# MASTERARBEIT | MASTER'S THESIS

Titel | Title

Calls in Context: An Acoustic Analysis of African Elephant Calf Vocalizations Across Behavioral Contexts

verfasst von | submitted by

Sara Bosch BSc

angestrebter akademischer Grad | in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien | Vienna, 2025

| | |
|---|---|
| Studienkennzahl lt. Studienblatt \| Degree programme code as it appears on the student record sheet: | UA 066 878 |
| Studienrichtung lt. Studienblatt \| Degree programme as it appears on the student record sheet: | Masterstudium Verhaltens-, Neuro- und Kognitionsbiologie |
| Betreut von \| Supervisor: | Univ.-Prof. Mag. Dr. Angela Stöger-Horwath<br>Privatdoz. |
| Mitbetreut von \| Co-Supervisor: | Dott.ssa Vesta Eleuteri MSc MSc |

# TABLE OF CONTENTS

# Abstract

African savannah elephants (*Loxodonta africana*) have a large vocal range and live in a complex social system making them a fascinating species to study mammalian communication. Many insights into their acoustic behavior have already been gathered by numerous studies, usually focusing on adult individuals and their most frequently used vocalization, the rumble. Elephant calves also produce rumbles but tend to express higher arousal states through different types of roar vocalizations, which they use to signal when they require assistance or care. Elephant calves display remarkable precocial abilities, being able to move with the herd from the first day of life onwards. Their ability to communicate effectively is crucial and their calls have been shown to signal arousal levels and, to some extent, encode social contexts.

The focus of this thesis is to explore the acoustic communication and associated behavior of African savannah elephant calves. Data was collected in Addo Elephant National Park, South Africa, providing the opportunity to investigate the vocalizations of calves in their natural habitat. Rumble and roar vocalizations were analyzed across various acoustic parameters to determine whether they differ between behavioral contexts. Based on the selected parameters, our rumble sample revealed an acoustic differentiation of rumbles across behavioral contexts. An acoustic distinction between the roar types has been described before and is confirmed by the analysis conducted in this thesis. Mixed, noisy and tonal roars differ in acoustic entropy parameters, and context-related tendencies in the use of specific roar types were found in our data. Furthermore, additional insights were gathered regarding the reaction time to the three roar types across different behavioral contexts, which are in line with previous findings while also extending them.

**Keywords**

African savannah elephants, elephant calf vocalizations, acoustic communication, behavioral context, natural habitat

# Zusammenfassung

Afrikanische Savannenelefanten (*Loxodonta africana*) verfügen über ein Lautrepertoire mit einem außergewöhnlich großen Stimmumfang und leben in komplexen Sozialgefügen. Diese Eigenschaften machen sie zu einer besonders faszinierenden Art für die Erforschung der Kommunikation von Säugetieren. Zahlreiche Studie haben bereits wertvolle Erkenntnisse über ihr akustisches Verhalten geliefert, wobei der Schwerpunkt meist auf erwachsenen Individuen und deren am häufigsten verwendeter Lautäußerung, dem sogenannten „Rumble“, liegt. Auch Elefantenkälber verwenden diesen Laut, tendieren jedoch in stressigen Situationen dazu, den „Roar“ zu äußern, um erhöhte Aufregung auszudrücken und so auf ihre Bedürfnisse aufmerksam zu machen. Neugeborene Elefantenkälber sind bereits weit entwickelt und besitzen die bemerkenswerte Fähigkeit, der Herde schon am ersten Lebenstag zu folgen. Eine effektive Kommunikation ist für sie von entscheidender Bedeutung. Es wurde gezeigt, dass in ihren Lautäußerungen Erregungszustände codiert sind und dass sich bestimmte Laute in verschiedenen Verhaltenskontexten akustisch voneinander unterscheiden.

Das Ziel dieser Arbeit ist es, die akustische Kommunikation und das damit verbundene Verhalten von Kälbern der Afrikanischen Savannenelefanten weiter zu untersuchen. Die Daten wurden im Addo Elefanten Nationalpark in Südafrika erhoben, was die Möglichkeit bot, die Lautäußerungen junger Elefanten in ihrem natürlichen Lebensraum zu untersuchen. Rumble- und Roar-Vokalisationen wurden hinsichtlich verschiedener akustischer Parameter untersucht, um festzustellen, ob und wie sich die Laute in Verhaltenskontexten unterscheiden. Die Analyse der Rumble Laute unseres Datensatzes zeigte eine akustische Unterscheidung in den unterschiedlichen Verhaltenskontexten. Eine Differenzierung der Roar-Typen wurde bereits in früheren Studien beschrieben und wird durch die Ergebnisse dieser Arbeit bestätigt. Die drei Subtypen der Roar-Vokalisationen unterscheiden sich deutlich in ihren Entropie-Parameter, und es zeigte sich, dass bestimmte Roar-Typen bevorzugt in spezifischen Verhaltenskontexten eingesetzt werden. Darüber hinaus konnten neue Erkenntnisse zu den Reaktionszeiten in Bezug auf die verschiedenen Roar-Typen und Verhaltenskontexte gewonnen werden, die mit bisherigen Forschungsergebnissen übereinstimmen und diese ergänzen.

**Schlüsselwörter**

Afrikanische Savannenelefanten, Vokalisationen von Elefantenkälbern, akustische Kommunikation, Verhaltenskontext, natürlicher Lebensraum

# INTRODUCTION

## Why Study Elephant Acoustic Communication?

The field of animal bioacoustics can help us understand the evolution of animal communication, cognition and culture, and can offer insights into animal conservation (Hardus et al., 2009; Janik, 2013; McComb et al., 2000; Zeppelzauer et al., 2015). African savannah elephants represent a compelling model species for animal bioacoustics, due to their large frequency range, complex cognition and IUCN status as endangered species (Bates et al., 2008; IUCN, 2020; Moss & Poole, 1983; Poole et al., 1988). Specifically, studying elephant acoustic communication can potentially inform and help improve elephant conservation (Zeppelzauer et al., 2015). African savannah elephants are endangered (IUCN, 2020) due to habitat loss and fragmentation (Wall et al., 2024), climate change (Turner et al., 2022) and ivory poaching (Milner-Gulland & Beddington, 1997). A major threat to elephants is human-elephant conflict, where elephants invade human settlements to forage on their crops and enter conflict with humans (Hoffman, 1993; Shaffer et al., 2019; Warner, 2008). Studying elephant bioacoustics can help mitigate human-elephant conflict by, for example, employing acoustic early warning systems (Zeppelzauer et al., 2015), in which the presence of elephants can be detected through their vocalizations from a distance, and warn nearby communities, giving them more time to prepare for their arrival.

Aside from the conservation perspective, African savannah elephants are an important model species to study the evolution of communication and cognition (Bates et al., 2008; Plotnik & Jacobson, 2022; Stoeger & Manger, 2014). Language is a capacity that makes humans unique and exploring evolutionary similarities or precursors to language in the communication of other animals can give insight into the evolution of this capacity and complex communication. Although elephants are evolutionarily distant from humans, they share with humans and other primates complex cognition (Bates et al., 2008; Poole et al., 2005; Rensch, 1957), long life history (Lee et al., 2016), and complex social systems (McComb et al., 2001; Moss & Poole, 1983), thus facing comparable challenges that may have led to convergent evolution of similar communicative strategies. Studying elephants is therefore not just highly relevant from the conservation perspective but also from a human evolution perspective to provide insight into the pressures leading to the evolution of complex communication.

## Social System of Elephants

African savannah elephants live in a dynamic, hierarchical social structure within a fission-fusion society (Archie et al., 2006; Wittemyer & Getz, 2007). Fission-fusion societies are complex, dynamic social structures. Fission describes the regular separation of some individuals from the family whereas fusion means that larger groups form through the merging of related herds or families (Wittemyer et al., 2005). The separation and merging of herds can depend on the seasons, since during the wet season it is possible for the land to sustain larger groups of elephants at once (Moss & Poole, 1983; Vance et al., 2009).

At the core of elephant social organization is the mother-offspring unit, or first tier unit (T1). The next level, the family unit (Douglas-Hamilton, 1972) or second tier unit (T2) (Wittemyer et al., 2005) consists of closely related adult females and their calves. These family units can form kinship groups (Douglas-Hamilton, 1972) also called bond groups (Moss & Poole, 1983) or third tier units (T3) (Wittemyer et al., 2005). A fourth tier (T4) exists as clans, which are aggregations of bond groups or unrelated family units that share overlapping home ranges during the dry season (Moss & Poole, 1983). To maintain consistency in the thesis, these categories will be referred to as mother-offspring unit, family unit, bond groups and clans. The family unit follows a matriarch, where an adult female is the leader with her daughters and their offspring forming the most stable social core. Upon reaching sexual maturity, usually around the age of 15, male elephants typically disperse from the family unit and join male-only social networks also called male alliances or male bond groups (Chiyo et al., 2011).

The high frequency of multilayered social interactions in elephants support the Social Complexity Hypothesis (SCH) which posits that species living in complex social systems require equally complex communication systems to navigate relationships and interactions within the group (Freeberg et al., 2012). This pattern is not found when comparing the two African elephant species of the African savannah and the African forest elephant (*Loxodonta cyclotis*). The African savannah elephants live in more complex social domains but display less vocal diversity (Hedwig et al., 2021). The application of SCH might still hold true in the mammalian domain overall and when comparing elephants to other mammals.

In the wild, group cohesion and coordinated movement are important for safety and location of resources (Wittemyer et al., 2005). In a family unit typically a dominant female signals to initiate departure from a site, but it has been found that other herd members also call interactively, overlapping or antiphonally during departures from the waterhole (O'Connell-Rodwell et al., 2012). While such vocal coordination is well documented in family units, similar patterns also occur in male alliances. In these groups similar communication has been documented, where dominant males initiate

departure with vocalizations that prompt responses from others, suggesting a form of consensus-based movement coordination (O'Connell-Rodwell et al., 2024).

## Multimodal Communication and Cognitive Flexibility in Elephants

Elephants utilize a range of modalities to communicate with each other. For instance, elephants produce chemical cues through temporal gland secretion, urine and feces which encode information about identity and the current hormonal state of an individual (von Dürckheim et al., 2022). An example of olfactory acuity of elephants is demonstrated by Hoerner and colleagues, who showed that two mother-daughter pairs could recognize each other's feces after 2 and 12 years of separation, suggesting a long-term memory for individual scent profiles (Hoerner, Lawrenz, et al., 2023). Sight is important for navigating the environment but also functions in perceiving signals. Elephants seem to understand the importance of visual attention even with a human experimenter. To request food, elephants gesture towards humans and produce visual signals more often when the human is facing them (Smet & Byrne, 2014). More recently, Eleuteri and colleagues found that semi-captive elephants persisted and elaborated on the gestures they used to request food, when their goal of getting all the food items from the experimenter was not fully met with their initial attempt (Eleuteri et al., 2025). This demonstrates goal-directed intentionality in elephant visual communication. Additionally, in separation experiments with semi-captive elephants, it was observed that upon reunion they use different communication modalities sensitive to their recipients visual attention (Eleuteri et al., 2024). These findings align with the elephants' fission-fusion structure in which groups frequently split and merge and therefore greeting behaviors like "Little Greetings" and "Greeting Ceremonies" are part of the natural behavior. Greetings can be observed at the arrival of a family or mother-offspring unit at the waterhole. At waterholes elephants frequently engage in affiliative contact (Hoerner, Rendle-Worthington, et al., 2023), in socio-sexual behavior or collective play. These interactions are often accompanied by vocalizations and body contact. A prominent example of a vocalization in combination with group cohesion and social cues is the "let's go rumble" often produced by the matriarch. During this event, the leading female typically faces away from the group, produces a rumble and pauses while the family gathers in response before departing the waterhole.

## Elephant Acoustic Communication and Social Relevance

Vocal repertoire of African savannah elephants

The study of elephants began in the late 18th century with Cuvier in 1796 and Blumenbach in 1797. Since then, many researchers have studied the species and their acoustic communication. Many call types have been proposed and defined (Berg, 1983; Langbauer, 2000; Leong, Ortolani, Burks, et al., 2003; Poole, 2011; Soltis, 2010; Stoeger-Horwath et al., 2007) some of which overlap, while others differ between studies. For the sake of clarity and relevance to this thesis, we will focus on the call type definitions described in Stoeger-Horwath et al., 2007 (see also Methods – Call Types).

Vocalizations produced by elephants can be divided into two groups. The rumble, bark, grunt, noisy roar, tonal roar and mixed roar are described as laryngeal call types with the source being the vibration of the vocal folds in the larynx (Herbst et al., 2012). By contrast, the snort and trumpet are referred to as trunk call types with these call types not being produced by the larynx but by airflow from the lungs traveling through the nasal cavity where the larynx only plays a role in regulating air pressure (Poole, 2011; Soltis, 2010). The rumble vocalization, defined as laryngeal call type, can be emitted through the oral tract (mouth) or the nasal tact (trunk) (Stoeger, Heilmann, et al., 2012). While the source for a rumble is always the vibration of the vocal folds, the sound can travel along different anatomical structures respectively, which modify the sound differently. This modification represents a filter for the sound, altering its properties depending on the structures is passes from the source to the utterance. Thus, the vocal tracts represent the filters in the source-filter theory (Fant, 1970; Fitch, 2000). Furthermore, it was found that Asian elephants (*Elephas maximus*) apply velopharyngeal coupling, meaning that calls can be emitted utilizing both vocal tracts at the same time, and this finding also applies to African elephants (Beeck et al., 2022; Stoeger, Heilmann, et al., 2012).

The rumble is the most used call type of African savannah elephants, with the fundamental frequency in the infrasonic range (Payne et al., 1986; Poole et al., 1988), depending on the size and age of the elephant (Baotic & Stoeger, 2017; Stoeger et al., 2014). The rumble vocalization generally has a harmonic structure. Barks are very short in duration and can be described as transient and noisy (Stoeger-Horwath et al., 2007). The grunt vocalization is noisy with slight indications of harmonic structure and was first described in Stoeger-Horwath et al., 2007. This call occurs only in newborn individuals in the first 2 months of life. Based on manner features, the roar can be grouped into three different subtypes. A roar with no tonal elements and just deterministic chaos is called a noisy roar whereas the opposite would be a tonal roar. They are tonal for most of the call, with deterministic chaos only appearing briefly at the end. The third subtype is the mixed roar, representing a mixture of the previous two with noisy and tonal elements alternating or combined in a way not matching the definitions of either noisy or tonal roars. The call type snort sounds like a strong exhalation and is

produced by blasting air out the trunk, with no tonal signal or proper sound produced (Stoeger-Horwath et al., 2007). The trumpet, produced by the trunk, is usually a loud, tonal call with the harmonics fully overlaid with noise (Stoeger-Horwath et al., 2007).

Social Contexts of Acoustic Communication

Elephants use vocalizations across a wide range of social contexts. Among adult African elephants, the most frequently produced call is the rumble, a low-frequency vocalization with a fundamental frequency of 15-25 Hz (Payne et al., 1986; Poole et al., 1988). Due to its low-frequency properties, this call is suggested to be used in long-distance communication capable of traveling up to 10 km in ideal environmental conditions, but with attenuating conditions only about 1 km (Garstang, 2004). Elephants might adjust the timing and frequency of calls depending on these conditions and therefore on time of the day, which has been supported by findings in Etosha National Park (Garstang et al., 2005). Propagation studies have identified rumble components detectable at over 1.5 km (Baotic et al., 2018). In playback experiments, elephants have been shown to recognize social information contained in rumbles from distances up to 2.5 km (McComb et al., 2003).

The fundamental frequency of African elephant rumbles varies with body size of the caller (Baotic & Stoeger, 2017; Stoeger et al., 2014). Adult male rumbles, for instance, tend to have lower fundamental frequency than those of adult females, reflecting sex-related size differences (Baotic & Stoeger, 2017). These acoustic features provide insight into the physical attributes and identity of the sender. Playback experiments in the field support this, where it was found that male elephants respond more strongly to rumbles from unfamiliar females by increased orientation in the direction of the speaker and looking duration. The response behavior was significantly reduced for rumbles of familiar females which indicates the ability to encode familiarity based on vocal cues (Stoeger & Baotic, 2017).

In a reproductive context male elephants produce a distinct variation of the rumble, exclusive to their state of musth, a hormonally driven period marked by increased aggression and dominance (Poole & Moss, 1981). Male elephants in musth can be visually identified through urine dribbling and temporal gland secretion. Heightened dominance and aggression is part of this state which makes them more likely to get a chance for mating (Poole & Moss, 1981). Males in musth produce a so-called musth rumbles, characterized by a temporally pulsed structure and lower mean fundamental frequency (Poole & Moss, 1981). Similarly, females in estrus produce rumbles with a longer duration (Leong, Ortolani, Graham, et al., 2003). Modifying vocalizations by longer duration or repetition is a way to increase the signal-to-noise ratio and enable better signal detection (Hamilton, 1957) which in these examples seem to enhance the advertisement of the reproductive state. While successful reproduction

is essential to maintain a population, the survival of the offspring is equally crucial. Effective communication during the vulnerable period of infants and calves plays an important role.

## Elephant Vocal Communication – Production and Learning

Vocal Production

The African savannah elephants' call repertoire comprises 8-10 call types (Berg, 1983; Langbauer, 2000; Poole, 2011; Soltis, 2010; Stoeger-Horwath et al., 2007). Vocalizations depend on the age of the individual, since infants and calves use call types, or variations not present in adult elephants and vice versa (Langbauer, 2000; Poole, 2011; Soltis, 2010).

The mechanism of vocal production is largely conserved across mammals (Fitch, 2000). Laryngeal calls of elephants follow the same principle as speech, and both can be explained by the source-filter theory (Herbst et al., 2012). Air expelled from the lungs, travels through the trachea and can set the vocal folds into vibration, generating sound. The fundamental frequency of this sound depends on the size, mass and tension of the vocal folds (Fant, 1970; Titze, 1994). As the sound travels through the supralaryngeal tract, consisting of pharynx, oral cavity, nasal cavity, it gets reshaped. While passing through these structures the sound is filtered with certain frequencies emphasized and others suppressed. Thus, the vocal tract gives each vocalization its final acoustic structure and functions as a filter shaping the sound spectrum (Fant, 1970; Titze, 1994).

Therefore, the source as well as the filter impact the output since the vocal folds influences the fundamental frequency, and the vocal tract modifies the sound and is responsible for the formant formation. The vocal folds of adult African elephants are 78 – 95 mm long and in juvenile and calf individuals have been reported to be 50 – 70 mm long (Forbes, 1879; Kühhaas & Weissengruber, 2011). Based on mandible measurements, the length from the larynx to the mouth is estimated to be around 75 cm in adult female African elephants (Soltis, 2010). Taking the trunk length into account, the larynx to trunk opening length is estimated to be about 2.5 meters (Soltis, 2010). However, the source and the filter are independent of each other, and elephants can vocalize using different either the oral or nasal vocal tract which can result in the same vocalization type with different acoustic properties (Stoeger, Heilmann, et al., 2012). Additionally, in elephants it has been found that sounds can be produced by vibrations of head structures and by air passing through nasal cavities (Stoeger et al., 2021). This means that the larynx is not the only source, but elephants also use various parts of their head and trunk to generate sound.

Physical production mechanisms of elephant infrasonic vocalizations have been tested by blowing air through an extracted anatomical structure of an elephant larynx (Herbst et al., 2012). It was demonstrated through this experimental setup that a rumble can be produced with airflow through the larynx alone. Therefore, active muscle contractions are not needed for the production of a rumble, but it can occur through the principles of myoelastic-aerodynamic (MEAD) forces from the vocal folds alone and without any neural signal (Herbst et al., 2012). With the larynx as the source, elephants can produce rumbles orally (mouth) or nasally (trunk) as shown with an acoustic camera array (Stoeger, Heilmann, et al., 2012). It has not been conclusively tested, but this study suggested that different production types also had a social component, since the nasal rumbles were produced more often as contact calls and oral rumbles were used in a bonding context. It has to be mentioned here, that elephants sometimes apply velopharyngeal coupling, using both oral and nasal vocal tract at the same time when vocalizing (Beeck et al., 2022) and therefore distinguishing context specific usage of different filters is difficult to discern.

Vocal Learning

Elephants are capable of vocal learning (Poole et al., 2005; Stoeger, Mietchen, et al., 2012; Stoeger & Manger, 2014). They exhibit vocal usage learning (Stoeger & Baotic, 2021) which refers to context-dependent call use and elephants also show vocal production learning meaning the modification of acoustic output to produce novel sounds (Stoeger et al., 2021).

Vocal usage learning involves acquiring the appropriate context for call use, for example when a calf is learning from their mother or other group members when to use which vocalization. Usage learning is strongly shaped by social interactions and, in certain species have a sensitive or critical period during early development (Janik et al., 1997; Janik & Knörnschild, 2021; Janik & Slater, 2000). When studying combinatorial calls in all three elephant species, it was found that the young African savannah elephants (calves and juveniles up to the age of 10) combine call types more often than adults (Pardo et al., 2019). In elephants, the use of roars or combined calls could be helpful to get attention from other individuals, as they have more nonlinear phenomena and are therefore more difficult to habituate to (Fitch et al., 2002; Herler & Stoeger, 2012; Poole, 2011; Stoeger et al., 2011). Combined or graded calls could also be necessary to encode different kinds of information at once (Soltis et al., 2005b), where a rumble could encode individual identity (McComb et al., 2003) and the roar signals arousal levels (Stoeger et al., 2011).

There is evidence that African savannah elephants imitate, and produce novel sounds based on acoustic experiences they made (Poole et al., 2005; Stoeger et al., 2021). Examples include elephants imitating

the noise of a truck, and an African savannah elephant that produced the chirp of an Asian elephant which is not part of their natural call repertoire but acquired it through experience since they were housed together (Poole et al., 2005). Another recorded instance involved an Asian elephant in captivity, imitating human speech, more specifically words which the elephant heard daily from his trainers (Stoeger, Mietchen, et al., 2012). The Asian elephant who produced human-like speech sounds accomplished this by putting the trunk in his mouth to modify the sound (Stoeger, Mietchen, et al., 2012). These recorded instances show that elephants are capable of vocal production learning and suggest that elephants meet the criteria for both vocal usage and vocal production learning among mammals. Looking at other species the underlying mechanisms for vocal production learning differ from each other and require more research to conclusively distinguish (Vernes, Kriengwatana, et al., 2021). In the process of learning a new sound, babbling is a phenomenon in development that has been hypothesized to be a prerequisite for vocal production learning (Fitch, 2006; Vernes, Janik, et al., 2021). For social species who also communicate acoustically, babbling might be a significant developmental step to learn and use calls right. This may occur as repetitive, variable utterances to explore the species' own vocal repertoire and has been found in bats, monkeys and birds (ter Haar et al., 2021).

## Acoustic Properties of Rumbles and Roars

Sound is a medium to communicate without visual attention and over relatively long distances. Although sound degrades over distances and is attenuated by obstacles in between the signaler and receiver, lower frequencies have the ability to travel longer distances, since their wavelengths are longer and are therefore not as easily attenuated or degraded by obstacles (Stokes, 1845). This is especially applicable for the rumbles of elephants since their fundamental frequency lies in the infrasonic range and is known to be used in long-distance communication, as mentioned before (Baotic et al., 2018; Garstang, 2004; McComb et al., 2003). Rumbles are common vocalizations in elephants and have a harmonic structure. This is typical for the baseline behavior of mechanical and aerodynamic coupling which results in synchronized vibrating vocal folds (Fitch et al., 2002). This leads to a harmonic vocalization where the periodic oscillations are called limit cycles, which are also the most common vibratory regime for the human voice (Fitch et al., 2002).

However, vocal folds are oscillators with a natural limit imposed by the properties of the tissue they are made of and the size of the larynx they are contained in (Fitch et al., 2002). These natural limits add nonlinearity to the behavior of the vocal folds and are responsible for certain phenomena visible in vocalizations like subharmonics, biphonation, and deterministic chaos. In elephants, the roar

vocalization is split into three subtypes which are defined by their manner features (Fant, 1970; Stoeger-Horwath et al., 2007) and the presence or absence of non-linear phenomena (NLP). Manner features describe properties of a sound like the opposing qualities of being tonal or noisy. These features can be identified through visual inspection of a spectrogram. For a tonal sound the frequency contours of the harmonics are visible in the spectrogram and their shape, for example, can be identified and reveal further distinctions (Stoeger-Horwath et al., 2007). For noisy calls, no such frequency contours are visible, since the energy of the call is roughly equally distributed along frequencies, making its properties and perceived sound noisy and not harmonic.

Nonlinear phenomena happen when the vibration of the two vocal folds is out of synchrony. When the differences are in a specific relation like 1:2 the NLP manifests as subharmonics and when the two folds vibrate at different arbitrary ratios the acoustic phenomenon is called biphonation (Fitch et al., 2002). Since coupling between the two vocal folds is relatively strong, biphonation is a relatively rare phenomenon (Fitch et al., 2002). In a study that investigated the NLPs of calf vocalizations for vocal cues indicating arousal levels, no biphonation was found in the roars of the sample (Stoeger et al., 2011). The NLP deterministic chaos can be identified in a spectrogram as a broadband sound with energy distributed across many different frequencies mentioned before as noisy calls. This phenomenon happens when the vocal folds are oscillating in a desynchronized, non-periodic, irregular manner (Fitch et al., 2002). The transitions from one vibratory state to another are called bifurcations. NLP in general as well as the transitions within one vocalization are observed in birds (Fee et al., 1998), humans (Herzel et al., 1994), and many other mammals (Fitch et al., 2002; Tokuda, 2018; Wilden et al., 1998).

The out of synchrony vibration responsible for nonlinear phenomena can have different causes. One reason for the emergence of NLPs can be the limitations of the tissue facing too much pressure for the standard synchronized vibratory regime. Fatigue or limits of control can cause irregularities in the vocal system, causing NLPs (Fitch et al., 2002). Overall NLPs are not pathological or system errors, but they are rather natural outcomes of a biophysical oscillator experiencing varying load or tension (Tokuda, 2018).

There are several explanations as to why NLPs are present in vocalizations of many different species. They make the signal stand out from the background noise or harmonic signals, making it easier to detect (Fitch et al., 2002). A recent study on the topic found that artificially editing vertebrate calls by adding NLPs makes them appear more alarming to human listeners (Terrade et al., 2025) which fits into their proposed function of attention grabbing. Vocalizations of many animals show the presence of NLPs in the context of alarm, aggression, distress and generally states of high arousal (Rendall, 2025; Stoeger et al., 2011). This is suggested to be a potential function to signal arousal and additionally

provide honest cues of physiological stress (Fitch et al., 2002; Fitch & Hauser, 1995). It has also been hypothesized that NLPs do not necessarily have to be an adaptation with advantages but could be just a byproduct of voice production not selected against by evolutionary processes (Fitch et al., 2002).

## African Savannah Elephant Calf Communication

Elephants are well-developed at birth and their precocial abilities are remarkable (Lee & Moss, 1986; Taylor et al., 2022). After birth, elephants are referred to as infants until the age of one, and as calves between 1-4 years of age (Stoeger et al., 2014). Even in the first days of life, infants are able to keep up with the rest of the herd traveling, without the herd having to slow down (Taylor et al., 2022). This has several advantages, such as enabling the mother to keep up with her nutritional needs and ensure herd protection for the calf and neonatal care from other herd members (Taylor et al., 2022). This enhances both the fitness of the calf and the inclusive fitness of the herd (Taylor et al., 2022). Thus, the new mother-offspring unit moves relatively quickly with the herd and especially in the wild, infants usually stay very close and calves relatively close to the mother at all times (Hoerner, Rendle-Worthington, et al., 2023).

In the mother-offspring relationship one of the most important contexts is suckling, the infant/calf nursing from the mother's breast. This behavior is crucial since at the start of life this is the main source of nourishment for the young elephant. In this context, touching each other as well as vocalizing is part of these interactions. The mother usually assumes the suckle stance, where she stands still and puts one front leg a bit forward to give the calf access to the breast. The calf sometimes touches the mother or her front legs with the trunk and stands or walks at the side of the adult female (Poole & Granli, 2011). When the suckling is interrupted or terminated, the calf will sometimes emit loud roars in protest or to request another suckling (Stoeger et al., 2011).

The mother or allomothers are usually in very close proximity, often even tactile contact with an infant. When the offspring reach a more mature state, from 1 year of age onwards, they will become more independent and will also start including food other than mother's milk in their diet (Lee & Moss, 1986). Calves will then also move further away from the family unit, still in the vicinity, to engage in play with other calves or walk up to other families at the waterhole. When they engage in play behavior, loud vocalizations indicating arousal can happen. Just like when young individuals slip in the mud or get pushed by someone, agonistic distress calls are common, and after such occurrence they will mostly seek comfort from the mother or family unit. During calm and affiliative interactions within the family, vocalizations can occur, which are usually soft sounding rumbles (Poole, 2011).

Many behaviors are accompanied by vocalizations and some even by different call types. In the suckling context for example this is the case where rumbles and roars are mostly used to communicate. Rumbles are common as a request to suckle. Roars can be produced when either wanting to initiate suckling and being denied the breast or when a suckle bout is terminated. Suckling is a particularly fascinating context to study vocalizations because it is a behavior only present in infants and calves and where both vocalizations are frequently used in Asian and African elephants (Herler & Stoeger, 2012; Stoeger-Horwath et al., 2007). It seems intuitive that mother-offspring communication often concerns sustenance, assistance or affiliation but more intriguingly, the levels of arousal are also reflected in the acoustic properties of vocalizations of calves. It was found that the duration and the harmonics-to-noise ratio (HNR) were different for vocalizations in an assistance context compared to suckling interactions (Stoeger et al., 2011).

## African Savannah Elephant Calf Acoustic Communication and Behavior

### Rumbles

Studies about young African savannah elephants reveal that they communicate various needs acoustically (Poole, 2011; Stoeger et al., 2011; Stoeger-Horwath et al., 2007). Different situations require different signals to unambiguously relay information of what their current call is referring to. Poole (2011) gives different calf rumbles names depending on the context of production and their acoustic features. Specifically, she found that "*begging rumbles" and "separated rumbles",* are acoustically different, also "*as-touched rumbles", "grumbling rumbles", "umbrage rumbles*" differ from each other significantly along acoustic parameters like duration, bandwidth, maximum frequency, maximum time, curve, fundamental frequency ($F_0$) maximum, contour, $F_0$ maximum to minimum and $F_0$ start (Poole, 2011). This suggests that context modifies the acoustic properties of calls. Behavioral contexts are associated with emotional states to some degree. This was found in adult individuals, where emotional states are reflected in rumble variation (Soltis et al., 2005b).

### Roars

Roars have been explored acoustically in different social contexts (Stoeger et al., 2011; Stoeger-Horwath et al., 2007) and it has been revealed, that acoustic structure including non-linear phenomena (NLP) provide cues indicating the level of arousal in elephant infant roars (Stoeger et al., 2011). NLPs like deterministic chaos may have been an adaptation in vocalizations to make them stand out of the background noise and therefore making them harder to ignore which is crucial in situations that are potentially dangerous (Fitch et al., 2002). African savannah elephant tonal roars are mostly harmonic

in structure, whereas noisy roars are stereotyped in their noisy acoustic characteristic. Mixed roars represent a combination of these two call types with various transitions. The roar subtypes in calves share some characteristics with each other but are acoustically distinct from each other, which presents a compelling case to explore to what extent they are used for a different purpose.

## Research Objectives

While adult elephant acoustic communication is well studied, there are few studies on calf acoustic communication (Stoeger et al., 2011; Stoeger-Horwath et al., 2007). Especially in the wild the vocalizations of African savannah elephant calves have not been studied separately but have been part of broader studies (O'Connell-Rodwell et al., 2007; Pardo et al., 2019; Stoeger et al., 2014). The aim of this thesis is to investigate the acoustic communication of African savannah elephant calves from the population of Addo Elephant National Park. Specifically, in this thesis I will focus on two call types, the rumble and the roar. My aims are to:

1. Provide a descriptive overview of the acoustic parameters and behavioral contexts in use of rumbles and roars in the Addo Elephant National Park.
2. Explore if calf rumbles have different acoustic properties in different contexts.
3. Explore the difference in acoustic parameters in the subtypes of roars.
4. Explore which roar subtype is used in which context and elicits faster reactions from other elephants.

# METHODS

## Study Site and Population

### Study Site

Data were collected at Addo Elephant National Park (Addo: 33°30'S, 25°45'E), Eastern Cape Province in South Africa. The Addo Elephant National Park covers 1 640 $km^2$ and is part of the South African National Parks. The elephants roam in a sub-section of the park encompassing the Main Camp and Matyholweni area (267 $km^2$) (Guldemond et al., 2022). Diverse wildlife can be found in the park, including buffalo (*Syncerus caffer*), black rhinoceros (*Diceros bicornis*), zebra (*Equus quagga*), lion (*Panthera leo*) and leopard (*Panthera pardus*), various antelopes such as red hartebeest (*Alcelaphus buselaphus*), kudu (*Tragelaphus strepsiceros*) and eland (*Taurotragus oryx*) as well as many bird and reptile species (Reardon, 2021). Because of the lack of a river and to manage herbivory, the management has established artificial waterholes throughout the park (Reardon, 2021).

### Population

In the past, this elephant population was highly affected by poaching to the extent that there were only 11 elephants left (Hall-Martin, 1992). In 1931 Addo Elephant National Park (AENP) was founded to protect the last elephants and buffalo of the Eastern Cape Province. A fence was built in 1954 and since then the population has grown steadily (Whitehouse & Hall-Martin, 2000; Whitehouse & Kerley, 2002). The small founding population led to a bottleneck in the gene pool of Addo elephants and therefore they have an unusual characteristic for African elephants: most adult females do not have tusks (Whitehouse, 2002). Individuals from other parks have been introduced to Addo to diversify the genes of the population (park management, personal communication). Whitehouse and Hall Martin determined a population size of 284 individuals at the end of the year 1998 (Whitehouse & Hall-Martin, 2000). The park has a population of 622 elephants as of 2019 (Brett, 2019). In 2024 when the data was collected in the Main Camp and Colchester area, the elephant population consisted of 626 individuals, as counted and reported by park rangers (park management, personal communication).

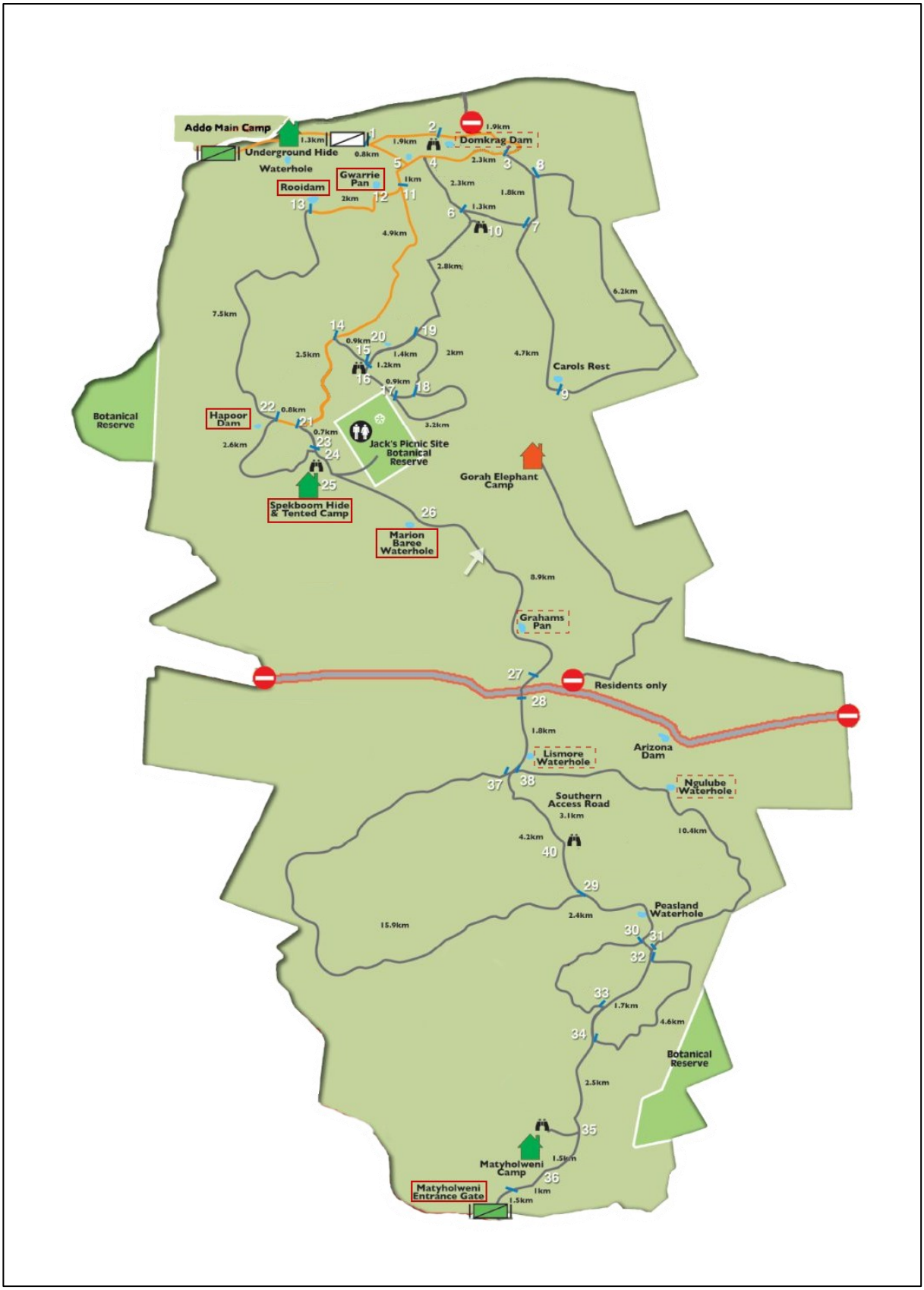


*Figure 1: Map of Addo Elephant National Park adapted from sanparks.org. Main Camp area and Camp Matyholweni (Colchester) area are separated by the road in the middle. Points of interest are highlighted by red border or dashed red border.*

## Data Collection

The data for this research were collected as part of the PhD thesis *Multimodal and intentional communication in African savannah elephants* conducted by Vesta Eleuteri and the Mammal Communication Lab at the University of Vienna.

Data were collected with an all-occurrence, non-invasive sampling approach (Altmann, 1974). Data collection was conducted from 15th January to 15th March 2024 from around 8 a.m. to 6 p.m. daily, depending on weather conditions and presence of elephants. We entered the park in the south through Matyholweni Entrance Gate and drove north by car along the main roads of the park. Elephants gather around waterholes during the warm months, so data collection focused on the main waterholes in the northern section of the Main Camp and Matyholweni. The waterholes where most data were recorded were Marion Baree Waterhole, Spekboom Hide, Hapoor Dam, Rooidam and Ghwarrie Pan (see Figure 2). On one or two occasions, we also collected data at Ngulube Waterhole, Lismore Waterhole, Grahams Pan and Domkrag Dam.

We conducted recordings while in the vehicle in accordance with safety rules of the park. The audio data were recorded with an omnidirectional Neumann condenser microphone (KM183) connected to a MixPre-6 portable recorder at 48 kHz sampling rate and 16-bit resolution. The microphone was positioned on a holster outside of the car door, pointing toward the vocalizing elephants. During recordings we took field notes on the file number of the audio recording, time of vocalization within the file and call type. If the vocalizing individual was seen, the age, sex, identity (if known) and behavioral context were recorded in the notes. We also noted the confidence level of the identification and if the vocalization was also recorded on video. The videos were recorded with a Panasonic HC-VXF1 and taken from inside the car. The date, time, location, weather and other general comments were also noted.

### Caller Identification

When a call occurred, the vocalizing individual was identified visually whenever possible. Elephants sometimes open their mouth while vocalizing, but calls can also be produced through the trunk. In addition, the calling elephant could be inferred from directionality or by matching the behavior of individuals to the perceived vocalization. For instance, if an intense call such as trumpet or roar was heard and one individual in the group simultaneously displayed excited behavior (e.g. sudden movement, head shaking, change in posture, mock charging, running) it was considered likely that this individual had produced the call. In such cases, the caller's ID was recorded with less than full confidence, since it could not be established with full certainty. When no vocalizing individual could be identified, the call was still documented but noted as having an unknown caller.

Individual Identification

Elephants can be individually identified through the shape, notches and tears in the ears. Wrinkles on their head or tusk characteristics can also be used for individual ID (Arivazhagan & Sukumar, 2008; Douglas-Hamilton, 1972; Moss, 1996). When using an ID kit for identification, it must be taken into consideration that tusks can be damaged or broken as well as new holes and notches in the pinna may form due to fights or interaction with the environment. Of the more than 600 individuals in the park, over 100 males and 25 females are included in the ID kits. Overall, we recorded and identified 15 adult females and 21 adult males based on the ID kits of the park during data collection. These were females from the families A, B, H, M, L, P, R, and prominent males with distinctive features that made it possible to identify them reliably within large groups of elephants. For 25 adult females, typically leaders of matrilines, the original family association is documented in the ID kits. This allowed us to know if part of a certain family was present at the waterhole, data which was also recorded in the field notes.

Sex identification

Adult elephants have a sexual dimorphism that is detectable by sight. Adult male elephants have a body height of around 300 cm, reaching up to 350 cm at the shoulder whereas adult females have an approximate shoulder height of 200–250 cm (Shrader et al., 2006). Furthermore, the shape of the head can help to identify the sex of the elephant in subadult individuals. Female elephants tend to have narrower heads and in subadult males, especially the area between the eyes is broader and the head in general bigger and bulkier (Moss, 1996). The best visual cue to identify the sex of an individual is the external reproductive organs. If these are clearly visible the elephants' sex can be unambiguously determined. However, this is often not the case because they are located between the hind legs and are often obscured from view. When elephants are urinating, identification of the gender becomes more obvious because males urinate with their penis outside the body which makes it clearly visible from all sides. When the penis retracted into the sheath, there is a difference in shape from behind in adult individuals. The vulva, seen from behind, extends approximately parallel to the ground with the opening facing downward. Adult females can also be distinguished by the mammary glands. They are located between their front legs and after giving birth to and nursing a calf, the female will have more pronounced breasts than males.

In addition, many females in Addo Elephant National Park do not have tusks because of the extensive poaching, which caused a genetic bottleneck of this population in the early 20th century (Whitehouse, 2002). Individuals lacking tusks due to genetic abnormalities were not targeted by poachers since they had no ivory to obtain. Therefore, the absence of tusks can serve as an indication to identify the sex, but only within this population. All adult males in Addo have tusks.

Age identification

The age was estimated using criteria such as height, behavior, and group composition. The age group categories are based on Stoeger et al., 2014 with infants (0-1 years), calves (1-4 years), juveniles (5-12 years), subadults and adults (>13 years) for females (Stoeger et al., 2014). The most accessible and obvious factor on-sight to determine age is the height of the elephant. Infants can usually fit underneath the belly of the mother or any other adult female. The behavior of infant elephants is often still uncoordinated and typically oriented toward the caregivers, primarily the mother but also older, typically female members of the core family. Calves are about one third of the size of an adult female. They engage in a lot of play with each other and are very vocally active. Calves are still nourished by their mothers' milk and can regularly be observed suckling. In comparison to infants, calves are a lot more independent and can be spotted further away from the core family than infants. Sometimes the tusks of calves are already visible but usually only as little stumps (Moss, 1996). Juveniles are about two-thirds to three-quarters (depending on age) the height of an adult African savannah elephant female (Moss, 1996; Shrader et al., 2006). They sometimes help with the caretaking roles within the family unit or bonding groups. They still engage in play behavior but are not as active and wild as calves. The most reliable factor apart from behavior is the height of an elephant to determine their age. At around 15-20 years of age the yearly growth rate declines and thus it is not possible to determine an exact age of adults based on the visual method alone (Arivazhagan & Sukumar, 2008). For our purpose of assigning the individuals to an age class, identifying age through visual assessment and comparison alone was sufficient, though with some degree of subjectivity.

## Behavior and Vocalizations

*Table 1: Ethogram of elephant behavior (adapted from Eleuteri, 2025)*

| **Name of context** | **Definition of context** |
|---|---|
| Unknown | When it is unknown which behavior it is. |
| Unclear | When it is unclear which behavior it is. |
| Affiliation | An Individual affiliates with another one in general. Usually included tactile behaviors like hugging with trunk, touching temporal glands touching mouth, touching genitals. |
| Reassurance | An individual performs affiliative behaviors to another individual after they have been attacked or were distressed. |
| Little greeting | An individual greeting another after a period of separation. Little greeting behavior includes: A rumbling greeting exchange between members of an elephant family in which one approaches another. Typically, the approaching elephant gives a 'little greeting rumble' and the elephant being approached, responds by head-raising, ear-lifting and sometimes backing-towards the approaching elephant and gives a 'little greeting rumble' in return. Often both |

| | |
|---|---|
| | individuals engage in the described body acts and may social-rub and ear-brush against one another or otherwise touch one another or greet trunk-to-mouth. |
| Greeting ceremony | An individual taking part in a group greeting. Greeting ceremony behavior includes: Members of a family or bond group may rush to meet one another while emitting loud, modulated, throaty greeting rumbles and sometimes social trumpets and roars. The elephants raise their heads, lift and spread their ears, secreting from the temporal gland. As they meet, they flap their lifted ears rapidly, while still vocalizing. Rubbing together they may stand in parallel or face to face and while holding heads high, open mouth to open mouth they may click their tusks together and entwine trunks. As the greeting continues, they may back into one another urinating and defecating. |
| Contact call | An individual calling to find family members or mother. Usually a young individual (calf) emits a contact call. Contact call behavior includes head raised, ears spread, walking and looking while rumbling. The individual can start running once a reply call was given or the other individuals searched for were found. |
| Initial contact call | An individual emits the first contact call. Initial contact call only happens when followed by a reply contact call otherwise it is labeled as contact call. |
| Reply contact call | An individual replies to the contact call of another individual and therefore helps the individual initial contact calling in finding them. |
| Defensive | An individual bunches together with others or protects an individual or group after hearing or seeing a threat. |
| Agonistic | An individual mocks, displaces or aggresses another individual (also from other species) to assert dominance or for competition over something. Also includes a protest or distress call when an individual has received any form of aggression like mock, displace or push. |
| Digging | An individual digs the ground with their tusks (or attempts to in case of missing tusks in females or calves) |
| Drinking | An individual drinks water. |
| Dusting | An individual dusts themselves with dry soil. |
| Bathing | An individual bathes in a water hole. |
| Feeding | An individual browsing or grazing. |
| Listening | An individual standing still, sudden freezing or tense posture, with ears spread and overall attentive body posture. Often listening includes having one foot up with just the front touching the ground. |
| Mud-Bathing | An individual is wallowing in mud or covering themselves with mud |
| Let's go rumble | An individual is rumbling while facing away from the site, waiting for the herd to gather, then leaving the site. |
| Suckling | An individual is engaged in a sucking interaction. Either the mother or the calf vocalizes directly before, after or during the calf is suckling. When it was not clear if it is suckling intention or termination. |
| Suckling intention | An individual (infant, calf) wants to initiate a suckling interaction, standing close to the mother, touching usually the front legs of the mother with their trunk. |
| Suckling termination | When the suckling interaction was terminated either by mother and offspring being interrupted an external event or by the mother moving. |

| | |
|---|---|
| Play social | An individual is playing in general with another individual. |
| Play solitary | An individual is playing by themselves, including playing with objects. |
| Play social water | An individual is playing with another individual in the water. |
| Sparring | An individual spars with another one and includes physical contact like pushing, tusking, entwining trunks and tusks and ramming while facing each other. |
| Resting | An individual is not engaged in any of the other active contexts like traveling, feeding etc. and is relaxed either standing up or laying down. An individual can flap ears for thermoregulation and move their trunk while resting. |
| Post copulation behavior | An individual performs signals/behaviors after he/she mated (may include vocalizations, visual displays, defecation, urination, touching genitals etc.) |
| Mating pandemonium | An individual performs signals/behaviors during or directly after the mating of other individuals in the close vicinity and/or of the same herd. Includes behavior like vocalize, display, urinate, defecate and touch genitals. |
| Sex | An individual has sex or produces sexual behavior (only with physical contact) with another one of the opposite sex. For example, if a male mounts a female. |
| Socio-sexual Behavior | An individual produces sexual behaviors towards another one of the same sex like mounting, showing erect penis. |
| Musth | An individual in musth (temporal gland secretion and urine dribbling) showing advertisement behaviors specific to males in musth towards any sex like musth stance and walk. |
| Consortship | An individual is in Consortship with another, typically a male following a female allegedly in estrus and spending time together |
| Swimming | An individual swimming in a body of water. Different from bathing in that the individual usually travels by swimming like crossing a river. |
| Traveling | An individual is locomoting. |
| Dominance | An individual performs behaviors believed to be signs of asserting dominance towards another individual like trunk curl, holding object with trunk or displacing another one. |
| Birth | An individual performs signals/behavior during or after the birth of a newborn. |
| Death | An individual performs signals/behaviors towards a dying individual, a carcass, or bones. |

For purposes of analysis, certain behaviors were grouped into the categories a*gonistic, affiliative, contact call, greeting, play* and *suckling*. The agonistic and affiliative context were not grouped further and contain only the behavior specified in the ethogram (Table1). Table 2 displays the behaviors that were combined into broader behavioral categories.

*Table 2: Main categories of grouped behaviors for the context analysis of rumbles and roars.*

| **Contact call** | **Greeting** | **Play** | **Suckling** |
|---|---|---|---|
| Contact call | Little Greeting | Play solitary | Suckling |
| Initial contact call | Greeting ceremony | Play social | Suckling intention |
| Reply contact call | | Play social water | Suckling termination |

The contexts *affiliative, contact call, greeting* and *suckling* were chosen for the rumble analysis because most rumbles qualifying for the analysis occurred in these contexts. Similarly, the contexts *agonistic, play* and *suckling* were chosen, because most roar vocalizations were collected in these social behaviors.

*Figure 2: Photo from data collection shows two calves nursing from their mothers, exhibiting suckling behavior. Both mothers display the typical suckle stance body position.*

*Table 3: Definitions of African savannah elephant call types (based on Stoeger-Horwath et al., 2007).*

| **Name** | **Definition** |
|---|---|
| Rumble | Tonal/tonal with noise. Low frequency calls with clear harmonics and often with formant formation that can contain more energy than the fundamental. |
| Trumpet | Noisy harmonics. Nasal sound, produced in the trunk, is tonal but overlaid with noise. |
| Tonal Roar | Tonal. Containing clear harmonics, show different grades of modulation, more than 50 percent of the call is tonal, the end can be noisy. |
| Noisy Roar | Noisy. Unmodulated, noisy sound with no harmonic elements to it. |
| Mixed Roar | Tonal and noisy. Roar with alternating or mixing structure of noisy and tonal segments. |
| Bark | Transient and mainly noisy call, very short duration. |
| Grunt | Noisy with first indications of harmonics, only recorded in the first 2 months of age. |
| Snort | Noisy. Short burst of air out the trunk without producing a tonal signal and a proper sound. |
| Unknown | Unclassifiable vocalization. |
| Unclear | Vocalization is not clearly identifiable. Either a mix of two vocalization types, none of the above-described vocalization types or unclear if even elephant vocalization. |

## Data Analysis

Acoustic Annotations

All calls recorded for this thesis were annotated in S_Tools-STx (STx), version 5.1.1 (Balazs et al., 2000), a software by the Austrian Academy of Sciences, Acoustic Research Institute. The calls were located through the noted time and file from the fieldnotes as well as through visual inspection of the spectrogram. The beginning and end of a call were marked and metadata, such as caller identity and behavioral context, were added following the field notes (see Figure 2, Table 4). With this method, each call was assigned an individual identification number, and the metadata saved alongside it. When there was a calling event with multiple overlapping calls, the annotation method consisted of first creating an event (e.g. addo.00512) containing all overlapping calls. Then the individual calls within the event were annotated with the same call ID adding a letter at the end, beginning with 'a' and following alphabetical order of occurrence of the calls (e.g. addo.00512a, addo.00512b etc.). For each call, the call type was chosen based on the initial field notes, the acoustic impression of the call, and the spectral characteristics of the spectrogram based on the classification in Table 3 (Stoeger-Horwath et al., 2007). The annotation panel in STx contained several categories that were filled out according to the field notes, the context of the call, and the properties of the sound file and call, as specified in Table 4. Out of all annotated calls, those from calves with known call type and context and with good quality were selected for further analysis. Specifically, all rumbles and roars with a quality rating of 1 to 3 (Table 4) and known context were chosen for analysis. The individual clips of the calls of interest were extracted from the original sound files and saved with a padding of 0.5 seconds at the beginning and end of each call for better view in the analysis process.

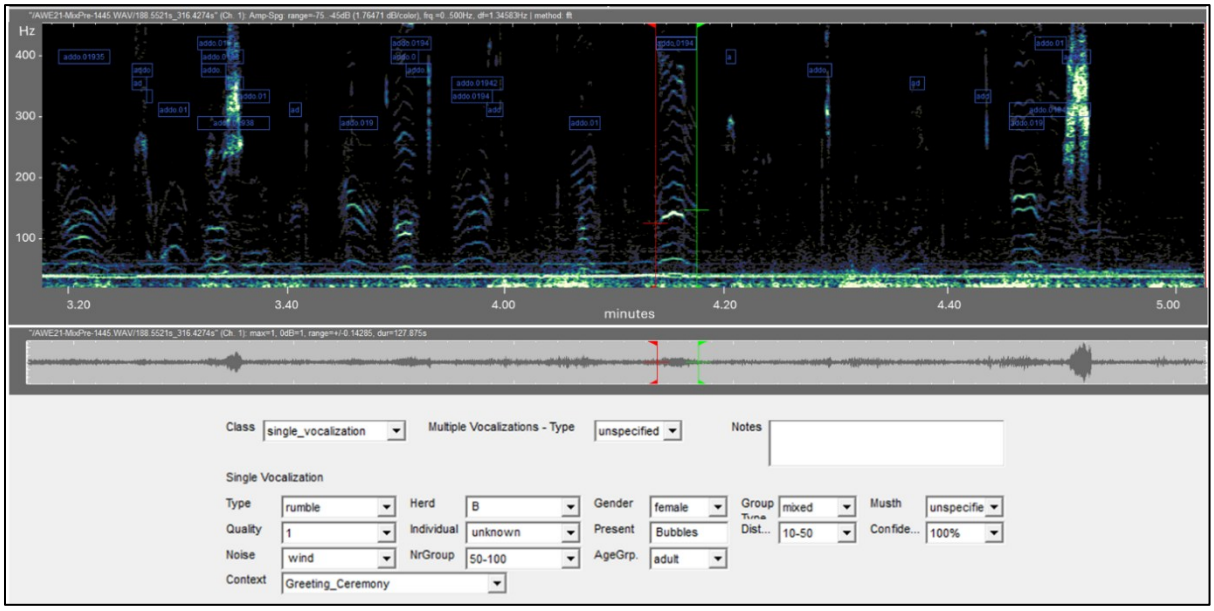


*Figure 3: Screenshot of the annotation in STx. Spectrogram displayed in the upper half of the image with vocalizations (mostly rumbles) visible. Lower half of the image shows the annotation panel where the metadata is entered and saved.*

*Table 4: Categories of STx annotation panel with all variables, their definitions and selection options during annotation.*

| **Variable** | **Definition** | **Options** |
|---|---|---|
| Class | Specifies if the annotated section defines one or multiple calls | single_vocalization, multiple_vocalization |
| Multiple vocalizations - type | Specifies what kind of multiple vocalizations are annotated | unspecified, combination, overlapping, chorus, unknown |
| Type | Call types based on call type definition | See Table 2: Definitions of African savannah elephant call types |
| Quality | Quality of the call based on amplitude and contrast from the background | 1, 2, 3, 4, 5 |
| Noise | Prominent background sound, or any sound masking the vocalization or overlapping with the vocalization. | unspecified, water, addo_noise, car_noise, plane, wind, rain, generator, talking_humans, animal (bird, lion, zebra, antelope, buffalo, cheetah, leopard, rhino, canoidea, unknown), unknown |
| Context | Behavioral context the call was produced in based on ethogram | See Table 1: Ethogram of elephant behavior |
| Herd | Specifies what herd/family was present when recording, based on identified individuals during the recording session | unknown, males, unspecified, alone_individual, unknown_family, A, B, H, L, M, P, R; |
| Individual | See individual identification | [type name of Individual], unknown, unspecified; |
| NrGroup | The number of individuals that were present at the waterhole during recording | 1, 2-5, 5-10, 10-20, 20-50, 50-100, 100+, unknown, unspecified; |
| Gender | Biological sex of the individual vocalizing | unspecified, male, female, unknown; |
| Present | For writing down the Names of identified Individuals to look up in ID kit and trace back to the correct family | [type name(s) of Individual(s)] |
| AgeGrp | Age group of the vocalizing individual | unspecified, infant, calf, juvenile, adult, unknown; |
| Group Type | Composition of the group of elephants present during the recoding | herd, males, mixed, alone_individual, unknown; |
| Distance | Estimated distance from the microphone to the vocalizing individual | unknown, 0-10, 10-50, 50-100, 100+; |
| Musth | If a male in Musth is present or not | unspecified, yes, no; |
| Confidence | Level of certainty with entering the sex and age identification of the vocalizing individual | unspecified, 100%, 80%, 50%, unsure; |

Rumble Annotations with MATLAB Contour Annotation Tool

After all recorded calls were annotated with STx, it was possible to filter the calls and select those of interest. All calf rumbles were selected and filtered for good recording quality (1-3), in total, 186 calf rumbles met this criterion. Using the contour annotation tool, individual harmonics were annotated, which provided precise output for time-frequency measurements. These served as foundation for calculating time-frequency related acoustic parameters (Table 8).

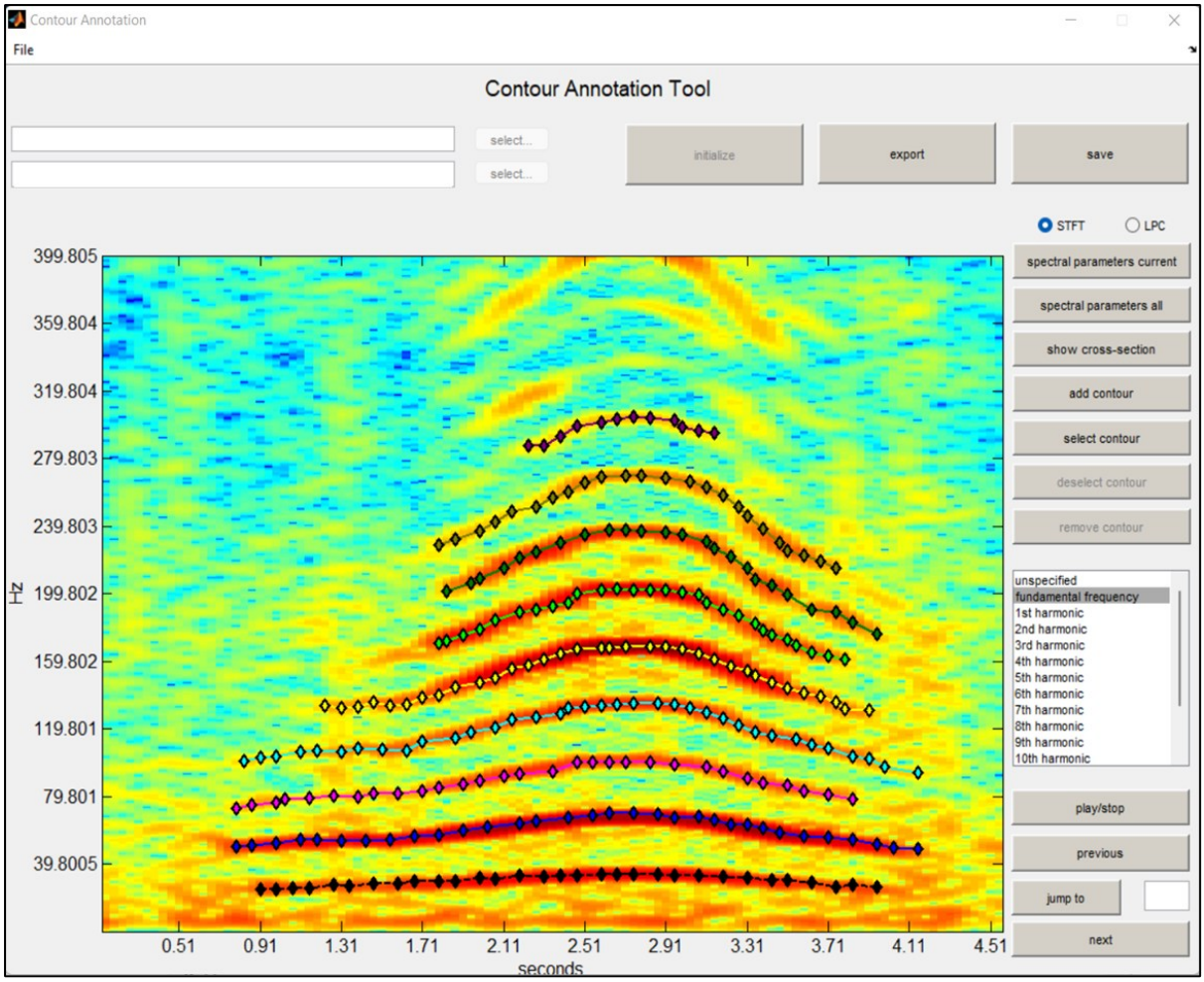


*Figure 4: Screenshot - Spectrogram of a rumble in the custom made semi-automatic annotation in MATLAB developed by Zeppelzauer & Stöger 2015. The tracking of frequency contours is shown for the fundamental frequency (black), 1st harmonic (blue) and following harmonic contours above in chronological order.*

The rumbles were further annotated with the contour-tracking tool in MATLAB developed by Zeppelzauer and Stoeger (Zeppelzauer & Stoeger, 2015). For each rumble (n=186) in the contour annotation tool, measurements of time and corresponding frequency were available in uniformly sampled steps of 0.01 seconds across the entire duration of all annotated contours. The same measurements were also obtained in non-uniformly sampled steps, with 60 time-frequency measures directly from the contour tracking, for each call.

Of 186 calf rumbles overall, the fundamental could be measured for 80 rumbles with the contour annotation tool. For 106 rumbles, the fundamental frequency was not visible in the spectrogram due to noise in the environment and therefore only harmonics could be measured, and the fundamental frequency was calculated from them. The fundamental frequency was calculated from the lowest harmonic annotated (Table 5) with the contour annotation tool (Zeppelzauer & Stoeger, 2015).

*Table 5: Overview of the numbers of fundamental frequencies measured and calculated.*

| **Way of the fundamental** | **Absolute amount (n)** | **Relative amount (%)** |
|---|---|---|
| Fundamental frequency measured | 80 | 43.0 % |
| Calculated from 1st harmonic | 78 | 41.9 % |
| Calculated from 2nd harmonic | 12 | 6.5 % |
| Calculated from 3rd harmonic | 7 | 3.8 % |
| Calculated from 4th harmonic | 3 | 1.6% |
| Calculated from 5th harmonic | 4 | 2.1 % |
| Calculated from 6th harmonic | 0 | 0 % |
| Calculated from 7th harmonic | 2 | 1.1% |

In total, for 57% of rumbles the fundamental frequency could not be measured because it was not visible for manual annotation due to strong background noise. For those calls, the lowest measurable harmonic (Table 5) with high energy was chosen to calculate the fundamental. This was done by dividing each frequency step, for the entire duration of the call by (n+1) where n is the harmonic number. For example, when calculated from the 2nd harmonic the time steps of 0.01 seconds were kept but the corresponding frequencies in this case were all divided by 3 (2+1). This provided a calculated estimate of the fundamental for the calls where measuring the fundamental was not possible. This approach was chosen for calculating the fundamental frequencies, since the general formula for the frequency of the $n^{th}$ harmonic ($f_n$) in acoustics is $f_n = (n+1) * f_0$ where $f_0$ is the fundamental frequency. Therefore, calculating the fundamental frequency, the relationship looks like this: $f_0 = f_n / (n+1)$. Thus, to obtain values for the fundamental frequency, the 2nd harmonic ($f_2$) had to be divided by 3.

### Roar Annotation with Raven Pro

Since roars are less uniformly harmonic than rumbles, Raven Pro (version 1.6) (K. Lisa Yang Center for Conservation Bioacoustics, 2024) was used to measure acoustic parameters for roar vocalizations. Different entropy parameters, as well as duration and peak frequency were measured using Raven Pro. To conduct these measurements a selection box was drawn over the entire visible spectrogram for each individual call which enabled a detailed investigation of average, minimum and maximum entropy

measurements. Example spectrograms of the three roar types, generated in Raven Pro are shown in Figure 5 without selection boxes for better visualization.

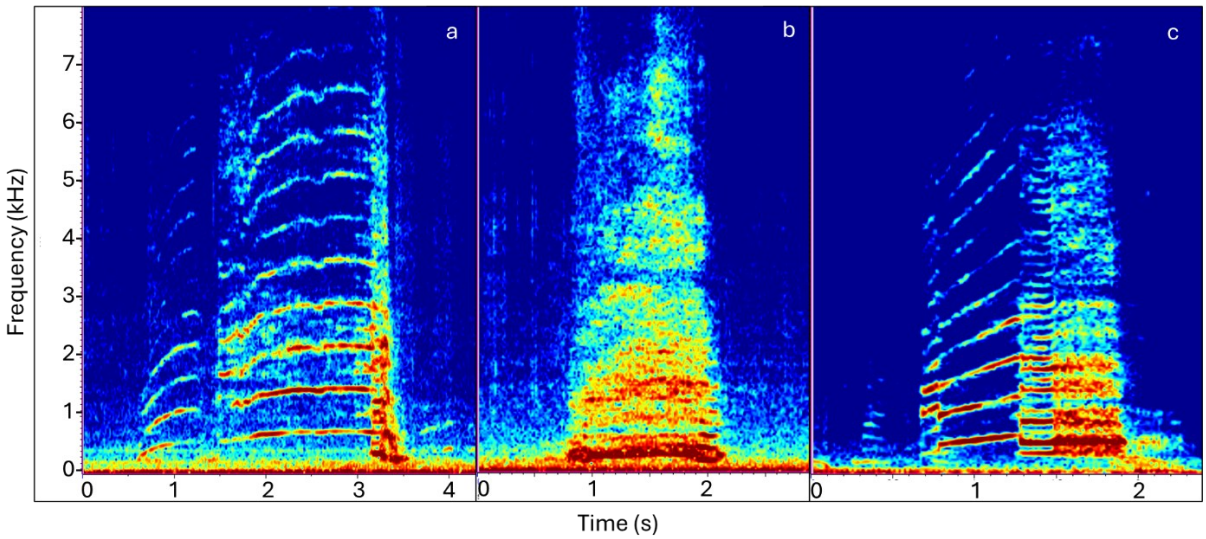


*Figure 5: Spectrogram of an exemplary tonal roar (a), noisy roar (b) and mixed roar (c) all emitted in a suckling context. Visualization with Raven Pro 1.6.*

### Classification based on Entropy Parameters

To quantify the acoustic spectrum and differences between roar subclasses, an acoustic analysis focusing on entropy was conducted. Raven Pro 1.6 (K. Lisa Yang Center for Conservation Bioacoustics, 2024) was used to obtain these measurements for each call. This was done to further support the audio-visual classification of the categories and to describe the different roar subtypes in greater detail.

*Table 6: Acoustic parameters and definitions for analysis of roars in Raven Pro 1.6.*

| **Acoustic parameter** | **Definition** |
|---|---|
| Duration (s) | Duration of the call in seconds |
| Peak Frequency (Hz) | Frequency with the highest amplitude within a given selection |
| Average Entropy (bits) | Entropy per slice, averaged across slices in the selection |
| Min Entropy (bits) | Minimum entropy observed across all spectrogram slices within the selection |
| Max Entropy (bits) | Maximum entropy observed across all spectrogram slices within the selection |

The selection boxes in Raven were drawn precisely around each individual call. Entropy in Raven is computed on a per-spectrogram-slice basis. This means that entropy was calculated by assessing the energy distribution across frequencies for each time slice. This can be treated as a probability distribution, and the use of logarithms allows for measurements of how widespread or distorted the energy of the sound is. The result is entropy in bits, indicating how many binary units of uncertainty

exist in the spectral distribution. A higher value of bits means the energy is more evenly distributed, which equals higher entropy (K. Lisa Yang Center for Conservation Bioacoustics, 2024).

### Non-Linear-Phenomena of Roar Vocalizations

Since the subcategories of roars are distinguished by the presence of specific NLPs, we investigated the presence of harmonics, subharmonics, deterministic chaos, and frequency jumps by visually inspecting the spectrogram. Each selected roar (single calls, known context, quality rating 1-3) was visually inspected and the presence of these acoustic features was documented. The analysis was carried out in Raven Pro (K. Lisa Yang Center for Conservation Bioacoustics, 2024) to provide a descriptive overview of NLP counts for each roar type and behavioral context.

## Behavior Coding

To further analyze the different roar subtypes, we conducted additional behavioral coding (see Table 7) using Behavioral Observation Research Interactive Software version 9.4 (BORIS) (Friard & Gamba, 2016). Specifically, videos that matched the annotated roars (if available) were coded to measure the reaction time of other elephants to different roar types. All behaviors in BORIS were coded as point events.

*Table 7: Variables used in behavioral coding showing names of variables, their definitions and additional information to the behaviors and coding scheme.*

| **Name** | **Definition** | **Additional information** |
|---|---|---|
| Vocalization | Marked the onset of the call from the focal calf, this marked the onset of the observation | Beginning of observation |
| Touch | AF/AM/J/C touches the calling calf with any body part | Behaviors were individually codable for each age group and sex for adults AF (adult female), AM (adult male), J (juvenile), C (calf) and are counted as reaction to that roar, if produced up to 15 seconds after the roar and in the direction of the focal calf |
| Touch mouth | AF/AM/J/C touches the calling calf's mouth | |
| Look | AF/AM/J/C adjusts head position to look to calling calf | |
| Move ears | AF/AM/J/C moves own ears, visibly different than before the calf call | |
| Move towards | AF/AM/J/C turns, walks, runs towards calling calf | |
| Move away | AF/AM/J/C turns, walks, runs away from calling calf | |
| Suckling | Calling calf starts suckling, indicated by mouth to nipple contact, trunk of calf usually lifted above head | Behaviors performed by the calling calf and for suckling context only |
| Suckle stop | Calling calf stops suckling, no more mouth to nipple contact, head of calf returns from lifted to straight position | |

| | | |
|---|---|---|
| AF Suckle stance start | Individual takes on suckle stance, by being stationary, standing with one of the front legs placed more to the front than other to give easy access to the breast | Behaviors specific for adult female (most likely the mother of calling calf) and suckling context, these are not only reaction to a call; variables were chosen to follow the structure of suckling interactions specifically. |
| AF Suckle stance stop | Individual tops suckle stance by putting forward front leg back or starts locomoting | |
| AF moves | Individual starts locomoting (turning, walking, running) or changing standing position without moving from the spot | |
| AF stops moving | Individual resumes located on one spot after turning, walking or running | |

Analysis of Reaction Time to Roars

The reaction time to calf roars was calculated by subtracting the onset time of the reaction behavior from that of the vocalization. Many vocalizations could not be analyzed because no suitable video of the call or the reaction behavior was available.

## Statistical Analysis

Analysis of Rumbles

After obtaining the uniform sampled and non-uniform sampled time-frequency measures of the fundamental frequency for each rumble, all shape and contour, absolute frequency, and temporal parameters (Table 8) were calculated based on these measurements. Only time- and frequency related parameters were calculated since no uniform amplitude measures were available for analysis because the distance to the vocalizing individual during data collection was not standardized. The acoustic parameters are entirely based on Wood et al., (2005) and were also used in investigating social rumbles of male African elephants by Stoeger & Baotic, (2016).

*Table 8: Acoustic parameters and their definition and calculation for analysis of rumbles based on (A. S. Stoeger & Baotic, 2016; Wood et al., 2005).*

| **Acoustic Parameter** | **Description** |
|---|---|
| Shape and Contour Parameters | |
| COFM (Coefficient of Frequency Modulation)<br>(McCowan & Reiss, 1995) | Represents the amount and magnitude of frequency modulation across a rumble, computed by summing the absolute values of the difference between sequential frequencies divided by 10 000:<br>$$COFM = \sum_{n=1}^{N-1} \lvert Y_{n+1} - Y_n \rvert \div 10\,000$$<br>Where $Y_n$ = frequency at the $n^{th}$ time step, N = total number of time steps |

| | |
|---|---|
| FVI (Frequency Variability Index) (Mitani & Brandt, 1994) | Represents the magnitude of frequency modulation across a rumble, computed by dividing the variance in the frequency by the square of the average frequency of a rumble and then multiplying the value by 10. $(Variance\ of\ average\ frequency) \div (average\ frequency)^2 * 10$ |
| Start Slope | Calculated as $(Frequency\ 20 - Frequency 1) \div (Time\ 20 - Time\ 1)$ |
| Middle Slope | Calculated as $(Frequency\ 40 - Frequency\ 20) \div (Time\ 40 - Time\ 20)$ |
| Final Slope | Calculated as $(Frequency\ 60 - Frequency\ 40) \div (Time\ 60 - Time\ 40)$ |
| Absolute Frequency Parameters | |
| SF (Start Frequency) | Fundamental frequency at the start of the rumble (Hz). |
| MF (Middle Frequency) | Fundamental frequency at the middle of the rumble (Hz). |
| FF (Finish Frequency) | Fundamental frequency at the end of the rumble (Hz). |
| MIN (Minimum Frequency) | Lowest measured frequency of the fundamental (Hz). |
| MAX (Maximum Frequency) | Highest measured frequency of the fundamental (Hz). |
| MEAN (Mean Frequency) | Calculated as average frequency across the fundamental (Hz). |
| FR (Frequency Range) | Calculated as maximum frequency minus minimum frequency (Hz). |
| Mean 1st Third | Mean fundamental frequency of the first third of the sound segment (Hz). |
| Mean 2nd Third | Mean fundamental frequency of the second third of the sound segment (Hz). |
| Mean 3rd Third | Mean fundamental frequency of the last third of the sound segment (Hz). |
| Temporal Parameters | |
| Duration | Temporal distance of the entire rumble measured in seconds (s). |
| Min Frequency Location | Location of the minimum frequency on the fundamental contour. Normalized not in seconds (0 indicating beginning and 1 indicating end of the call, calculated as: $(t_{event} - t_{first}) \div (t_{last} - t_{first})$ Where $t_{event}$ is the time of the minimum frequency |
| Max Frequency Location | Location of the maximum frequency on the fundamental contour. Normalized not in seconds (0 indicating beginning and 1 indicating end of the call, calculated as: $(t_{event} - t_{first}) \div (t_{last} - t_{first})$ Where $t_{event}$ is the time of the maximum frequency |

Before analyzing the acoustic differences of rumbles between contexts, the acoustic differences of single and combined rumbles were investigated. For this, all acoustic parameters (Table 8) were tested using a Mann-Whitney U test (Mann & Whitney, 1947) to see if they show differences between rumbles produced as single calls and rumbles produced as combined calls. Assumption checks including Shapiro-Wilk (Shapiro & Wilk, 1965) and Levene (Levene, 1960) were applied before testing and Benjamini-Hochberg false discovery rate (BH FDR) (Benjamini & Hochberg, 1995) and Bonferroni (Bonferroni, 1936) were used to perform required corrections. Error bars were created for parameters with significant results. The tests and visualizations were done in R Studio (version 4.4.2) (R Core Team, 2024) using the packages stats, car and ggplot2.

### Principal Component Analysis (PCA)

To analyze the differences of acoustic parameters (Table 8) between contexts, we conducted a PCA (Hotelling, 1933) with varimax rotation and Kaiser normalization. For this all variables were z-scored beforehand to correct for different units making their variances comparable. Kaiser-Meyer-Olkin (KMO) and Bartlett's test of Sphericity were conducted to ensure the data is adequate for PCA analysis. Retaining components of the PCA was based on parallel analysis and scree plot inspection. The factor scores of the PCA were used to further conduct the discriminate function analysis. For the computation and visualization of the PCA results the packages psych, GPArotation, nFactors and ggplot2 in R Studio version 4.4.2 (R Core Team, 2024) were used for this analysis.

### Discriminate Function Analysis (DFA)

The first three principal components were used for the DFA as justified by scree plot and parallel analysis. A nested permuted discriminant function analysis (pDFA) (Mundry & Sommer, 2007) was conducted because of the given data structure. We did not obtain true individual identity when collecting the data, therefore we created a proxy ID parameter. This means the same ID was assigned for calls that were in consecutive order (with up to 2 calls in between allowed) and from the same context. Like this we could make sure that calls coming certainly from the same individual are classified as such. Therefore, each caller (proxy ID) only exists in one context which makes caller identity and context confounded (ID nested within context). To account for this, a nested pDFA with cross validation blocked by ID and permutations within IDs was used. The nested pDFA was performed on all rumbles with known context where context was the test factor and individual (proxy ID) the control factor. Since acoustic discrepancies between single and combined rumbles exist and the proportion of them was not the same between contexts (Table 10) we conducted the pDFA on all rumbles as well as on the subset of rumbles containing only single calls. The tests were performed in R Studio (version 4.4.2) (R Core Team, 2024) using the package MASS: :lda and applying Roger Mundry's R function for nested pDFA (Mundry & Sommer, 2007).

## Analysis of Roars

To analyze acoustic differences between the roar types, statistical tests were carried out. Assumption checks included tests for normal distribution with the Shapiro-Wilk test (Shapiro & Wilk, 1965) and for homogeneity of variances with Levene's test (Levene, 1960). Data for each entropy parameter and roar type were tested to assess distributional properties of the data before examining group mean differences.

As an initial step, a PERMANOVA (Anderson, 2001) was conducted on all entropy parameters together. PERMANOVA is a permutation-based test that was used on the z-scored entropy parameters and is robust to non-normality and unequal variances. It was conducted because the entropy parameters are correlated and fit together conceptually, to see if roar type explains variation across entropy parameters. This test is sensitive to differences in dispersion which is why it is followed by a PERMDISP to investigate whether the PERMANOVA can be taken as a true mean difference. Further the pairwise PERMANOVA was conducted, and the p-values were corrected with the Benjamini-Hochberg False Discovery Rate (BH FDR) test (Benjamini & Hochberg, 1995). This allows us to see which roar types differ from each other considering all entropy parameters together. These tests do not give detailed insight into the magnitude or direction of differences. Therefore, tests for each individual parameter of entropy but also for duration and peak frequency were conducted to determine differences between the roar types.

The tests for each individual parameter were chosen considering the assumption checks performed beforehand. The parameter average entropy was tested with Welch's ANOVA (Welch, 1951) and Games Howell. Maximum entropy differences between roar types were investigated with an ANOVA (Fisher, 1992) and Tukey. Minimum entropy, duration and peak frequency were tested with a Kruskal Wallis (Kruskal & Wallis, 1952) test, Dunn and Cliff's delta to examine differences between roar types. The packages vegan, stats, rstatix, effectsize, effsize, rcompanion, ggplot2, dplyr, and tidyr were used in the process of computing and visualizing the results for the roar analysis.

For all statistical tests in the analysis of rumbles and roars R version 4.4.2 was used for computation (R Core Team, 2024) and ChatGPT (OpenAI, 2025) was consulted to partially assist with the drafting and troubleshooting of R scripts.

# RESULTS

## Calf Rumbles

Single Rumble vs Part of a Combination Rumble

Of all 186 calf rumbles, 122 (65.6%) were single rumbles and 64 (34.4%) rumbles were part of a combined call either roar-rumble (Figure 6, a & b), rumble-roar, rumble-roar-rumble or roar-rumble-roar. To test whether single rumbles and combined rumbles differ acoustically, first a Shapiro-Wilk (Shapiro & Wilk, 1965) and Levene test (Levene, 1960) were performed and showed that data within these groups were not normally distributed and that variances were not homogenous. Therefore a Mann-Whitney U test (Mann & Whitney, 1947), with BH-FDR (Benjamini & Hochberg, 1995) and Bonferroni corrections (Bonferroni, 1936) was performed for each acoustic parameter defined by Wood et al., (2005). The test revealed that single calls and combined calls differ in duration, start frequency, finish frequency, start slope, and maximum frequency (Table 9) with the Bonferroni correction indicating a strong effect. Furthermore, the parameters minimum frequency, mean 1st third frequency, mean 3rd third frequency, mean frequency and final slope were different in single versus combined calls considering BH-FDR correction.

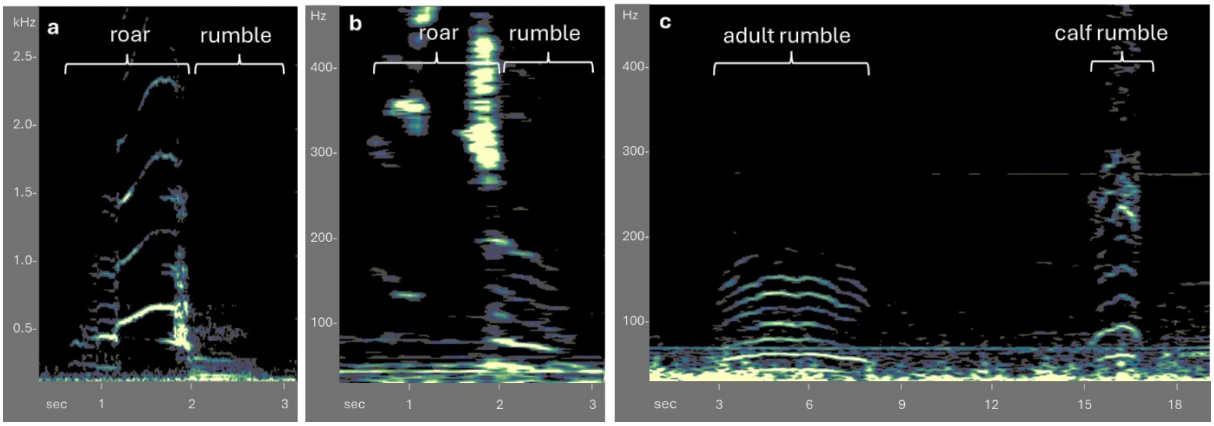


*Figure 6: Spectrograms of a roar-rumble (a & b) and a calf rumble next to an adult rumble (c). Figures a & b show the same combined call in different frequency views highlighting the roar (a) and rumble (b). Brighter areas of the spectrogram encode higher amplitude.*

*Table 9: Median values for single and combined rumbles with results of Mann-Whitney U test of significant different acoustic parameters between groups.*

| **Acoustic parameters** | **Single (n = 122)** | **Combined (n = 64)** | **Mann-Whitney U** | **p-value** | **Cliff's δ** |
|---|---|---|---|---|---|
| Duration | 1.84 s | 0.92 s | 6836 | < 0.001 | 0.75 (large) |
| Start frequency | 25.4 Hz | 29.8 Hz | 2413 | < 0.001 | -0.38 (medium) |
| Max frequency | 29.9 Hz | 33.3 Hz | 2812 | 0.0018 | -0.28 (small) |
| Finish frequency | 24.2 Hz | 27.9 Hz | 2413 | < 0.001 | -0.38 (medium) |
| Start slope | 3.99 Hz/s | -0.89 Hz/s | 5288 | < 0.001 | 0.35 (medium) |

The Mann-Whitney U test (Mann & Whitney, 1947) revealed that the parameters duration, start frequency, maximum frequency, finish frequency and start slope were significantly different between single and combined calls (Table 9). Duration differed significantly between single and combined calls. The median duration was higher for single calls than for combined calls. The difference remained significant after Bonferroni correction ($p < 0.001$). A difference between single and combined rumbles could also be shown for start and finish frequency with the median for both being lower in single calls than in combined calls. These differences remained significant after Bonferroni correction with $p > 0.001$ for start frequency and $p = 0.001$ for finish frequency. The start slopes were different between single rumbles and combined rumbles. Median start slopes indicated that frequency tended to increase more steeply during single rumbles. Significant differences in maximum frequency were found between single and combined calls, with single rumbles displaying lower median maximum frequencies than combined rumbles (for exact values see Table 9). These parameter differences were most prominent and are visually represented by error bars in Figure 7.

In the Mann-Whitney U test, parameters with $p < 0.05$ included minimum frequency, mean 1$^{st}$ third, mean 3$^{rd}$ third, mean frequency and final slope (Figure 8) which were considered in further analysis. They were not significant under Bonferroni correction but showed significant differences in BH-FDR correction. Cliff's delta values indicated small effects for these parameters. No difference between single and combined rumbles could be found for measurements of COFM, middle slope, maximum frequency location, frequency range, frequency variability index, mean 2$^{nd}$ third, middle frequency and minimum frequency location.

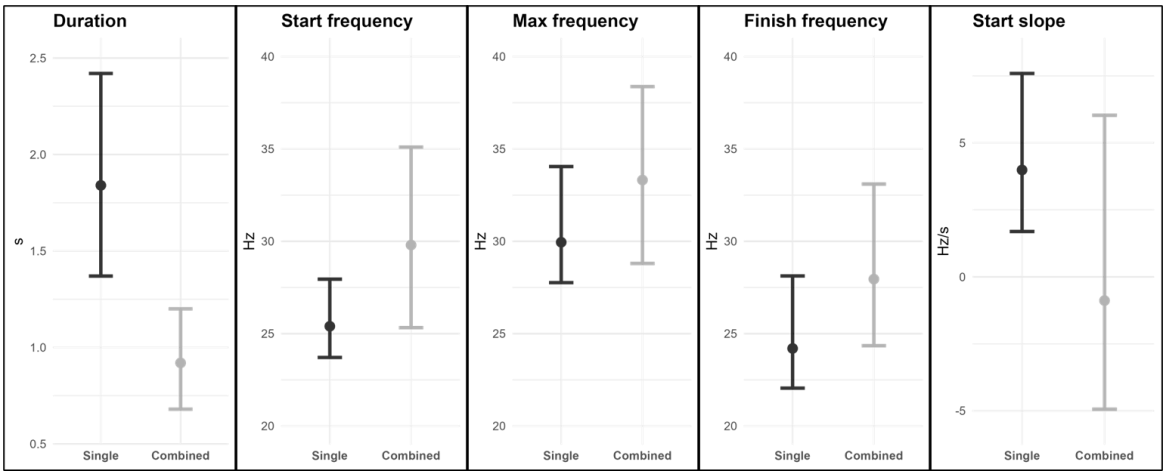


*Figure 7: Error bars (y-axis: time in seconds, frequency in hertz, slope in hertz per second). Acoustic parameters differing significantly between single and combined rumbles indicated by p-values for Mann-Whitney U test and Bonferroni correction.*

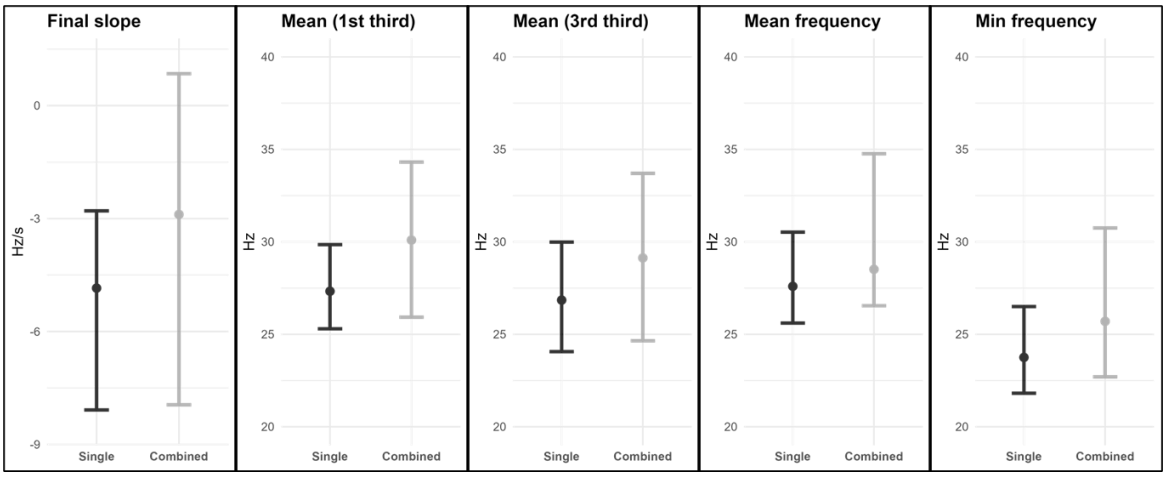


*Figure 8: Error bars (y-axis: slope in hertz per second, frequency in hertz). Acoustic parameters with differences for single rumbles compared to combined rumbles by testing Mann-Whitney U and correcting for false detection rate (BH).*

## Rumbles in Behavioral Contexts

An overview of the contextual occurrence of single and combined calls is shown in Table 10. The affiliation context contained no combined rumbles. The sample for contact call and greeting rumbles contained one rumble which was part of a combined call. Rumbles of the suckling context contained six calls that were part of a combined call which made up a total of 31.6% of all rumbles in this context.

*Table 10: List displaying the parts of single rumbles and combined rumbles for each behavioral context used in analysis*

| **Context** | **Single n (%)** | **Combined n (%)** |
|---|---|---|
| Affiliation | 12 (100%) | 0 (0%) |
| Contact call | 25 (96.2%) | 1 (3.8%) |
| Greeting | 10 (90.9%) | 1 (9.1%) |
| Suckling | 13 (68.4%) | 6 (31.6%) |

The fundamental frequencies for all calls were either calculated from the harmonics or measured directly by the contour annotation tool (Table 8). The acoustic parameters (Stoeger & Baotic, 2016; Wood et al., 2005) for the statistical analysis were calculated from the fundamental frequency for each call. The values for mean and standard deviation per behavioral context and for each acoustic parameters are displayed in Table 11.

*Table 11: Descriptive statistics overview of acoustic parameters measured for rumbles in four different behavioral contexts.*

| **Acoustic parameters** | Mean ± SD | | | |
|---|---|---|---|---|
| | **Affiliation (n = 12)** | **Contact call (n = 26)** | **Greeting (n = 11)** | **Suckling (n = 19)** |
| Shape and Contour Parameters | | | | |
| COFM | 0.00133 ± 0.00059 | 0.00182 ± 0.00105 | 0.00139 ± 0.00069 | 0.0011 ± 0.00074 |
| FVI | 0.412 ± 0.035 | 0.112 ± 0.373 | 0.059 ± 0.070 | 0.037 ± 0.040 |
| Start Slope (Hz/s) | 4.09 ± 6.06 | 4.46 ± 4.89 | 7.22 ± 7.34 | 1.42 ± 4.11 |
| Middle Slope (Hz/s) | -1.56 ± 5.36 | -1.29 ± 5.03 | -4.77 ± 10.25 | -3.94 ± 7.59 |
| Final Slope (Hz/s) | -4.36 ± 3.21 | -5.36 ± 3.41 | -5.37 ± 4.52 | -5.34 ± 5.77 |
| Absolute frequency parameters (Hz) | | | | |
| Start Frequency | 25.58 ± 2.24 | 27.43 ± 5.63 | 27.37 ± 5.22 | 25.78 ± 3.94 |
| Middle Frequency | 28.41 ± 3.92 | 30.46 ± 6.38 | 29.97 ± 4.62 | 26.52 ± 3.15 |
| Finish frequency | 24.38 ± 2.30 | 26.23 ± 6.25 | 25.47 ± 4.83 | 23.35 ± 3.95 |
| Min Frequency | 23.87 ± 2.00 | 25.18 ± 6.11 | 24.80 ± 4.34 | 23.10 ± 3.79 |
| Max Frequency | 29.65 ± 4.02 | 32.31 ± 5.49 | 31.91 ± 7.21 | 28.11 ± 4.01 |
| Mean Frequency | 27.16 ± 3.11 | 29.46 ± 5.64 | 29.08 ± 5.18 | 25.94 ± 3.30 |
| Frequency Range | 5.78 ± 3.01 | 7.13 ± 4.12 | 7.12 ± 4.51 | 5.01 ± 3.01 |
| Mean 1st Third | 27.08 ± 3.07 | 29.55 ± 5.46 | 30.01 ± 6.80 | 26.68 ± 3.71 |
| Mean 2nd Third | 28.30 ± 3.85 | 30.24 ± 6.08 | 29.84 ± 4.85 | 26.38 ± 3.21 |
| Mean 3rd Third | 26.03 ± 2.85 | 28.50 ± 6.23 | 27.29 ± 4.48 | 24.72 ± 3.43 |
| Temporal Parameters | | | | |
| Duration (s) | 2.13 ± 0.77 | 2.09 ± 0.66 | 2.09 ± 0.84 | 1.37 ± 0.67 |
| Min Frequency Location (normalized) | 0.82 ± 0.38 | 0.55 ± 0.49 | 0.72 ± 0.46 | 0.70 ± 0.40 |
| Max Frequency Location (normalized) | 0.44 ± 0.20 | 0.42 ± 0.23 | 0.37 ± 0.21 | 0.24 ± 0.21 |

Principal Component Analysis (PCA)

Sampling adequacy was marginal (KMO overall = 0.5; per variable = 0.5) while Bartlett's test was significant ($\chi^2(153) = 4\,914.5$, $p < 0.001$) indicating sufficient correlation between variables to proceed. As a conservative retention strategy, we used parallel analysis in combination with scree plot to only use well defined components for further analysis with DFA.

Parallel analysis supported three components from the PCA. The first three observed eigenvalues (8.4, 3.5, 2.3) are greater than their simulated counterparts (2.0, 1.8, 1.6) whereas the fourth observed eigenvalue (1.1) did not exceed parallel analysis (1.5). The scree plot (Figure 9) shows an inflection on the fourth component, suggesting a three-component solution as adequate representation.

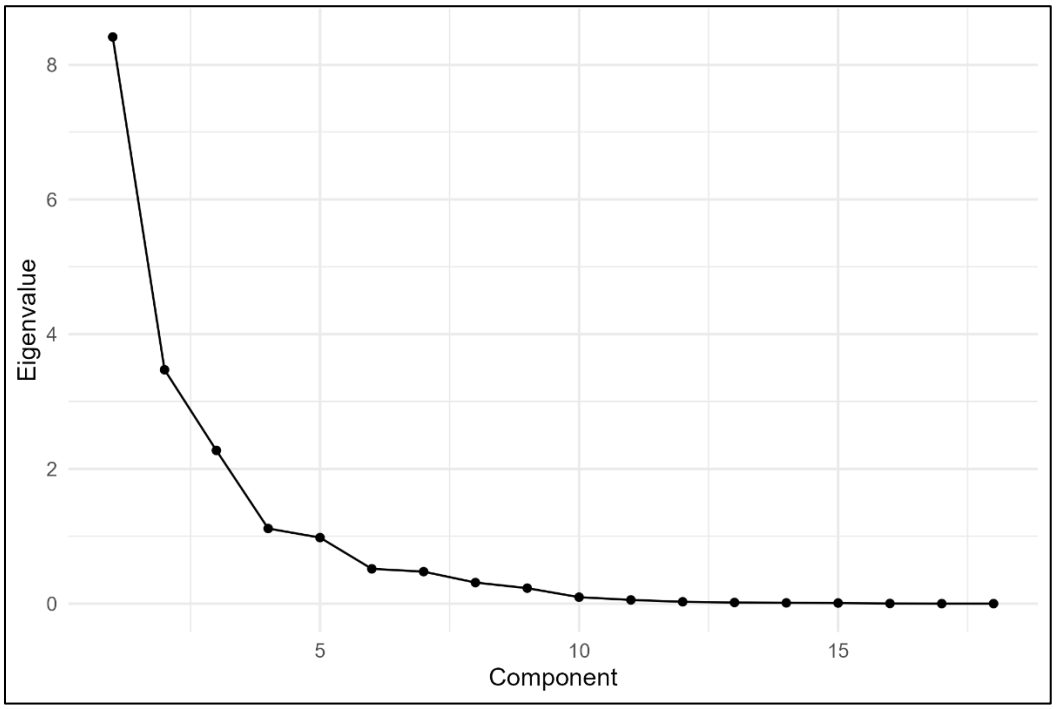


*Figure 9: Scree plot displaying the observed eigenvalues of all principal components calculated by the PCA.*

The PCA reduced 18 acoustic parameters (Table 11) to three principal components (PC) explaining 78,7% variance overall. The first PC explained 46.1% of the variance and all absolute frequency parameters correlated with PC 1 except for frequency range. The shape and contour related parameters loaded high on PC 2 explaining 19.8% of the variance. Frequency range was also assigned to PC 2 but middle slope as the exception for shape and contour parameter was assigned to the PC 3. Together with duration and location of minimum and maximum frequency these four parameters correlated with PC3 and explained 12.8% of the variance.

Discriminate Function Analysis (DFA)

The nested pDFA with ID-blocked 5-fold cross-validation classified context above chance (p = 0.014, 5000 permutations). The observed balanced accuracy = 0.366 shows a correct classification of calls to contexts above chance level (permutation mean = 0.260, SD = 0.048). The correct reclassification of contexts was best for the suckling context with 57.9% of calls being classified correctly shown in the confusion matrix (Table12). This is followed by the contact call achieving 46.1% correct reclassification. The greeting context had the lowest reclassification (9.1%), getting mainly confused with the affiliation context (54.5%).

*Table 12: Confusion matrix of pDFA containing all rumbles with known context. Bold numbers represent correct reclassification for contexts, numbers in brackets are absolute numbers of calls.*

| **True** | Affiliation | Contact call | Greeting | Suckling | Total |
|---|---|---|---|---|---|
| **Affiliation** | **33.3% (4)** | 25% (3) | 25% (3) | 16.7% (2) | 100% (12) |
| **Contact call** | 15.4% (4) | **46.1% (12)** | 7.7% (2) | 30.8% (8) | 100% (26) |
| **Greeting** | 54.5% (6) | 18.2% (2) | **9.1% (1)** | 18.2% (2) | 100% (11) |
| **Suckling** | 21.1% (4) | 10.5% (2) | 10.5% (2) | **57.9% (11)** | 100% (19) |

The same procedure of nested pDFA yielded different results when testing only with rumbles produced as single calls. The test was significant p = 0.011, 5000 permutations, with a balanced accuracy of 0.392. Calls were correctly assigned to the right context above a chance level (permutation mean = 0.284, SD = 0.061).

*Table 13: Confusion matrix of pDFA containing only rumbles produced as single calls. Bold numbers represent correct reclassification for contexts, numbers in brackets are absolute numbers of calls.*

| **True** | Affiliation | Contact call | Greeting | Suckling | Total |
|---|---|---|---|---|---|
| **Affiliation** | **25.0% (3)** | 25.0% (3) | 16.7% (2) | 33.3% (4) | 100% (12) |
| **Contact call** | 8.0% (2) | **48.0% (12)** | 20.0% (5) | 24.0% (6) | 100% (25) |
| **Greeting** | 30.0% (3) | 20.0% (2) | **30.0% (3)** | 20.0% (2) | 100% (10) |
| **Suckling** | 15.4% (2) | 0.0% (0) | 30.8% (4) | **53.8% (7)** | 100% (13) |

The confusion matrix (Table 13) for single rumbles shows differences in correct reclassification compared to the results containing all rumbles. Correct reclassification was better for the greeting (30.0%) and contact call (48.0%) context and worse for the affiliation (25.0%) and suckling (53.8%) context. The suckling context still achieved the most relatively correct reclassification. It must be mentioned that the sample size dropped by one for contact call and greeting context. For the suckling context six samples of combined rumbles were excluded, and affiliation contained no combined rumbles therefore numbers of calls stayed the same.

## Calf Roars

Descriptive Statistics

*Table 14: Descriptive values for roar parameters: Mean ± SD. In total 120 calls were analyzed for the three subclasses of mixed roars, noisy roars and tonal roars.*

| Acoustic Parameters | Mixed (n=76) | Noisy (n=64) | Tonal (n=70) |
|---|---|---|---|
| Duration (s) | 1.6 ± 0.6 | 1.2 ±0.5 | 1.2 ± 0.6 |
| Peak Frequency (Hz) | 544 ± 298 | 504 ± 296 | 458 ± 257 |
| Minimum Entropy (bits) | 1.8 ± 0.4 | 2.1 ± 0.5 | 1.7 ± 0.4 |
| Average Entropy (bits) | 3.5 ± 0.6 | 3.7 ± 0.7 | 2.9 ± 0.5 |
| Maximum Entropy (bits) | 5.1 ± 0.6 | 5.1 ± 0.7 | 4.6 ±0.7 |

Table 14 shows a descriptive overview of the measured parameters in Raven Pro (K. Lisa Yang Center for Conservation Bioacoustics, 2024) showing the mean and standard deviation for each parameter and roar type. For this analysis, all roars with a quality of 1-3 were considered, including those with unknown contexts. A Shapiro-Wilk test conducted on all parameters returned p-values greater than 0.05 for average and maximum entropy, suggesting the data can be considered approximately normally distributed, therefore parametric tests could be performed to determine if the subclasses of roars differ from each other. Minimum entropy, duration and peak frequency datapoints did not follow normal distribution, allowing only non-parametric tests to investigate differences between roar types.

The PERMANOVA comparing all entropy parameters yielded significant results with $p < 0.001$. The PERMDISP was also significantly different with $p = 0.009$ indicating that the PERMANOVA result might be driven by group variability which is why further tests are needed and will give more insight. Pairwise PERMANOVA showed significant differences between all three roar type pairs but to different degrees. The roar types tonal vs. noisy show the biggest separation ($F = 35.5$, $R^2 = 0.21$, $p < 0.001$), followed by tonal vs. mixed roars ($F = 24.9$, $R^2 = 0.14$, $p < 0.001$) and mixed roars vs. noisy roars show the smallest differences of all pairs ($F = 5.63$, $R^2 = 0.04$, $p = 0.006$) with all p-values representing BH FDR adjusted values. Since the three roar types differed significantly in the pairwise PERMANOVA, we also conducted individual tests for each parameter as a follow-up procedure to investigate further details.

### Duration

Differences of duration for the three roar types were tested using Kruskal-Wallis $\chi^2(2) = 18.55$, $p < 0.001$ and effect size $\varepsilon^2 = 0.08$. Table 15 shows the post-hoc Dunn test statistic with BH FDR adjusted p-values and values for Cliff's $\delta$ and 95% confidence intervals.

*Table 15: Post-hoc test statistic results for the duration parameter showing group contrasts of all roar type pairs.*

| Group contrasts | Dunn | | Cliff's δ | |
|---|---|---|---|---|
| | statistic | p-value adjusted | δ | 95% CI |
| tonal – mixed | 3.74 | p < 0.001 | -0.35 (medium) | [-0.51, -0.16] |
| tonal – noisy | 0.01 | p > 0.05, n. s. | -0.02 (negligible) | [-0.21, 0.18] |
| mixed – noisy | -3.64 | p < 0.001 | 0.37 (medium) | [0.18, 0.53] |

### Peak Frequency

Peak frequency differed by roar type, Kruskal-Wallis $\chi^2(2) = 6.48$, $p < 0.05$, with an effect size of $\varepsilon^2 = 0.02$. Post-hoc Dunn statistic with adjusted p-values after BH FDR correction are shown together with Cliff's δ and 95% confidence intervals in Table 16.

*Table 16: Post-hoc test statistic results for the peak frequency showing group contrasts of all roar type pairs.*

| Group contrasts | Dunn | | Cliff's δ | |
|---|---|---|---|---|
| | statistic | p-value adjusted | δ | 95% CI |
| tonal – mixed | 2.55 | p < 0.05 | -0.24 (small) | [-0.42, -0.06] |
| tonal – noisy | 1.27 | p > 0.05, n. s. | -0.13 (negligible) | [-0.31, 0.07] |
| mixed – noisy | -1.20 | p > 0.05, n. s. | -0.12 (negligible) | [-0.08, 0.30] |

The data points for the individual calls per roar type are displayed as boxplots in Figure 10a for the duration and in Figure 10b for the peak frequency parameter also highlighting the significant differences with mixed roars being the longest in duration and exhibiting the highest peak frequency on average.

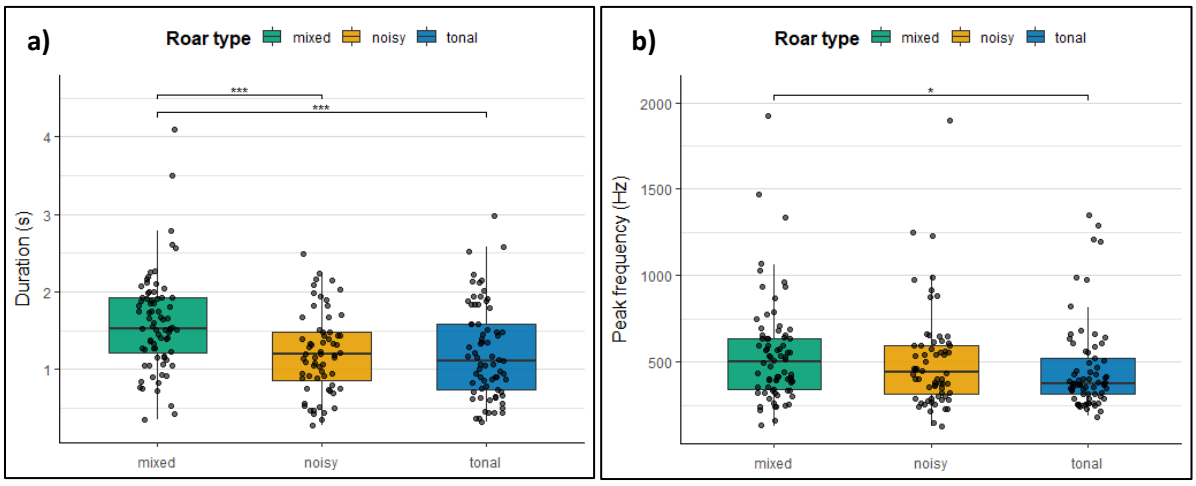


*Figure 10: Boxplots for a) duration and b) peak frequency showing contrasts between tonal (n= 70), mixed (n= 76) and noisy roars (n= 64). Significance levels indicated by stars as p < 0.001 (***), p < 0.01 (**), p < 0.05 (*).*

### Minimum Entropy

A Kruskal-Wallis test revealed that minimum entropy differs significantly among roar types $\chi^2(2) = 24.34$, $p < 0.001$ with the effect size of $\varepsilon^2 = 0.12$. The results for Dunn post-hoc comparisons with BH FDR adjusted p-values and Cliff's δ values with 95% confidence interval are displayed in Table 17.

*Table 17: Post-hoc test statistic results for minimum entropy parameter showing group differences of all roar type pairs.*

| Group contrasts | Dunn | | Cliff's δ | |
|---|---|---|---|---|
| | statistic | p-value adjusted | δ | 95% CI |
| tonal – mixed | 2.19 | p < 0.05 | -0.22 (small) | [-0.39, -0.03] |
| tonal – noisy | 4.92 | p < 0.001 | -0.48 (large) | [-0.63, -0.30] |
| mixed – noisy | 2.88 | p < 0.01 | -0.29 (small) | [-0.46, -0.11] |

### Average entropy

Average entropy differed significantly by roar type, Welch's ANOVA, $F(2, 133.04) = 41.97$, $p < 0.001$, generalized $\eta^2 = 0.28$, 95% CI [0.20, 1.00] with the post-hoc Games-Howell results reported in Table 18.

*Table 18: Post-hoc test statistic results for average entropy showing group contrasts of all roar type pairs.*

| Group contrasts | GH estimate | 95% CI | p-value adjusted |
|---|---|---|---|
| tonal – mixed | 0.65 | [0.44, 0.87] | p < 0.001 |
| tonal – noisy | 0.88 | [0.62, 1.13] | p < 0.001 |
| mixed – noisy | 0.22 | [-0.03, 0.48] | p > 0.05, n. s. |

### Maximum Entropy

An ANOVA showed significant differences of roar type on maximum entropy, $F(2, 207) = 13.92$, $p < 0.001$, with an effect size of $\eta^2 = 0.12$, CI [0.05, 1.00], $\omega^2 = 0.11$, CI [0.05, 1.00]. Tukey post-hoc comparisons are shown in Table 19.

*Table 19: Post-hoc test statistic results for maximum entropy showing group differences of all roar type pairs.*

| Group contrasts | Tukey estimate | 95% CI | p-value adjusted |
|---|---|---|---|
| tonal – mixed | 0.50 | [0.24, 0.76] | p < 0.001 |
| tonal – noisy | 0.54 | [0.26, 0.81] | p < 0.001 |
| mixed – noisy | 0.04 | [-0.23, 0.31] | p > 0.05, n. s. |

Regarding entropy, tonal roars show significant differences between noisy and mixed roars in all three parameters minimum, average and maximum entropy. Noisy and mixed roars are not statistically different from each other regarding average and maximum entropy. The biggest difference in minimum

entropy lies between tonal and noisy roars whereas tonal and mixed roars show smaller differences than mixed and noisy roars (Figure 11).

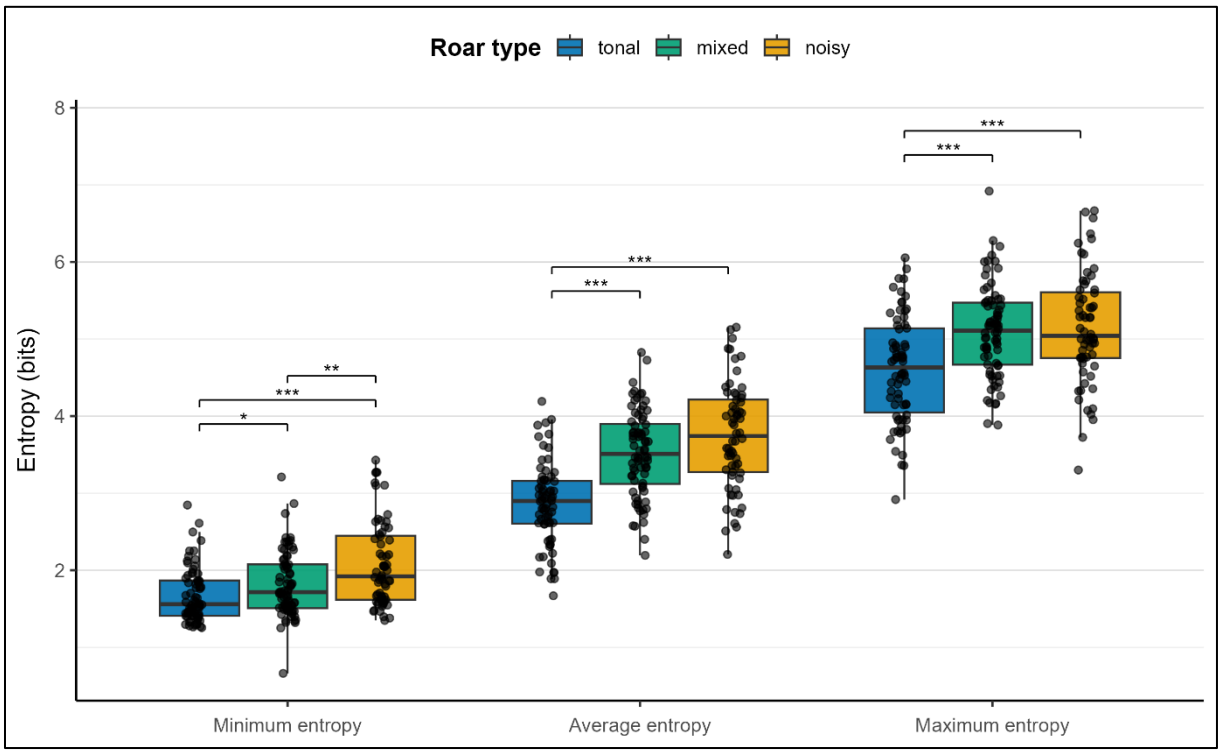


*Figure 11: Boxplots with individual data points for the entropy parameters depicting differences between tonal (n = 70), mixed (n = 76) and noisy roars (n = 64), with significance levels indicated by stars as p < 0.001 (***), p < 0.01 (**), p < 0.05 (*).*

## Roars in Context

For roar types in the selected behavioral contexts, a quantitative analysis was conducted (Figure 12). For the suckling context (n = 35) most roars were either mixed (n = 15) or tonal (n = 18). The play context consisted of five mixed roars, four noisy roars and one tonal roar, totaling ten play roars in the sample. Half of all agonistic roars were noisy (n = 9), with the other half roughly equally distributed between mixed roars (n = 4) and tonal roars (n = 5).

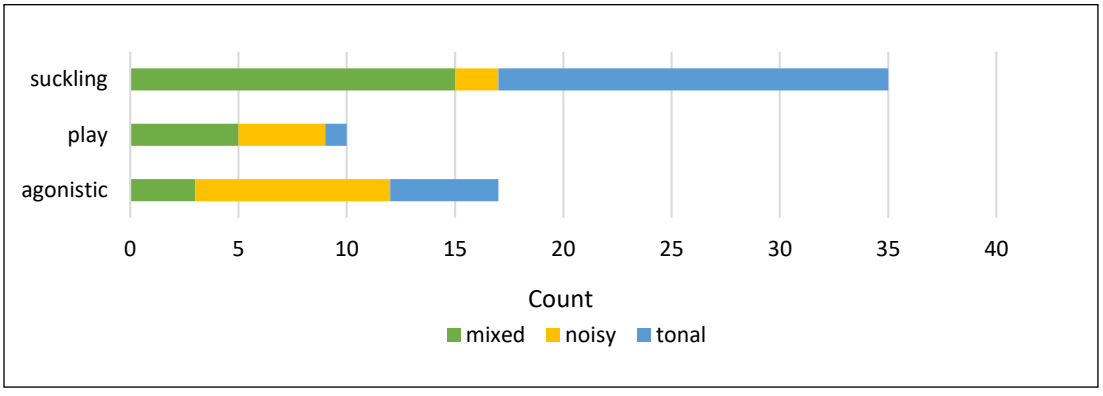


*Figure 12: Total number of roar subtypes for each selected behavioral context.*

Non-Linear Phenomena (NLP) of Context Roars

For the descriptive overview of roars in context containing NLP only calls produced as single roars were considered. Since good audio quality is required to analyze details such as subharmonics, only roars of quality 1-3 were analyzed.

*Table 20: Overview of non-linear phenomena of roar subtypes in different behavioral contexts.*

| Non-linear Phenomena | **Mixed roars (n = 14)** | | | | **Noisy roars (n = 12)** | | | | **Tonal roars (n = 18)** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Agon. (n=3) | Play (n=4) | Suckl. (n=7) | all | Agon. (n=9) | Play (n=2) | Suckl. (n=1) | all | Agon. (n=3) | Play (n=1) | Suckl. (n=14) | all |
| **Harmonics** | 3 | 4 | 7 | 14 | - | - | - | - | 3 | 1 | 14 | 18 |
| **Sub-harm.** | 1 | 2 | 3 | 6 | - | - | - | - | 2 | 1 | 5 | 8 |
| **Chaos** | 3 | 4 | 7 | 14 | 9 | 2 | 1 | 12 | 1 | - | 5 | 6 |
| **Freq jump** | - | - | - | - | - | - | - | - | - | - | 5 | 5 |

All mixed roars contained harmonics, subharmonics as well as deterministic chaos. Noisy roars only contained deterministic chaos in all behavioral contexts. Frequency jumps are rare and could only be observed in tonal roars within the subsample used for the analysis of NLP. The different types of NLP are visualized with an exemplary call in Figure 13. The call starts with a harmonic structure containing a frequency jump in the beginning and when transitioning to subharmonics and further into deterministic chaos. The vocalization displayed is a combined call transitioning from high frequency chaos into a low frequency rumble.

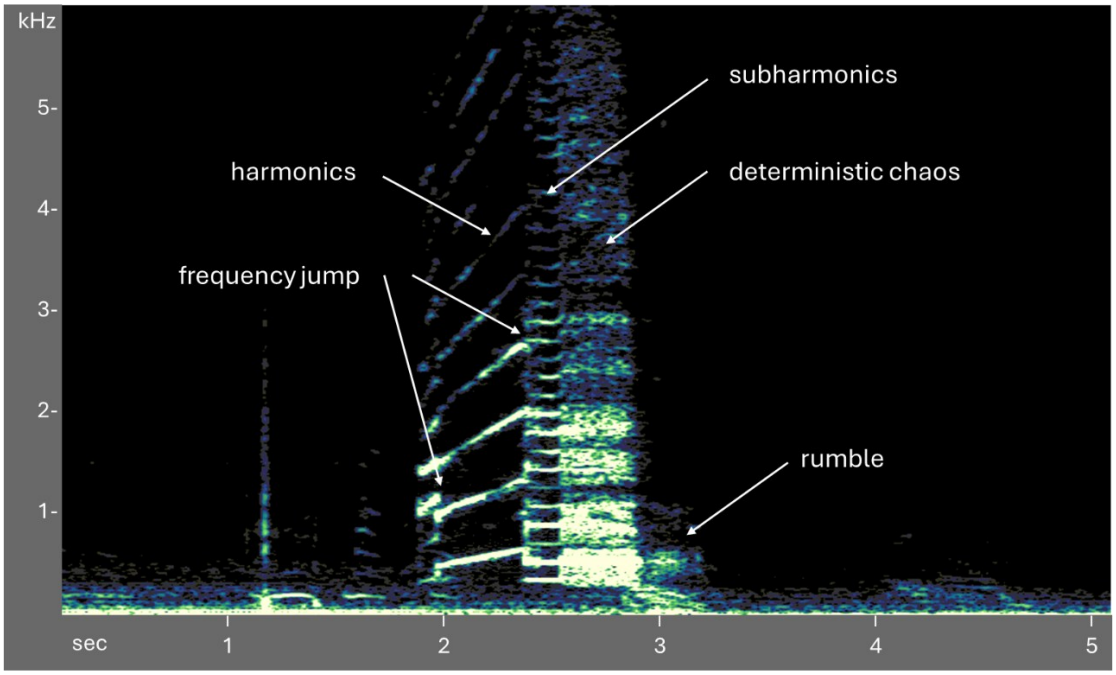


*Figure 13: Spectrogram of a combined call (mixed roar-rumble) showing different types of NLP investigated in the analysis of roars.*

Reaction Time to Calf Roars

The quickest reactions from other individuals were achieved by noisy roars when considering the roar type. Almost identical average reaction time achieved roars emitted in an agonistic context. Noisy roars were often used with the agonistic context, but not exclusively and considering the two dimensions separately both were answered by conspecifics within the shortest time.

*Table 21: Overview of behavioral context, roar subtype, reaction time and reaction behavior for the analysis of reaction time to calf roars.*

| Context | Roar subtype | Reaction Time (s) | Rection Behavior |
|---|---|---|---|
| agonistic | noisy | 2.54 | AF touch |
| agonistic | noisy | 0.75 | AM moves away |
| agonistic | noisy | 4.71 | AF touch mouth |
| agonistic | mixed | 5.84 | AF touch |
| agonistic | noisy | 1.08 | AF move ears |
| agonistic | tonal | 5.17 | AF look |
| agonistic | noisy | 0.20 | AF move ears |
| play | mixed | 2.57 | AF look |
| play | noisy | 7.67 | AF move towards |
| suckling | tonal | 1.83 | AF suckle stance start |
| suckling | tonal | 6.21 | AF touch |
| suckling | tonal | 12.38 | AF suckle stance start |
| suckling | mixed | 2.29 | AF stops moving |
| suckling | tonal | 1.37 | AF stops moving |
| suckling | mixed | 4.80 | AF stops moving |
| suckling | mixed | 5.92 | AF stops moving |
| suckling | tonal | 1.84 | AF stops moving |
| suckling | tonal | 7.84 | AF stops moving |
| suckling | tonal | 1.50 | AF stops moving |

In total, 19 calls could be included in the reaction time analysis. Agonistic roars (n = 7) had the fastest reaction time with an average of 2.90 seconds, followed by suckling roars (n = 10) with an average of 4.60 seconds. The slowest reaction time was observed context in the play context (n = 2) with an average of 5.13 seconds. For the different roar subclasses, noisy roars (n = 6) elicited a reaction within an average of 2.83 seconds. Mixed roars (n = 5) elicited a reaction after an average of 4.29 seconds, followed by tonal roars (n = 8) with an average reaction time of 4.77 seconds. Mainly adult females were reacting to calf roars with one exception of an adult male moving away from the vocalizing calf.

# DISCUSSION

This thesis aims to provide a more detailed understanding of the communication of wild African savannah elephant calves. The rumble, as the most common vocalization of this species, is known to be used in many different socially relevant contexts (Baotic & Stoeger, 2017; McComb et al., 2003; Poole, 2011; Soltis et al., 2005b; Stoeger & Baotic, 2016, 2017) and also shows acoustic variation across contexts (Leong, Ortolani, Graham, et al., 2003; Poole & Moss, 1981). When examining the calf rumbles for this thesis, the first distinction made was whether the call occurred as part of a combination or as a single call, and this distinction was reflected in various acoustic parameters. An acoustic differentiation between behavioral contexts was possible with the examined sample. Rumbles differed acoustically across affiliation, contact call, greeting and suckling contexts. The results provide new insight in the field of calf acoustic communication but also point towards areas in need of further investigation. The subtypes of roars have been described as distinct call types before (Stoeger et al., 2011; Stoeger-Horwath et al., 2007). The findings of this thesis support this distinction. Additionally, we provide details of the use and reaction to these vocalizations, showing contextual preferences for certain roar types.

## Calf Rumbles

The first consideration when examining calf rumbles was whether they had been produced as a single call or as part of a combinatorial call. For that, acoustic parameters (Wood et al., 2005) were used to determine if their means differed. Significant differences were found in duration, start frequency, maximum frequency, finish frequency and start slope when applying BH and Bonferroni correction, which indicates strong results. The differences in start and finish frequency could be attributed to the fact that when a rumble is combined with a roar (either before or after) there is a transition from one to the other call. This can influence the start frequency and the finish frequency in rumble combinations resulting in higher values. Differences in the duration were also observed, with the individual rumbles of a combined call being shorter in total duration than single rumbles just like for combined rumbles of the African forest elephant (Hedwig & Kohlberg, 2024). African forest elephants combine calls more frequently than African savannah elephants (Pardo et al., 2019) but there is no detailed previous analysis of combined vs. single calls in African savannah elephants available. The acoustic parameters final slope, mean 1$^{st}$ third, mean 3$^{rd}$ third, mean frequency and minimum frequency also showed differences between single and combined rumbles when correcting for BH FDR but not for Bonferroni.

This suggests a smaller difference but still a noticeable effect. When examining these differences, it should be mentioned that the sample was imbalanced containing 122 (65.6%) single rumbles and 65 (34.4%) combined rumbles. Furthermore, we did not investigate which kind of combinations are part of this sample. This analysis helps to understand the overall acoustic properties of combinatorial calls compared to single calls.

The next step was analyzing the rumbles using principal component analysis to reduce many acoustic parameters to fewer components but still accounting for all of them. The first principal component mainly contained absolute frequency parameters, each with similarly high loadings, explaining 46.1% variance overall. The second (19.8% variance) principal component featured mainly shape and contour measurements as well as the frequency range. Mainly temporal parameters were assigned to the third principal component which accounted for 12.8 % of the variance. The first three principal components therefore accounted for all acoustic parameters of absolute frequency, shape and contour as well as temporal aspects of the vocalizations and were selected for the discriminant function analysis.

The results of the discriminate analysis (nested pDFA) showed a balanced accuracy of 0.366 ($p = 0.014$) yielding significant differentiation between the rumbles of different contexts. This means that correct classification of rumbles to context based on acoustic properties was possible exceeding chance level. Because for some contexts high misclassifications happened an additional explorative analysis was conducted. Since the single rumbles and combined rumbles differ in some parameters significantly it could be valuable to include this limitation. Because of the unequal distribution of single and combined rumble cases it could not be taken as restriction factor in the original pDFA analysis and therefore another test was conducted including only single rumbles. The test results (balanced accuracy = 0.392, $p = 0.011$) were slightly more significant than with samples including combined and single calls. With a correct reclassification per context rising for contact call and greeting context, whereas dropping for affiliation and suckling context. The contact call and suckling context showed the highest reclassification in both tests. The overall significant results of both pDFA speak for the fact that calls show acoustic properties specific to certain contexts, particularly considering our sample size was relatively small. Furthermore, this analysis would profit from an exact age and sex of the caller. Even though we only analyzed only one age group, limiting the acoustic variation depending on height and maturity (Stoeger & Baotic, 2016) an effect sexual dimorphism on frequency has been observed in adult individuals (Baotic & Stoeger, 2017) and could not be accounted for in this analysis of calf calls. Nevertheless, the acoustic differences of females and males, even in calves, could be crucial when testing for small differences between contexts.

Context dependent acoustic differences have been shown before in the analysis of Poole, (2011) where the rumbles of a begging context (corresponding to our suckling intention context within the suckling

context category) and a separated context (corresponding to our contact call context) could be distinguished reliably. In the same publication the contexts as touched, grumbling and umbrage also showed acoustic distinction between each other using a different set of acoustic parameters (Poole, 2011). The sample size in their study was substantially larger and included known individuals.

It has been shown that rumbles reflect individual identity in adult females (Soltis et al., 2005a) which we could not test because no individual identification of calves was possible during data collection. In African elephant calf roars, investigating the vocal cues as indicator to arousal level, individual identity was analyzed but shows a lower effect than in adult rumbles (Stoeger et al., 2011). The possibility that a context in our analysis is driven by one individual cannot be excluded for this analysis, the probability is low since data were recorded from many different herds but nevertheless it is possible the same calf was recorded on multiple occasions for the same context. According to Poole (2011) younger calves elicit more begging rumbles than older calves with an almost linear yearly decline from age 1 to age 6. This means the sample for the thesis could be skewed towards having unequal age distribution across contexts. The growth rate for young individuals has the steepest curve from ages 0-5 (Shrader et al., 2006) with the size of vocal folds growing with the body meaning older, bigger calves also have longer vocal folds influencing the fundamental frequency of their vocalizations (Stoeger et al., 2014). This is also what Poole (2011) referred to when addressing the rather low reclassification of the DFA between begging and separated rumbles, also stating that the frequency and duration of calf calls change drastically with age (Poole, 2011). To what extent this influences the performance of tests conducted for this analysis is unknown but indicates another aspect of the differences in frequencies of vocalizations which our data does not provide and therefore potentially interferes with the results.

Vocalizations are a complex composition of frequency, contour shape and temporal aspects of sound and can all be relevant for certain aspects of communication. In the analysis for this thesis the small sample size and data lacking reliable information of sex and individual identity limits the detailed interpretation of the results. Nevertheless, the procedure of conducting the DFA with principal components representing all acoustic aspects has shown to contain meaningful results since calls could be statistically attributed to the right context above chance level.

The last but substantial limitation for the results of the rumble-analysis is that during data collection, many sources of noise, mainly cars, were present, masking the fundamental frequency of many calls. This is the reason why the fundamentals had to be calculated for 106 (57%) out of 186 calls. With 43% of all calls containing measured fundamental frequency data, it could have primarily influenced the shape and contour parameters because the relation of fundamental frequency to harmonics is constant regarding the frequency but not necessarily regarding the shape and contour of harmonics.

## Calf Roars

Calf roars can be distinguished by entropy parameters. The results show that tonal roars are significantly different from noisy and mixed roars regarding the parameters minimum entropy, average entropy and maximum entropy. Overall tonal roars had significantly lower values for these parameters meaning they are less noisy and show more harmonic structure. Mixed roars often alternate between tonal and noisy segments which is reflected in the minimum entropy parameter. Here noisy roars have significantly higher minimum entropy than tonal roars ($p < 0.001$) and significantly higher than mixed roars ($p < 0.01$). Mixed roars contain elements of deterministic chaos, differing significantly from tonal roars regarding minimum entropy by a smaller margin ($p < 0.05$). These results are as expected along the standard definitions of the roar subtypes but nevertheless confirmed the accuracy of call classification. Duration was on average longest in mixed roars, being significantly longer than both noisy and tonal roars which did not differ from each other in their mean duration overall. The frequency with the highest amplitude, was on average not significantly different for noisy roars compared to the other types, although mixed roars showed a higher mean peak frequency than tonal roars ($p < 0.05$).

The data indicate a context specific trend in roar type usage. The suckling context mainly contains tonal and mixed roars whereas in an agonistic context a preference for the use of noisy roars is shown. Because broadband calls do not seem to be individually distinctive (Stoeger et al., 2011) and are suggested to function primarily as distress signals. This fits the idea that certain NLPs like chaos are harder to ignore (Fitch et al., 2002) and therefore used in contexts of high arousal where the vocalizing individual requires assistance or attention (Herler & Stoeger, 2012). This is coherent with our findings that half of all agonistic calls are noisy roars consisting of deterministic chaos. One suggestion of Stoeger et al., (2011) is that probably roars do not encode individual identity, suggesting that elephants may rely on the combination of calls to signal all needed information.

A descriptive analysis of NLPs for roar types per context shows that noisy roars in our sample contained only deterministic chaos, in line with their original call type description (Stoeger-Horwath et al., 2007). All the examined mixed roars of our sample contained harmonic elements as well as elements of chaos and with subharmonic structures present in about half of them. As part of their definition all tonal roars contained harmonics whereas about half show subharmonic structures as well. Of the 18 tonal roars, six ended in deterministic chaos and five exhibited frequency jumps. Most tonal roars with subharmonics and frequency jumps were produced in a suckling context, suggesting that the NLP could be important towards communication specifically with the mother (Fitch et al., 2002).

NLPs have been suggested to play a role in the communication of individuality, motivation and status (Wilden et al., 1998). Vocal cues of roar vocalizations indicating arousal levels and physiological

condition have been confirmed previously (Stoeger et al., 2011). It is not clear yet what the underlying mechanisms are to produce NLPs. Both anatomy and neural control are thought to play a role in the vocal production mechanisms which might serve as an indicator for individual differences in call morphology (Fitch et al., 2002). The individual differences in calves regarding the use of roar types or nonlinearities for specific contexts may therefore enhance recognition especially in mother-infant pairs (Fitch et al., 2002) which is in line with our findings regarding the tonal roars in a suckling context.

Furthermore, the reaction time to calf roars was measured to refine the picture of their usage by looking at the reaction of other individuals. Almost exclusively adult females (alleged mother) reacted to the calf roars with just one exception where an adult male reacted to a calf roar. The adult male moved away from the calf as a reaction to the agonistic, noisy roar from the calf. The adult male first pushed the calf with its trunk which was followed by the calf roar. The reactions came almost exclusively from adult females and can be traced back to the general structure of African elephant society (Douglas-Hamilton, 1972; Moss & Poole, 1983; Wittemyer et al., 2005) and the strong mother-offspring bond where calves depend on their mothers for nutrition during the first years of their lives (Lee & Moss, 1986). Female individuals of a family sometimes stay together, or at least in contact, over their whole life spans (Moss & Poole, 1983). The reaction time was shortest for roars produced in an agonistic context. This supports the use of roars in distress situations with a need for imminent care and support. Furthermore, noisy roars elicited the fastest reaction when considering call types, since vocalizations containing deterministic chaos will stand out most against background noise and may therefore elicit faster reactions because of their alarming sound quality (Fitch et al., 2002).

The results regarding the context specific use of roar types found in this thesis are in accordance with previous findings (Stoeger et al., 2011) and extend the knowledge of the role NLPs play in communicative function. It seems that the roar types are used with varying preferences across different contexts and therefore potentially signal information about urgency and context (Fitch et al., 2002; Wilden et al., 1998) to some degree. Our findings cannot conclusively assess this with our limitation of a small sample size and insufficient data for individuality, which could also have a potential effect. Nevertheless, a trend is there for the preferred usage of tonal and mixed roars in a suckling context and noisy roars in an agonistic context. These results have not been demonstrated before and give further insight into the potential function of NLP and their utilization in socially relevant communication.

## Conclusion and Future Directions

After exploring the acoustic differences of rumbles in four different behavioral contexts, it can be concluded that the calls in our sample can be differentiated above chance level by acoustic properties between the four contexts that were tested. Since the reclassification was low for some parameters, more testing must be done. Rumbles are known to be specific to certain social contexts (Poole et al., 1988; Poole & Moss, 1981) and individuals (Stoeger & Baotic, 2017) and it has been shown before that rumbles differ acoustically between some contexts (Poole, 2011; Stoeger, Heilmann, et al., 2012). This potential is also shown in this thesis since even with unknown individuals and small sample sizes the discriminant function analysis showed distinction between contexts is possible. A future path for investigation is to explore if the two production types of rumbles (orally and nasally) are used in different social situations. Further research combining knowledge of acoustic communication with other modalities has great potential for understanding communication on a deeper level. Studies of this kind might reveal language universals among species and with the help of emerging machine learning technologies the analysis process should also become more accessible.

The differences in acoustic parameters between combined and single rumbles raise the question of whether combined calls overall have additional communicative functions. It should be further explored which combinations are used in specific behavioral contexts, by which individuals and age groups and if the different parts of a combined call serve distinct functions. The abundance of combinations of calls in calf vocalizations provides an interesting opportunity to study rumbles as well as roars and any potential benefits for individuals when combining them.

For the calf roar vocalizations an intensive study already exists investigating their communicative function in different arousal states (Stoeger et al., 2011). This thesis shows that different roar subtypes are used with a preference for certain contexts and gives further detail about the non-linear phenomena contained within them. An interesting direction for future research is the possibility that NLP are used to varying extents for each individual and social context. It should be further investigated if there are distinct patterns for individuals concerning the expression of NLP and how they are associated with roar type and behavioral context.

A particularly striking part of our analysis is that rumble and roar vocalizations were both used in the suckling context. This social behavior marks a unique time in an elephant's life and is intertwined with the relationship to the mother but also represents a crucial period in life for survival and learning. It should be investigated what communicative strategies surround the suckling context. Specifically, which calls and combinations are used and what function they serve potentially combined with other modalities.

# Acknowledgements

I want to take this opportunity to mention everyone who has contributed to this thesis in one way or another. First and foremost, I want to thank Angela Stöger, for her supervision of this thesis, but also for her trust in me, for her patience and for providing valuable knowledge, guidance and support along all aspects of the way towards finishing the master's. I am deeply grateful to Vesta, for being a mentor and friend during my first time in the field collecting data. Her love for elephants and knowledge of their behavior was a joy and fascinating to witness every day. I learned a lot during the fieldwork, and I will always remember and cherish the time in Addo. I want to thank you both for this opportunity and all the help.

I am grateful we were able to be in Addo, and I want to thank the South African National Parks, the Addo management team and Heston McCabe. The elephants played an essential part in this thesis, so I also want to express my gratitude towards them, for being vocally active and especially for being so calm and gentle around us.

I want to thank all the members of the mammal communication lab for being great colleagues. Even though we are mostly not working directly together we are united by the same interests, even outside of research. It means a lot to have gotten support and encouragement from this group and on this note special thanks to Jure. I want to mention and thank all my other friends for providing distractions and fun when needed and for being there for me and listening to me talk about elephants.

Finally, I want to thank my family, their support has been invaluable, not just financially but mostly emotionally. They are truly amazing, I can always count on them, which is such an honor, and I wouldn't take it for granted.

# References


Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3/4), 227–267.

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*(1), 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Archie, E. A., Morrison, T. A., Foley, C. A. H., Moss, C., & Alberts, S. C. (2006). Dominance rank relationships among wild female African elephants, *Loxodonta africana*. *Animal Behaviour*, *71*(1), 117–127. https://doi.org/10.1016/j.anbehav.2005.03.023

Arivazhagan, C., & Sukumar, R. (2008). Constructing Age Structures of Asian Elephant Populations: A Comparison of Two Field Methods of Age Estimation. *Journal of the Asian Elephant Specialist Group*, *29*, 11–16.

Balazs, P., Noll, A., Deutsch, W., & Laback, B. (2000). *Concept of the integrated signal analysis software system STx* (p. ROM).

Baotic, A., Garcia, M., Boeckle, M., & Stoeger, A. (2018). Field Propagation Experiments of Male African Savanna Elephant Rumbles: A Focus on the Transmission of Formant Frequencies. *Animals*, *8*, 1–19. https://doi.org/10.3390/ani8100167

Baotic, A., & Stoeger, A. (2017). Sexual dimorphism in African elephant social rumbles. *PLOS ONE*, *12*(5), e0177411. https://doi.org/10.1371/journal.pone.0177411

Bates, L., Poole, J., & Byrne, R. (2008). Elephant cognition. *Current Biology : CB*, *18*, R544-6. https://doi.org/10.1016/j.cub.2008.04.019

Beeck, V. C., Heilmann, G., Kerscher, M., & Stoeger, A. (2022). Sound Visualization Demonstrates Velopharyngeal Coupling and Complex Spectral Variability in Asian Elephants. *Animals: An Open Access Journal from MDPI*, *12*(16), 2119. https://doi.org/10.3390/ani12162119

Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, *57*(1), 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Berg, J. K. (1983). Vocalizations and Associated Behaviors of the African Elephant (Loxodonta africana) in Captivity. *Zeitschrift Für Tierpsychologie*, *63*(1), 63–79. https://doi.org/10.1111/j.1439-0310.1983.tb00741.x

Bonferroni, C. E. (1936). *Teoria Statistica Delle Classi e Calcolo Delle Probabilità*. Pubblicazioni del R Istituto Superiore di Scienze Economiche e Commerciali di Firenze.

Brett, M. R. (2019). From game camps to landscape conservation: The evolution and development of the Addo Elephant National Park, South Africa. *Tourism and Leisure*, *8*.

Chiyo, P. I., Archie, E. A., Hollister-Smith, J. A., Lee, P. C., Poole, J. H., Moss, C. J., & Alberts, S. C. (2011). Association patterns of African elephants in all-male groups: The role of age and genetic relatedness. *Animal Behaviour*, *81*(6), 1093–1099. https://doi.org/10.1016/j.anbehav.2011.02.013

Douglas-Hamilton, I. (1972). *On the ecology and behaviour of the African elephant* [Http://purl.org/dc/dcmitype/Text, University of Oxford]. https://ora.ox.ac.uk/objects/uuid:fa9636ab-ce2f-4a45-8b2e-29d2452e25d5

Eleuteri, V., Bates, L., Nyaradzo Masarira, Y., Plotnik, J. M., Hobaiter, C., & Stoeger, A. (2025). Investigating intentionality in elephant gestural communication. *Royal Society Open Science*, *12*(7), 242203. https://doi.org/10.1098/rsos.242203

Eleuteri, V., Bates, L., Rendle-Worthington, J., Hobaiter, C., & Stoeger, A. (2024). Multimodal communication and audience directedness in the greeting behaviour of semi-captive African savannah elephants. *Communications Biology*, *7*(1), 472. https://doi.org/10.1038/s42003-024-06133-5

Fant, G. (1970). *Acoustic Theory of Speech Production: With Calculations Based on X-ray Studies of Russian Articulations* (2nd edn). Mouton.

Fee, M. S., Shraiman, B., Pesaran, B., & Mitra, P. P. (1998). The role of nonlinear dynamics of the syrinx in the vocalizations of a songbird. *Nature*, *395*(6697), 67–71. https://doi.org/10.1038/25725

Fisher, R. A. (1992). Statistical Methods for Research Workers. In *Breakthroughs in Statistics* (pp. 66–70). Springer, New York, NY. https://doi.org/10.1007/978-1-4612-4380-9_6

Fitch, W. T. (2000). The evolution of speech: A comparative review. *Trends in Cognitive Sciences*, *4*, 258–267. https://doi.org/10.1016/S1364-6613(00)01494-7

Fitch, W. T. (2006). The biology and evolution of music: A comparative perspective. *Cognition*, *100*(1), 173–215. https://doi.org/10.1016/j.cognition.2005.11.009

Fitch, W. T., & Hauser, M. D. (1995). Vocal production in nonhuman primates: Acoustics, physiology, and functional constraints on 'honest' advertisement. *American Journal of Primatology*, *37*(3), 191–219. https://doi.org/10.1002/ajp.1350370303

Fitch, W. T., Neubauer, J., & Herzel, H. (2002). Calls out of chaos: The adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour*, *63*(3), 407–418. https://doi.org/10.1006/anbe.2001.1912

Forbes, W. A. (1879). On the Anatomy of the African Elephant (Elephas africanus, Blum.). *Proceedings of The Zoological Society of London*, *1879*, 420–435. https://doi.org/10.1111/j.1096-3642.1879.tb02673.x

Freeberg, T. M., Dunbar, R. I. M., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1597), 1785–1801. https://doi.org/10.1098/rstb.2011.0213

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*, 1325–1330. https://doi.org/10.1111/2041-210X.12584

Garstang, M. (2004). Long-distance, low-frequency elephant communication. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, *190*, 791–805. https://doi.org/10.1007/s00359-004-0553-0

Garstang, M., Fitzjarrald, D. R., Fristrup, K., & Brain, C. (2005). *The Daily Cycle of Low-Frequency Elephant Calls and Near-Surface Atmospheric Conditions*. https://doi.org/10.1175/EI147.1

Guldemond, R. A. R., Louw, C. J., Maré, C., Nørgaard, C., & van Aarde, R. J. (2022). Demographic responses of an insular elephant population to removal as a management intervention. *Conservation Science and Practice*, *4*(8), e12741. https://doi.org/10.1111/csp2.12741

Hall-Martin, A. J. (1992). Distribution and status of the African elephant Loxodonta africana in South Africa, 1652-1992. *Koedoe : African Protected Area Conservation and Science*, *35*(1). https://doi.org/10.4102/koedoe.v35i1.390

Hardus, M., Lameira, A., Schaik, C., & Wich, S. (2009). Tool use in wild orang-utans modifies sound production: A functionally deceptive innovation? *Proceedings. Biological Sciences / The Royal Society*, *276*, 3689–3694. https://doi.org/10.1098/rspb.2009.1027

Hedwig, D., & Kohlberg, A. (2024). Call combination in African forest elephants Loxodonta cyclotis. *PLOS ONE*, *19*, e0299656. https://doi.org/10.1371/journal.pone.0299656

Hedwig, D., Poole, J., & Granli, P. (2021). Does Social Complexity Drive Vocal Complexity? Insights from the Two African Elephant Species. *Animals : An Open Access Journal from MDPI*, *11*(11), 3071. https://doi.org/10.3390/ani11113071

Herbst, C., Stoeger, A., Frey, R., Lohscheller, J., Titze, I., Gumpenberger, M., & Fitch, W. T. (2012). How Low Can You Go? Physical Production Mechanism of Elephant Infrasonic Vocalizations. *Science (New York, N.Y.)*, *337*, 595–599. https://doi.org/10.1126/science.1219712

Herler, A., & Stoeger, A. S. (2012). Vocalizations and associated behaviour of Asian elephant (Elephas maximus) calves. *Behaviour*, *149*(6), 575–599. https://doi.org/10.1163/156853912X648516

Herzel, H., Berry, D., Titze, I. R., & Saleh, M. (1994). Analysis of vocal disorders with methods from nonlinear dynamics. *Journal of Speech and Hearing Research*, *37*(5), 1008–1019. https://doi.org/10.1044/jshr.3705.1008

Hoerner, F., Lawrenz, A., Oerke, A.-K., Müller, D. W. H., Azogu-Sepe, I., Roller, M., Damerau, K., & Preisfeld, A. (2023). Long-Term Olfactory Memory in African Elephants. *Animals (MDPI)*, *13*(4), 679. https://doi.org/10.3390/ani13040679

Hoerner, F., Rendle-Worthington, J., Lawrenz, A., Oerke, A.-K., Damerau, K., Santos, S., Hard, T., & Preisfeld, G. (2023). Differences in Mother–Infant Bond and Social Behavior of African Elephant Calves Living In Situ and Ex Situ. *Animals (MDPI)*, *13*(19), 3051. https://doi.org/10.3390/ani13193051

Hoffman, M. T. (1993). Major P.J. Pretorius and the decimation of the Addo elephant herd in 1919-1920: Important reassessments. *Koedoe: African Protected Area Conservation and Science*, *36*. https://doi.org/10.4102/koedoe.v36i2.372

Hotelling, H. (1933). Analysis of a complex of statistical variables into principal components. *Journal of Educational Psychology*, *24*(6), 417–441. https://doi.org/10.1037/h0071325

IUCN. (2020). *The IUCN Red List of Threatened Species*. IUCN Red List of Threatened Species. https://www.iucnredlist.org/en

Janik, V. M. (2013). Cognitive skills in bottlenose dolphin communication. *Trends in Cognitive Sciences*, *17*(4), 157–159. https://doi.org/10.1016/j.tics.2013.02.005

Janik, V. M., Janik, V. M., Slater, P. J., & Slater, P. J. B. (1997). Vocal Learning in Mammals. *Advances in The Study of Behavior*. https://doi.org/10.1016/s0065-3454(08)60377-0

Janik, V. M., & Knörnschild, M. (2021). Vocal production learning in mammals revisited. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1836). https://doi.org/10.1098/rstb.2020.0244

Janik, V. M., & Slater, P. J. B. (2000). The different roles of social learning in vocal communication. *Animal Behaviour*, *60*(1), 1–11. https://doi.org/10.1006/anbe.2000.1410

K. Lisa Yang Center for Conservation Bioacoustics. (2024). *Raven Pro: Interactive Sound Analysis Software* (Version 1.6) [Computer software]. The Cornell Lab of Ornithology. https://www.ravensoundsoftware.com/

Kruskal, W. H., & Wallis, W. A. (1952). Use of Ranks in One-Criterion Variance Analysis. *Journal of the American Statistical Association*, *47*(260), 583–621. https://doi.org/10.1080/01621459.1952.10483441

Kühhaas, P., & Weissengruber, G. E. (2011). *Der Larynx des Afrikanischen Elefanten: Eine anatomische Studie*. Südwestdeutscher Verlag für Hochschulschriften.

Langbauer, W. R. Jr. (2000). Elephant communication. *Zoo Biology*, *19*(5), 425–445. https://doi.org/10.1002/1098-2361(2000)19:5%253C425::AID-ZOO11%253E3.0.CO;2-A

Lee, P., Fishlock, V., Webber, C. E., & Moss, C. (2016). The reproductive advantages of a long life: Longevity and senescence in wild female African elephants. *Behavioral Ecology and Sociobiology*, *70*, 337–345. https://doi.org/10.1007/s00265-015-2051-5

Lee, P., & Moss, C. (1986). Early maternal investment in male and female African elephant calves. *Behavioral Ecology and Sociobiology*, *18*, 353–361. https://doi.org/10.1007/BF00299666

Leong, K., Ortolani, A., Burks, K., Mellen, J., & Savage, A. (2003). Quantifying acoustic and temporal characteristics of vocalizations for a group of Captive African Elephants Loxodonta Africana. *Bioacoustics*, *13*, 213–231. https://doi.org/10.1080/09524622.2003.9753499

Leong, K., Ortolani, A., Graham, L. H., & Savage, A. (2003). The use of low-frequency vocalizations in African elephant (Loxodonta africana) reproductive strategies. *Hormones and Behavior*, *43*(4), 433–443. https://doi.org/10.1016/S0018-506X(03)00025-4

Levene, H. (1960). *Robust tests for equality of variances* (pp. 278–292). Stanford University Press.

Mann, H. B., & Whitney, D. R. (1947). On a Test of Whether one of Two Random Variables is Stochastically Larger than the Other. *The Annals of Mathematical Statistics*, *18*(1), 50–60. https://doi.org/10.1214/aoms/1177730491

McComb, K., Moss, C., Durant, S., Baker, L., & Sayialel, S. (2001). Matriarchs As Repositories of Social Knowledge in African Elephants. *Science (New York, N.Y.)*, *292*, 491–494. https://doi.org/10.1126/science.1057895

McComb, K., Moss, C., Sayialel, S., & Baker, L. (2000). Unusually extensive networks of vocal recognition in African elephants. *Animal Behaviour*, *59*(6), 1103–1109. https://doi.org/10.1006/anbe.2000.1406

McComb, K., Reby, D., Baker, L., Moss, C., & Sayialel, S. (2003). Long-distance communication of acoustic cues to social identity in African elephants. *Animal Behaviour*, *65*(2), 317–329. https://doi.org/10.1006/anbe.2003.2047

McCowan, B., & Reiss, D. (1995). Whistle contour development in captive-born infant bottlenose dolphins (Tursiops truncatus): Role of learning. *Journal of Comparative Psychology*, *109*(3), 242–260. https://doi.org/10.1037/0735-7036.109.3.242

Milner-Gulland, E. J., & Beddington, J. R. (1997). The exploitation of elephants for the ivory trade: An historical perspective. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *252*(1333), 29–37. https://doi.org/10.1098/rspb.1993.0042

Mitani, J. C., & Brandt, K. L. (1994). Social Factors Influence the Acoustic Variability in the Long-distance Calls of Male Chimpanzees. *Ethology*, *96*(3), 233–252. https://doi.org/10.1111/j.1439-0310.1994.tb01012.x

Moss, C. (1996). Getting to know a population. In K. Kadzo (Ed.), *Studying Elephants* (pp. 58–74). African Wildlife Foundation.

Moss, C., & Poole, J. (1983). *Relationships and social structure in African elephants* (pp. 315–325).

Mundry, R., & Sommer, C. (2007). Discriminant function analysis with nonindependent data: Consequences and an alternative. *Animal Behaviour*, *74*(4), 965–976. https://doi.org/10.1016/j.anbehav.2006.12.028

O'Connell-Rodwell, C. E., Berezin, J. L., Pignatelli, A., & Rodwell, T. C. (2024). The use of vocal coordination in male African elephant group departures: Evidence of active leadership and consensus. *PeerJ*, *12*, e17767. https://doi.org/10.7717/peerj.17767

O'Connell-Rodwell, C. E., Wood, J. D., Wyman, M., Redfield, S., Puria, S., & Hart, L. A. (2012). Antiphonal vocal bouts associated with departures in free-ranging African elephant family

groups (Loxodonta africana). *Bioacoustics*, *21*(3), 215–224. https://doi.org/10.1080/09524622.2012.686166

O'Connell-Rodwell, C. E., Wood, J., Kinzley, C., Rodwell, T., Poole, J., & Puria, S. (2007). Wild African elephants (Loxodonta africana) discriminate between familiar and unfamiliar conspecific seismic alarm calls. *The Journal of the Acoustical Society of America*, *122*, 823–830. https://doi.org/10.1121/1.2747161

OpenAI. (2025). *ChatGPT* (Version 5) [Computer software]. https://chat.openai.com/

Pardo, M., Poole, J., Stoeger, A., Wrege, P., O'Connell-Rodwell, C., Padmalal, U., & de Silva, S. (2019). Differences in combinatorial calls among the 3 elephant species cannot be explained by phylogeny. *Behavioral Ecology*. https://doi.org/10.1093/beheco/arz018

Payne, K. B., Langbauer, W. R., & Thomas, E. M. (1986). Infrasonic calls of the Asian elephant (Elephas maximus). *Behavioral Ecology and Sociobiology*, *18*(4), 297–301. https://doi.org/10.1007/BF00300007

Plotnik, J. M., & Jacobson, S. L. (2022). A "thinking animal" in conflict: Studying wild elephant cognition in the shadow of anthropogenic change. *Current Opinion in Behavioral Sciences*, *46*, 101148. https://doi.org/10.1016/j.cobeha.2022.101148

Poole, J. (2011). The Behavioral Context of African Elephant Acoustic Communication. In *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal* (pp. 125–161). University of Chicago Press. https://doi.org/10.7208/9780226542263-011

Poole, J., & Granli, P. (2011). Signals, Gestures, and Behavior of African Elephants. In *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal* (pp. 109–124). University of Chicago Press. https://doi.org/10.7208/chicago/9780226542263.003.0008

Poole, J., & Moss, C. (1981). Musth in the African elephant, Loxodonta africana. *Nature*, *292*, 830–831. https://doi.org/10.1038/292830a0

Poole, J., Payne, K., Langbauer, W., & Moss, C. (1988). The social contexts of some very low frequency calls of African elephants. *Behavioral Ecology and Sociobiology*, *22*(6), 385–392. https://doi.org/10.1007/BF00294975

Poole, J., Tyack, P. L., Stoeger-Horwath, A. S., & Watwood, S. (2005). Elephants are capable of vocal learning. *Nature*, *434*(7032), 455–456. https://doi.org/10.1038/434455a

R Core Team. (2024). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Reardon, M. (2021). *Shaping Addo: The Story of a South African National Park*. Penguin Random House South Africa (Struik Nature).

Rendall, D. (2025). Nonlinear phenomena in animal vocalizations: Do they reflect alternative functional modes of voice control, 'leaked' cues to quality or condition, or both? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *380*(1923). https://doi.org/10.1098/rstb.2024.0010

Rensch, B. (1957). The Intelligence of Elephants. *Scientific American*, *196*(2), 44–49.

Shaffer, L. J., Khadka, K. K., Van Den Hoek, J., & Naithani, K. J. (2019). Human-Elephant Conflict: A Review of Current Management Strategies and Future Directions. *Frontiers in Ecology and Evolution*, *6*. https://doi.org/10.3389/fevo.2018.00235

Shapiro, S. S., & Wilk, M. B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, *52*(3–4), 591–611. https://doi.org/10.1093/biomet/52.3-4.591

Shrader, A., Ferreira, S., McElveen, M., Lee, P., Moss, C., & van Aarde, R. (2006). Growth and age determination of African savanna elephants. *Journal of Zoology*, *270*, 40–48. https://doi.org/10.1111/j.1469-7998.2006.00108.x

Smet, A. F., & Byrne, R. W. (2014). African elephants (Loxodonta africana) recognize visual attention from face and body orientation. *Biology Letters*, *10*(7), 20140428. https://doi.org/10.1098/rsbl.2014.0428

Soltis, J. (2010). Vocal communication in African Elephants (Loxodonta africana). *Zoo Biology*, *29*(2), 192–209. https://doi.org/10.1002/zoo.20251

Soltis, J., Leong, K., & Savage, A. (2005a). African Elephant Vocal Communication I: Antiphonal Calling Behaviour Among Affiliated Females. *Animal Behaviour*. https://epublications.marquette.edu/data_drdolittle/26

Soltis, J., Leong, K., & Savage, A. (2005b). African elephant vocal communication II: Rumble variation reflects the individual identity and emotional state of callers. *Animal Behaviour*, *70*, 589–599. https://doi.org/10.1016/j.anbehav.2004.11.016

Stoeger, A., & Baotic, A. (2016). Information content and acoustic structure of male African elephant social rumbles. *Scientific Reports*, *6*(1), 27585. https://doi.org/10.1038/srep27585

Stoeger, A., & Baotic, A. (2017). Male African elephants discriminate and prefer vocalizations of unfamiliar females. *Scientific Reports*, *7*, 46414. https://doi.org/10.1038/srep46414

Stoeger, A., & Baotic, A. (2021). Operant control and call usage learning in African elephants. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1836), 20200254. https://doi.org/10.1098/rstb.2020.0254

Stoeger, A., Baotic, A., & Heilmann, G. (2021). Vocal creativity in elephant sound production. *Biology*, *10*(8). https://doi.org/10.3390/biology10080750

Stoeger, A., Charlton, B. D., Kratochvil, H., & Fitch, W. T. (2011). Vocal cues indicate level of arousal in infant African elephant roars. *The Journal of the Acoustical Society of America*, *130*(3), 1700–1710. https://doi.org/10.1121/1.3605538

Stoeger, A., Heilmann, G., Zeppelzauer, M., Ganswindt, A., Hensman, S., & Charlton, B. D. (2012). Visualizing Sound Emission of Elephant Vocalizations: Evidence for Two Rumble Production Types. *PLOS ONE*, *7*(11), e48907. https://doi.org/10.1371/journal.pone.0048907

Stoeger, A., & Manger, P. (2014). Vocal learning in elephants: Neural bases and adaptive context. *Current Opinion in Neurobiology*, *28*, 101–107. https://doi.org/10.1016/j.conb.2014.07.001

Stoeger, A., Mietchen, D., Oh, S., de Silva, S., Herbst, C. T., Kwon, S., & Fitch, W. T. (2012). An Asian Elephant Imitates Human Speech. *Current Biology*, *22*(22), 2144–2148. https://doi.org/10.1016/j.cub.2012.09.022

Stoeger, A., Zeppelzauer, M., & Baotic, A. (2014). Age-group estimation in free-ranging African elephants based on acoustic cues of low-frequency rumbles. *Bioacoustics*, *23*(3), 231–246. https://doi.org/10.1080/09524622.2014.888375

Stoeger-Horwath, A., Stoeger, S., Schwammer, Harald. M., & Kratochvil, H. (2007). Call repertoire of infant African elephants: First insights into the early vocal ontogeny. *The Journal of the Acoustical Society of America*, *121*(6), 3922–3931. https://doi.org/10.1121/1.2722216

Stokes, G. G. (1845). On the theories of the internal friction in fluids in motion, and of the equilibrium and motion of elastic solids. *Transactions of the Cambridge Philosophical Society*, *8*(2), 287–342.

Taylor, L. A., Wittemyer, G., Lambert, B., Douglas-Hamilton, I., & Vollrath, F. (2022). Movement behaviour after birth demonstrates precocial abilities of African savannah elephant, *Loxodonta africana*, calves. *Animal Behaviour*, *187*, 331–353. https://doi.org/10.1016/j.anbehav.2022.03.002

ter Haar, S. M., Fernandez, A. A., Gratier, M., Knörnschild, M., Levelt, C., Moore, R. K., Vellema, M., Wang, X., & Oller, D. K. (2021). Cross-species parallels in babbling: Animals and algorithms. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1836), 20200239. https://doi.org/10.1098/rstb.2020.0239

Terrade, A., Massenet, M., Pernel, L., Mathevon, N., Anikin, A., & Reby, D. (2025). Nonlinear phenomena make animal calls alarming for human listeners. *iScience*, *28*(6). https://doi.org/10.1016/j.isci.2025.112600

Titze, I. R. (1994). *Principles of Voice Production*. Prentice Hall.

Tokuda, I. (2018). Non-linear dynamics in mammalian voice production. *Anthropological Science*, *126*. https://doi.org/10.1537/ase.171130

Turner, W. C., Périquet, S., Goelst, C. E., Vera, K. B., Cameron, E. Z., Alexander, K. A., Belant, J. L., Cloete, C. C., du Preez, P., Getz, W. M., Hetem, R. S., Kamath, P. L., Kasaona, M. K., Mackenzie, M., Mendelsohn, J., Mfune, J. K. E., Muntifering, J. R., Portas, R., Scott, H. A., … Kilian, J. W. (2022). Africa's drylands in a changing world: Challenges for wildlife conservation under climate and land-use changes in the Greater Etosha Landscape. *Global Ecology and Conservation*, *38*, e02221. https://doi.org/10.1016/j.gecco.2022.e02221

Vance, E., Archie, E., & Moss, C. (2009). Social networks in African elephants. *Computational & Mathematical Organization Theory*, *15*, 273–293. https://doi.org/10.1007/s10588-008-9045-z

Vernes, S. C., Janik, V. M., Fitch, W. T., & Slater, P. J. B. (2021). Vocal learning in animals and humans. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *376*(1836), 20200234. https://doi.org/10.1098/rstb.2020.0234

Vernes, S. C., Kriengwatana, B. P., Beeck, V. C., Fischer, J., Tyack, P. L., Ten Cate, C., & Janik, V. M. (2021). The multi-dimensional nature of vocal learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1836). https://doi.org/10.1098/rstb.2020.0236

von Dürckheim, K. E. M., Hoffman, L. C., Poblete-Echeverría, C., Bishop, J. M., Goodwin, T. E., Schulte, B. A., & Leslie, A. (2022). A pachyderm perfume: Odour encodes identity and group membership in African elephants. *Scientific Reports*, *12*(1), 16768. https://doi.org/10.1038/s41598-022-20920-2

Wall, J., Hahn, N., Carroll, S., Mwiu, S., Goss, M., Sairowua, W., Tiedeman, K., Kiambi, S., Omondi, P., Douglas-Hamilton, I., & Wittemyer, G. (2024). Land use drives differential resource selection by African elephants in the Greater Mara Ecosystem, Kenya. *Movement Ecology*, *12*(1), 11. https://doi.org/10.1186/s40462-023-00436-8

Warner, Z. (2008). *Examining Human-Elephant Conflict in Southern Africa: Causes and Options for Coexistence* [Master of Environmental Studies Capstone Project]. Department of Earth and Environmental Studies, University of Pennsylvania.

Welch, B. L. (1951). ON THE COMPARISON OF SEVERAL MEAN VALUES: AN ALTERNATIVE APPROACH. *Biometrika*, *38*(3–4), 330–336. https://doi.org/10.1093/biomet/38.3-4.330

Whitehouse, A. M. (2002). Tusklessness in the elephant population of the Addo Elephant National Park, South Africa. *Journal of Zoology*, *257*(2), 249–254. https://doi.org/10.1017/S0952836902000845

Whitehouse, A. M., & Hall-Martin, A. J. (2000). Elephants in Addo Elephant National Park, South Africa: Reconstruction of the population's history. *Oryx*, *34*(1), 46–55. https://doi.org/10.1046/j.1365-3008.2000.00093.x

Whitehouse, A. M., & Kerley, G. I. H. (2002). Retrospective assessment of long-term conservation management of elephants in Addo Elephant National Park, South Africa. *Oryx*, *36*(3), 243–248. https://doi.org/10.1017/S0030605302000455

Wilden, I., Tembrock, G., Herzel, H., & Peters, G. (1998). Subharmonics, biphonation, and deterministic chaos in mammal vocalization. *Bioacoustics*, *9*(3), 171–196. https://doi.org/10.1080/09524622.1998.9753394

Wittemyer, G., Douglas-Hamilton, I., & Getz, W. M. (2005). The socioecology of elephants: Analysis of the processes creating multitiered social structures. *Animal Behaviour*, *69*(6), 1357–1371. https://doi.org/10.1016/j.anbehav.2004.08.018

Wittemyer, G., & Getz, W. M. (2007). Hierarchical dominance structure and social organization in African elephants, Loxodonta africana. *Animal Behaviour*, *73*(4), 671–681. https://doi.org/10.1016/j.anbehav.2006.10.008

Wood, J. D., Mccowan, B., Langbauer, W. R., Viljoen, J. J., & Hart, L. A. (2005). *CLASSIFICATION OF AFRICAN ELEPHANT LOXODONTA AFRICANA RUMBLES USING ACOUSTIC PARAMETERS AND CLUSTER ANALYSIS* (pp. 143–161).

Zeppelzauer, M., Hensman, S., & Stoeger, A. (2015). Towards an automated acoustic detection system for free-ranging elephants. *Bioacoustics*, *24*(1), 13–29. https://doi.org/10.1080/09524622.2014.906321

Zeppelzauer, M., & Stoeger, A. (2015). Establishing the fundamentals for an elephant early warning and monitoring system. *BMC Research Notes*, *8*, 409. https://doi.org/10.1186/s13104-015-1370-y