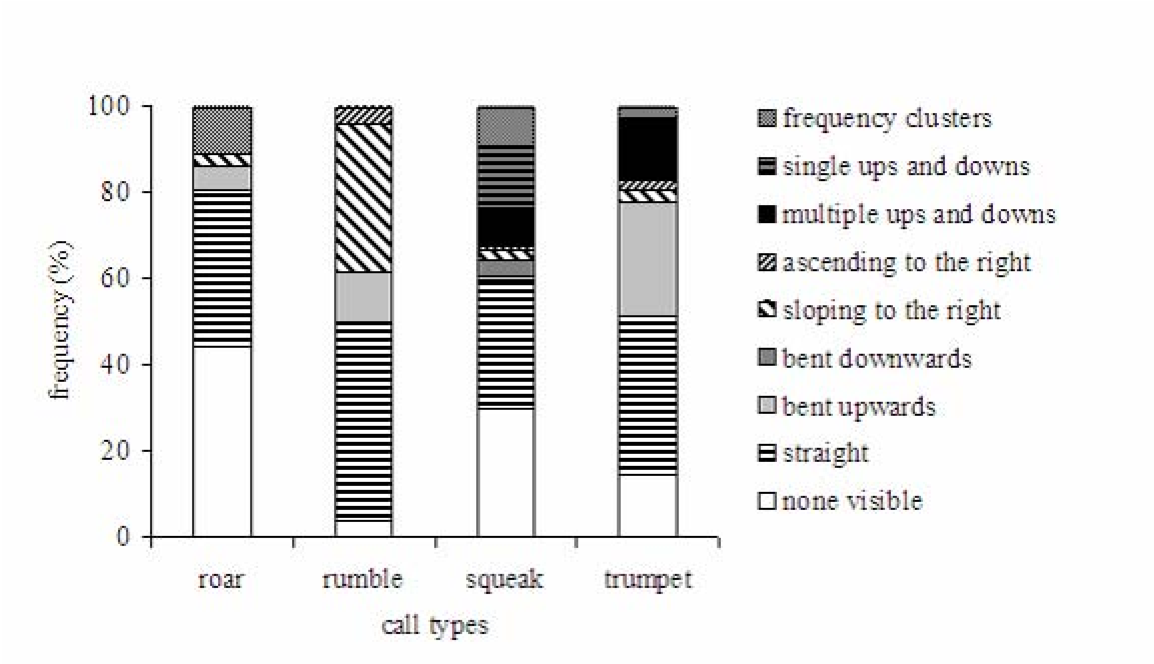


Figure 9. Frequency distribution of 8 types of frequency contours in the call types roar, rumble, squeak and trumpet.

An average linkage hierarchical cluster analysis based on Pearson correlation distances was performed to investigate similarities of frequency contours between call types (Figure 10). The cluster analysis displayed three groups, revealing that roars and squeaks were very homogenous and therefore strongly clustered in regard to frequency contours, whereas trumpets and rumbles are well separated.

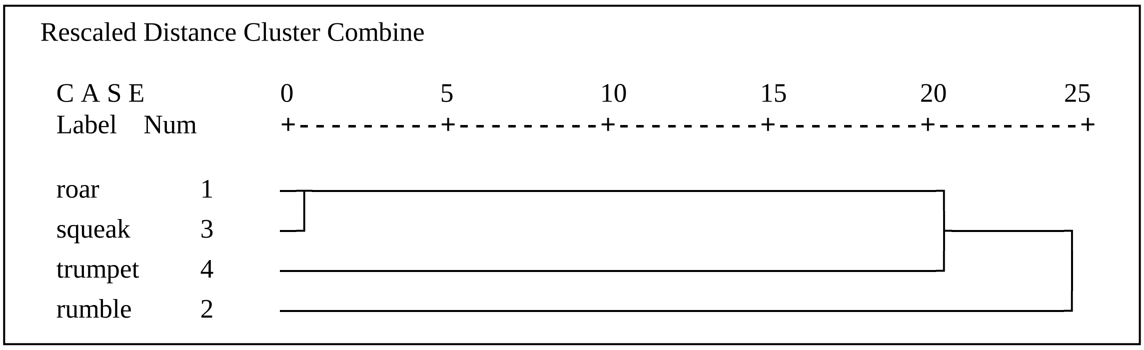


Figure 10. Average linkage hierarchical cluster (based on Pearson correlation distance) performed on the relative frequency of eight frequency contours of four call types (total: n_{CALL}=327,roar n_{CALL}=36, rumble n_{CALL}=26, squeak n_{CALL}=224, trumpet n_{CALL}=41).

Further hierarchical cluster analyses based on Pearson correlation distance comparing individuals regarding each call type showed no age-dependent clustering within the four call types. Gender-dependent similarities could only be found in the call type rumble, clustering females together and separating them from the males (Figure 11).

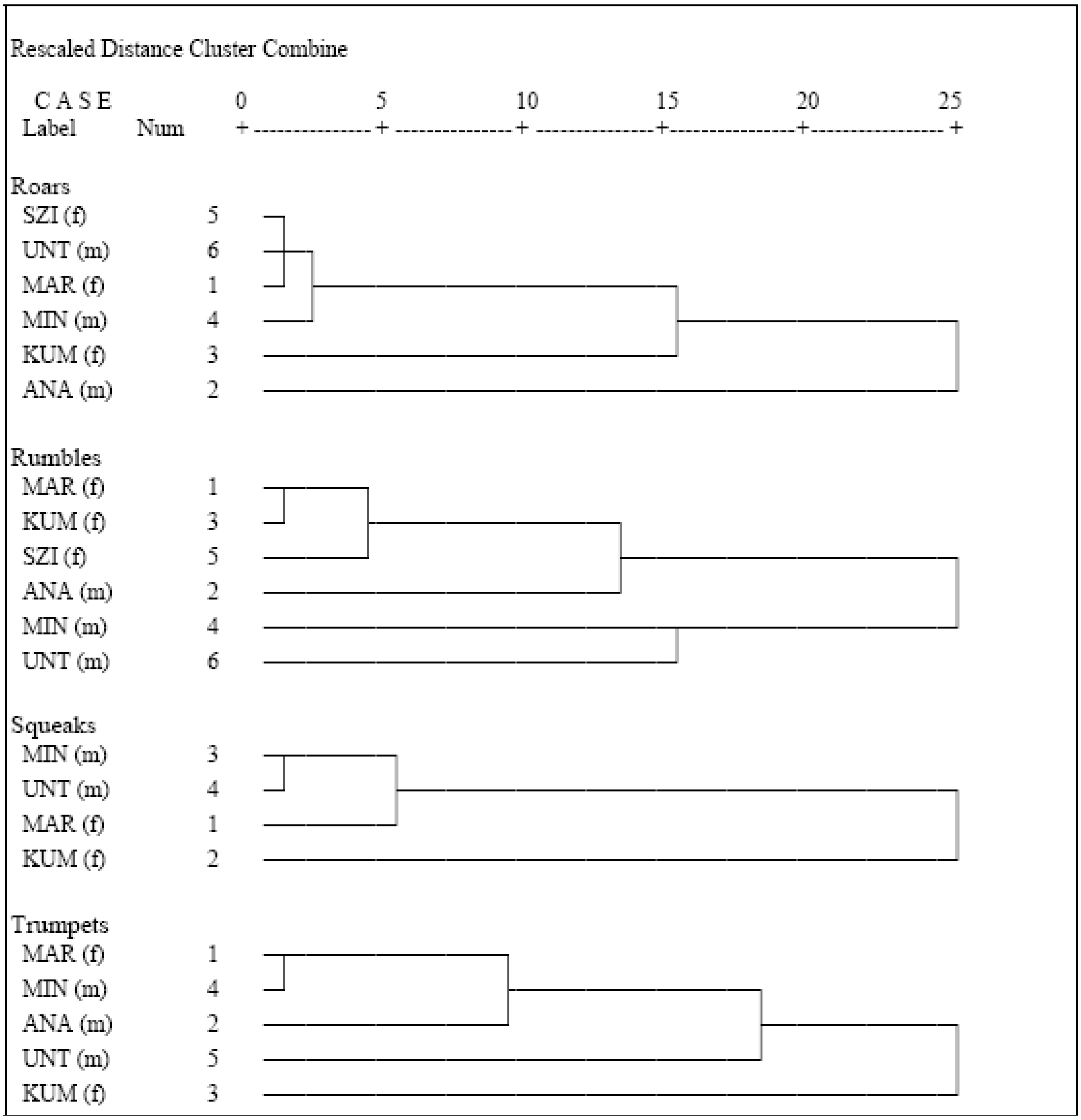


Figure 11. Dendogram of four average linkage hierarchical clustering with Pearson correlation distance regarding individuals and the relative frequency of frequency contours within each call type (roar n_{CALL}=17, n_{IND}=6, rumble n_{CALL}=25, n_{IND}=6, squeak n_{CALL}=134, n_{IND}=4, trumpet n_{CALL}=33, n_{IND}=5). 3-letter-codes are abbreviations for the individuals (see Table 1 for full names), brackets indicate gender (f= female, m=male).

5.4. Nonlinear phenomena in the 4 call types

5.4.1. General analysis

Roars, rumbles, squeaks and trumpet produced by calves revealed seven nonlinear phenomena (NLP). Frequency and duration of five NLP (harmonic, harmonic overlaid with deterministic chaos ('harmonic overlaid'), subharmonic, deterministic chaos, biphonation) were analysed in each call type. Harmonic windows were not considered, as they are integrated in the nonlinear phenomenon harmonic and occurred only seldom. Also frequency jumps were excluded as their duration is not measurable.

Trumpets contained primarily harmonic overlaid features (duration 88.6 %, frequency 82.2 %), while rumbles were composed mostly of harmonic features (duration 42.1 %, frequency 34.4 %). Roars consisted mainly of deterministic chaos (duration 77.5 %, frequency 67.4 %.) Squeaks contained quite equally harmonic overlaid features (duration 46.62 %, frequency 35.14 %) and deterministic chaos (duration 35.7 %, frequency 41.7 %). Biphonation was only found in squeaks (Figure 12). G-test confirmed that the frequency of each nonlinear phenomenon is significantly different compared to all other call types (harmonic, n_{CALL}=58, G=51.839, p<0.001, harmonic overlaid, n=139, G=139.288, p<0.001, subharmonic, n=24, G=20.45, p<0.001 and deterministic chaos, n_{CALL}=151, G=164.821, p<0.001, all p-values are two-tailed and Williams' continuity corrected).

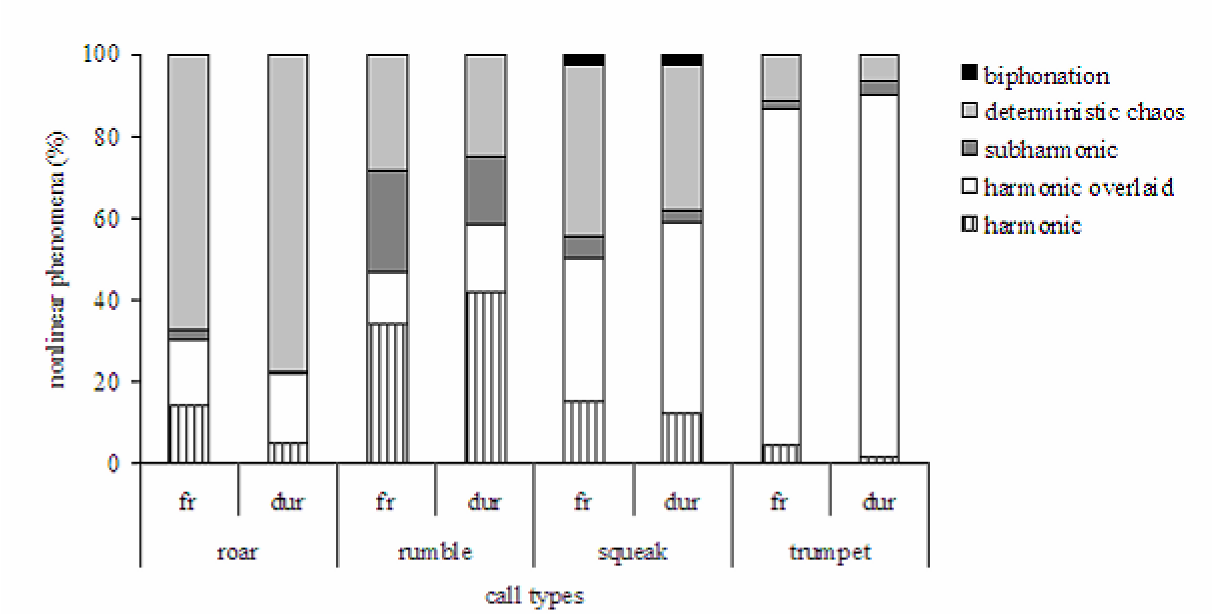


Figure 12. Relative frequencies (fr) and relative durations (dur) of the NLP determined in four call types

5.4.2. Call structure regarding nonlinear phenomena

Calls were classified according to which NLP occurred in each call and whether they occurred solely or in combination. In most calls (85.6 %) only a single nonlinear phenomenon was found. Biphonation always occurred in combination with other NLP. Combinations of two to four NLP including frequency jumps appeared in 14.4 % of the calls. Only 35 out of 327 calls were purely harmonic (three roars = 8.3 %, seven rumbles = 26.9 %, 24 squeaks = 10.7 % and one trumpet = 2.4 %).

Most roars (77.8 %) contained only a single nonlinear phenomenon as deterministic chaos, harmonic overlaid and harmonic (Figure 13). All other roars were combinations of different NLP as ‘harmonic and deterministic chaos’ (11.1 %), ‘harmonic overlaid and deterministic chaos’ (2.8 %) and other combinations with two to four phenomena in one call (8.3 %). A frequency jump occurred only in one roar (2.8 %). Bifurcations were found in 22.3 % of all roars (mean 0.25±0.5s, range 0-2).

Rumbles usually (80.7 %) consisted of only a single phenomenon such as harmonic, deterministic chaos, subharmonic or harmonic overlaid (Figure 13). All other rumbles were composed of different combinations of NLP such as 'harmonic and deterministic chaos' (3.8 %). Other combinations with two to four phenomena in one call were documented in 15.4 % of rumbles. Frequency jumps did not occur. Bifurcations were found in 19.2 % of all rumbles (mean 0.27±0.67, range 0-3).

Most squeaks (86.6 %) contained only a single nonlinear phenomenon such as deterministic chaos, harmonic overlaid, harmonic and subharmonic (Figure 13). All other squeaks were combinations of different NLP as 'harmonic and deterministic chaos' (2.7 %), 'harmonic overlaid and deterministic chaos' (2.2 %) and other combinations with two to four phenomena in one call (8.5 %). Frequency jumps occurred in only 2 squeaks (0.9 %). Bifurcations were found in 12.9 % of all squeaks (mean 0.21±0.66s, range 0-4s).

Most trumpets (90.2 %) contained only a single nonlinear phenomenon such as harmonic overlaid, harmonic and deterministic chaos. All other trumpets were combinations of different NLP as 'harmonic overlaid and deterministic chaos' (4.9 %). Other combinations with two to four phenomena in one call were documented in 4.9 % of trumpets (Figure 13). A frequency jump occurred only once (2.4 %), whereas bifurcations were found in 9.8 % of all trumpets (mean 0.15±0.48, range 0-2).

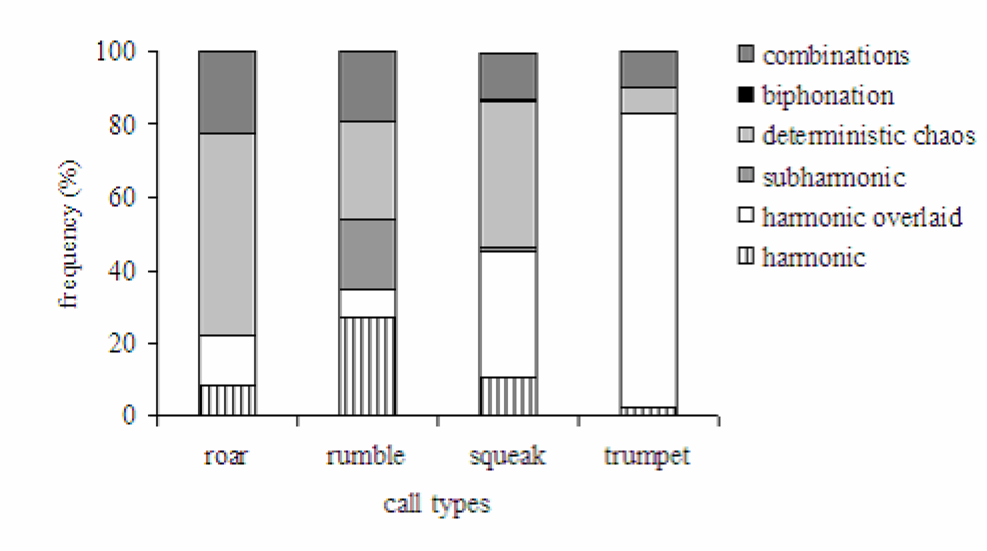


Figure 13. Frequency distribution of NLP of four call types expressed solely (harmonic, harmonic overlaid, deterministic chaos, subharmonic and biphonation) or in combination (includes frequency jumps).

An average linkage hierarchical cluster analysis based on Pearson correlation distances was performed to investigate similarities between call types (Figure 14). The analysis displayed three groups, revealing that roars and squeaks are very similar in call structure, whereas rumbles and trumpets are separate groups.

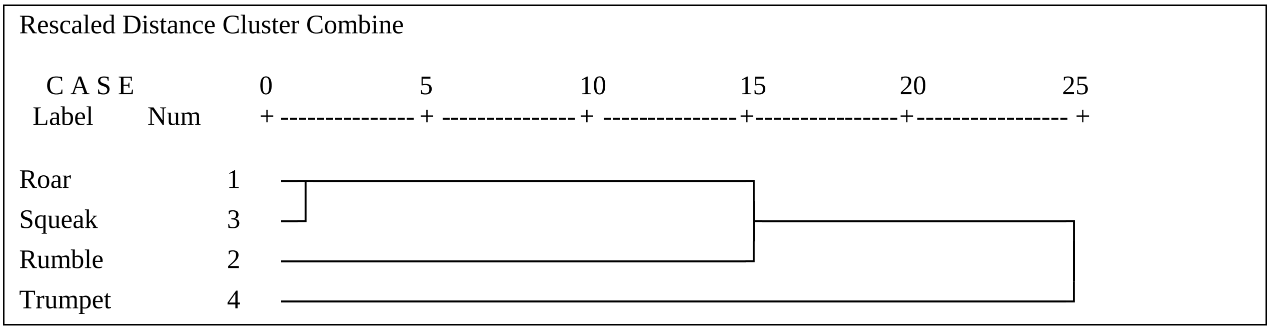


Figure 14. Average linkage hierarchical cluster analysis (based on Pearson correlation distances) performed on the relative frequency of call structures of four call types (n_{CALL}=327).

5.5. Functional context during vocalisations of the four call types

Calves vocalised during specific behaviours, which were assigned to different categories. Most vocalisations occurred during calf play behaviours (39.6 %), followed by group coordination and cohesion (18.9 %), unknown or unseen behaviours (15.9 %) and calf-mother and/or calf-other elephant interactions (14.5 %). Interactions with keepers (8.4) and agonistic behaviours (2.6) were rarely accompanied by vocalisations (Figure 15).

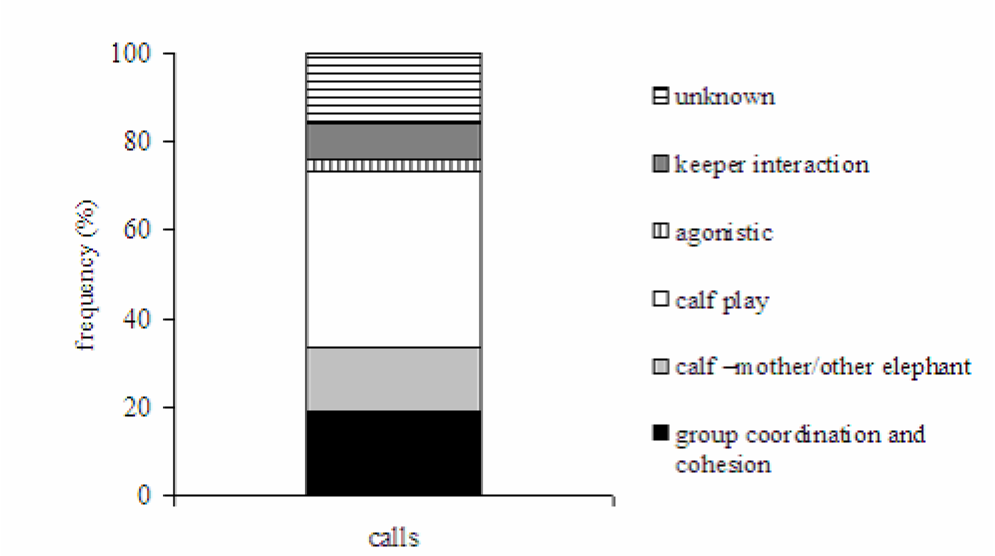


Figure 15. Relative frequency (%) of behavioural categories in all calls (n_{CALL}=227) of the four call types produced by calves.

When examining the different age groups, age group 1 vocalised equally frequent during calf-mother and calf-other elephant interactions, group coordination and cohesion behaviours and calf play (24.4 %). Age group 2 clearly vocalised mainly during play behaviours (42 %), followed by group coordination and cohesion (17 %). Calf-mother or calf-other elephant interactions (11.6 %) and keeper interactions (12.5 %) were uttered quite equally in age group 2. Calls during agonistic behaviours were very rare (age group 1: 3.7 % and age group 2: 0.9 %; Figure 16). Individuals of age group 1 produced five times more calls during interactions with their mother or other elephants than during behaviours relating to keepers or other humans, whereas age group 2 called equally often in these categories (Fishers exact test, χ^2=7.6448, $p<0.05$).

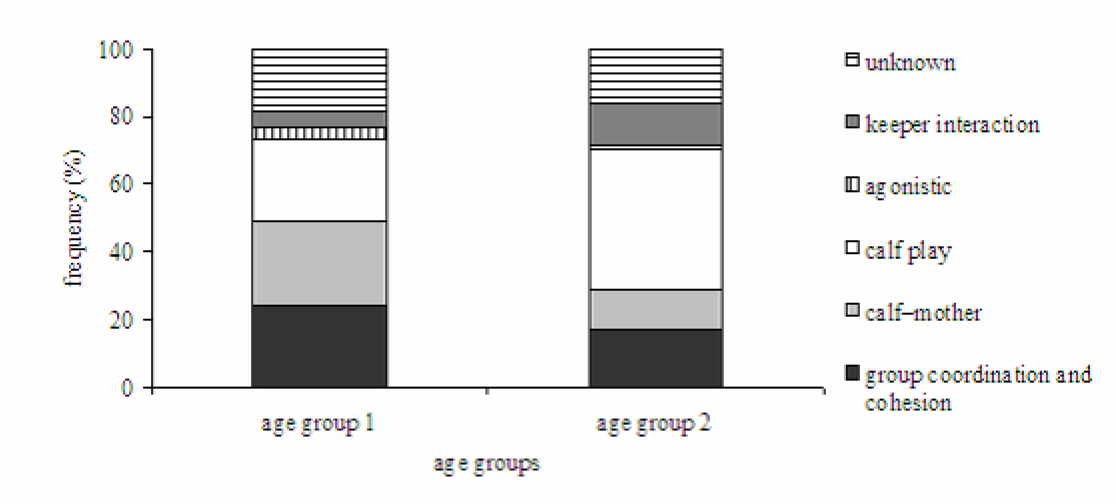


Figure 16. Relative frequency (%) of behavioural categories (n_{CALL}=227) uttered by the different age groups (age group 1, n_{IND}=4, n_{CALL}=82 and age group 2, n_{IND}=2, n_{CALL}=112).

By comparing the relative frequency of calls in the different behavioural categories, group coordination and cohesion interactions as well as playing were mainly accompanied by squeak sequences as well as solely uttered squeaks. In calf-mother and/or calf-other elephant interactions roars were most often used, whereas keeper interactions were attended by rumbles. Most trumpets were vocalised during calf playing behaviours (Figure 17).

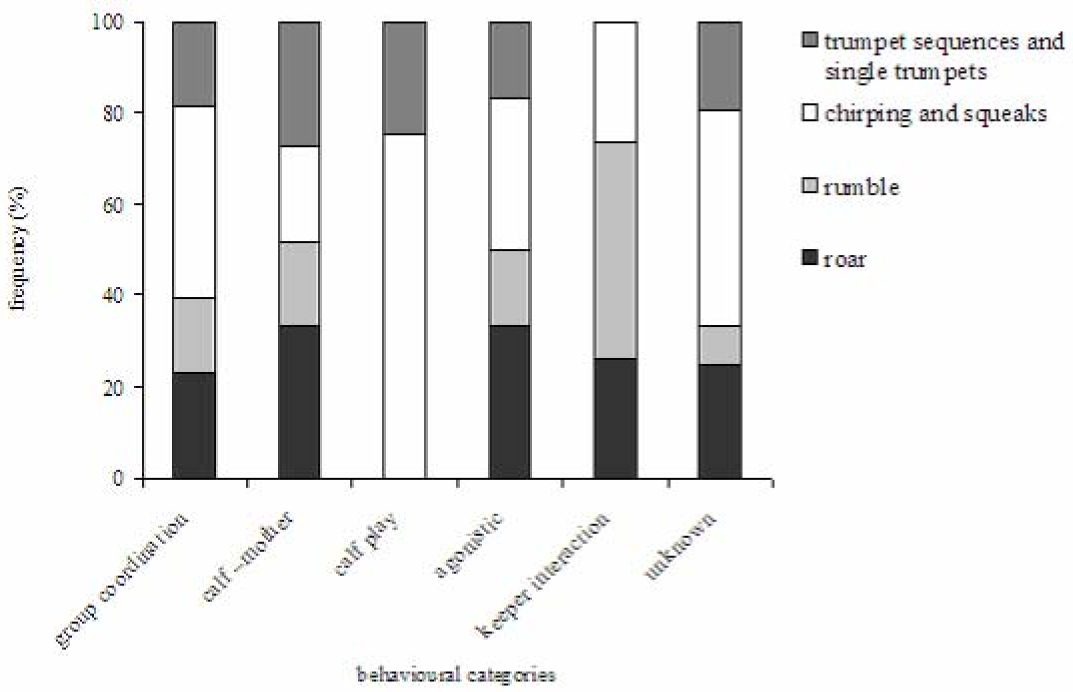


Figure 17. Relative frequency (%) of the four call types (roar n_{CALL}=37, rumble n_{CALL}=26, chirping (=squeak sequence) and single squeaks n_{CALL}=117 as well as trumpets n_{CALL}=47, total n_{CALL}=227) produced in different behavioural categories.

The relative duration of NLP in five behavioural categories was compared within each call type (roar: n_{CALL}=36, rumble: n_{CALL}=26, squeak: n_{CALL}=224, trumpets n_{CALL}=41). Independent of the behavioural category roars were dominated by deterministic chaos and trumpets by harmonic overlaid features, Squeaks that were uttered during keeper interactions contained purely deterministic chaos, while the other behavioural categories showed no striking differences among each other. One purely harmonic rumble occurred during an agonistic behaviour. The nonlinear phenomenon 'harmonic overlaid' occurred in rumbles only during keeper interactions. Duration of the NLP in squeaks (as well as in rumbles) showed no distinct differences during group coordination and cohesion and during calf-mother or calf-other elephant interactions.

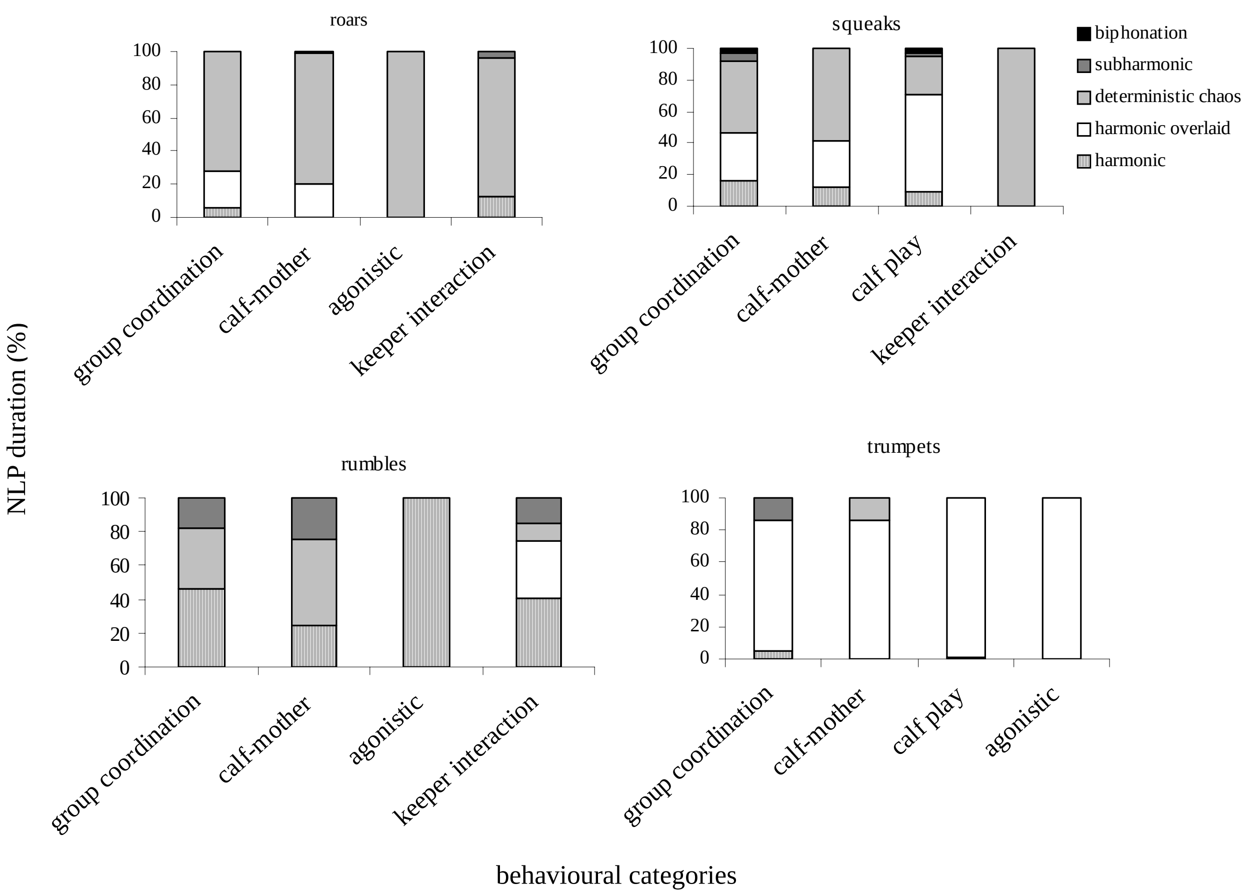


Figure 18. Relative duration (%) of the NLP produced in different behavioural categories within each call type (roar n_{CALL}=36, rumble n_{CALL}=26, squeaks n_{CALL}=224,trumpets n_{CALL}=41, total n_{CALL}=327).

6. Discussion

Due to the elephant's social system of mother-calf units, acoustic communication between adults and calves is of particular interest. Only one previous study provided first insights in the vocal ontogeny in elephants. Stoeger-Horwath *et al.* (2007) examined calls of infant African elephants from the Vienna Zoo and the Daphne Sheldrick orphanage in Nairobi National Park, Kenya, from neonatal to 18 months of age. Differences exist in social structure and vocal communication of Asian and African elephants (McKay, 1973; Fernando and Lande, 2000). Therefore studies of African elephants cannot be simply transferred to Asian elephants and more information on the latter is required to protect this endangered species. Two former studies provided insights on the vocal repertoire of Asian elephants (McKay, 1973; Artelt, 2006). Artelt (2006) described acoustic features of Asian elephants in a zoo in Berlin (Tierpark Berlin Friedrichsfelde, Germany), but the high age range of examined individuals (2 months to 32 years) restricts the opportunity of direct comparisons with the present study. In Artelt (2006), acoustic parameters of the trumpet and roar included calf calls, whereas they were excluded in rumbles and squeaks.

Furthermore, nonlinear phenomena (NLP) and their relevance in mammal vocal communication have been ignored for a long time and have only recently become subject to detailed investigation. The present study is the first to describe the acoustic structure, the functional context and nonlinear phenomena in Asian elephant calves and provide information on the vocal ontogeny in Asian elephants.

6.1. Basic acoustic information on calf vocalisations

The four call types (roar, rumble, squeak and trumpet) examined in the present study could be distinguished from each other through statistical analysis. No subcategories were investigated except in the squeak.

Roars of calves were higher in frequency and shorter in duration than those of adults and calves investigated by Artelt (2006).The lower range of the minimum frequency in the fundamental frequency (f0 min) overlapped but reached a four times higher level than those of two roar subcategories of the elephants in Berlin. In respect to African elephant infants, duration of all roar subtypes and the mean fundamental frequency (± SD) of infant's tonal roars overlapped well with those of the calves of this study. However, infant African elephants expressed even higher fundamental frequencies in mixed and noisy roars than roars of Asian calves (Stoeger-Horwath *et al.*, 2007).

In the study of Artelt (2006), rumbles did not include infant calls. Minimum frequencies measured in the fundamental frequency overlapped only slightly in the highest frequencies, showing that adult Asian elephants rumbled generally at lower frequencies than calves. Duration and dominant frequencies overlapped, although the upper range of dominant frequencies was almost four times higher in calf vocalisations. Rumbles produced by Asian calves were about two times higher in mean fundamental frequency and almost four times higher in dominant frequency than those of African infants, while call duration overlapped (Stoeger-Horwath *et al.*, 2007). Congruent to findings in African elephant infants, roars and rumbles often merged into each other. Half of the roars and 80 % of the rumbles produced by the Asian calves were uttered in this combination.

Trumpets of the Asian elephants (adults and calves) in Berlin overlapped with those of the calves of the present study in the deepest frequency in the fundamental frequency, although again calf calls were higher in the upper range. With respect to the dominant frequency, calves of Asian elephants were well within the range of their conspecifics in Berlin. Compared to infant African elephants, the mean fundamental frequencies of Asian elephant calves overlapped in the lower frequencies, while mean dominant frequency range is higher in African than in Asian elephant calves.

Squeaks produced by one adult elephant in Berlin overlapped well in the minimum frequency of the fundamental frequency compared to squeaks of the calves. Frequencies of the dominant frequency overlapped as well, although again calves reached a higher lever in the upper range. Squeak duration in adults was very short (0.1-0.35 s), whereas calf squeaks varied from 0.05 to 2.54 s. While all calves of this study squeaked, only two elephant mothers used this call type and then mostly in serial utterance (chirping). Chirping of these two mothers consisted only of short and pulsated squeaks, while calves produced long as well as short squeaks. These two squeak subtypes (short and long squeaks) could be statistically distinguished.

Long vocal folds or huge larynxes are needed to produce lower frequencies (Fitch, 2006). It is therefore not surprising, that calves utter calls with higher frequencies than fully-grown adults. No infrasonic frequencies were measured in the calf calls. Payne *et al.* (1986) were the first to detect that one reason for infrasonic calls of Asian elephants could be long-distance communication. As elephant calves live in stable mother-calf units and usually remain in close proximity to their mothers or other family members (Lee, 1987), long-distance communication is probably not needed for young elephants. Body size is related to length and elasticity of vocal folds and thereby influences the fundamental frequency (Garstang, 2004). Higher frequencies in calls may therefore be an indicator for adults to distinguish calf from adult vocalisations.

6.2. Frequency contours

Three frequency contours occurred in all four call types, ‘straight’ being the most common one. The other frequency contours were used in a variable way depending on the call type. Therefore, no similar pattern of frequency contours could be found when comparing call types except in squeaks and roars. Although frequency contours vary between call types, the above results indicate that no safe discrimination of call types is possible. However, frequency contours may be gender-, age- or individual-dependent. Gender-dependent variations were only present in rumbles, where usage of various frequency contours linked females with each other. No age-dependent variations were found. Due to low sample size, individual differences could not be tested for.

6.3. Nonlinear phenomena in calls of Asian elephant calves

Only in recent years have nonlinear phenomena (NLP) been investigated more thoroughly, revealing that NLP such as subharmonics (Fischer *et al.*, 2001), deterministic chaos (Wilden *et al.*, 1998; Tokuda *et al.*, 2002), biphonation (Riede *et al.*, 2000; Fischer *et al.*, 2001; Riede *et al.*, 2004) and frequency jumps (Riede *et al.*, 1997; Fitch *et al.*, 2002; Riede *et al.*, 2004) seem to be quite common in mammal vocalisation, but occur also in birds (Fee *et al.*, 1998; Fletcher, 2000), healthy human infant vocalisations (Robb and Saxman, 1988) and human pathological voices (Herzel *et al.*, 1994; Herzel *et al.*, 1995; Yu *et al.*, 2001; Zhang and Jiang, 2008).

The present study shows that NLP also exist in vocalisations of Asian elephant calves. Only about 10% (35 out of 327) of the calls were purely harmonic. The frequent appearance of nonlinear phenomena (NLP) other than harmonics in all four call types, in particular the deterministic chaos in roar and squeak, made it sometimes impossible to detect the fundamental frequency in the respective call spectrogram.

Similar to findings in infant African elephants (Stoeger-Horwath *et al.*, 2007), trumpets contained primarily harmonics overlaid with deterministic chaos, while rumbles consisted mainly of harmonic features. Most roars of African elephant infants were termed noisy roars (Stoeger-Horwath *et al.*, 2007), similarly, most roars of Asian calves consisted of deterministic chaos. Squeaks contained harmonics overlaid with deterministic chaos and deterministic chaos equally often, while squeaks of adult Asian elephants were described as harmonic by Artelt (2006). This was the only call type that included biphonation. Occurrence of NLP showed significant differences between call types.

Calls were structured according to which NLP occurred either solely or in combination. Independent of call types, only a single nonlinear phenomenon was found in most calls. Combinations of different NLP were highest in roars (22.2 %) and lowest in trumpets (9.8 %). Roars of African elephant infants were divided into three subtypes (tonal, noisy and mixed roars) based on their harmonic and noisy components (Stoeger-Horwath *et al.*, 2007). Most of these roars recorded were totally noisy, followed by mixed roars (multiple switches between tonal and noisy segments) and tonal roars. Similarly, most roars of Asian calves consisted of deterministic chaos, followed by combinations of several NLP as well as harmonics overlaid with deterministic chaos and harmonics. Frequency jumps occurred rarely: only once in roars and trumpets, twice in squeaks and never in rumbles. Again, according to hierarchical cluster analysis, squeaks and roars were similar in call structure, whereas rumbles and trumpets were distinct.

Although noisy components did exist in vocalisations of infant African elephants, especially in the roar, fundamental frequency could be clearly seen in most cases (personal communication with Stoeger-Horwath, 2009). In contrast, various NLP occurred highly in the four selected call types of Asian elephant calves, whereas adult Asian elephants seem to produce mainly harmonic rumbles, squeaks and trumpets (Artelt, 2006). Whether Asian and African elephant calves differ in the development of their vocal production mechanism needs to be investigated.

6.4. Call types and behavioural categories

All four call types were produced during three behavioural categories (group coordination and cohesion behaviours, calf-mother and calf-other elephant interactions and agonistic behaviours). Rumbles and roars were not used during calf play behaviours and trumpets were not used during keeper interaction. Most vocalisations recorded occurred during calf play behaviours, the squeak being the most frequent call type. Agonistic behaviours of adult elephants towards calves have rarely led to vocal protest. This is similar to the finding that low-ranking females of African elephants remain silent more often, when receiving aggression than high-ranking females do (Leong *et al.*, 2005). Except for the squeak no safe conclusions can be drawn for behavioural categories from call type utterance.

6.5. Age groups and behavioural categories

Age groups show differences in call rates during various behavioural categories. When examining the different age groups, age group 1 (6 to 12 months) vocalised equally frequent during calf-mother and calf-other elephant interactions, group coordination and cohesion behaviours and calf play. Age group 2 (24 to 27 months) clearly vocalised mainly during play behaviours, followed by group coordination and cohesion, calf-mother or calf-other elephant interactions and keeper interactions. Calls during agonistic behaviours were very rare in both groups. While individuals of age group 1 are considered as infants due to their milk dependency, it seems reasonable that calf-mother and group coordination behaviours are vocalised on an equal frequency. The 24-month old calf in age group 2 is still considered to be an infant, but in this case was an orphan, which behaved similar like the 27-month old calf, vocalising mainly during play but also during calf-mother or calf-other elephant behaviours. Allomothering is found frequently in elephants (Lee, 1987; Schulte, 2000) and was also observed – especially towards the orphan - during this study. Furthermore, significant difference is found between these two age groups regarding human and elephant interactions. Individuals of age group 2 communicated during keeper and calf-mother or calf-other elephant interactions equally often, while individuals of age group 1 produced five times more calls during interactions with their mother or other elephants than during keeper interactions.

6.6. Nonlinear phenomena and behavioural categories

Studies have shown that acoustic structure of elephant calls reflect the emotional state of callers (Soltis *et al.*, 2005b), e.g. by leading to an increased and more variable fundamental frequency (Soltis et al., 2009). Wesolek et al. (2009) found that the motivational state of African elephant infants increases the energy in higher frequencies of rumbles. As NLP occur frequently in Asian elephant calves, they may also provide information on the emotional state of the caller. To conclude on this, data on behaviour with respect to vocalisation are required. Roars were dominated by deterministic chaos and trumpets by harmonic overlaid features, showing no relation to the behavioural context in which they were uttered. During keeper interactions squeaks consisted purely of deterministic chaos, while rumbles contained harmonic overlaid features only in this category. Yet no distinct differences in occurrence of NLP within a call type could be found. This indicates that NLP in Asian elephant calves vocalisation do not differ due to emotional state, but may be due to the immature physical development.

Another possible function of NLP in vocalisation is that these calls become unpredictable, which fights habituation and thereby increases auditory impact (Fitch *et al.*, 2002; Riede *et al.*, 2007). This is plausible in the case of infants and calves, which depend on the reaction of the group in case of danger or when in need for assistance. Adult elephants may recognise these calls as calf calls due to these instabilities in vocalisation. Adult female African elephants in Amboseli National Park, Kenya, were able to recognise the contact calls of about 100 other females in the population, when playback was conducted within one km of the study animals (McComb *et al.*, 2000; McComb *et al.*, 2003). The latter indicates that identity information in the call is lost in long-distance communication and therefore individual identity may be in frequencies above infrasonic frequencies (McComb *et al.*, 2003). It is therefore likely that the occurrence of NLP provides crucial information on an individual's identity. Therefore further investigation of nonlinear phenomena in infant or calf vocalisations is needed.

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