What the rhino's voice tells: Information encoded in the vocalizations of Southern White Rhinoceros (*Ceratotherium simum simum*)

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“The vocal utterance of the Rhinoceros consists of a dull growl,
changing into a ferocious snorting and panting in anger.
In a state of natural freedom these snorts may be frequently heard; for the rage of a Rhinoceros is easily excited and its habitual indifference toward everything that does not come under the classification of food, may very soon turn to the direst anger.”

Alfred Brehm, 1895

CONTENT

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1. ABSTRACT

In many mammalian species, acoustic communication is essential as a mode of signalling for the transmission of information and thus for coordinating social interactions. It is assumed that animals living in a more complex social environment will exhibit greater complexity in their acoustic communication system.

The aim of this thesis was to provide new insights into vocal communication and information encoded in vocalizations of the Southern white rhinoceros (*Ceratotherium simum simum*), a species we still know too little about. The White rhinoceros is said to be the rhinoceros species with the most developed social system. Several attributes, which may contribute to vocal complexity of this species, have been analysed and their potential biological significance within and between species has been discussed.

In the first study, the vocal repertoire of infant and juvenile Southern white rhinoceros and age-dependent variations were investigated by analysing functional and structural characteristics of call types and by comparing infant and adult vocal repertoires. Results revealed a strong innate component to the development of vocal usage and production, but also a certain degree of flexibility during development with regard to call usage and contextual usage. Several adult call types were already present in new born White rhinoceros, whereas other call types were restricted to infancy or adulthood, or altered with regard to usage during development. In the second study, the acoustic encoding of an individual's identity was investigated for several call types. These showed varying levels of individual distinctiveness as a function of the context of social interactions. In particular calls emitted in affiliative social interactions were characterised by the highest level of individual distinctiveness.

The presented thesis showed that the restricted plasticity of vocal communication during development seems to play only a minor role in the context of communication complexity. The potential of encoding indexical information, clearly contributes to the complexity of the communication system. Even if extensive data in the different rhinoceros species is still lacking, variability in vocal communication across these species is evident. Social and ecological factors may have shaped acoustic communication, in terms of both when to call and how signals look like.

Key words: *White rhinoceros, acoustic communication, vocal ontogeny, sender identity*

2. ZUSAMMENFASSUNG

Die Kommunikation mittels akustischer Signale ist für viele Säugetiere eine wichtige Form der Informationsübertragung und damit für die Koordination sozialer Interaktionen. Man nimmt daher an, dass sich in Abhängigkeit von der Komplexität des Sozialsystems einer Art, eine komplexere akustische Kommunikation entwickelt hat. Zielsetzung dieser Arbeit war die Untersuchung der akustischen Kommunikation des Südlichen Breitmaulnashorns, die Nashornart mit dem ausgeprägtesten Sozialsystem, um neue Einblicke zu erhalten, welche Informationen in ihren Vokalisationen enthalten sind. Im Rahmen dieser Arbeit wurden verschiedene Attribute untersucht, die zur Komplexität der akustischen Kommunikation beitragen könnten. Darüber hinaus wurde ihre mögliche biologische Bedeutung diskutiert, auch im Vergleich mit anderen Nashornarten. In der ersten Studie dieser Arbeit wurde das vokale Repertoire von Jungtieren und Juvenilen des Südlichen Breitmaulnashorns untersucht. Dazu wurden sowohl die funktionellen, als auch die strukturellen Charakteristika der Ruftypen analysiert und mit denen von adulten Breitmaulnashörnern verglichen. Diverse Ruftypen adulter Nashörner konnten bereits bei neugeborenen Nashörnern beobachtet werden. Das Auftreten anderer Ruftypen schien sich hingegen ausschließlich auf bestimmte Altersgruppen zu beschränken, oder veränderte sich hinsichtlich ihrer Verwendung im Laufe der Entwicklung. Die Ergebnisse zeigten damit sowohl eine stark angeborene Komponente hinsichtlich der Produktion und Verwendung von Vokalisationen, aber auch eine gewisse Flexibilität bei der Verwendung bestimmter Ruftypen. In der zweiten Studie wurde das Potenzial die individuelle Identität eines Individuums akustisch zu kodieren für verschiedene Ruftypen untersucht. Individuelle akustische Unterschiede waren, in Abhängigkeit von ihrer Bedeutung in sozialen Interaktionen, bei verschiedenen Ruftypen unterschiedlich stark ausgeprägt. Besonders Ruftypen, die in affiliativen sozialen Interaktionen eine Rolle spielen, zeigten das größte Maß an Individualität. Mit dieser Arbeit konnte gezeigt werden, dass, im Gegensatz zur nur begrenzten Plastizität der akustischen Kommunikation des Breitmaulnashorns, das Potenzial diverser Ruftypen, die individuelle Identität des Senders zu kodieren, deutlich zur Komplexität beiträgt. Auch wenn umfangreiche Daten zur akustischen Kommunikation diverser Nashornarten nach wie vor fehlen, so zeichnen sich doch Unterschiede zwischen den Arten ab, für die sowohl soziale, als auch ökologische Faktoren ursächlich sein könnten.

Schlagwörter: *Breitmaulnashorn, akustische Kommunikation, vokale Ontogenie, Senderidentität*

3. GENERAL INTRODUCTION: WHAT THE ANIMAL'S VOICE TELLS

An effective communication is critical for the lives of all animals regardless of the species. Communication, in the classical sense, is defined as the interplay between the action or the cue of one animal (sender) on the one hand, and the perception and the associated altered behaviour in another animal (receiver) on the other hand, in a manner adaptive to either one or both of the animals involved (Wilson, 1975). Especially mammals use a variety of signal modalities for communication serving different functions. Each signal modality has its advantages and disadvantages depending on when, where, and which information needs to be transmitted. In many mammalian species, acoustic communication is essential as a mode of signalling for coordinating social interactions. Sounds can vary substantially in acoustic parameters such as amplitude, duration, or frequency and can thus be adjusted to various behavioural situations and environmental conditions (Wilson, 1975). These differences in the physical properties impact, for example, how fast and how far the sound can be transmitted in the environment, how easily the position of the sender can be localized, or how effective information can be encoded.

Given the fact that vocalizations evolved mainly for the purpose of communication a multitude of questions arises such as: How are vocalizations produced? What information do vocalizations transmit and how are they encoded? What are the specific functions of a given vocalization? How do vocalizations change during ontogeny?

3.1. Vocal production mechanism

Mammals are capable of emitting vocalizations through the interaction of several structures that can be assigned to three functional areas and that are also involved in other primary functions such as breathing or swallowing: the respiratory organs, the larynx including the vocal folds, and the supralaryngeal cavities (the pharynx, the oral cavity, and the nasal cavity). The vocal production apparatus is the complex system by which air is transformed into sound. The air enters the body through the nasal or oral cavity, flows down the trachea and finally into the lungs. For the process of moving air into and out of the lungs various structures are involved such as the ribs, the intercostal muscles, and the diaphragm (e.g. Lieberman & Blumstein, 1988; Fitch, 2010). The respiratory organs generate the air flow that reaches the larynx through the trachea. The larynx is the place in which the sound is produced ("source"; e.g. Fant, 1960; Fitch, 2010) and therefore the key area of the vocal production apparatus. The larynx is composed of several cartilages, connected by ligaments, muscles, and membranes, and houses the vocal folds. It is divided into three parts: the supraglottis (contains the false vocal cords), the glottis (contains the true vocal cords), and the subglottis. The opening or closing of the vocal folds by contraction movements allows a greater or smaller amount of air to pass and thereby determines the pitch of the resulting sound (e.g. Fitch, 2010). The elementary transformation of this sound results from the resonance properties and modulation mechanism of the supralaryngeal vocal tract ("filter"; e.g. Fant, 1960; Fitch, 2010). In this area of the vocal production apparatus, certain frequencies of the sound are attenuated and others amplified (e.g. Fitch, 2010; Taylor & Reby, 2010).

The above-described mammalian vocal production apparatus exerts strong anatomical and physiological constraints on the acoustic characteristics of vocalizations. The capacity of the respiratory organs generating the air flow thereby often determines temporal parameters. The animal's body size correlates, for example, to the shape and the size of the vocal tract and thus determines the acoustic features of the voice (e.g. Fitch, 1997; Gamba et al., 2017; Garcia et al., 2016; Ravignani et al., 2017). In this context, the anatomy and physiology of the larynx, sub-laryngeal and laryngeal structures (e.g. vocal fold length) influence "source-related" parameters, whereas "filter-related" parameters depend on the anatomy and physiology of the supralaryngeal vocal tract. Various acoustic variations can be directly linked to phenotypical variation of the caller. To name just a few examples: Longer and thicker vocal folds lead to lower fundamental frequencies and longer vocal tracts result in formants with energy concentrated at lower frequencies (e.g. Ey et al., 2007). Larger lungs lead to longer vocalizations. Moreover, maturational processes such as growth or changes in hormonal levels and the associated effects on the vocal tract are linked to modifications of vocalizations (e.g. Briefer & McElligott, 2011b; Hammerschmidt et al., 2000a; Stoeger et al., 2014). However, not only long-term hormonal changes, but also short-term hormonal fluctuations can affect vocal production mechanism. It is assumed that the release of sex hormones has a direct influence on the larynx. Progesterone, for example, increases the viscosity and acidity levels of glandular laryngeal cells leading to a decreased volume (Abitbol et al., 1999). Oestrogen has a hypertrophic effect on laryngeal mucus and increases glandular cell secretion.

3.2. Information encoded in mammalian vocalizations

Determining the information content of animal vocalizations can give valuable insights into the potential functions of vocal signals. Information encoded in animal vocalizations can be grouped into two broad categories: (1) Information about the physical and physiological attributes of the caller (indexical information) and (2) contextual information, including information about the caller's emotional state and information about external events or objects (referential information). The differentiation between indexical and contextual information has developed historically. However, one has to keep in mind that these two categories are not entirely separate from one another, as for example emotions trigger hormonal secretions (Butnariu & Sarac, 2019) and are thus also related to physiological changes.

3.2.1. Indexical information - information on physical and physiological attributes

Indexical information is related to morphological and physiological characteristics and attributes of the caller. As the production of sounds depends largely on these parameters, morphological and physiological constraints may influence both the inter- as well as the intra-specific acoustic variability, ranging from variations on a (sub-) species level (see Table 3-1; e.g. Esser et al., 2008; Gouzoules & Gouzoules, 2000), to population or group membership (e.g. Delgado, 2007; Symmes et al., 1979), kinship or social affiliations (e.g. Kessler et al., 2012; Levréro et al., 2015), up to variations on an individual level such sex, age, or size differences (e.g. Baotic & Stoeger, 2017; Charlton, et al., 2011; Pfefferle & Fischer, 2006), and can even be linked to hormonal variation (e.g. Barelli et al., 2013; Charlton, et al., 2011).

Closely related species or subspecies, especially sympatric species, have often evolved significant structural differences in vocalizations (see Table 3-1; e.g. Esser et al., 2008; Gouzoules & Gouzoules, 2000). Inter-specific variation provides information for discriminating between conspecifics and heterospecifics and thus may act as premating isolation mechanism in order to avoid hybridisation (e.g. Andersson, 1994; Templeton, 1989).

Intra-specific acoustic variability may be related to the population affiliation of individuals with different populations having different acoustic signatures (see Table 3-1; e.g. Delgado, 2007; Symmes et al., 1979). Furthermore, vocalizations may vary depending on the group membership (Capybara: Barros et al., 2011; Goitred gazelle: Volodin et al., 2014; Spix´s disc-winged bat: Gillam & Chaverri, 2012). Those variations may be important for cohesion between group members and for spacing between groups. As individuals of a social group are often highly related, group-related acoustic signatures may also signal kinship (e.g. Barros et al., 2011). Indeed, acoustic features are heritable components which may be suitable for determining genetic relatedness. Evidence was found for some primate and carnivore species, in which vocalizations are an important cue for the recognition of kinship (e.g. Charlton et al., 2009a ; Kessler et al., 2012; Levréro et al., 2015). Vocalizations containing reliable innate information about genetic relatedness of individuals constitute an effective mechanism for inbreeding avoidance (Kessler et al., 2012). On the other hand, kinship-related signatures also offer the opportunity for kin selection as individuals can give preferential treatment to those with calls similar to their own.

Indexical information can, last but not least, be related to individual-specific attributes, physical and physiological characteristics. Vocalizations can provide reliable information on the sex (see Table 3-1; e.g. Baotic & Stoeger, 2017; Charlton, 2015), the size (e.g. Casey et al., 2015; Charlton et al., 2011; Stoeger & Baotic, 2016), the age (e.g. Charlton, 2015; Stoeger & Baotic, 2016) and, thus, on the identity of an individual (e.g. Bouchet et al., 2012; Fan et al., 2019). In several mammalian species, acoustic variations are even linked to hormonal fluctuations. Vocalizations of females of various mammalian orders contain, for example, information about their receptivity (see Table 3-1; Rodentia: Matochik et al., 1992; Carnivora: Charlton et al., 2010; Graham et al., 1995; Lindburg et al., 2001; Rogers et al., 1996; Umapathy et al., 2007; Wielebnowski & Brown, 1998; Artiodactyla: Schön et al., 2007; Perissodactyla: Zainal Zahari et al., 2005; Proboscidea: Leong et al., 2003; Primates: Buesching, et al., 1998; Daschbach et al., 1981; Semple et al., 2002). Vocalizations of males, on the other hand, seem to have the potential to signal reliably differences in androgen- and testosterone-levels (e.g. Barelli et al., 2013; Charlton et al., 2011; Higham et al., 2013; Koren & Geffen, 2009).

The assessment of the identity of others is important for separating individuals as well as for bringing and keeping them together, and thereby for creating and regulating social relationships that are critical for fitness and survival. Especially in complex social systems, it is essential for an individual to assess the identity of others for maintaining group structures and dominance hierarchies, avoiding of inbreeding, attraction of mates, determent of rivals, parent-offspring recognition, or the detection of reliable and unreliable callers (e.g. Bouchet et al., 2012; Charlton et al., 2007; Kessler et al., 2012; Müller & Manser, 2008; Reby et al., 2005a). Physical and physiological attributes such as the sex, the body size, the age, or the hormonal state such as differences in androgen- and testosterone-levels of an individual (e.g. Barelli et al., 2013; Charlton et al., 2011a; Higham et al., 2013; Koren & Geffen, 2009) are key determinants of resource holding potential, mate quality, fighting ability, and dominance rank, as these factors can determine the potential outcome of agonistic contests and are positively correlated with reproductive success (Hollister-Smith et al., 2007).

Nonetheless, the question remains whether acoustic signals convey reliable or honest information about the caller. It is often argued that such acoustic features cannot easily be faked as they are directly linked to the caller's phenotype (Maynard Smith & Harper, 2003). Although this may be true in many cases, there are also instances where this is not the case (Charlton & Reby, 2016). In some species, males are, for example, able to retract their larynx during vocalization and thus to elongate their vocal tracts (Red deer, Fallow deer: Fitch & Reby, 2001; Koala: Charlton et al., 2011b). Through this elongation and the resulting formant lowering, males convey the impression, via their vocalizations, of an exaggerated body size (Fitch & Reby, 2001). In such cases, individual differences in vocalizations sire not only from unselected individual differences in vocal morphology, but rather have been intensified by sexual selection pressure to advertise caller identity to increase mating success. In contrast, ground squirrels (*Spermophilus sp.*) are pursuing a completely different objective when using a form of "vocal mimicry" (Matrosova et al., 2007). Despite the fact that there are prominent differences in body size between juvenile and adult ground squirrels, acoustic cues to body size are absent (Matrosova et al., 2007). It has been suggested that the imitation of adult vocal pattern in juvenile ground squirrels protects them from age-dependent predation risks (Matrosova et al., 2007).

In summary therefore, it can be said that in most cases indexical information encoded in vocalizations provide honest information about the physical and physiological attributes of the sender as the production of sounds highly depends on morphological and physiological parameters. However, some species seem to have developed specific mechanisms to manipulate acoustic features of the voice to enhance biological fitness (Charlton et al., 2011b; Fitch & Reby, 2001; Matrosova et al., 2007).

Table 3-1. Overview of selected studies which investigated indexical information encoded in vocalizations of different mammalian orders including information on: the species (Sp.), the population/ subspecies (Pop./Subsp.), the social group/ social affiliation (Soc. aff.), the dominance rank (Rank), the kinship (Kin.), the sex, the age, the body weight/ size (Size), the individual identity (ID), and the reproductive/ hormonal state (Repro.).

Species	**Call type**	**Indexical information**										**Reference**
		Sp.	**Pop./ Subsp.**	**Soc. aff.**	**Rank**	**Kin.**	**Sex**	**Age**	**Size**	**ID**	**Repro.**	
PRIMATES												
Ringtailed lemur (*Lemur catta*)	cohesion call					(+)	-	-		+		Gamba et al., 2017; Macedonia, 1986
	nasal click grunt									+		
Grey mouse lemur (*Microcebus murinus*)	short whistle					-				+		Hafen et al., 1998; Kessler et al., 2012; Leliveld et al., 2011; Zimmermann & Lerch, 1993
	grunt									+		
	tsak									+		
	trill		+			+				+		
Squirrel monkey (*Saimiri sciureus*)	isolation peep		+							+		Symmes & Biben, 1985; Symmes et al., 1979
Pygmy marmosets (*Cebuella pygmaea*)	trill			+								Snowdon & Elowson, 1999
White-faced capuchins (*Cebus capucinus*)	lost call				+		+			+		Digweed et al., 2007
Campbell´s monkey (*Cercopithecus campbelli campbelli*)	B series									+		Lemasson & Hausberger, 2004, 2011; Lemasson et al., 2010, 2011
	CH6			+	-	-						
	contact call			+		-						

Species	**Call type**	**Indexical information**										**Reference**
		Sp.	**Pop./ Subsp.**	**Soc. aff.**	**Rank**	**Kin.**	**Sex**	**Age**	**Size**	**ID**	**Repro.**	
Putty-nosed monkey (*Cercopithecus nictitans*)	pyow		-							+		Price et al., 2009
	hack		-							-		
Golden snub-nosed monkey (*Rhinopithecus roxellana*)	coo call									+		Fan et al., 2019
Red-capped mangabey (*Cercocebus torquatus*)	Whoop-Gobble, loud call									+		Bouchet et al., 2012
	WaHoo, alarm call									+		
	Ti+(Uh), food call									+		
	A+(Uh), food call									+		
	Un+(Uh), threat call									+		
	Ro+(Uh), contact call									+		
Barbay macaque (*Macaca sylvanus*)	copulation call										+	Fischer et al., 1995; Pfefferle et al., 2011; Semple & McComb, 2000
	shrill bark									+		
Japanese macaque (*Macaca fuscata*)	coo call			+								Tanaka et al., 2006

Species	**Call type**	**Indexical information**										**Reference**
		Sp.	**Pop./ Subsp.**	**Soc. aff.**	**Rank**	**Kin.**	**Sex**	**Age**	**Size**	**ID**	**Repro.**	
Pigtailed monkey (*Macaca nemestrina*)	scream	+										Gouzoules & Gouzoules, 2000
Sulawesi crested black macaque (*Macaca nigra*)	scream											Gouzoules & Gouzoules, 2000
Stumptailed macaque (*Macaca arctoides*)	scream											Gouzoules & Gouzoules, 2000
Rhesus monkey (*Macaca mulatta*)	scream											Fitch, 1997; Fukushima et al., 2015; Ghazanfar et al., 2007; Gouzoules & Gouzoules, 2000; Hammerschmidt et al., 2000; Higham et al., 2013; Rendall et al., 1998
	coo							+	+	+		
	bark				-			-	+		+	
	grunt									+		
	noisy scream									-		
	threat								+			
Mandrill (*Mandrillus sphinx*)	contact call					+						Levréro et al., 2015
Hamadryas baboon (*Papio hamadryas*)	grunt								+			Pfefferle & Fischer, 2006

Species	Call type	Indexical information										Reference
		Sp.	Pop./ Subsp.	Soc. aff.	Rank	Kin.	Sex	Age	Size	ID	Repro.	
Chacma baboon (*Papio ursinus*)	infant contact call									+		Kitchen et al., 2003; Rendall, 2003; Rendall et al., 2009
	wahoo call				+			+	-			
	infant distress scream									+		
	vowel-like grunt									+		
White-handed gibbon (*Hylobates lar*)	male solo song							+		+	+	Barelli et al., 2013
Müeller's gibbon (*Hylobates muelleri*)	great call		-							+		Clink et al., 2017
Western Gorilla (*Gorilla gorilla*)	single grunt									+		Salmi et al., 2014
	double grunt									+		
	grumble									+		
	copulation grunt									+		
	threat grunt									+		
	scream									+		
	hum									+		
	hoot series									+		
Orangutan (*Pongo spp.*)	long call		+							+		Delgado, 2007

Species	**Call type**	**Indexical information**										**Reference**
		Sp.	**Pop./ Subsp.**	**Soc. aff.**	**Rank**	**Kin.**	**Sex**	**Age**	**Size**	**ID**	**Repro.**	
Chimpanzee (*Pan troglodytes*)	infant whimper									+		Crockford et al., 2004; Levréro & Mathevon, 2013; Marshall et al., 1999; Mitani et al., 1996; Mitani & Brandt, 1994; Notman & Rendall, 2005; Slocombe & Zuberbühler, 2005
	infant scream									+		
	scream						+					
	pant hoot		+	+						+		
	pant grunt									-		
CHIROPTERA												
Spix´s disc-winged bat (*Thyroptera tricolor*)	inquiry call			(+)						+		Gillam & Chaveri, 2012
	response call			(+)						+		
Greater spear-nosed bat (*Phyllostomus hastatus*)	screech call			+								Boughman, 1998
Greater sac-winged bat (*Saccopteryx bilineata*)	isolation call			+			-			+		Knörnschild et al., 2012
CARNIVORA												
Domestic cat (*Felis silvestris*)	kitten isolation call									+		Scheumann et al., 2012

Species	**Call type**	**Indexical information**										**Reference**
		Sp.	**Pop./ Subsp.**	**Soc. aff.**	**Rank**	**Kin.**	**Sex**	**Age**	**Size**	**ID**	**Repro.**	
Koala (*Phascolarctos cinereus*)	bellow						+		+	+		Charlton, 2015; Charlton et al., 2011a
	tonal rejection call							+		+		
	snarl							-		-		
Giant panda (*Ailuropoda melanoleuca*)	chirp										+	Charlton et al., 2009b, 2010a,b, 2011b, 2018; Lindburg et al., 2001
	bleat					+	+	+	+	+	+	
Banded mongoose (*Mungos mungo*)	pup distress call									+		Jansen et al., 2012; Müller & Manser, 2008
	escort contact call									+		
	close call			(+)			-			+		
Dwarf mongoose (*Helogale parvula*)	contact call									+		Rubow et al., 2018
	snake call									+		
	isolation call									+		
Giant otter (*Pteronura brasiliensis*)	contact call									+		Mumm et al., 2014
	hum									-		
Asian small-clawed otter (*Amblonyx cinerea*)	U3							+	+	+		Lemasson et al., 2014

Species	**Call type**	**Indexical information**										**Reference**
		Sp.	**Pop./ Subsp.**	**Soc. aff.**	**Rank**	**Kin.**	**Sex**	**Age**	**Size**	**ID**	**Repro.**	
Sea otter (*Enhydra lutris lutris*)	scream call									+		McShane et al., 1995
Spotted hyena (*Crocuta crocuta*)	giggle call				+		-	+		+	-	Mathevon et al., 2010; Theis et al., 2007
	whoops						+	+				
Meerkat (*Suricata suricatta*)	alarm call							+		+		Hollén & Manser, 2007; Manser, 2001; Schibler & Manser, 2007; Townsend et al., 2014
	bark									+		
Domestic dog (*Canis familiaris*)	bark									+		Riede & Fitch, 1999; Sibiryakova et al., 2020; Yin & McCowan, 2004
	whine								+			
	growl								+			
Maned wolf (*Chrysocyon brachyurus*)	extended-bark									+		Balieiro & Monticelli, 2019; Brady, 1981
Dingoe (*Canis lupus dingo*)	bark		-				-			+		Déaux et al., 2016
	howl		-				-			+		
Mediterranean monk seal (*Monachus monachus*)	bark									+		Charrier et al., 2017
	scream									+		

Species	**Call type**	**Indexical information**										**Reference**
		Sp.	**Pop./ Subsp.**	**Soc. aff.**	**Rank**	**Kin.**	**Sex**	**Age**	**Size**	**ID**	**Repro.**	
Northern elephant seal (*Mirounga angustirostris*)	clap threats				-				+	+		Casey et al., 2015
South American fur seal (*Arctocephalus australis*)	female call									+		Phillips & Stirling, 2000
	pup call									+		
Bearded seal (*Erignathus barbatus*)	trill		+							+		Risch et al., 2007
Ribbon seal (*Histriophoca fasciata*)	down sweep		+									Mizuguchi et al., 2016
	roar		-									
	yowl		-									
	grunt		-									
	hiss		-									
Weddell seal (*Leptonychotes weddellii*)	contact call		+									Collins & Terhune, 2007
ARTIODACTYLA												
Goat (*Capra hircus*)	contact call			+		+	+	+	+			Briefer & McElligott, 2011a, 2011b

Species	**Call type**	**Indexical information**										**Reference**
		Sp.	**Pop./ Subsp.**	**Soc. aff.**	**Rank**	**Kin.**	**Sex**	**Age**	**Size**	**ID**	**Repro.**	
Sheep (*Ovis aries*)	bleat									+		Ligout et al., 2004; Sèbe et al., 2007, 2010
Goitre gazelle (*Gazella subgutturosa*)	nasal call			+								Volodin et al., 2014
Fallow deer (*Dama dama*)	groan				+			+		+		Briefer et al., 2010; Torriani et al., 2006; Vannoni & McElligott, 2007
	contact call									+		
	infant contact call									-		
Red deer (*Cervus elaphus*)	roar								+			Reby et al., 2005; Reby & McComb, 2003; Sibiryakova et al., 2015, 2018; Volodin et al., 2016, 2018
	contact call		+									
	bugle call		+									
	oral contact call							+		+		
	nasal contact call							+		+		
Domestic pig (*Sus scrofa*)	grunt								+	+		Blackshaw et al., 1996; Chan, 2011; Garcia et al., 2016
	bark							+				
RODENTIA												
Capybara (*Hydrochoerus hydrochaeris*)	click call			+								Barros et al., 2011

Species	Call type	Indexical information										Reference
		Sp.	**Pop./ Subsp.**	**Soc. aff.**	**Rank**	**Kin.**	**Sex**	**Age**	**Size**	**ID**	**Repro.**	
Speckled ground squirrel (*Spermophilus suslicus*)	alarm whistle		+				-	- / +	-	+		Matrosova et al., 2007, 2009, 2011, 2016
Yellow ground squirrel (*Spermophilus fulvus*)	alarm whistle						+	- / +	-	+		Matrosova et al., 2007, 2011
European ground squirrel (*Spermophilus citellus*)	alarm call									+		Schneiderová et al., 2017
Yellowe-bellied marmot (*Marmota flaviventris*)	alarm call/ whistle						+	+		+		Blumstein & Daniel, 2004; Blumstein & Munos, 2005; Matrosova et al., 2011
African woodland dormouse (*Graphiurus murinus*)	contact call									+		Ancillotto & Russo, 2016
	aggressive call									-		
Neotropical singing mice (*Scotinomys*)	trill										+	Pasch et al., 2011

Species	Call type	Indexical information										Reference
		Sp.	**Pop./ Subsp.**	**Soc. aff.**	**Rank**	**Kin.**	**Sex**	**Age**	**Size**	**ID**	**Repro.**	
Naked mole-rat (*Heterocephalus glaber*)	soft chirp			+								Barker et al., 2021; Buffenstein, 2021
PROBOSCIDEA												
African elephant (*Loxodonta africana*)	infant roar									(+)		Baotic & Stoeger, 2017; McComb et al., 2000, 2003; Soltis et al., 2005; Stoeger et al., 2011, 2014; Stoeger & Baotic, 2016, 2017
	rumble						+	+	+	+	+	
HYRACOIDEA												
Rock hyrax (*Procavia capensis*)	male song				+				+		+	Koren & Geffen, 2009
SCANDENTIA												
Tree shrew (*Tupaia belangeri*)	chatter call	+					-	-	-	+		Esser et al., 2008; Schehka & Zimmermann, 2009
Tree shrew (*Tupaia glis*)	chatter call											Esser et al., 2008
Tree shrew (*Tupaia chinensis*)	chatter call											Esser et al., 2008

+ positive results; - negative results; (+) found tendencies but not significant differences

3.2.2. Contextual information – emotional or referential information?

In former times, it has been argued that animal vocalizations are primarily manifestations of an individual´s internal state and thereby expressions of emotions (Darwin, 1872). It was assumed that arousal results in contractions of the muscles of the body and thus also in contractions of the muscles of the chest and glottis and that, as a consequence, loud sounds are uttered (Darwin, 1872). For a long time, this view was largely shared and even more recent works have still highlighted the meaning of the affective state of the caller for call production (e.g. Briefer, 2012; Fischer & Price, 2017). However, today it is also clear that vocalizations are much more than just a pure expression of emotions. Vocalizations contain information about the behavioural context and even about a specific external events or objects.

When talking about contextual information, there is always the central question of why an individual produces a certain type of vocalization in a particular situation. There is an ongoing controversial discussion about whether or not acoustic communication in mammals is intentional or rather unintentional (e.g. Schamberg et al., 2018; Townsend et al., 2017). However, these two approaches are not necessarily mutually exclusive. There is no doubt that animals acquire information from the vocalizations of conspecifics. Thereby, it should rather be considered that natural selection has favoured vocalizations of callers that change the behaviour of listeners and simultaneously listeners who detect the links between particular vocalizations and specifics events or environmental conditions (Seyfarth & Cheney, 2003). In this context, evolution might have favoured the development of acoustically distinct vocalizations in different circumstances to convey more specific information (Seyfarth & Cheney, 2003). Nevertheless, there are still two different approaches in this field: the one emphasising the role of emotions and the other emphasising the role of external stimuli.

Emotions are essential for the survival of an individual as they facilitate proper responses to external or internal stimuli enhancing or threatening fitness, for example, approach behaviour versus avoidance behaviour (Mendl et al., 2010). By communicating emotional states, individuals can alert conspecifics to danger (e.g. Blumstein, 1995; Blumstein & Armitage, 1997). Moreover, by perceiving emotions of conspecifics, individuals can assess the emotional state of others, their intention of behaviour, and are thus able to react in a proper manner (e.g. Fichtel et al., 2001; Schehka et al., 2007). Emotions can affect vocalizations directly or indirectly through the brain, lungs, larynx, or vocal tract (Briefer, 2012). Different emotional states induce changes in the somatic and autonomic nervous system leading to tension of muscles and changes in respiration and salivation and, thereby, to modifications of the vocal apparatus and changes of voice parameters (Scherer, 2003).

The existence of general rules regarding the vocal expression of emotions have been suggested by Morton (1977). Morton’s (1977) motivation-structural rules propose that there is a general relationship between the physical structure of vocalizations and the motivation underlying their use, or to be more precisely: Relatively low frequency and harsh sounds are associated with aggressive contexts, whereas high frequency sounds with a tonal structure are associated with a friendly or fearful context. Whereas different studies confirmed Morton´s rules (e.g. Compton et al., 2001; Feighny et al., 2006; Giampaoli, 2017; Keesom et al., 2015; Knotková et al., 2009; Lin et al., 2015; Yin & McCowan, 2004), August & Anderson, (1987) suggested to make a distinction between the friendly and fearful context by using additional acoustic parameters. Ehret (1980) extended the model even further and slightly changed the point of view. He proposed that vocalizations of mammals convey three basic meanings: aversion (aggression), attraction (appeasing or fearful emotions/motivations), and cohesion (friendliness). Aversion should be associated with vocalizations covering a broad frequency range of varying frequency spectrum with noisy component. Attraction should be associated with high frequency tonal sounds, whereas cohesion should be associated with low frequency rhythmic vocalizations (Ehret, 1980). Thus, different types of sounds are linked to context-specific emotions and, thereby, vocalizations are generated by affective states as a result of social-affective interactions.

While Morton’s (1977) approach distinguishes between basic emotional categories, a dimensional approach distinguishes between the two basic dimensions of emotions: emotional arousal (intensity of an emotion, calm versus excited) and valence (positive versus negative emotion; Mendl et al., 2010). Valence in this context is the affective quality referring to the intrinsic attractiveness, for example, in a positive context, such as friendly social interactions, or averseness, such as fear or anger, between the sender and another individual, an object or a situation, and thereby characterizes and categorizes specific emotions (e.g. Frijda, 1986; Mendl et al., 2010). Even if only few studies have focused on vocal indicators of emotional valence, it has been found for several mammalian orders that vocalizations have the potential to indicate positive or negative emotions (see Table 3-2; e.g. Carnivora: Collins et al., 2011; Gogoleva et al., 2010; Taylor et al., 2009; Yin & McCowan, 2004; Perissodactyla: Briefer et al., 2015; Maigrot et al., 2017; Pond et al., 2010; Primates: Fichtel et al., 2001; Jovanovic & Gouzoules, 2001; Scheumann et al., 2007; Rodents: Brudzynski, 2007; Burman et al., 2007; Knutson et al., 2002; Proboscidea: Soltis et al., 2011).

Most of the studies, however, dealing with emotional information encoded in animal vocalizations, focused on encoding of emotional arousal, and here particularly on negative arousal (Briefer, 2012; see Table 3-2). Vocal indicators of arousal in positive situations have rarely been investigated (Briefer, 2012; see Table 3-2). It appears, that vocal indicators of negative arousal show a high degree of similarity across species, with regard to both temporal and spectral parameters, such as an increase in the fundamental and peak frequency, the amplitude, the energy distribution, the duration and call rate, and thus, a decrease in the inter-call interval (Briefer, 2012). Encoding of emotional arousal plays, amongst others, an important role in alarm and food calling behaviour. It is assumed, that food and alarm calls reflect the signaller’s level of arousal, or in other words, the perceived level of threat or the level of urgency to react in the presence of a predator and the level of excitement in response to the presence of a food source or a feeding event (e.g. Macedonia & Evans, 1993b; Owren & Rendall, 2001; Price et al., 2015). In some sciurid species, for example, differences in alarm calling are interpreted as due to urgency, usually defined as distance of threat from caller or suddenness of its approach (see Table 3-2; e.g. Blumstein, 1995; Blumstein & Armitage, 1997) and, thereby, provide information about the response urgency.

Another approach, however, suggests that food and alarm calls contain referential information and that some call systems have a surprising degree of specificity (see Table 3-2; e.g. Evans, 1997; Fichtel & Kappeler, 2002). Referential information, in this discipline, is defined as information about specific events or objects in the environment (Evans, 1997). Moreover, referential signals are not only context-specific but also stimulus-independent, that is the receiver reacts to a referential signal even in the absence of the stimulus eliciting the signal. In order to demonstrate referential specificity for a call, two components, productional specificity and perceptual specificity, are necessary. Productional specificity suggests that specific information about the external event or object is encoded in the call by the animal producing that call. Perceptual specificity suggests that the encoded information is perceived by other animals that hear the call and that they react in the appropriate way. Indeed, even if in some squirrels species different alarm calls reflect the signaller´s level of arousal (see Table 3-2; e.g. Blumstein, 1995; Blumstein & Armitage, 1997), at least some other sciurid species have been shown to use different alarm calls for different predator types (see Table 3-2; McRae &

Green, 2014, 2017; Kiriazis & Slobodchikoff, 2006; Placer & Slobodchikoff, 2000, 2001; Slobodchikoff et al., 1991, 2009; Slobodchikoff & Placer, 2006).

It was, however, above all some primate calls, the alarm call system of vervet monkeys, which first raised the question whether animal vocalizations may have referential quality (e.g. Marler, 1977; Seyfarth et al., 1980a, 1980b). Like most primate species, East African vervet monkeys have a large vocal repertoire which includes calls produced by both males and females upon discovering food, in aggressive interactions, but also structurally-distinct alarm calls specific to the approach of three major predator types, eagles, leopards, and snakes (e.g. Price et al., 2015; Seyfarth et al., 1980a, 1980b). When detecting a predator, vervet monkeys give alarm calls that contain information about the type of predator that has been detected and conspecifics react with particular and adaptive antipredator responses. Over the years the impression has been strengthened and evidence has accumulated that besides expression of the emotional state of an individual, vocalizations contain referential information and that some systems have a surprising degree of specificity (see Table 3-2; e.g. Evans, 1997; Fichtel & Kappeler, 2002). Structurally distinct alarm calls that are predator-class specific and evoke adaptive responses from conspecific receivers have, for example, also been developed in some other primate species (see Table 3-2; Cercopithecidae: Zuberbühler et al., 1997, 1999; Callitrichidae: Kirchhof & Hammerschmidt, 2006; Lemuridae: Macedonia, 1990; Pereira & Macedonia, 1991). Similarly, food-associated calls from several species are said to be referential signals and to provide not only information about food preference, but also about specific food types (see Table 2; Clay et al., 2012; Clay & Zuberbühler, 2009, 2011; Hauser et al., 1993; Kalan et al., 2015; Slocombe & Zuberbühler, 2006).

The alarm calls of meerkats (*Suricata suricatta*) have shown that both kind of information, emotional and referential, can simultaneously be communicated even via the same signal (Hollén & Manser, 2006, 2007; Manser, 2001; Manser et al., 2001, 2002; Townsend et al., 2014). The acoustic structure of these alarm calls varies depending on different predator types and can be classified into discrete call categories (Manser, 2001). In conspecifics these alarm calls elicit different responses according to the different predator types (Manser et al., 2001). In addition, meerkat alarm calls also differ within a predator type in their acoustic structure in relation to the distance of the predator and thus signal response urgency (Manser, 2001). As the urgency increased, call structure changes from harmonic to noisy consistently across all alarm call types.

The major challenge still remains the identification of the actual stimulus or the eliciting event of a specific call and to understand the mechanisms mediating the link between a specific event and the emission of a certain call. It remains questionable what exactly triggers the production of vocalization, the external event itself or intrinsic processes associated with the event. Under natural conditions it still remains difficult to objectively determine the emotional state of an animal. Experimental paradigm as well as social and behavioural contexts in behavioural studies can be used to discriminate between different arousal levels (e.g. Scheumann et al., 2012). Quantifying species specific behavioural displays that indicate arousal is another approach to determine arousal states (e.g. Bastian & Schmidt, 2008; Stoeger et al., 2011, 2012).

Moreover, it can be assumed that, on the basis of instinctual emotional vocalizations, a variety of more complex and specialised vocalizations have developed (Panksepp, 2010). Instinctual vocalizations signalling sexual readiness may have evolved to vocalizations for coordinating various sustaining activities, such as mother-infant proximity calls (e.g. Okabe et al., 2012). Separation calls as a simple expression of pain, on the one hand, may have been the basis for complex alarm calls that alert others to the presence of specific dangers (e.g. Manser et al., 2002). Thereby, there is still considerable controversy about what is encoded when animal produces, for example, alarm or food calls to an external event (e.g. Clay et al., 2012; Fischer, 2017; Fischer & Price, 2017; Ghazanfar et al., 2019; Macedonia & Evans, 1993; Manser, 2010; Schamberg et al., 2018; Wheeler & Fischer, 2012). Assuming that the ultimate goal is maximizing fitness, there might be a number of advantages to attract conspecifics to food sources, by enhancing fitness indirectly via kin selection as well as by enhancing fitness directly (e.g. Hauser & Marler, 1993b, 1993a). With regard to alarm calls, information that might be relevant to maximize fitness can differ depending on, for example, the social organization, the habitat, or the different flight responses of a species. As many squirrel species, for example, have essentially only one escape response, an urgency-based alarm system would fit with the hypothesis that the predator type is irrelevant and that it is more important for them to know how intensely to respond.

The question of which information is encoded in a vocal signal might have to be addressed separately from different perspectives, the signaller’s and receiver’s perspective (Seyfarth & Cheney, 2003). From the signaller’s perspective, these calls might be purely arousal based. The receiver, on the other hand, might have learned to interpret these calling patterns to gain information about the environment, relevant objects, or events (Seyfarth &

Cheney, 2003). In this context, it has been suggested that vocal signals should rather been considered as “goal-directed”, with signallers that have developed a keen sense for the relation between their signals and the receivers’ responses, and receivers that are able to use these signals to predict signallers’ behaviour (Fischer & Price, 2017). Based on this emerging evidence that calls are “goal-directed”, a more recent approach, the “caller-goal framework” (Schamberg et al., 2018), suggests that a call type is a signal of a caller’s goal. In this context, the term “goal” implies that the caller has a motivation that the receiver behaves in a certain way. Thereby, the “caller-goal framework” (Schamberg et al., 2018) tries to clarify the contributions of the caller´s emotional state and the caller´s goal on call production.

Table 3-2. Overview of selected studies which investigated contextual information encoded in vocalizations of different mammalian orders (including emotional and referential information).

Species	**Call type**	**Contextual information**[1]		**Encoding mechanism (intra vs. inter)**[2]	**(Behavioural) Context**	**Reference**
		referential	**emotional**			
PRIMATES						
Gray mouse lemur (*Microcebus murinus*)	purr		V (?)	inter (V)	grooming context (positive)	Scheumann et al., 2007
	whistle				isolation (and threat) context (negative)	
	tsak				threat context (negative)	
Red lemur (*Eulemur rufus*)	chutter	P		inter (P)	predator encounter (aerial predator)	Fichtel & Kappeler, 2002
Verreaux's sifaka (*Propithecus verreauxi*)	roaring bark	P		inter (P)	predator encounter (aerial predator)	Fichtel & Kappeler, 2002
Ringtailed lemur (*Lemur catta*)	rasp	P		inter (P)	predator encounter (raptor)	Macedonia, 1990; Pereira & Macedonia, 1991
	shriek	P			predator encounter (raptor)	
	yap	P			predator encounter (carnivore)	
Brown-mantled tamarin (*Leontocebus fuscicollis*)	aerial alarm call	P		inter (P)	predator encounter (aerial predator)	Kirchhof & Hammerschmidt, 2006
	terrestrial alarm call	P			predator encounter (terrestrial predator)	
Moustached tamarin (*Saguinus mystax*)	aerial alarm call	P		inter (P)	predator encounter (aerial predator)	Kirchhof & Hammerschmidt, 2006
	terrestrial alarm call	P			predator encounter (terrestrial predator)	

Species	Call type	Contextual information[1]		Encoding mechanism (intra vs. inter)[2]	(Behavioural) Context	Reference
		referential	emotional			
Cotton-top tamarin (*Saguinus oedipus*)	C-chirp	F(?)		intra (call rate; F)	food encounter (food preference)	Elowson et al., 1991; Roush & Snowdon, 1994, 2001
	D-chirp	F(?)		intra (call rate; F)	food encounter (food preference)	
Common marmoset (*Callithrix jacchus*)	Call C	F		inter (F)	discovering of insects	Rogers et al., 2018
Black-fronted titi monkey (*Callicebus nigrifrons*)	A-call (chirp)	P		inter (P)	predator encounter (raptor/monkey, threats in the canopy)	Cäsar et al., 2012a, 2012b, 2013
	B-call (cheep)	P		inter (P)	predator encounter (terrestrial predator, disturbances on the ground)	
White-faced capuchin (*Cebus capucinus*)	alarm call	P and/or U		intra (spectral and temporal structure; P)	disturbances and predator encounter (predatory/non-predatory type: aeria predator, human, monkey, terrestrial predator, snake)	Digweed et al., 2005; Fichtel et al., 2005; Gros-Louis et al., 2008
	mild vocal threat		A (-)	inter (temporal and spectral structure; A)	low-level aggression	
	intense vocal threat				high-level aggression	
Tufted capuchin (*Sapajus apella*)	bark	P		inter (P)	predator encounter (aerial predator)	Di Bitetti, 2003, 2005; Wheeler, 2010
	hiccup	U(?)		intra (call rate; U)	risk urgency	
	peep	P(?)		inter (P)	predator encounter (terrestrial predator)	
	grgrs	F(?)		inter (F)	food encounter (fruit at a highly productive source)	
	whistle series	F(?)		inter (F)	food encounter (fruit at a highly productive source)	

Species	Call type	Contextual information[1]		Encoding mechanism (intra vs. inter)[2]	(Behavioural) Context	Reference
		referential	emotional			
Squirrel monkey (*Saimiri sciureus*)	bawl		A (-)	intra (spectral structure; A)	different states of aversion (fighting, predator encounter)	Fichtel et al., 2001
	shriek				different states of aversion (aggressive interactions)	
	growl				different states of aversion (agonistic interactions, mating behaviour)	
	cackle				different states of aversion (social mobbing, aggressive encounters)	
	yap				different states of aversion (predator encounter)	
Campbell's monkey (*Cercopithecus campbelli*)	male loud/alarm call	P		intra (spectral and temporal structure, call rate; P)	predator encounter (predator type: eagle, leopard)	Lemasson et al., 2010a; Ouattara et al., 2009a, 2009b; Zuberbühler, 2001
	female RRA call	P		intra (spectral and temporal structure, call rate; P)	predator encounter (predator type: eagle, leopard)	
	K+ series	U(?)	A(-)	intra (call rate; A/U)	disturbances and predations	
	K series	U(?)	A(-)	intra (call rate; A/U)	disturbances and predations	

Species	Call type	Contextual information[1]		Encoding mechanism (intra vs. inter)[2]	(Behavioural) Context	Reference
		referential	emotional			
Diana monkey (*Cercopithecus diana*)	male long-distance call	P		intra (spectral and temporal structure; P)	predator encounter (predator type: eagle, leopard)	Zuberbühler et al., 1997, 1999
	female eagle alarm call	P		inter (P)	predator encounter (eagle encounter)	
	female leopard alarm call	P			predator encounter (leopard encounter)	
Stuhlmann's blue monkey (*Cercopithecus mitis stuhlmanni*)	pyows	P+U		inter (P); intra (call sequence composition, call rate; U)	predator encounter (leopard encounter), other disturbances	Murphy et al., 2013; Papworth et al., 2008
	hacks	P+U		inter (P); intra (call sequence composition, call rate; U)	predator encounter (eagle encounter)	
Vervet monkey (*Chlorocebus pygerythrus*)	alarm call (leopard)/ chirp	P		inter (P)	predator encounter (leopard encounter)	Price et al., 2015; Seyfarth et al., 1980a, 1980b
	alarm call (eagle)/ rraup	P(?)		inter (P)	predator encounter (eagle encounter)	
	alarm call (snake)/ chutter	P(?)		inter (P)	predator encounter (snake encounter)	

Species	**Call type**	**Contextual information[1]**		**Encoding mechanism (intra vs. inter)[2]**	**(Behavioural) Context**	**Reference**
		referential	**emotional**			
Guereza colobus monkey (*Colobus guereza*)	roaring (+snort)	P		intra (call rate, call sequence composition, temporal structure; P)	predator encounter (predator type: eagle, leopard)	Schel et al., 2009, 2010; Schel & Zuberbühler, 2009
King colobus (*Colobus polykomos*)	roaring (+snort)	P		intra (call rate, call sequence composition, temporal structure; P)	predator encounter (predator type: eagle, leopard)	Schel et al., 2009
Rhesus monkey (*Macaca mulatta*)	noisy scream		A (-)	inter (A)	agonistic interactions	Gouzoules et al., 1984; Hauser & Marler, 1993a, 1993b; Hauser, 1998; Jovanovic & Gouzoules, 2001
	arched scream					
	tonal scream					
	pulsed scream					
	undulated scream					
	grunt	F(?)	A (-)	inter (F); intra (call rate; A)	food encounter (food preference/ food types, low-quality food)	
	harmonic arch	F(?)	A (-)	inter (F); intra (call rate; A)	food encounter (food preference/ food types, high-quality food)	
	chirp	F(?)	A (-)	inter (F); intra (call rate; A)	food encounter (food preference/ food types, high-quality food)	
	warble	F(?)	A (-)	inter (F); intra (call rate; A)	food encounter (food preference/ food types, high-quality food)	

Species	Call type	Contextual information[1]		Encoding mechanism (intra vs. inter)[2]	(Behavioural) Context	Reference
		referential	emotional			
Japanese macaques (*Macaca fuscata*)	coo call		A (-)	intra (spectral and temporal structure; A)	within-group contact, separation, maintaining group cohesion	Sugiura, 2007
Bonnet Macaques (*Macaca radiata*)	alarm call	U		intra (spectral and temporal structure; U)	predator encounter	Coss et al., 2007
Barbary macaque (*Macaca sylvanus*)	shrill bark (disturbance call, alarm call)	P		intra (spectral structure; P)	disturbances and predator encounter (disturbance/ predator type: dog, human, snake)	Fischer et al., 1995; Fischer & Hammerschmidt, 2001
Chacma baboon (*Papio ursinus*)	vowel-like grunt		A	intra (temporal and spectral structure; A)	mother-infant interactions (high and low arousal), group movement (high and low arousal)	Fischer et al., 2001; Rendall, 2003
	bark	P	A(?)	intra (temporal and spectral structure, A; spectral structure, P)	group separation and predator encounter (predator type: lion, crocodile)	
Chimpanzee (*Pan troglodytes*)	rough grunt	F		intra (spectral and temporal structure; F)	food encounter (food preference, food types)	Hauser et al., 1993; Kalan et al., 2015; Siebert & Parr, 2003; Slocombe & Zuberbühler, 2005, 2006
	"food calls" (diverse)	F		intra (spectral structure; F)	food encounter (food preference, food quantity)	
Bonobo (*Pan paniscus*)	call sequence (bark, peep, peep-yelp, yelp, grunt)	F		intra (call sequence composition; F)	food encounter (food preference)	Clay & Zuberbühler, 2009, 2011

Species	**Call type**	**Contextual information[1]**		**Encoding mechanism (intra vs. inter)[2]**	**(Behavioural) Context**	**Reference**
		referential	**emotional**			
PERISSODACTYLA						
Horse (*Equus ferus caballus*)	whinnies		A(-/+) and V	intra (spectral structure, A; spectral and temporal structure, V)	social separation, social reunion	Briefer et al., 2015, 2017; Pond et al., 2010
Przewalski's horse (*Equus ferus przewalskii*)	whinnies		V	intra (call rate, spectral structure,	anticipation for a food reward, affiliative interactions, agonistic interactions, social separation	Maigrot et al., 2017
	squeal					
	nicker					
ARTIODACTYLA						
Goat (*Capra hircus*)	n.m.		A(-/+) and V	intra (spectral structure; A, V)	anticipation of a food reward, food-related frustration, isolation away from conspecifics	Briefer et al., 2015
Domestic pig (*Sus scrofa domesticus*)	grunt		V	intra (spectral and temporal structure, call rate; V)	maintain social contact; positive context, negative context	Briefer et al., 2019a, 2019b; Chan, 2011; Friel et al., 2019; Leliveld et al., 2016; Tallet et al., 2013
	closed-mouth grunt		V	intra (spectral and temporal structure; V)	positive context, negative context	
	bark		V	intra (spectral structure; V)	alarm context, play context	
	n.m. (diverse)		A(-/+) and V	intra (spectral and temporal structure; V, A)	positive contexts, negative contexts	

Species	Call type	Contextual information[1]		Encoding mechanism (intra vs. inter)[2]	(Behavioural) Context	Reference
		referential	emotional			
CARNIVORA						
Silver fox (*Vulpes vulpes*)	whine		A (-/+) and V (?)	intra (call rate, A; spectral structure, V, A); inter (proportion of different call types; V, A)	approaching of humans (positive and negative context)	Gogoleva et al., 2010a, 2010b
	moo					
	growl					
	cough					
	snort					
	bark					
	pant					
	cackle					
Domestic dog (*Canis familiaris*)	bark		V (?)	intra (spectral and temporal structure, call rate; V)	aggression/disturbance context, play context, isolation context	Molnár et al., 2010; Pongrácz et al., 2006; Taylor et al., 2009; Yin & McCowan, 2004
	growl		V (?)	intra (temporal structure, call rate; V)	aggression context, play context	
Spotted hyena (*Crocuta crocuta*)	whoops		A	intra (spectral structure, call rate; A)	general activities, social excitement	Theis et al., 2007
White nose coatis (*Nasua narica*)	chirp		V (?)	inter (V)	relaxed context (foraging, allogrooming, exploration)	Compton et al., 2001; Giampaoli, 2017
	squeak				relaxed context (inquisitive)	
	trill				aggressive context (threat)	
	grunt				aggressive context (territorialism)	
	squawk				aggressive context (agonistic interactions)	

Species	Call type	Contextual information[1]		Encoding mechanism (intra vs. inter)[2]	(Behavioural) Context	Reference
		referential	emotional			
Meerkat (*Suricata suricatta*)	aerial alarm call	P and U		inter (P); intra (call rate, spectral structure; U)	predator encounter (aerial predator)	Hollén & Manser, 2006, 2007b; Manser, 2001; Manser et al., 2001, 2002; Townsend et al., 2014
	terrestrial alarm call			inter (P); intra (call rate, duration, spectral structure; U)	predator encounter (terrestrial predator)	
	recruitment call			inter (P); intra (call rate, duration, spectral structure; U)	predator encounter (snakes and deposits on the ground)	
	bark	P(?)		intra (spectral structure; P)	predator encounter (predator type: aerial predator, terrestrial predator)	
Domestic cat (*Felis silvestris*)	kitten isolation call		A (-)	intra (spectral and temporal structure; A)	isolation from the mother	Scheumann et al., 2012
Giant panda (*Ailuropoda melanoleuca*)	cub vocalization		A	intra (temporal and spectral structure; A)	handling and feeding context procedure (hand-rearing)	Stoeger et al., 2012
Weddell seal (*Leptonychotes weddellii*)	mother contact call		A	intra (call rate; A)	reunion, nursing, separation	Collins et al., 2011
	pup contact call		A	intra (call rate, temporal and spectral structure; A)	reunion, nursing, separation	

Species	Call type	Contextual information[1]		Encoding mechanism (intra vs. inter)[2]	(Behavioural) Context	Reference
		referential	**emotional**			
RODENTIA						
American red squirrel (*Tamiasciurus hudsonicus*)	alarm call sequence (seet, bark-seet)	U(?)		intra (call rate; U)	predator encounter	Digweed & Rendall, 2009a, 2009b, 2010; Greene & Meagher, 1998
	bark	P(?)		inter (P)	predator encounter (terrestrial danger)	
	seet	P(?)		inter (P)	predator encounter (aerial danger)	
Eastern gray squirrel (*Sciurus carolinensis*)	alarm call sequence (moan, quaa, kuk)	P		intra (call rate, call sequence composition; P)	predator encounter (predator type: aerial predator, terrestrial predator)	McRae & Green, 2014, 2017
Eastern chipmunk (*Tamias striatus*)	chipping	P and/or U (?)		inter (P); intra (call rate; U)	predator encounter (avian predator)	Couchoux et al., 2018; da Silva et al., 1994; Weary & Kramer, 1995
	chucking				predator encounter (mammalian predator)	
Golden marmot (*Marmota caudata*)	alarm call	U		intra (syllable number/rate; U)	predator encounter	Blumstein, 1995
Yellow-bellied marmot (*Marmota flaviventris*)	whistle	U		intra (call rate; U)	predator encounter	Blumstein & Armitage, 1997
	trill	U(?)		inter (U)	predator encounter	
	chuck				predator encounter	

Species	Call type	Contextual information[1]		Encoding mechanism (intra vs. inter)[2]	(Behavioural) Context	Reference
		referential	emotional			
Alpine marmot (*Marmota marmota*)	single whistle	P and/or U (?)		inter (P/U)	predator encounter (aerial predator)	Blumstein & Arnold, 1995; Boero, 1992
	multiple whistle				predator encounter (terrestrial predator)	
Gunnison's prairie dog (*Cynomys gunnisoni*)	alarm call	P		intra (temporal and spectral structure; P)	predator encounter (hawk)	Kiriazis & Slobodchikoff, 2006; Placer & Slobodchikoff, 2000, 2001; Slobodchikoff et al., 1991, 2009; Slobodchikoff & Placer, 2006
					predator encounter (domestic dog)	
					predator encounter (coyote)	
					predator encounter (human, incl. descriptors of size, shape, color)	
Richardson's ground squirrel (*Urocitellus richardsonii*)	whistle	P and/or U (?)		inter (P/U); intra (call rate; U)	predator encounter (terrestrial predator)	Davis, 1984; Hare & Atkins, 2001; Sloan et al., 2005; Swan & Hare, 2008; Warkentin et al., 2001
	chirp				predator encounter (aerial predator)	
	repetitive alarm call (chuck, chirp, whistle)	U(?)		intra (call sequence composition; U)	predator encounter	
Belding's ground squirrel (*Urocitellus beldingi*)	trill	U (?)		inter (U)	predator encounter (low risk, slow-moving predators)	Mateo, 1996; Robinson, 1980, 1981
	chirp/ whistle				predator encounter (high risk, fast-moving predator)	
Common rat (*Rattus norvegicus*)	22-kHz USV		V	inter (V)	emotional state (negative state, distress situation)	Brudzynski, 2007; Burman et al., 2007; Knutson et al., 2002; Saito et al., 2019
	50-kHz USV				emotional state (positive state, pleasant situation)	

Species	**Call type**	**Contextual information[1]**		**Encoding mechanism (intra vs. inter)[2]**	**(Behavioural) Context**	**Reference**
		referential	**emotional**			
SCANDENTIA						
Tree shrew (*Tupaia belangeri*)	chatter call		A (-)	intra (call rate, spectral and temporal structure; A)	disturbance	Schehka et al., 2007; Schehka & Zimmermann, 2009, 2012
	squeak		A (-)	intra (call rate, spectral and temporal structure; A)	context of agonism	
PROBOSCIDEA						
African elephant (*Loxodonta africana*)	rumble		A/V	intra (temporal and spectral structure; A/V)	negative social context (dominance interactions), neutral social context (minimal social activity), positive social context (affiliative interactions)	Soltis et al., 2005, 2009, 2011; Stoeger et al., 2011; Wesolek et al., 2009
			A (-)	intra (spectral structure; A)	"tense" social context (caller in proximity to a dominant animal), "calm" social context (caller not in proximity to a dominant animal)	
	infant roar		A (-)	intra (spectral and temporal structure; A)	distress context (low and high urgency)	
	infant rumble		A and/or V	intra (temporal and spectral structure; A,V)	affiliative social interactions, nurse cessation	

Species	**Call type**	**Contextual information**[1]		**Encoding mechanism (intra vs. inter)**	**(Behavioural) Context**	**Reference**
		referential	**emotional**			
CHIROPTERA						
Greater false vampire bat (*Megaderma lyra*)	aggression call		A (-)	intra (call rate, temporal structure; A)	agonistic interactions	Bastian & Schmidt, 2008
	response call		A (-)	intra (call rate, temporal and spectral structure; A)	agonistic interactions	

[1] A: arousal (- negative, + positive); V: valence; U: urgency; P: predator type; F: food source

[2] intra: within call type variation; inter: variation at the level of call type

(?): supposed/inconsistent results; n.m.: not mentioned

3.3. Development of vocalizations during ontogeny

To understand fully the relationship between vocalizations, the encoded information and their functions, it is important to investigate not only the acoustic structure and the context of call production, but also vocal ontogeny. Infancy and adolescence are important periods in the lives of all mammals as the basis for their future life is laid here. Although acoustic communication has been studied in mammals for decades, a stronger focus on the development of vocalizations in mammals is a relatively new trend (e.g. Baotic et al., 2014; Herler & Stoeger, 2012; Pistorio et al., 2006; Stoeger-Horwath et al., 2007).

Vocal ontogeny must be considered in the context of various factors that change during development. On the one hand, there are physical and hormonal changes, including growth processes, through which the infant´s body matures into an adult body. On the other hand, in addition to the development within the sender, changes of its environment during development have to be considered. Some behavioural contexts disappear (e.g. infant-specific contexts), whereas others emerge over time (e.g. sexual and territorial behaviour) and, thereby, external stimuli change. It thus must be assumed that the information encoded in animal vocalizations also change over time depending on both physical changes and environmental changes.

In general, it is assumed that large parts of the vocal repertoire of a given species are already genetically predisposed at birth (e.g. Seyfarth & Cheney, 2010). Most call types are fully formed and appear to undergo relatively little modification during development. A number of studies have supported this assumption (e.g. Egnor & Hauser, 2004; Seyfarth & Cheney, 1997, 2010). Especially studies investigating vocal behaviour of isolated infants provide evidence for vocal production with no modification during development (e.g. Hammerschmidt et al., 2001; Owren et al., 1993; Winter et al., 1973).

The mammalian vocal production apparatus and its underlying mechanism exert strong anatomical and physiological constraints also on the acoustic characteristics of vocalizations of infants. It is therefore not surprising that even infant vocalizations of various mammalian species already exhibit well-defined individual vocal signatures based on spectral cues (e.g. chimpanzees: Levréro & Mathevon, 2013; banded mongoose: Müller & Manser, 2008; sea otter: McShane et al., 1995; domestic cat: Scheumann et al., 2012; greater sac-winged bat: Knörnschild et al., 2012; goitred gazelles: Lapshina et al., 2012). Individual vocal signatures in infants are essential for mother-infant recognition, for coordinating mother-infant interactions and, thereby, for the survival of the infant (e.g. Briefer & McElligott, 2011a; McShane et al., 1995; Müller & Manser, 2008; Symmes & Biben, 1985). However, when assuming that the structure of mammalian vocalizations is largely related to the morphology of the vocal apparatus, one has to conclude, that maturational processes, such as growth or changes in hormonal levels, also affect the vocal production apparatus and thereby lead to modifications in vocalizations. Studies on vocal development in several mammalian species provide evidence for this hypothesis showing gradual modifications in call structure depending on morphological changes with infants producing calls with adult-like structure from the first week of life with only little variation during development that could be explained solely by changes in size and weight and thereby maturational growth (e.g. Primates: Hammerschmidt et al., 2000; Hauser, 1989; Carnivora: Hollén & Manser, 2007; Elephants: Herler & Stoeger, 2012; Stoeger-Horwath et al., 2007; Stoeger et al., 2014; Artiodactyla: Briefer & McElligott, 2011b; Rodentia: Blumstein & Munos, 2005; Randall et al., 2005).

Even though call structure might be largely innate and influenced mainly by morphological changes, there is, however, growing evidence for vocal plasticity. Some species across various mammalian orders, such as primates, ungulates, seals, elephants, bats, and cetaceans, seem to have control over the acoustic structure of their calls and are even able to further modify certain acoustic features (e.g. Boughman, 1998; Boughman & Moss, 2003; Briefer & McElligott, 2012; Favaro et al., 2016; Janik, 2014; Knörnschild, 2014; Knörnschild et al., 2010, 2012; Lattenkamp & Vernes, 2018; Lemasson et al., 2011; Levréro et al., 2015; Prat et al., 2017; Reichmuth & Casey, 2014; Stoeger & Manger, 2014; Volodin et al., 2014). Acoustic development thus seems to result not only from maturational development but also to be guided socially with young individuals modifying their calls based on vocal influences from their social environment (e.g. Briefer & McElligott, 2012; Lemasson et al., 2011; Levréro et al., 2015; Volodin et al., 2014). Thereby, familiar individuals exhibit voice similarities suggesting that vocal learning enables them to adapt call structure (Janik & Slater, 2000).

There is a long lasting debate on whether, or not, non-human mammals are capable of "vocal learning" and over the definition of the term "vocal learning" (e.g. Fischer & Hammerschmidt, 2020; Lattenkamp & Vernes, 2018; Seyfarth & Cheney, 2010). Some authors have suggested that "vocal learning" should refer only to cases in which acoustic parameters of calls are modified based on social experience, either by gradual changes of already existing signals (social modification) or by the acquirement of new signals (learned acquisition; Boughman & Moss, 2003; Knörnschild, 2014; Lattenkamp & Vernes, 2018). While strong evidence has been found for this type of "vocal learning" in seals, cetaceans, elephants, and bats (e.g. Boughman, 1998; Boughman & Moss, 2003; Favaro et al., 2016; Janik, 2014; Knörnschild, 2014; Knörnschild et al., 2010, 2012; Lattenkamp & Vernes, 2018; Prat et al., 2017; Reichmuth & Casey, 2014; Stoeger & Manger, 2014), the presence of this type of "vocal learning" in primates is debated (e.g. Fischer, 2017; Fischer et al., 2015; Fischer & Hammerschmidt, 2020; Watson et al., 2015). Moreover, different levels of complexity have to be distinguished. Animals might be able, by comparatively simple modifications in breathing patterns, to modify temporal parameters or the amplitude of acoustic signals that are already existing in their vocal repertoire (e.g. Marshall et al., 1999). Changes in frequency parameters of vocal signals require control over the muscles of the vocal apparatus and, thereby, represent a more sophisticated form of vocal learning that is regarded as being rare in mammals (e.g. Boughman, 1998; Janik & Slater, 1997; Knörnschild et al., 2012; Lemasson & Hausberger, 2004; Seyfarth & Cheney, 1997).

The situation is not less complex when it comes to contextual information. As the environment changes during development, animals that use calls to signal about features of their environment must be able to adjust accordingly. Some call types seem not to appear before infants have reached a particular age whereas other disappear at a certain age (e.g. Baotic et al., 2014; Barros et al., 2011; Darden & Dabelsteen, 2006; Mumm & Knörnschild, 2014; Pistorio et al., 2006; Stoeger-Horwath et al., 2007). Several authors therefore have suggested that mammalian vocal repertoires often have specific vocal signals that are either restricted to certain juvenile periods or to adulthood (e.g. Baotic et al., 2014; Barros et al., 2011; Peters & Wozencraft, 1989; Stoeger-Horwath et al., 2007; Zimmermann, 1991). It cannot be ruled out that experience plays a role in these processes. Therefore, it should be considered that encoding contextual information need to a certain degree be socially influenced or even learned. Evidence from various mammalian species suggests that the development of encoding contextual information is rather a mix between non-learned and learned components (e.g. Ghazanfar et al., 2019; Hollén et al., 2008; Hollén & Manser, 2007; Hollén & Radford, 2009; Roush & Snowdon, 2001; Seyfarth & Cheney, 1997, 2010). Infants seem to be predisposed from birth to produce a specific call type in a broader context, not entirely random from the adult context, but over time the association between call type and context becomes more precise as producing and correctly using calls encoding referential information may require practice (e.g. Janik & Slater, 1997, 2000). The call type already present within the repertoire thus gets associated with a new context based on experiences of how other individuals use this signal. These changes in call usage and comprehension should be regarded as "contextual learning" (Janik & Slater, 1997).

There is evidence throughout the order of mammals that infants learn from adult conspecifics how to use vocalizations in the appropriate context. This seems to be particularly important with regard to referential calls (food-associated calls: Roush & Snowdon, 2001; predator-specific calls: Cheney & Seyfarth, 1990). Meerkat (*Suricata suricatta*) infants, for example, already emit adult-like alarm calls. However, in contrast to adults, in which the majority of alarm calls is predator specific, alarm calls of infants are non-predator type specific (Hollén et al., 2008). When infants start using predator-specific alarm calls, these calls are often emitted in the wrong context. In contrast to the acoustic features encoding predator type information, features related to the level urgency seem to develop much earlier in infant alarm (Hollén & Manser, 2007). It might be more crucial for infants to signal urgency early on (Hollén et al., 2008).

Indeed, infants of various mammalian species are already capable of expressing the level of arousal or urgency by vocalizations at an early stage (e.g. Scheumann et al., 2012; Stoeger et al., 2011, 2012). This might be of particular importance in situations in which the infants rely heavily on the support of their mothers or caregivers, for example, during isolation or in case of danger. Mammalian infants are entirely dependent upon their care-takers with regard to nutrition, thermoregulation and protection and cannot survive in the absence of maternal care (e.g. Lubach et al., 1992; Nowak et al., 2000). Expressing the level of urgency might allow mothers to react appropriately according to the infants' needs and might thus play an important role in infants' survival. Indeed, it has been shown that mothers or caregivers respond faster towards high-arousal calls as compared to low-arousal calls (e.g. Konerding et al., 2016).

Investigating vocal ontogeny, vocal interaction between young and adults as well as among young, differences between infant and adult vocal repertoires and thereby the development of encoding information in vocalizations in a given species is crucial to understand the role of innate mechanism, maturational effects, and vocal learning.

3.4. The Southern White Rhinoceros (*Ceratotherium simum simum*) as a model for studying information encoded in vocalizations

Rhinoceros are some of the largest remaining megafauna. There are five extant species of rhinoceros: The Black rhinoceros, the White rhinoceros, the Indian rhinoceros, the Sumatran rhinoceros, and the Javan rhinoceros. These species inhabit different socio-ecological niches, ranging from forest- to savanna living, and from solitary to semi-social. Common to all rhinoceros species is poor eyesight, which is why the auditory system, apart from the olfactory system, is the major sensory modality for communication (e.g. Cinková & Policht, 2015; Freeman et al., 2014; Linklater et al., 2013; Marneweck et al., 2017a, 2017b, 2018). Although rhinoceros in general are said to be highly vocal, there are only few studies investigating vocal behaviour of this large-bodied species (Muggenthaler et al., 1993; White rhinoceros: Cinková & Policht, 2014, 2016; Cinková & Shrader, 2020; Jenikejew et al., 2020; Owen-Smith, 1973; Policht et al., 2008; Black rhinoceros: Budde & Klump, 2003; Sumatra rhinoceros: Muggenthaler et al., 2003; Muggenthaler & Reinhart, 2003; Greater one-horned rhinoceros: Bhattacharya, 2020; Laurie, 1978, 1982), which are also suggested to be one of the few mammals producing infrasound vocalizations (Muggenthaler et al., 1993; Policht et al., 2008).

Since sociality has been hypothesized to drive the evolution of communicative complexity (e.g. Blumstein & Armitage, 1997b), especially the White rhinoceros (*Ceratotherium simum*) represents an excellent animal model to investigate information encoded in vocalizations as the White rhinoceros is the most gregarious of the five rhinoceros species with the most developed social system (e.g. Hutchins & Kreger, 2006). In White rhinoceros, long-lasting and temporary associations of up to six individuals can be observed (e.g. Estes, 1991; Owen-Smith, 1972; Owen-Smith, 1973; Pienaar, 1994; Shrader & Owen-Smith, 2002). Most of these groups are based on a mother-offspring bond, consisting of an adult female and her offspring (Estes, 1991; Owen-Smith, 1973; Pienaar, 1994). Adolescents often attach themselves to similar aged companions or mother-offspring dyads. Females remain in adolescent-groups until the birth of their first calf at six to seven years of age (Estes, 1991; Owen-Smith, 1973; Pienaar, 1994). Adult White rhinoceros bulls live solitarily and are regarded as socially matured at ten to twelve years of age (Estes, 1991; Owen-Smith, 1973; Pienaar, 1994). Female home range usually overlaps several males' territories (Estes, 1991).

Given the above described social system, effective communication is not only essential for coordinating mating encounters for dispersed living males and females, but also for coordinating social interactions within the groups. It therefore makes sense that the more developed social system of this rhinoceros species leads to a more complex acoustic communication system with the largest variety of vocalizations (e.g. Owen-Smith, 1973; Policht et al., 2008) compared to other rhinoceros species.

At the onset of the present thesis, two publications on the vocal repertoire of the White rhinoceros existed describing ten to eleven distinct vocalizations, but both coincide only in five call types (Owen-Smith, 1973; Policht et al., 2008). Whereas Owen-Smith (1973) characterised these call types only based on onomatopoetic descriptions, Policht et al. (2008) conducted a detailed multi-parametric sound analysis combined with statistical methods. Moreover, Policht et al. (2008) investigated the Northern subspecies (*Ceratotherium simum cottoni*), whereas Owen-Smith (1973) investigated the Southern subspecies (*Ceratotherium simum simum*). Thus, subspecies differences may also affect the results. The vocal repertoire of the White rhinoceros includes noisy as well as some harmonic sounds (calls containing narrow frequency bands: Whine, Squeak, Squeal). Vocalizations in White rhinoceros play an important role in coordinating mating behaviour, mother-offspring interactions, but also during agonistic and affiliative interactions. For the Pant call, which is composed of bouts of repetitive noisy calls produced during inhalation or exhalation, it is already known that it contains not only information about the sender, such as individuality, subspecies, age class, sex, and dominance status, but also about the motivation of the sender (Cinková & Policht, 2014b, 2016; Cinková & Shrader, 2020). Moreover, it has been shown that conspecifics are able to extract these information (Cinková & Policht, 2016; Cinková & Shrader, 2020).

3.5. Aims of this thesis

In this thesis I will provide further insights into vocal communication of the Southern white rhinoceros (*Ceratotherium simum simum*) and the information encoded in vocalizations by investigating two topical foci: (1) the vocal repertoire of infant and juvenile Southern white rhinoceros and (2) information on the identity of the sender encoded in the vocalizations of this species.

The vocal repertoire of the White rhinoceros comprises ten to eleven distinct vocalisations emitted in different behavioural contexts (Owen-Smith, 1973; Policht et al., 2008). So far, data on the vocal repertoire of infant and juvenile White rhinoceros were still lacking. To fill up this gap, the aim of the first study was to provide the first vocal repertoire of infant and juvenile Southern white rhinoceros by defining structural and functional characteristics of call types. By comparing these findings with adult vocal repertoires, age-dependent variations were determined as a basis to understand the role of innate mechanism, maturational effects, and vocal learning during development. For this purpose, the vocal behaviour of seven mother-reared and one hand-reared calf at the age of one month to four years of age was simultaneously audio and video-recorded at three different zoos.

In the second study individual distinctiveness across call types of the Southern white rhinoceros was investigated. So far, there was only a first evidence, that one call type, the Pant call, contains information about the sender such as individuality, subspecies, age class, sex, and dominance status, but also about the motivation of the sender (Cinková & Policht, 2014b, 2016; Cinková & Shrader, 2020). Information on other call types and their potential for encoding information about the sender were still lacking. This study, therefore, aimed to explore whether further vocalizations of the Southern white rhinoceros have the potential to encode information on the individual identity of the sender and whether the level of individual distinctiveness varies between the different call types. Moreover, it should be clarified to what extent factors such as the behavioural context, the distance of the caller to the receiver, and the acoustic structure of the call account for differences in individual distinctiveness. For this purpose, the variation in individual distinctiveness across the three most common call types, namely the Grunt, the Hiss, and the Snort, was investigated for 25 adult Southern white rhinoceroses recorded in six different zoos.

In the discussion, I will relate the variability and complexity of acoustic communication in the White rhinoceros to that of other rhinoceros species. These aspects will be discussed based on the “social complexity hypothesis for communicative complexity” (e.g. Freeberg et al., 2012; Krams et al., 2012; Pika, 2017; Sewall, 2015). As the White rhinoceros is said to be the rhinoceros species with the most complex social system, one should expect a high level of communicative complexity. I will present and discuss which attributes of the acoustic communication system of the White rhinoceros contribute to the communicative complexity of this species by referring to my findings, but also to the literature.

4. STUDY 1 - FIRST INSIGHTS INTO THE VOCAL REPERTOIRE OF INFANT AND JUVENILE SOUTHERN WHITE RHINOCEROS *[1]

Describing vocal repertoires represents an essential step towards gaining an overview about the complexity of acoustic communication in a given species. The analysis of infant vocalisations is essential for understanding the development and usage of species-specific vocalisations, but is often underrepresented, especially in species with long inter-birth intervals such as the white rhinoceros. Thus, this study aimed for the first time to characterise the infant and juvenile vocal repertoire of the Southern white rhinoceros and to relate these findings to the adult vocal repertoire. The behaviour of seven mother-reared white rhinoceros calves (two males, five females) and one hand-reared calf (male), ranging from one month to four years, was simultaneously audio and video-taped at three zoos. Normally reared infants and juveniles uttered four discriminable call types (Whine, Snort, Threat, and Pant) that were produced in different behavioural contexts. All call types were also uttered by the hand-reared calf. Call rates of Whines, but not of the other call types, decreased with age. These findings provide the first evidence that infant and juvenile rhinoceros utter specific call types in distinct contexts, even if they grow up with limited social interaction with conspecifics. By comparing our findings with the current literature on vocalisations of adult white rhinoceros and other solitary rhinoceros species, we discuss to which extent differences in the social lifestyle across species affect acoustic communication in mammals.

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4.1. Introduction

In many mammalian species vocal communication is essential to coordinate social interactions such as mating rituals (e.g. Hanson & Hurley, 2012; Pfefferle et al., 2011), alarm calling (e.g. Schibler & Manser, 2007; Schneiderová & Policht, 2012), mother-infant care (e.g. Herler & Stoeger, 2012; Scheumann et al., 2007), group cohesion (e.g. Braune et al., 2005; Soltis et al., 2005a), or territorial displays (e.g. Ramanankirahina et al., 2016; Reby et al., 2005). One of the first steps towards understanding the complexity of acoustic communication in a given species is to establish a vocal repertoire (Fischer & Hammerschmidt, 2002). This provides definitions of different types of vocalisation by describing the acoustic parameters of these vocalisations and displaying exemplary sonograms as well as a description of the context in which they were uttered. Thereby, vocal repertoires play not only an important role in the bioacoustic discipline but also help to understand complex social behavioural patterns.

Even though a number of previous studies established vocal repertoires in many different mammalian species of different mammalian taxa (e.g. Rodentia: Barros et al., 2011; Scandentia: Binz & Zimmermann, 1989; Chiroptera: Knörnschild, et al., 2010; Carnivores: Cao et al., 2016; Lemasson et al., 2014; Perissodactyla: Policht et al., 2008; Artiodactyla: Passilongo et al., 2013; Cetacea: Dunlop et al., 2007; Primates: Fischer & Hammerschmidt, 2002; Röper et al., 2014), infant vocalisations have been understudied especially in species with a long inter-birth interval and a low number of offspring. By investigating infant vocal behaviour and comparing infant and adult vocal repertoires the role of innate mechanism, vocal learning or ontogenetic changes during development such as maturational effects can be clarified (e.g. Briefer & McElligott, 2012; Egnor & Hauser, 2004; Esser, 2003; Janik & Slater, 1997; Lea & Blumstein, 2011; Volodin et al., 2014, 2015). Therefore, research on vocal communication of infants has recently been of great interest (e.g. Baotic et al., 2013; Benson et al., 1992; Mumm & Knörnschild, 2014; Pokrovskaya, 2013; Scheumann et al., 2012; Stoeger-Horwath et al., 2007; Zaytseva et al., 2015).

While data on the vocal communication systems of many mammalian taxa have grown in recent decades, so far relatively little effort has been dedicated to the study of vocal communication in rhinoceros. Pioneering bioacoustic studies (Muggenthaler et al., 1993; White rhinoceros: Cinková & Policht, 2014b, 2016; Owen-Smith, 1973; Policht et al., 2008; Black rhinoceros: Budde & Klump, 2003; Sumatra rhinoceros: Muggenthaler et al., 1993; Greater one-horned rhinoceros: Laurie, 1982) have provided first insights into the field of rhinoceros vocal communication. Focussing on the White Rhinoceros, two studies exist documenting the vocal repertoire of this species (Owen-Smith, 1973; Policht et al., 2008). Both showed a distinct acoustic communication system with ten to eleven different call types emitted in a variety of different contexts ranging from aggressive to cohesive interactions (e.g. Cinková & Policht, 2014b, 2016; Owen-Smith, 1973; Policht et al., 2008). Furthermore, there is first evidence, that the Pant call of white rhinoceros carries information about the sender such as individuality, sex or subspecies (Cinková & Policht, 2014b, 2016). However, only one of these former studies provided a comprehensive vocal repertoire with displays of sonograms and a multi-parametric sound analysis (Policht et al., 2008, the other study was based on onomatopoetic descriptions). Furthermore, infants and juveniles were not included in their investigations (the youngest individual within this study was six years old). Thus, until now systematic data on the vocal repertoire of infant and juvenile white rhinoceros are still missing.

To fill this gap, we investigated the vocal behaviour of infant and juvenile white rhinoceros at three different zoological institutions. White rhinoceros are described as "semi-social". Long-lasting associations of adult females and subadults have been observed (Owen-Smith, 1975; Shrader & Owen-Smith, 2002) whereas the adult bulls live solitarily (Owen-Smith, 1975; Shrader & Owen-Smith, 2002; this semi-social lifestyle is in contrast to all other rhinoceros species). Females give birth to their first calf at approximately six to seven years of age, whereas males are socially matured between ten to twelve years of age (Owen-Smith, 1974). After a 16-month gestation period, a female gives birth to one calf (Owen-Smith, 1974). The calf can stand up after birth (Estes, 1991). However, it remains in close proximity to the mother and as soon as there is any disturbance the calf returns to her (Owen-Smith, 1974). Calves start to graze at two months of age, but continue suckling for over 12 months (Owen-Smith, 1974). Calves maintain a close bond to their mothers usually until the birth of the next calf (Owen-Smith, 1973, 1974). After that the mothers chase them away and the infants have to search for other rhinoceros to form a stable social associations (Owen-Smith, 1974). The more complex social organisation of this rhinoceros species may lead to a more pronounced acoustic communication system as compared to all the other solitary living rhinoceros species.

The aim of this study was to provide the first vocal repertoire of infant and juvenile white rhinoceros by defining structural and functional characteristics of call types and determining age-dependent variations by comparing our findings with the adult vocal repertoires of Owen-Smith (1973) and Policht et al. (2008). Recordings were made from eight Southern white rhinoceros ranging from one month to four years of age at different zoos. One calf had been rejected by his mother and was therefore hand-raised, which provided us with an opportunity to investigate whether social interactions are required to establish species-specific vocal behaviour.

4.2. Materials and Methods

4.2.1. Ethic statement

The article contains only observational data of zoo animals during their daily routine. No animal was manipulated by the authors. The authors received the permission to record the data of the animals on the private land of the respective zoo.

4.2.2. Subjects and study site

Recordings were made on eight Southern white rhinoceros (*Ceratotherium simum simum*) ranging from one month to four years of age at the following zoological institutions: Serengeti-Park Hodenhagen (February - March 2012, May-June 2014, April-May 2015), Dortmund Zoo (September – October 2014) and Augsburg Zoo (April 2016; Table 4-1). At Serengeti-Park Hodenhagen the whole rhinoceros group consisted of nine individuals in 2012 (six adult females, one adult male, two infants) and of eleven individuals in 2014 and 2015 (five adult females, one adult male, two juveniles, three infants). The adult male was occasionally separated from the herd. Two calves were recorded in all three years and three calves in two consecutive years. The rhinoceros were mainly observed in their 9 ha drive-through outdoor enclosure where they live together with watusis (*Bos primigenius f. taurus*), zebras (*Equus quagga chapmani*), ostriches (*Struthio camelus*), lechwes (*Kobus leche*), addax antelopes (*Addax nasomaculatus*), and dromedaries (*Camelus dromedaries*). Rhinoceros were used to being followed by car (also off the visitor route; (Boeer & Hamaz, 1996). Thus, we could approach them up to a distance of approximately five metres. Occasionally when the rhinoceros had to stay indoors due to inclement weather conditions, recordings were made in the indoor enclosure, where the animals were observed from the keeper area. At Dortmund Zoo we recorded a five-month-old female calf that was kept together with her mother and an adult female in their outdoor enclosure. At Augsburg Zoo we recorded a two-month-old male and a one-month-old female calf. Due to the young age of the female calf her mother did not leave the indoor area. Thus, recordings were made in the indoor enclosure where both were observed from the keeper area. The male calf had been rejected by his mother at birth. Therefore, he was hand-reared and bottle-fed (approximately every two hours) in the indoor enclosure by zookeepers. He was kept in a separate stable within the rhinoceros facility. Recordings were made in the indoor as well as in the outdoor enclosure.

We assigned our subjects to two main age classes: Infant and juvenile. Moreover, the acoustic analyses also included some calls (N = 41) of subadult individuals (N = 2; Table 4-1), which had already been recorded as infant and juvenile and which still lived together with their mothers and the current calves. Due to the fact that for white rhinoceros intercalving intervals of less than two years can be observed (Skinner et al., 2006, personal observations), subjects were classified as infants from birth to 18 months of age. All infant subjects were reared by their mothers with one exception. Subjects were classified as juvenile from 18 months to 3.5 years of age, which can be considered as nutritionally independent (Table 4-1). As white rhinoceros females can be regarded as adults from the age of six years and males from the age of ten years (Owen-Smith, 1973), subjects were classified as subadults up to this age.

Table 4-1. Demographic data of subjects and number of selected high-quality calls per call type used for the acoustic analyses.

Name	Zoo	Sex	Age in months	Pant	Snort	Threat	Whine
Keeva	Augsburg Zoo	Female	1	-	-	5	-
Kibo^{+}	Augsburg Zoo	Male	2	20	21	10	21
Abasi*	Serengeti-Park Hodenhagen	Male	4-5	20	6	-	21
			32	47	13	21	-
			42	3	-	-	-
Abebi	Dortmund Zoo	Female	5	-	29	2	21
Tatu*	Serengeti-Park Hodenhagen	Female	8-9	-	5	-	6
			19-20	-	1	-	15
Dinari*	Serengeti-Park Hodenhagen	Male	9-10	-	6	2	16
			19-20	4	4	-	-
Lara*	Serengeti-Park Hodenhagen	Female	11-12	7	6	2	20
			39-40	3	16	47	-
			49-50	9	6	23	-
Makena*	Serengeti-Park Hodenhagen	Female	15	2	5	7	-
			25-26	5	2	1	-

* subjects were recorded in different years ; $^{+}$ hand-reared calf

4.2.3. Data collection

For all subjects of the rhinoceros groups audio and video data were collected using the focal animal sampling method (Altmann, 1974). Each subject of the group was observed for a ten-minute interval. The order in which the subjects were observed was block randomised. After all subjects had been observed once in a randomised order, a new block of focal observation started. It was not possible to record data blind because our study involved focal animals. In general, recordings took place between 6.00 a.m. and 5.00 p.m.. Overall, a total of 164 hours of data were recorded and analysed. We recorded 91 hours at Serengeti-Park Hodenhagen, 52 hours at Dortmund Zoo and 21 hours at Augsburg Zoo.

Audio recordings were made with a Sennheiser omni-directional microphone (MKH 8020; Sennheiser, Wedemark, Germany; frequency response: 10 – 60000 Hz, flat frequency response from 10 – 20000 Hz ± 5db) equipped with a wind shield and a boom pole. The microphone was connected to a Sound Devices 722 State Recorder (Sound Devices, LLC, Reedsburg, USA; frequency response of the recorder: 10 – 40000 Hz; settings: 44.1 Hz sampling rate, 16 Bit, uncompressed.wav format). Due to logistic reasons in 2015 we had to change the audio recording system for the infants of the Serengeti-Park Hodenhagen. Thus, we used a Sennheiser microphone (ME 67, Sennheiser, Wedemark, Germany; frequency response: 40–20000 Hz ± 2.5db) linked to a Marantz recorder (PMD 660, Marantz, D&M Holdings Inc., Mahwah, NJ, USA; settings: 44.1 kHz sampling rate, 16 Bit, uncompressed.wav format). The behaviour was videotaped using a digital camcorder (Sony DCR-SR36E, Tokyo, Japan). The identity of the caller was identified by hearing and was noted for each call.

4.2.4. Acoustic analysis

We inspected the spectrograms of all audio recordings visually using Batsound Pro 4.1 (Pettersson Elektronik AB, Uppsala, Sweden; settings: FFT 512, Hanning window) and visually classified four different call types according to the literature (Policht et al., 2008): Whine, Snort, Threat and Pant (Figure 4-1). No other call types were found. A call was defined as a continued sound element having no sound gap (Holy & Guo, 2005). A series of consecutive sound elements of the same call type was defined as a bout. Call types were defined as sound elements of the same pattern of spectral content.

For the acoustic characterisation of infant calls, we selected all calls of high sound quality (no overlap with other sound, not over-amplified, good signal to noise ratio). Since Pants were the call type with the lowest number of high quality calls (N=120, Table 4-1), we randomly selected 120 calls for each of the other call types for acoustic analysis to have a balanced data set. Thus, 120 calls per call type were included in the acoustic analysis using PRAAT (self-written script; http.//www.praat.org; Phonetic Sciences, University of Amsterdam, the Netherlands; Boersma, 2001) and AVISOFT (Avisoft Bioacoustics, Glienicke, Germany).

First, we measured the following six acoustic parameters to describe the spectral composition of the call types (for definition of acoustic parameters see Table 4-2): call duration (DUR), percentage of voiced frames (VOI), centre of gravity (COG), standard deviation of the frequency in the spectrum (SD), Skewness (SKE) and Kurtosis (KUR) of the spectrum. To measure the number of voiced frames (VOI), we used a semiautomatic procedure for pitch tracking. Thus, if necessary, we corrected the pitch tracking manually by matching the extracted contour with the sonogram (settings: Submenu: “To pitch”: min pitch: 100 Hz; max pitch: 3000 Hz; time steps: 0.005). If no fundamental frequency contour could be determined in the sonogram (noisy calls) we set all frames at unvoiced. For the tonal calls, we additionally measured four parameters characterising the contour of the fundamental frequency (F0): Minimum F0 (MINF0), maximum F0 (MAXF0), mean F0 (MEANF0), and standard deviation of the F0 (SDF0).

Second, using the automatic measurement routine of AVISOFT, we additionally measured the following five parameters at the point of maximum energy of the call (FFT 1024, Hanning window) to compare measurements with Policht et al. (2008): Quartiles of the spectrum (25%QUART, 50%QUART, 75%QUART), entropy (ENTR), and harmonic-to-noise ratio (HNR).

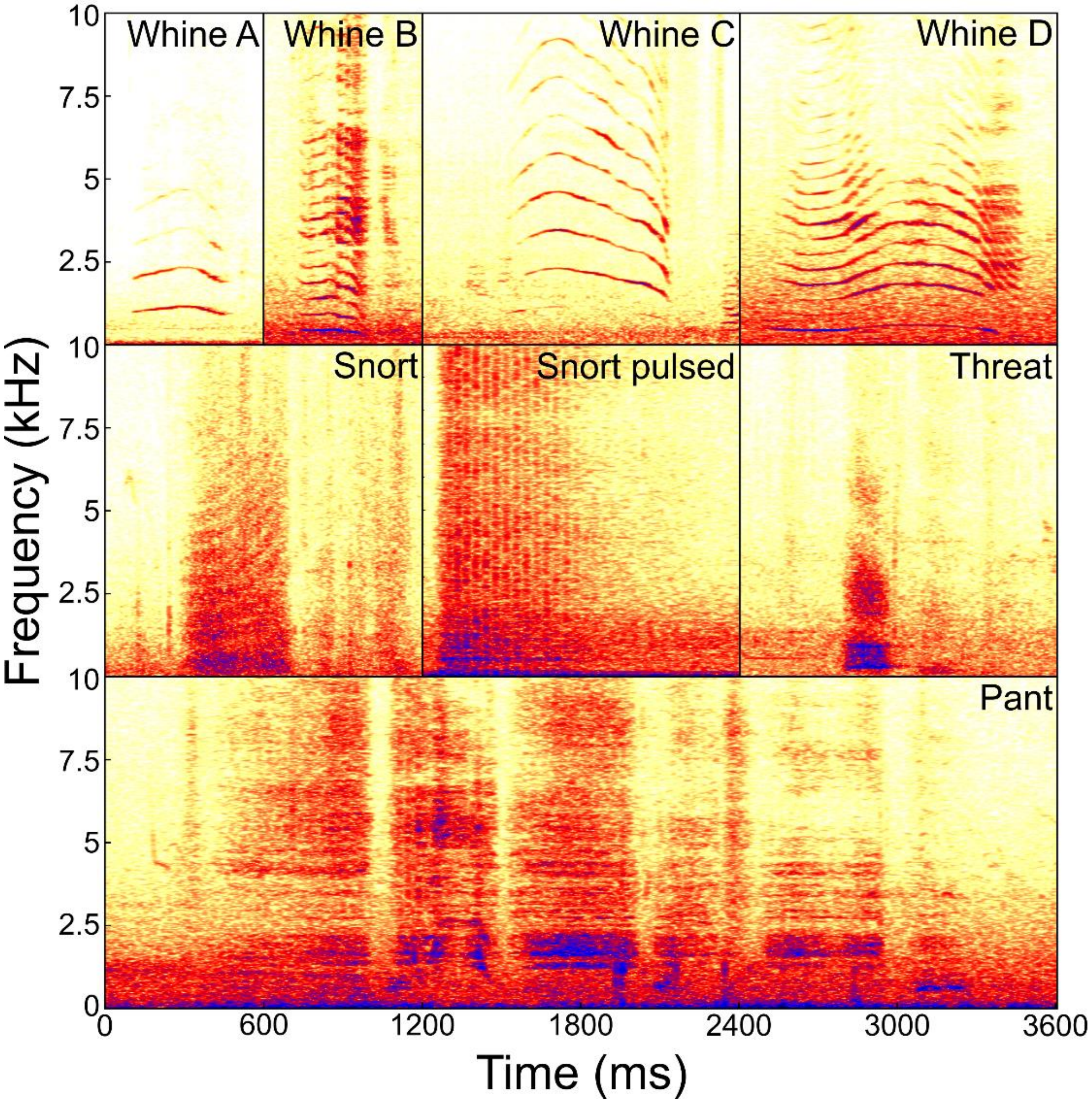

Figure 4-1. Examples of Sonograms for the different call types. Whines (A-D) showing temporal and spectral variations of the contour of the fundamental frequency; Snort without and with pulsed structure; Threat and Pant.

Table 4-2. Description of measured acoustic parameters.

Parameter	**Definition**
DUR [s] [1]	Time between the onset and the offset of a call.
VOI [%] [1]	Percentage of voiced frames of a call.
COG [Hz] [1]	Centre of gravity - mean frequency of the spectrum.
SD [Hz] [1]	Standard deviation of the frequency in a spectrum.
SKE [1]	Skewness of the spectrum - difference between the spectral distribution below and the spectral distribution above the COG.
KUR [1]	Kurtosis of the spectrum - difference between the spectral around the COG and a Gaussian distribution.
25% QUART [Hz] [2]	Frequency of the first quarter (25%) of total energy in the spectrum.
50% QUART [Hz] [2]	Frequency of the second quarter (50%) of total energy in the spectrum.
75% QUART [Hz] [2]	Frequency of the third quarter (75%) of total energy in the spectrum.
ENTR [2]	Wiener entropy - ratio of geometric to arithmetic energy.
HNR [db] [2]	Harmonic-to-noise ratio as the ratio of harmonic to atonal energy.
MINF0 [Hz] [1,*]	Minimum fundamental frequency of a call.
MAXF0 [Hz] [1,*]	Maximum fundamental frequency of a call
MEANF0 [Hz][1,*]	Mean fundamental frequency of a call.
SDF0 [Hz] [1,*]	Standard deviation of the fundamental frequency of a call.

[1] measured in PRAAT; [2] measured in AVISOFT at the location of maximum amplitude; *only measured for tonal calls (Whine)

4.2.5. Behavioural analysis

For analysing call rate, behavioural context, mouth and tail position, we focussed our analyses only on focal observations of infants and juveniles and on dyadic observations of mothers when infants were younger than 18 months. Due to the fact that infants maintain a close bond to their mothers until the birth of the next calf (Owen-Smith, 1973), infants younger than 18 months were almost always visible in the focal observations of the mother. Therefore, we decided to include these focal observations to increase observation time. As observation time varied between infants (dependent on the size of the group and number of infants in the group), we focussed our analysis on approximately ten hours of focal observation per infant and analysed the video recordings using VLC Player. Based on the video recordings we noted for each call: (1) the identity of the caller (the identity of the caller was noted for each call during the recording), (2) the behavioural context, (3) the interaction partner and the distance to the interaction partner with regard to social behaviours, (4) the nearest-neighbour and the distance to the nearest neighbour with regard to non-social behaviours, (5) the reaction of the interaction partner or nearest neighbour, (6) the aperture angle of the mouth during vocalisation, as well as (7) the position of the tail. For the behavioural contexts we established the following categories based on an ethogram (Table 4-3): General activity, comfort & manipulation behaviour, olfactory behaviour, social interactions, suckling behaviour, and isolation. For the interaction partner and the nearest neighbour we classified three categories: The mother, other group members, or foreign species (keeper/other species in mixed-species enclosures). For the distance of the sender to the interaction partner/nearest neighbour, we defined three categories: Distance less than one adult body length (approximate body length is 3.5 to 4 m; Owen-Smith, 1973, personal observations), distance of approximately one adult body length, and distance greater than one adult body length. For the aperture angle of the mouth, we distinguished between open mouth, closed mouth, and feeding. For the position of the tail we classified hanging or curled (tail was lifted at least 90°) as a sign of excitement (Schenkel et al., 1969). As reactions to vocalisations by other rhinoceros were only rare, we only counted whether there was a behavioural reaction in response to the vocalisation or not. In cases where the behavioural context, the position of other rhinoceros, the position of mouth and tail, or a reaction of other rhinoceros could not clearly be determined (e.g. not visible in the video recording), the respective category was coded as unknown.

Table 4-3. Description of behavioural categories.

Behaviour	**Definition**
General activity	
Resting	Subject stood, sat or lay and showed no activity or locomotion.
Feeding	Subjects took food (grass, pellets, salt) or water into its mouth and chewed.
Locomotion	Subject changed position or moved around.
Comfort & Manipulation behaviour	
Comfort behaviour	Subject wallowed in mud or rubbed its body on objects in the enclosure.
Manipulation	Subject pawed with its horn on the ground or pushed/lifted objects.
Olfactory behaviour	
Sniffing	Subject sniffed the ground/objects or urine/faeces of other group members.
Defaecation & Urination	Subject voided faeces or urine.
Social behaviour	
Active approach	Subject moved directly to other group members or followed other group members.
Passive approach	Other group members moved directly towards the subject or followed the subject.
Socio-positive behaviour	Subject made physical contact with any body part of another group member or another group member made physical contact with the subject (e.g. rubbing, sniffing). Thereby, rhinoceros can touch each other with their nose (naso-nasal contact).
Socio-negative behaviour	Subject (was) pushed or chased (by) another group member. Subject fled or avoided the other group members. Attacks using their horns could be observed.
Suckling behaviour	
Suckling	Subject drank from the cow`s udder.
Suckling attempt/begging	Subject repeatedly approached and touched the mother´s hind legs or teats attempting to make nipple contact and was nursed shortly after that.
Isolation	
Isolation	Subject was alone; group members were at a distance greater than 2 adult body lengths.

4.2.6. Statistical analysis

The raw data for the statistical analyses can be found in the supporting information S1 Table (see Appendix). To validate our visual classification of call types, a statistical analysis of the acoustic measurements was performed. In the first step, we performed univariate ANOVAs using the subject as random factor to investigate which acoustic parameters differ significantly between call types. To control for multiple testing, we performed the Fisher-Omnibus test (Haccou & Meelis, 1994). In the second step, we performed a stepwise discriminant function analysis (DFA) using the one-leave-out method for cross-validation. We tested whether classification results were above chance level using Binomial tests and calculated the level of agreement using the Kappa test. For each call type we calculated the call rate [calls/hour] by dividing the number of calls by the analysed observation time. We used the Wilcoxon signed-rank test to assess whether the call rates for infant and juvenile white rhinoceros differ. For the description of the acoustic parameters, we calculated the mean and the standard deviation for each acoustic parameter for all subjects. To test for Snort subtypes, we performed a step-wise discriminant function analysis according to the description above. To investigate the occurrence across context and interaction partner/nearest neighbour for each call type, we calculated the percentage of calls by dividing the number of calls of the respective context and the interaction partner/nearest neighbour respectively by the total number of calls of the respective call type. The same was performed for the distance of the interactions partner/nearest neighbour, mouth and tail positions as well as reaction of other group members with the exception that we excluded calls for which these parameters could not clearly be determined. For the calves of the Serengeti-Park Hodenhagen, we tested whether calls were more emitted in proximity to or during social interactions with the mother as compared to other group members than expected by chance for each call type using the Binomial test (chance level was adapted to group size: 9% or 11%). All tests were performed using the statistical software SPSS 24 except the Fisher Omnibus test. The Fisher Omnibus test was calculated manually using Excel. The level of significance was set to $p \leq 0.05$.

4.3. Results

4.3.1. Call Repertoire

We recorded 3660 calls which were classified by visual inspection of the spectrograms into four call types (Figure 4-1): Whine, Snort, Threat, and Pant. To validate the visual classifications, a stepwise DFA was performed to prove whether the calls can statistically be classified based on their acoustic measurements. Four out of 11 acoustic parameters differed significantly between call types (ANOVA: $F \geq 4.65$, df=3, $p \leq 0.015$ for DUR, VOI, ENTR, HNR; Fisher Omnibustest: $\chi 2 = 116.77$, df=22, $p<0.001$; Table 4-4; see Appendix, Table A in S1 Table). The stepwise DFA selected eight out of these 11 acoustic parameters (in decreasing order: VOI, HNR, DUR, 75%QUART, ENTR, 25%QUART, SD, COG) to calculate three discriminant functions which significantly correctly classified 79.0% of the calls to the respective call type ($p<0.001$; cross-validation: 78.5%; $p<0.001$; Figure 4-2). Thus, 92.5% of the Whines, 79.2 % of the Snorts, 73.3% of the Threats and 70.8% of the Pants were classified correctly above chance level ($p<0.001$; for all call types). The Kappa test confirmed the good agreement between the results of the DFA and the visual classification (Kappa=0.719). The first DFA function explained 91.4% of the variance and correlated strongly with the tonality-related acoustic parameter VOI (r=0.890) separating the Whines from the three noisy call types (Figure 4-2a). The second and third DFA function showed strongest correlations with measurements of hoarseness (DFA2: r=0.777 for HNR) and spectral parameters (DFA3: r>0.369 for SD and 75%QUART) separating the three noisy call types (Figure 4-2b).

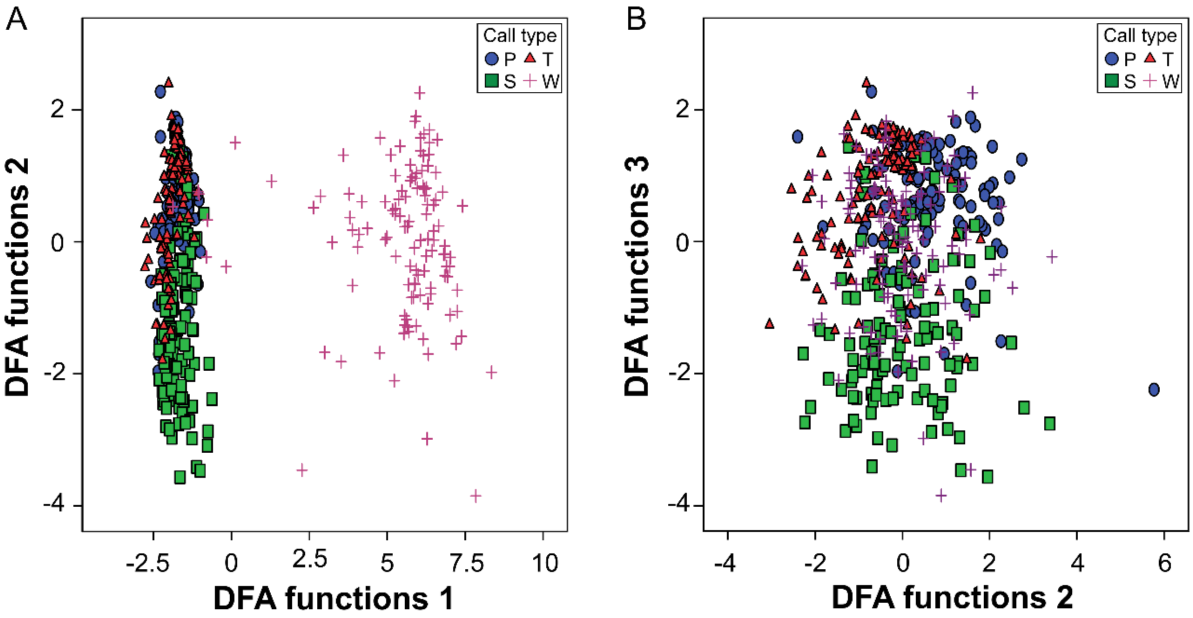

Figure 4-2. Scatterplot of the Discriminant function analysis. **(a)** DFA function 1 separates the Whines from the noisy call types. **(b)** DFA functions 2 and 3 separate the three noisy call types Snort, Threat and Pant.

Table 4-4. Mean and standard deviation of the acoustic parameters for each call type as well as results of the univariate ANOVA comparing the four call types.

Parameter	**WHINE (N=120)**	**SNORT (N=120)**	**THREAT (N=120)**	**PANT (N=120)**	**F**	**p**
Nind	8 (6)	8 (7)	8 (7)	6 (5)		
DUR [s]	0.65±0.59	0.55±0.29	0.27±0.13	0.32±0.19	4.645	0.015
VOI [%]	84.35±26.61	0.00±0.00	0.00±0.00	0.00±0.00	124.77	<0.001
COG [Hz]	837.02±644.87	460.55±371.81	405.95±424.86	474.87±489.91	2.37	0.109
SD [Hz]	877.66±396.08	943.95±449.21	538.03±368.58	759.76±467.79	1.47	0.261
SKE	6.56±6.83	9.21±5.93	13.45±10.77	10.74±10.22	1.49	0.253
KUR	186.64±397.97	185.44±260.79	635.91±824.61	388.73±673.30	1.27	0.314
25% QUART [Hz]	618.42±668.21	281.25±288.52	296.25±318.02	348.75±481.50	2.41	0.105
50% QUART [Hz]	1192.50±927.04	986.92±798.64	654.58±540.22	864.67±804.62	0.75	0.538
75% QUART [Hz]	2296.83±1313.67	2880.75±1659.07	1585.42±1120.83	2253.67±1374.78	1.92	0.164
ENTR	0.16±0.06	0.23±0.10	0.19±0.08	0.18±0.08	5.02	0.011
HNR [db]	31.87±6.23	19.49±7.92	29.54±7.46	31.38±6.28	30.46	<0.001

Nind: number of subjects from which the respective call type was recorded;

( ): number of subjects from which high-quality calls could be used for the acoustic analysis; Significant p values ($p<0.05$) are marked in bold.

4.3.2. Call rate

Whines (x̅±SD=12.31±7.35 calls/hour, see Appendix, Table B in S1 Table) were the most common calls recorded from the infants followed by Snorts (x̅±SD=3.18±1.96 calls/hour), Threats (x̅±SD=1.32±2.18 calls/hour) and Pants (x̅±SD=0.51±0.88 calls/hour). Thereby, Whines showed a significant decrease in call rate when comparing the call rate for the five subjects of the Serengeti-Park Hodenhagen when they were younger than 18 months (x̅±SD=20.77±15.73 calls/hour) with the call rate when they were older than 18 months (x̅±SD=2.99±3.92 calls/hour; T=0, N=5, p=0.043). This age-dependent decrease was not observed for the other call types.

4.3.3. Description of call types

Whine

Whines (Figure 4-1) occur singly or in bouts and can be easily distinguished from the other call types by their high-frequency tonal structure. We recorded Whines in all eight individuals ranging from one to 20 months of age. Whines showed, compared to the other call types, a higher HNR (x̅±SD=31.87±6.23 db), higher COG (x̅±SD=837.02±644.87 Hz) and lower entropy values (x̅±SD=0.16±0.06). Furthermore, Whines were characterised by a highly variable fundamental frequency contour ranging from almost constant to modulated F0 contours (Figure 4-1) and a highly variable call duration ranging from 0.111 to 3.511 seconds. Whines were mainly uttered when the mouth was closed (72.79%) or emitted during feeding/suckling (27.04%).

Whines were mainly recorded in the suckling context (58.22%, N = 517, Figure 4-3a, see Appendix, Table C and Table D in S1 Table) in proximity to or during interactions with the mother (92.79%, N=824, Figure 4-3b, see Appendix, Table E in S1 Table). Testing this statistically for the subjects of the Serengeti-Park Hodenhagen revealed that all subjects emitted Whines more often in proximity to or during interactions with the mother than expected by chance (p<0.001 for all subjects). Only in 2.08% of the cases did the mother/group members show a behavioural reaction in response to the call such as following, social pushing, or position changes.

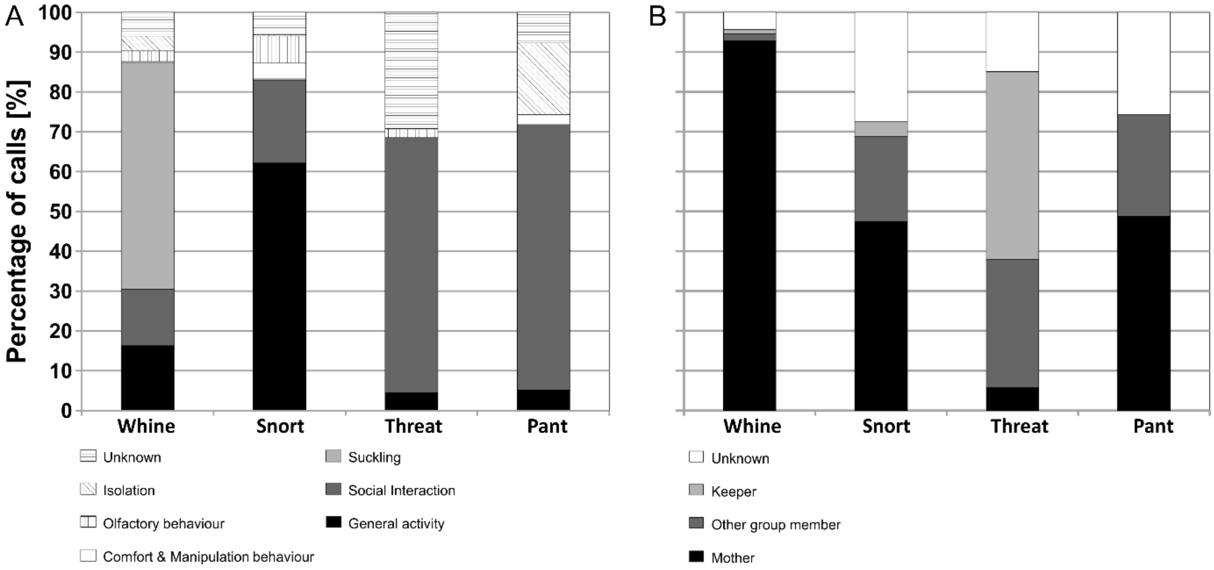

Figure 4-3. Cumulative barplots for the occurrence of calls **(a)** in different behavioural contexts and **(b)** directed to different interaction partners (in case of non-social behaviours the nearest neighbour).

Snort

Snorts are noisy calls which occur mainly singly and seem like air blows through the nostrils or the mouth. We recorded Snorts in all eight infants ranging from one to 50 months of age. Snorts differed in their acoustic structure from Threats and Pants by their higher SD ($\bar{x}$±SD=943.95±449.21 Hz), higher entropy ($\bar{x}$±SD=0.23±0.10) and lower HNR ($\bar{x}$±SD=19.49±7.92 db) values. Based on visual inspection of the spectrogram two potential subtypes of Snorts could be identified; constant air blows (N=58) and Snorts with a pulsed structure (N=62, Figure 4-1). However, performing a stepwise DFA failed to classify these two potential subtypes statistically and also the Kappa test showed only a fair agreement (original: 64.2%; cross-validated: 64.2%; Chance level: 50%; Kappa = 0.276). Thereby, Snorts without pulses were classified by chance (p=0.535). Snorts with and without pulses were mainly recorded in the context of general activity (with pulses: 72.58%, N=45; without pulses: 67.24%, N=39; Figure 4-3a, see Appendix, Table C and Table D in S1 Table). Thereby, Snorts with pulses occurred more often during feeding context (46.67%, N=21), whereas Snorts without pulses occurred during resting (48.72%, N=19). Infants mainly emitted Snorts when the mouth was closed (56.28%) or during feeding (37.69%), in proximity to or during interactions with the mother (47.37%, N = 117, Figure 4-3b, see Appendix, Table E in S1 Table).

Threat

Threats are low frequency noisy calls which can occur singly or in bouts. We recorded Threats in all eight individuals ranging from one to 50 months of age. Threats differed in their acoustic structure from Snorts by their lower entropy (x̅±SD=0.19±0.08), lower SD (x̅±SD=538.03±368.58 Hz), and higher HNR values (x̅±SD=29.54±7.46 db), and from Pants by their lower Cog (x̅±SD=405.95±424.86 Hz). Threats were normally uttered with a closed mouth (78.18%) or during feeding (20.00%).

Threats were mainly used in social interactions (65.52%, N = 57, Figure 4-3a, see Appendix, Table C and Table D in S1 Table) during active and passive approach, following (51.73%, N=45) and during socio-negative interactions (11.49%, N=10). While calling, the infant often walked several steps towards other group members. In comparison to Pant and Snorts, Threat calls were mainly emitted in proximity to or during interactions with group members (32.18%, N=28, Figure 4-3b, see Appendix, Table E in S1 Table) and only rarely in proximity to or during interactions with the mother (5.75%, N=5). One infant regularly emitted Threats in proximity to the keepers and to the observer. In one case, an infant was observed emitting a Threat during an interaction with an ostrich. In almost all these cases, infants were in close proximity to the interaction partner (less than one adult body length away: 92.96%, N=66, see Appendix, Table E in S1 Table). In 22.06% (N=15) of the cases recipients responded to the Threats by avoiding, fleeing or by also producing Threat vocalisations.

Pant

Pants consist of bouts of repetitive noisy calls produced during inhalation or exhalation (in rare cases a single call can occur). Thereby, a bout consists on average of four calls (min: 1 to max: 17). Pants were recorded in six infants ranging from two to 50 months of age. Pants were acoustically characterised by higher COG (x̅±SD=474.87±489.91) and a higher 25QUART (x̅±SD=348.75±481.50) compared to the other two noisy call types. The mouth of the infants was normally closed (95.65%).

Pants were mainly emitted during social cohesive interactions when approaching or following an individual or a group of rhinoceros (66.67%, N=26, Figure 4-3a, see Appendix, Table C and Table D in S1 Table) and mainly during interactions with the mother (48.72%, N=19, Figure 4-3b, see Appendix, Table E in S1 Table). While calling, infants were normally further away from the mother/other group members (distance greater than one body length; 68.97%, N = 20, see Appendix, Table E in S1 Table). Only in 40.00% (N=8) of the cases could behavioural reactions (following/approaching or vocalisations) be observed. Interestingly, in comparison to the other call types, where the tail of the infants was in more than 87.65% of the cases in a hanging position, when producing Pants infants lifted their tail in 42.31% (N=11) of the cases.

4.3.4. Vocal communication of a hand-reared infant rhinoceros

Comparable to the mother-reared calves, we recorded all four call types Whines, Snorts, Threats, and Pants also for Kibo, the two-month-old hand-reared calf. However, we found differences in the call rate for the Whine. The call rate for Whines (169.29 calls/hour) exceeded the call rate in mother-reared calves ($\bar{x}$ ±SD=12.31±7.35 calls/hour) tremendously. Since Kibo was isolated from the other rhinoceros, behavioural contexts were not comparable with mother-reared calves. Whines and Pants were exclusively emitted in proximity to or during interactions with the keepers. The call rate of Whines was particularly high in the morning (after a long period of isolation, when keepers entered the enclosure) and before and during bottle-milk feeding, whereas Pants were uttered when Kibo approached the keepers. Snort production was predominantly associated with general activity such as resting and locomotion. Threats were only observed when the adult females were in the indoor enclosure next to him and approached the edge of his enclosure.

4.4. Discussion

This study provides first systematic data on the vocal repertoire of infant and juvenile white rhinoceros and on the behavioural contexts in which they are emitted. Four different call types could be acoustically distinguished which were used in different behavioural contexts. Whines were mainly uttered in proximity to the mother to signal suckle intention or as a reaction when being disturbed during suckling. Snorts were also emitted in close proximity to the mother but mainly uttered during general activity. Threats were directed at other rhinoceros, animals or keepers and were uttered during social interactions as a response to the approach or proximity of another individual as well as socio-negative social interactions. Pants were uttered in proximity to the mother or other group members while approaching/ following them or during socio-positive interactions. Moreover, even the hand-reared infant produced the same call types in a similar context, suggesting that these call types are already present at birth and maybe based on innate mechanisms of vocal production and usage.

Comparing our results to the literature (Owen-Smith, 1973; Policht et al., 2008), the important role of Whines in mother-infant interactions especially during suckling could be supported. However, Owen-Smith (1973) reported a second tonal call type, the Squeak, specific for mother-infant communication. The Squeak was also observed by Policht et al. (2008) for a subadult female communicating with its mother. In comparison to the Whine, the Squeak seems to be a shorter, high-pitched call produced when the calf is separated from the mother. There are two possible explanations why we did not find Squeaks in our dataset. First, during our observations infants were rarely separated from the mother, thus, they might have had no need to use this call type. Second, we observed a high variability in duration and frequency contour including very short, high-pitched calls reaching the maximum amplitude very fast as described by Owen-Smith (1973) and Policht et al. (2008). These calls may correspond to the Squeak call type described by Owen-Smith (1973) and Policht et al. (2008). However, all kind of Whines were emitted during suckling or suckling attempts and could not clearly be associated with a specific context. It cannot be ruled out that differences in temporal or spectral parameters just code a different degree of sender urgency as found in a variety of other mammalian species (e.g. Schehka et al., 2007; Scheumann et al., 2012; Stoeger et al., 2011, 2012). Thus, we suggest that in infant white rhinoceros tonal calls (termed here Whines) signal general discomfort or distress of the infant in various behavioural contexts such as isolation or hunger. They might serve to maintain contact or to draw the mother`s attention. The fact that the occurrence of Whines decreases with age supports this theory as the infants become more independent of their mothers.

In contrast to Whines, the other three call types (Snort, Threat, Pant) have also been described for adult rhinoceros (Table 4-5). We recorded Snorts in non-social situations such as feeding, resting, or locomotion. Thus, our data correspond to those of Policht et al. (2008). We assumed that they were mainly addressed to the mother since mothers were almost always within a close distance to the calves. In contrast, Owen-Smith (1973) described the Snort as a mild “keep-away warning”. However, based on the call description we think that the call type Snort of Owen-Smith (1973) is related to the term Threat of Policht et al. (2008) as well as in our study. In addition to the Snort, Policht et al. (2008) describe a further puffing sound also recorded mainly during foraging; the Puff, which is longer compared to the Snort. We found a high variability in call duration of Snorts. However, since there is no distinct context and receiver for both acoustic variations, we assume that both belong to the same call type, termed here Snort. Pulsed Snorts were mainly recorded during feeding, whereas Snorts without pulses were mainly recorded during resting. Thus, we presume that the pulsed structure may be the result of forced air out of the nostrils (thereby nostrils vibrate) to clear them from grass, straw, or insects but did not appear to have any communicational function.

Threat vocalisations of the infant and juvenile white rhinoceros occurred during approach (active and passive) of group members/keepers and socio-negative interactions comparable to adult white rhinoceros. Policht et al. (2008) observed Threats in adults as a “first warning”, for example, as a reaction to the approaching or presence of another individual. When the recipient did not react, Threats were followed by agonistics displays (e.g., growling, horn clashing).

Similar to adults (Table 4-5), infant white rhinoceros produced Pants during cohesive interactions such as approaching or following, serving as a kind of contact or greeting call (Owen-Smith, 1973; Policht et al., 2008). During infancy, Pants were mainly addressed to the mother, but when infants became older, Pants were also directed towards other group members. Thereby, call series in infants (average: 4 calls per bout) seem to be much shorter compared to those of adults (average: 13 calls per bout; Policht et al., 2008). In adults, the Pant carries various information about the sender (species, age class and context; Cinková & Policht, 2014b, 2016). Nevertheless, further research is necessary to clarify the information encoded in infant white rhinoceros Pants.

Table 4-5. Comparison of infant white rhinoceros vocalisations (present study) and the literature on adult vocalisations of the Northern (Policht et al., 2008) and Southern white rhinoceros (Owen-Smith, 1973).

Adult				**Infant**	
Northern White Rhinoceros		**Southern White Rhinoceros**		**Southern White Rhinoceros**	
Call type	**Context**	**Call type**	**Context**	**Call type**	**Context**
Tonal call types					
-	-	-	-	Whine	Suckling, distress
-	-	Squeal	Territorial behaviour, boundary blocking	-	-
-	-	Shriek	Elicited by fear, attack inhibition	-	-
Noisy call types					
Pant	Contact call, greeting	Pant	Contact call, friendly approach	Pant	Socio-positive interactions, contact call
		Hic	Male courtship call	-	-
Threat	Aggressive interactions, first warning	Snort*	Aggressive interactions, first warning	Threat	Socio-negative interactions
Snort	Not obvious, but mainly during foraging			Snort	General activities
Puff	Not obvious, but mainly during foraging			-	-
Grunt	Aggressive interactions, powerful warning	Snarl*	Aggressive interactions, powerful warning	-	-
Snarl	Aggressive interaction, passive approach, first warning			-	-
-	-	Gruff-squeal	Territorial behaviour, chasing	-	-
-	-	Gasp-puff	Response to a sudden fright	-	-
Groan	Moan, body discomfort	-	-	-	-

Grouch	Foraging and other activities in proximity of other members of the herd	-	-	-	-
Hoarse	Feeding, approach to female	-	-	-	-

* call descriptions of Owen-Smith (1973) correspond to different call types in Policht et al. (2008)

To sum up, we found that infant white rhinoceros are vocally active from birth on. The Whine seems to be an infant-specific call type, whereas the three noisy call types Snort, Threat, and Pant are also part of the adult vocal repertoire and correspond in acoustic pattern and context to those of adults. Moreover, all call types were also uttered by the hand-reared calf and even used in the appropriate behavioural context, suggesting that there is a strong innate component to the development of vocal usage and production in white rhinoceros. These findings support the assumption that in most mammalian species both vocal production and usage are largely fixed at birth (e.g. Janik & Slater, 1997; Seyfarth et al., 2010). We observed no sex-dependent variations, neither in call rate, nor in call structure or usage. However, separating males and females was limited by sample size and a skewed ratio of sexes. Owen-Smith (1973) and Policht et al. (2008) described further adult call types (Table 4-5), which we did not find in infants (Owen-Smith, 1973: Snarl, Hic, Shriek, Squeal, Grasp-puff, Gruff-Squeal; Policht et al., 2008: Snarl, Grunt, Grouch, Groan, Hoarse). Even though, sometimes the terminology and the definition of call types are not clear, most of these call types are uttered during aggressive interactions, mating attempts or territory defence, contexts which might not be relevant for infants. Further studies targeting different ontogenetic stages by collection longitudinal data will be necessary to determine the onset of adult vocalisations and potential vocal sexual dimorphism. Moreover, payback studies could help to validate the hypothesised function of the different call types.

Comparing infant vocalisations of white rhinoceros with those of other rhinoceros species reveals that tonal vocalisations similar to Whine seem to be common in other rhinoceros species, too (Sumatran rhinoceros: Abdullah et al., 1987; Muggenthaler & Reinhart, 2003; Black rhinoceros: Schenkel et al., 1969; Schenkel & Schenkel-Hulliger, 1969; Greater one-horned rhinoceros: Schenkel et al., 1969; Java rhinoceros: Ammann, 1986). However, the usage of tonal calls during adulthood differs between the species. For the Asiatic rhinoceros species, these tonal calls seem to function as mating calls or songs (Sumatra rhinoceros: Muggenthaler et al., 2003; Zahari et al., 2005; Greater one-horned rhinoceros: Hazarika & Saikia, 2010) or at least as long distance contact calls between dispersed individuals (Java rhinoceros: Schenkel & Schenkel-Hulliger, 1969; Schenkel et al., 1969). Adult black rhinoceros emit tonal Whines, for example, when begging for food (Budde & Klump, 2003; Schenkel et al., 1969). In contrast, we found that for white rhinoceros the call rate of Whines decreased with age. It seems that the tonal call type Whine is not used in adulthood. Nonetheless, there is some evidence that adult white rhinoceros bulls emit tonal calls comparable to the infant Whine, the Shriek and the Squeal, in dominant, mating, and territory behaviour (personal observations, Owen-Smith, 1973). It is argued that this infant-like call might inhibit aggression by the female (Owen-Smith, 1973). Unfortunately, our knowledge about rhinoceros vocalisation is very limited. Thus, it is difficult to compare the vocal behaviour among different species. Despite everything, rhinoceros vocal communication is a highly interesting area of research, not only due to the fact that rhinoceros are one of the largest terrestrial mammals, but also in terms of the different socio-ecological niches they inhabit, ranging from semi-social to solitary and from forest- to savanna living species. Thus, rhinoceroses would be a promising group to investigate how different socio-ecological adaptations effect vocal communication in mammals.

4.5. Appendix

Supporting information are available at PLoS ONE online.
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Supporting information S1 Table. Data sets. (Table A) Acoustic Measurements of selected high-quality calls. (Table B) Call rates for different call types. (Table C) Context analysis. (Table D) Absolute number (N) and percentage of calls (%) recorded in the different behavioural contexts. (Table E) Absolute number (N) and percentage of calls (%) for interaction partner (in case of non-social behaviours the nearest neighbour), distance to interaction partner/nearest neighbour and reaction of other group members.

5. STUDY 2 - INDIVIDUAL DISTINCTIVENESS ACROSS CALL TYPES OF THE SOUTHERN WHITE RHINOCEROS (*CERATOTHERIUM SIMUM SIMUM*) *[2]

Individual distinctiveness in the acoustic structure of vocalizations provides a basis for individual recognition in mammals and plays an important role in social behaviour. Within a species, call types can differ in individual distinctiveness, which can be explained by three factors, namely differences in the social function, the distance of the caller to the receiver, and the acoustic structure of the call. We explored the variation in individual distinctiveness across three call types (Grunt, Hiss, Snort) of the southern white rhinoceros (*Ceratotherium simum simum*) and investigated to what extent the above-mentioned factors account for individual distinctiveness. Calls were recorded from 25 adult southern white rhinoceroses in six different zoos. We used three methods to compare the level of individual distinctiveness across call types, namely discriminant function analysis (DFA), potential information coding (PIC), and the information criterion (Hs). The three call types possessed an acoustic structure capable of showing individual variation to different extents. Individual distinctiveness was lowest for Snorts, intermediate for Hisses, and highest for Grunts. The level of individual distinctiveness of all three call types was lower than that previously reported for Pant calls of this species. Calls functioning to mediate intragroup social interactions had the highest individual distinctiveness. This highlights that a given communicative function and the need for individual discrimination during a social interaction have a major influence on the degree of individual distinctiveness.

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5.1. Introduction

Vocal communication can be important for coordinating social interactions between animals. Acoustic signals can vary substantially in frequency-time contours and amplitude, and can thus reflect a wide variety of behavioural situations and environmental conditions. Moreover, animals living in a complex social environment have been suggested to use complex communication systems with signals carrying multiple information (e.g. Bouchet et al., 2013; Knörnschild et al., 2019; Peckre et al., 2019). Acoustic signals may convey information about the external environment with which the sender is confronted (e.g. Manser, 2001; Seyfarth et al., 1980a), about the internal state of the sender (e.g. Bastian & Schmidt, 2008; Schehka & Zimmermann, 2009; Scheumann et al., 2012), and also about physical characteristics of the sender (e.g. Charlton et al., 2011; Stoeger & Baotic, 2016). Thus, vocalization can encode the identity of the individual, which provides the basis for vocal individual discrimination. Individual discrimination is important for regulating social relationships to govern cohesion, attraction, and avoidance between conspecifics(August & Anderson, 1987; Ehret, 2006) such as mother-infant reunions, support of specific group members, or avoidance of inbreeding (e.g. Bouchet et al., 2012; Kessler et al., 2012; Müller & Manser, 2008; Phillips & Stirling, 2000; Rubow et al., 2018; Torriani et al., 2006; Wittig et al., 2007). It therefore, can be assumed that the more complex social organization will favour individual distinctiveness in call types. We investigated the encoding of sender identity in the southern white rhinoceros (*Ceratotherium simum simum*), which, in contrast to all the other solitarily living rhinoceros species, has been described as semi-social (e.g. Hutchins & Kreger, 2006).

It has been shown across a wide range of mammalian species (Appendix 5-2) that even if the majority of adult call types show individual distinctiveness, the degree of distinctiveness can vary among different call types within a given species. This suggests that different selection pressures have affected the evolution of individual distinctiveness across different call types. To explain differences in individual distinctiveness related to call type, three major hypotheses have been proposed, which are not mutually exclusive (see Appendix 5-2): the "social function hypothesis" (e.g. Charrier et al., 2001; Snowdon et al., 1997), the "distance communication hypothesis" (Mitani et al., 1996), and the "acoustic structure hypothesis" (e.g. Leliveld et al., 2011).

The "social function hypothesis" assumes that calls functioning in individualized intragroup social interactions, such as contact or aggression calls, should have a higher degree of individual distinctiveness than calls directed to the whole group, such as food, alarm, or loud calls (e.g. Snowdon et al., 1997). Lemasson and Hausberger (2011) expanded the social function hypothesis and proposed that individual distinctiveness was highest in calls related to affiliative contexts, intermediate in calls related to agonistic contexts, and lowest in calls related to general activities or directed to the whole group. Evidence for the social function hypothesis was found in several mammalian orders such as Primates (Chacma baboon: Rendall et al., 2009; rhesus monkeys: Rendall et al., 1998; red-capped mangabeys: Bouchet et al., 2012, 2013), Carnivora (dwarf mongoose: Rubow et al., 2018; domestic dog: Yin & McCowan, 2004; giant otter: Mumm et al., 2014), and Rodentia (African woodland dormouse: Ancillotto & Russo, 2016).

The “distance communication hypothesis” suggests that individual distinctiveness is related to the transmission distance (Mitani et al., 1996). Thus, long distance calls emitted out of visual contact with the receiver should have a higher level of individual distinctiveness than calls uttered in close distance where visual or tactile information are additionally available (Mitani et al., 1996). Evidence for the distance communication hypothesis was found in primates (chimpanzees: Mitani et al., 1996; rhesus monkeys: Rendall et al., 1998; gray mouse lemurs: Leliveld et al., 2011), carnivorans (giant otters: Mumm et al., 2014), and rodents (Ancillotto & Russo, 2016).

The “acoustic structure hypothesis” is related to call-type specific vocal production mechanisms. In mammals, the vocal production apparatus is evolutionarily conserved and consists of the lung, the larynx with the vocal folds, and the supra-laryngeal system with the throat, mouth, and nose (e.g. Fant, 1960; Fitch, 2010; Lieberman & Blumstein, 1988). Thus, source- and filter-related factors, namely the anatomical variation of the vocal folds defining the fundamental frequency and the anatomical variations of the supra-laryngeal vocal tract creating formants (source-filter theory; see Fitch, 2010; Taylor & Reby, 2010), determine individual distinctiveness (e.g. Belin et al., 2004; Fitch, 1997; Pfefferle & Fischer, 2006; Plotsky et al., 2013; Scherer, 1989). In narrow-band tonal calls of high to ultrasonic fundamental frequencies, harmonics at the source level are widely spaced, resulting in little inter-harmonic energy that can be filtered by the vocal tract. Thus, individual distinctiveness in these calls is critically coded by variation in the fundamental frequency (Leliveld et al., 2011; Yin & McCowan, 2004). In contrast, in broad-band calls of low fundamental frequency, or without detectable harmonic structure (termed noisy calls), there is a dense energy distribution at the source level. In these calls, the filter function of the vocal tract is the predominant factor determining individual distinctiveness (e.g. Rendall et al., 1998; Taylor & Reby, 2010). Even if both factors can encode individual identity, it has been hypothesized that narrow-band harmonic calls are better suited to code for sender identity than broad-band noisy calls (Leliveld et al., 2011; Yin & McCowan, 2004). Here, the question arises to what extent animal species that predominantly use noisy calls encode sender identity in their vocalizations. Thus, we investigated the encoding of sender identity in the southern white rhinoceros, a species in which noisy calls dominate the vocal repertoire and little is known about information encoded in the vocalizations.

In southern white rhinoceroses, adult bulls live solitarily, but cows occur in groups of different composition (Owen-Smith, 1973). Most southern white rhinoceros groups are based on a mother-offspring bond and consist of an adult female and her offspring (Owen-Smith, 1973). Adolescents often join with similar-aged companions or mother-offspring dyads. These groupings can persist for extended periods of more than a month or only a couple of days. Group sizes of over 10 individuals can occur (Owen-Smith, 1973; Shrader & Owen-Smith, 2002). The mating system of southern white rhinoceroses is territorial-based, with males defending their own territories and females ranging freely between male territories (Kretzschmar et al., 2020; Owen-Smith, 1973). Given the poor eyesight of rhinoceroses, this more pronounced social organization may favour a more complex acoustic communication system. Indeed, acoustic signals play an essential role in the coordination of mother-infant interactions (Linn et al., 2018), during friendly encounters, during aggressive interactions (Jenikejew et al., 2020; Owen-Smith, 1973; Policht et al., 2008), and during mating behaviour of southern white rhinoceroses (Cinková & Shrader, 2020; Owen-Smith, 1973). For example, vocalizations play a very important role in coordinating male and female behaviour during consortship (Owen-Smith, 1973) where bulls follow a single cow for two to three weeks. Thereby bulls emit Pant calls suggested to contain cues about the physical characteristics of the sender, signalling male quality (Cinková & Policht, 2014b; Cinková & Shrader, 2020). If cows are not ready to accept pre-copulatory contact, they do not tolerate such approaches and usually respond with aggressive calls such as Hisses and Grunts (Owen-Smith, 1973).

The southern white rhinoceros has a distinct acoustic communication system in which 10 to 11 different call types have been discriminated onomatopoetically (Owen-Smith, 1973) or based on the acoustic structure (Policht et al., 2008). The majority of calls were described as noisy calls (e.g. Linn et al., 2018; Owen-Smith, 1973; Policht et al., 2008). There is, moreover, some evidence for a strong innate component to the development of vocal usage and production in southern white rhinoceroses (Linn et al., 2018).

Only one call type, the Pant (Figure 5-1), has been studied in detail. The Pant consists of bouts of repetitive noisy calls produced during inhalation or exhalation and is emitted during isolation from the group, when approaching other conspecifics, or in the mating context (e.g. Cinková & Policht, 2014b, 2016; Cinková & Shrader, 2020; Linn et al., 2018; Owen-Smith, 1973; Policht et al., 2008). It has been found that the Pant encodes information not only about the sender, such as individuality, subspecies, age class, sex, and dominance status, but also about the motivation of the sender (Cinková & Policht, 2014b, 2016; Cinková & Shrader, 2020) and that conspecifics were able to extract sex and subspecies in playback experiments (Cinková & Policht, 2016; Cinková & Shrader, 2020). For the other call types, the potential for individual signatures is still unknown.

In this study, we investigated the potential for coding sender identity in three of the most common call types of the vocal repertoire of the southern white rhinoceros (*Ceratotherium simum simum*; Figure 5-1). These three call types were emitted in different contexts, at different distances of the caller from their recipient, and differed in their level of harmonicity. Therefore, rhinoceros calls are a promising model to explore the above hypotheses on call-type-related differences in distinctiveness. The Snort is uttered during general activities, such as feeding or resting. It is a noisy call, which sounds like an air blow through the nostrils or the mouth (e.g. Cinková & Policht, 2014b; Owen-Smith, 1973; Policht et al., 2008). The Hiss and the Grunt are uttered during agonistic interactions (e.g. Cinková & Policht, 2014b; Owen-Smith, 1973; Policht et al., 2008; in previous publications, the Hiss has been termed Threat, but we aim to be consistent in labelling all call types using onomatopoetic labels). The Hiss is suggested to serve as first warning, for example, as a reaction to the approach or presence of another individual, whereas the Grunt signals a more pronounced motivation to fight. When the recipient does not react, Hisses are often followed by Grunts in combination with agonistic displays such as horn clashing (Owen-Smith, 1973; Policht et al., 2008). Hisses and Grunts are commonly emitted by females or adolescents in response to the presence of a male (Owen-Smith, 1973; Policht et al., 2008; personal observations). Hisses are sometimes also emitted in interactions between females or adolescents (Owen-Smith, 1973; Policht et al., 2008; personal observations). Both call types differ in their level of tonality. Thus, the Grunt is a broad-band call that contains low-frequency harmonic components, whereas the Hiss is a broad-band call without tonal structure. To compare our data with the results of Cinková and Policht (2014b) for Pant calls, we calculated the information criterion (Hs), which is rather insensitive to differences in sample size (Beecher, 1989). Additionally, we used discriminant function analysis (DFA) and potential of identity coding (PIC) as reported in the literature (see Appendix 5-2) to compare the level of individual distinctiveness between different call types.

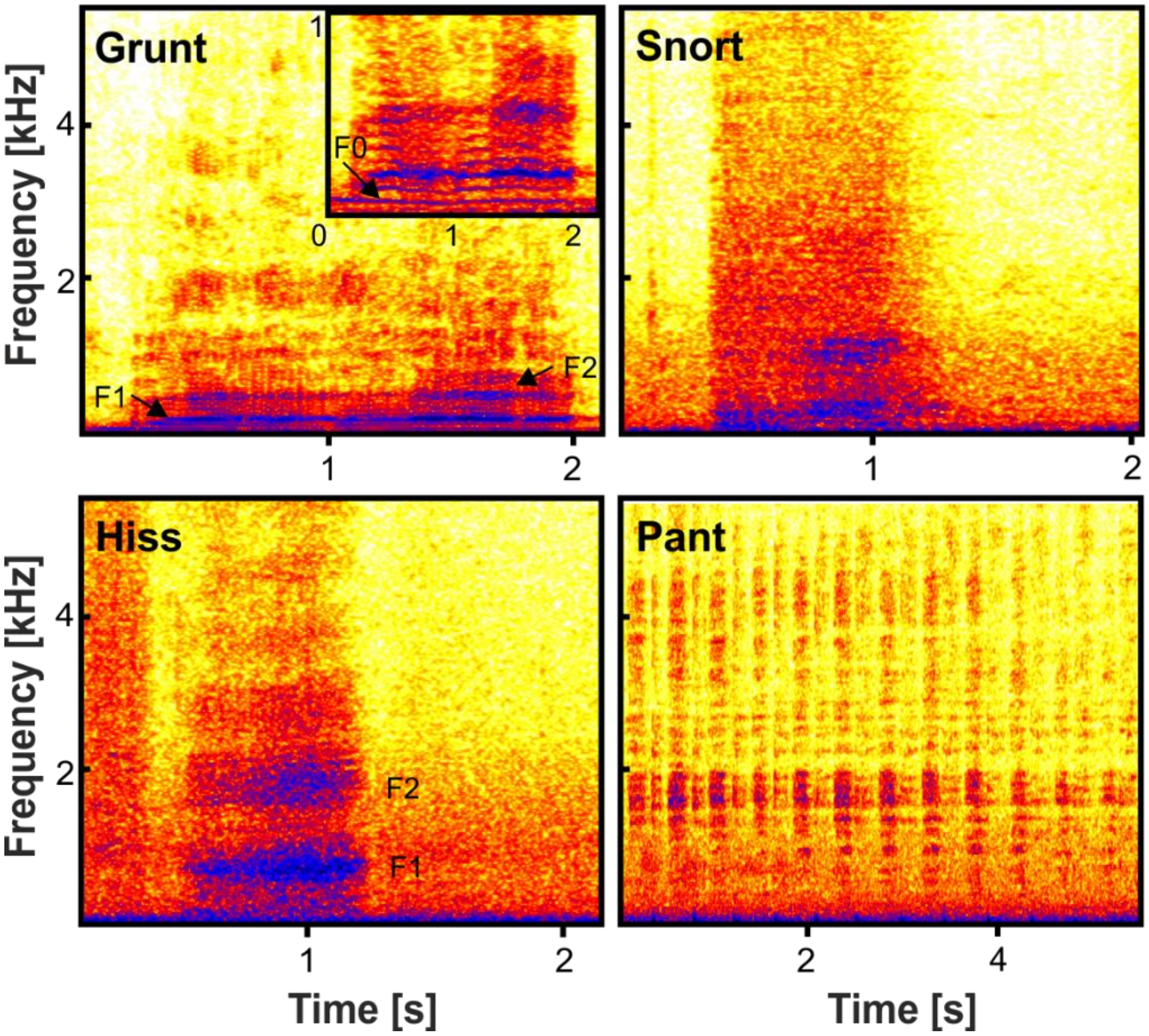


Figure 5-1. Sonograms of the common call types of the southern white rhinoceros: Grunt, Hiss, Snort, and Pant. The panel for Grunt includes a zoomed-in sonogram to show the harmonic structure of the call. F0 – fundamental frequency, F1 – first formant, F2 – second formant.

To test the three hypotheses, we made the following predictions about how the level of individual distinctiveness should differ between call types (Table 5-1). For the social function hypothesis, we predict that the Pant, the Hiss, and the Grunt, uttered during specific social interactions, will have a higher level of individual distinctiveness than Snorts uttered during general activities, such as resting or feeding. Moreover, the level of individual distinctiveness should be higher for the Pant uttered during affiliative social interactions than for the Hiss and Grunt uttered during agonistic interactions. For the distance communication hypothesis, we predict that Pant and Snort uttered at variable distances will show a higher level of individual distinctiveness than Hiss and Grunt uttered during close-distance interactions. For the acoustic structure hypothesis, we predict that the Grunts in which a harmonic structure and formants are obvious will show the highest level of individual distinctiveness, Hisses and Pants containing formant-like structures will show an intermediate level, and nasal Snorts will show the lowest level of individual distinctiveness.

Table 5-1. Predictions of level of individual distinctiveness for southern white rhinoceros call types (including acoustic structure, mouth position, context in which they are given, and typical distance at which they are exchanged) and predictions for acoustic variability and individual distinctiveness based on the different hypotheses; SF = Social function hypothesis, DC = Distance communication hypothesis, AS = Acoustic structure hypothesis; inter. = intermediate.

Call type	**Acoustic structure**	**Mouth position**	**Context**	**Distance**	**Hypotheses and Predictions**		
					SF[1]	**DC[2]**	**AS[3]**
Snort	noisy	closed	not obvious, during general activities	various distances (close /inter./ far)	low	high /inter.	low
Grunt	low frequency, harmonic components	open	aggressive interactions, powerful warning	close	inter.	low	high
Hiss	low frequency, noisy	closed	aggressive interactions, first warning	close	inter.	low	inter.
Pant	bouts of repetitive noisy calls	closed/ open	friendly approach, during isolation	various distances (close/ inter./ far)	high	high/ inter.	inter.

5.2. Materials and Methods

5.2.1. Subjects and study site

Recordings were made on two juvenile and 23 adult southern white rhinoceroses ranging from two to 45 years of age at the following six zoological institutions (Table 5-2): Serengeti-Park Hodenhagen (February - March 2012, May -June 2014), Dortmund Zoo (September - October 2014), Augsburg Zoo (July - August 2014), Osnabrück Zoo (April - May 2014), Erfurt Zoo (April - May 2015), and Gelsenkirchen Zoo (August - September 2015). Due to the fact that there is no evidence for seasonal trends in reproduction in female rhinoceroses in zoos (Roth, 2006), and that reproductive cyclicity in females occurs throughout the year (Brown et al., 2001; Patton et al., 1999), we do not expect that the different dates had an influence on vocalizations. For five of the six institutions, the groups were observed when the adult bull was kept together with the adult females and their offspring. In the Dortmund Zoo the adult bull was physically separated during the whole observation period, however, he had visual and olfactory contact with the adult females.

At Augsburg Zoo, the rhinoceros group consisted of three adult females and one adult male. The rhinoceroses were observed in a 14,000-m2 outdoor enclosure where they lived together during the day with Cameroon sheep (*Ovis aries*) and blesbok (*Damaliscus pygargus phillipsi*). At Osnabrück Zoo, we recorded three adult females and one adult bull that were kept in a 2,000-m2 outdoor enclosure together with red river hogs (*Potamochoerus porcus*) and Chapman's zebras (*Equus quagga chapmani*). At Dortmund Zoo, we observed two adult females in their 2,250-m2 outdoor enclosure. One of the females had a 5-month old calf. At Gelsenkirchen Zoo, the rhinoceros group consisted of two adult females and one adult bull. The rhinoceroses were observed in a 5,000-m2 outdoor enclosure where they lived together with several antelope species. At Erfurt Zoo, we recorded two adult females and one adult bull kept together in a 3,500-m2 outdoor enclosure during the day. At Serengeti-Park Hodenhagen, the rhinoceros group consisted of nine to 11 individuals (2012: six adult females, one adult male, two infants; 2014: five adult females, one adult male, two juveniles, three infants). The adult male was occasionally separated from the herd. Data were mainly recorded in the 9-ha drive-through outdoor enclosure where the rhinoceroses lived together with several other species (e.g. watusis, *Bos primigenius f. taurus*; zebras, *Equus quagga chapmani*; ostriches, *Struthio camelus*; lechwes, *Kobus leche*; addax antelopes, *Addax nasomaculatus*; dromedaries - *Camelus dromedarius*). Our research followed the ASM guidelines (Sikes, 2016). The article contains only observational data of zoo animals during their daily routine without any manipulation of the animals.

Table 5-2. Demographic data of southern white rhinoceroses included in the study and number of selected high-quality calls per call type used for the acoustic analyses.

Individual	Sex	Age* (years)	Zoo	No. of analyzed calls		
				Grunt	Hiss	Snort
Floris	M	37	Osnabrück	-	6	8
Amalie	F	7	Osnabrück	-	8	12
Marsita	F	9	Osnabrück	-	5	20
Lia	F	11	Osnabrück	-	-	20
Bantu	M	8	Augsburg	-	13	11
Baby	F	42	Augsburg	10	20	20
Chris	F	9	Augsburg	11	20	17
Kibibi	F	9	Augsburg	12	20	14
Shakina	F	9	Dortmund	-	20	18
Natala	F	44	Dortmund	-	12	11
Dino	M	21	Erfurt	-	-	14
Temba	F	17	Erfurt	-	-	7
Numbi	F	19	Erfurt	-	7	-
Lekuru	M	11	Gelsenkirchen	-	5	20
Cera	F	11	Gelsenkirchen	-	20	15
Tamu	F	12	Gelsenkirchen	-	20	8
Martin	M	18	Hodenhagen	-	8	-
		21				
Abasi	M	2	Hodenhagen	-	5	8
Molly	F	43	Hodenhagen	-	-	5
		45				
Doris	F	42	Hodenhagen	-	16	13
		44				
Uzuri	F	6	Hodenhagen	17	20	13
		8				
Kiyanga	F	8	Hodenhagen	-	20	14
		10				
Claudia	F	13	Hodenhagen	5	20	14
		15				
Jessica	F	17	Hodenhagen	5	6	6
Lara	F	3	Hodenhagen	-	15	17

* white rhinoceros females can be regarded as adults from the age of six years, males from the age of ten years (Owen-Smith, 1973)

5.2.2. Data collection

Recordings took place throughout the day between 06:00 h and 17:00 h. Audio and video data were collected using the focal animal sampling method (Altmann, 1974). Each rhinoceros of a group was observed for a 10-minute interval in block-randomized order. When all subjects had been observed once, the next block of focal observations started. Overall, a total of 384 hours of data were recorded and analysed. We recorded 81 h at Augsburg Zoo, 54 h at Osnabrück Zoo, 60 h at Erfurt Zoo, 95 h at Serengeti-Park Hodenhagen, 40 h at Gelsenkirchen Zoo, and 54 h at Dortmund Zoo. Recordings were mainly made in the outdoor enclosures from the visitor or keeper area. Occasionally recordings were made in the indoor enclosures, when the rhinoceroses had to stay indoors due to weather conditions.

Since it has been suggested that white rhinoceros produce infrasound vocalizations (Muggenthaler et al., 1993) acoustic data were obtained using a Sennheiser omni-directional microphone (MKH 8020; Sennheiser, Wedemark, Germany) with a frequency response of 10 to 60,000 Hz (frequency response from 10-20,000 Hz ± 5 db) equipped with a windshield and a boom pole. The microphone was connected to a Sound Devices 722 State Recorder (Sound Devices, LLC, Reedsburg, Wisconsin; frequency response of the recorder: 10 ± 20,000 Hz; settings: 44.1 kHz sampling rate, 16 Bit, uncompressed.wav format). Concomitant video recordings were done using a digital camcorder (Sony DCR-SR36E, Tokyo, Japan). In order to allocate vocalizations to individuals, the observer (SL) noted the identity of the caller.

5.2.3. Acoustic analysis

The spectrograms of all audio recordings were inspected visually using Batsound Pro (2013; settings: FFT 512, Hanning window). Calls were visually classified based on previously published vocal repertoires (Linn et al., 2018; Policht et al., 2008). In these studies, call classification was validated using multivariate statistics. For further acoustic analyses, we only selected calls of high quality (no overlap with other sounds, good signal-to-noise ratio, no clipping). The recordings from different zoos were affected by different ambient noise (e.g. Baker & Logue, 2007; Maciej et al., 2011) such as urban, traffic, and building construction noise. Since low frequency signals travel over long distance, even noise sources far away from the recording site necessarily affect the sound recordings, even in high-quality recordings. We used a noise reduction method as applied in other studies, when animal vocalizations were hampered by site specific noise (e.g. Baker & Logue, 2007; Liu et al., 2003; Nair et al., 2009). Namely, we pre-processed the sound files using a bandpass filter of 10 - 10,000 Hz followed by the Wiener Noise Suppressor with Harmonic Regeneration Noise Reduction (HRNR) algorithm (Plapous et al., 2006, 2005) in Matlab (2018) (script modified from Pascal Scalart version 1.1.0.0.). We determined a 200-ms noise segment shortly prior to or after the vocalization of interest, which was used as a statistical estimate of the ambient noise and filtered from the original recording of the vocalization to obtain an estimate of the underlying vocalizations (Wiener Filter). Since the Grunts contained a fundamental frequency with harmonics, we decided to use additionally the Harmonic Regeneration Noise Reduction method, which is suggested to reduce harmonic distortions for small signal-to-noise ratios (Plapous et al., 2006, 2005). Afterwards, the pre-processed audio files were stored as separate wave files for further acoustic analysis.

We are aware of the fact that filtering the acoustic recordings might influence the acoustic measurements and that filtering can cause harmonic distortions known as musical notes. We tried to reduce these effects as much as possible by using (1) high-quality calls, (2) the same procedure for all recordings, (3) a long noise segment directly preceding or following the respective vocalizations without any distinct sound events (e.g., bird calls, human speech) to calculate the statistical background noise, and (4) by using a noise reduction method suggested to reduce harmonic distortions. For Hisses and Snorts, we listened to all filtered vocalizations and selected only calls where musical notes could not be perceived by the experimenter. Taking a random sample of all Hisses and Snorts led to comparable statistical results as taking a sample of these call types including only filtered vocalizations without detectable musical notes. Thus, for the Grunts, for which a limited sample size was available, all calls were used. Sonograms of examples of the original and filtered calls are presented in Appendix 5-1 (Supplementary Data SD1).

Because the number of calls per call type and individual varied widely, we randomly selected five to 20 calls per individual of every call type for acoustic analysis to have a call balanced data set. Individuals with less than five calls per call type were not taken into account. In total, 651 calls were included in the acoustic analysis (Table 5-2; 60 Grunts, 286 Hisses, 305 Snorts). We also recorded Pants in the present study. However, due to their low amplitude and interferences with environmental sounds in the outdoor enclosures, most of these Pants did not satisfy our quality criteria. Therefore, we referred to the results reported in Cinková and Policht (2014b) for comparisons.

The spectral and temporal parameters that were measured differed depending on the call types. We described the spectral composition using Praat (2018; self-written script, Boersma, 1993, 2001) by measuring the following nine acoustic parameters for all call types: call duration (DUR), time of maximum amplitude (timeMAXPEAK), percentage of voiced frames (VOI), the center of gravity (COG) of the spectrum, standard deviation of the frequency (SD) in the spectrum, the skewness (SKE) as a measure of symmetry of the spectrum, the kurtosis (KUR) describing the deviation of the spectrum from a Gaussian distribution, harmonic-to-noise ratio (HNR) and Wiener entropy (ENTR). For full definitions of all acoustic parameters see Table 5-3. Since harmonic-to-noise ratio and Wiener entropy values are based on logarithmic scaling, we have converted these logarithmic values to a linear scale for all subsequent calculations.

If no fundamental frequency contour could be determined in the sonogram (noisy calls) for a time frame, the time frame was set as unvoiced for the calculation of the percentage of voiced frames (VOI). For the harmonic Grunt, we included four additional parameters characterizing the contour of the fundamental frequency (F0): minimum F0 (MINF0), maximum F0 (MAXF0), mean F0 (MEANF0), standard deviation of the F0 (SDF0). We used a semiautomatic procedure for pitch tracking. If necessary, we corrected the pitch tracking manually by matching the extracted contour with the sonogram (settings: sub-menu: “To pitch”; min pitch: 10 Hz; max pitch: 3,000 Hz; time steps: 0.005). However, since it has been suggested that noisy calls might be well suited for extraction of filter-related formants (e.g. Gamba, 2014; Plotsky et al., 2013), we additionally measured four formant parameters using Praat sub-menu “quantify formant”: first formant (F1), bandwidth of the first formant (BDF1), second formant (F2), and bandwidth of the second formant (BDF2). For the Grunts, we estimated the expected number of formants based on the following formula (Pfefferle & Fischer, 2006):

$$N=(2 \times L)/c \times f_c$$

where N = number of formants, L = vocal tract length [m], c = speed of sound (340 m/s), and f_c = cut-off frequency of the measurement range [Hz]. We based our calculation on the oral vocal tract length (0.72 m) of a cadaver measured by Roland Frey (Leibniz Institute for Zoo and Wildlife Research, personal communication, 9 February 2015) to get an indication of how many formants we can expect. Based on the calculated values and on visual inspections of the sonogram, we used the following setting for Grunts: number of formants: 4; max. formant value: 1,000 Hz; time steps: 0.05 s. For the Hiss we were not able to use the formula since the expected formant frequencies did not correspond to the dominant frequency bands in the sonogram. To track these frequency bands we based our setting on visual inspection of the sonograms and used the following settings: number of formants: 3; max. formant value: 5,000 Hz; time steps: 0.05 s. For Snorts, the frequency band of high energy was reflected by the center of gravity. Further emphasized frequency bands were barely detected. Therefore, we measured no formants for Snort calls.

In addition, we measured the minimum frequency (MIN), maximum frequency (MAX), and bandwidth (BAND), as well as the frequencies of the first, second, or third quarter of total energy in the spectrum (25%QUART, 50%QUART, 75%QUART; FFT 1024, Hanning window) for all call types using the automatic measurement routine of Avisoft (2018). Measurements were taken at the time point of maximum amplitude (max) as well as across the whole call (mean).

Table 5-3. Description of measured acoustic parameters.

Parameter	**Definition**
DUR [s] [a]	Time between the onset and the offset of a call
Time MAXPEAK [s] [a]	Time between the onset and the time point of maximum amplitude of a call
VOI [%] [a]	Percentage of voiced frames of a call
COG [Hz] [a]	Center of gravity - mean frequency of the spectrum weighed by the amplitude
SD [Hz] [a]	Standard deviation of the frequency in a spectrum
SKE [a]	Skewness of the spectrum - difference between the spectral distribution below and above the COG providing a measure of symmetry
KUR [a]	Kurtosis of the spectrum - difference between the spectrum around the COG and a Gaussian distribution
F1[Hz] [a**]	First formant - First frequency band in the sonogram
BDF1 [Hz] [a**]	Bandwidth of the first formant
F2 [Hz] [a**]	Second formant - second frequency band in the sonogram
BDF2 [Hz] [a**]	Bandwidth of the second formant
HNR [a]	Harmonic-to-noise ratio
ENTR [a]	Wiener entropy - ratio of geometric to arithmetic energy
MIN (max) [Hz] [b]	Minimum frequency at which the amplitude is 20 db below the peak amplitude measured at the time window of maximum amplitude
MAX (max) [Hz] [b]	Maximum frequency at which the amplitude is 20 db below the peak amplitude measured at the time window of maximum amplitude
BAND (max) [Hz] [b]	Bandwidth difference between maximum and minimum frequency using a threshold of 10 db to the peak amplitude measured at the time point of maximum amplitude
25% QUART (max) [Hz] [b]	Frequency of the power spectrum at which 25% of the total energy is reached measured at the time point of maximum amplitude
50% QUART (max) [Hz] [b]	Frequency of the power spectrum at which 50% of the total energy is reached measured at the time point of maximum amplitude
75% QUART (max) [Hz] [b]	Frequency of the power spectrum at which 75% of the total energy is reached measured at the time point of maximum amplitude
MIN (mean) [Hz] [b]	Minimum frequency at which the amplitude is 20 db below the peak amplitude measured over the mean spectrum of the entire call
MAX (mean) [Hz] [b]	Maximum frequency at which the amplitude is 20 db below the peak amplitude measured over the mean spectrum of the entire call
BAND (mean) [Hz] [b]	Bandwidth difference between maximum and minimum frequency using a threshold of 10 db to the peak amplitude measured over the mean spectrum of the entire call
25% QUART (mean) [Hz] [b]	Frequency of the power spectrum at which 25% of the total energy is reached measured over the mean spectrum of the entire call
50% QUART (mean) [Hz] [b]	Frequency of the power spectrum at which 50% of the total energy is reached measured over the mean spectrum of the entire call
75% QUART (mean) [Hz] [b]	Frequency of the power spectrum at which 75% of the total energy is reached measured over the mean spectrum of the entire call
MINF0 [Hz] [a*]	Minimum fundamental frequency of a call

MAXF0 [Hz] [a*]	Maximum fundamental frequency of a call
MEANF0 [Hz] [a*]	Mean fundamental frequency of a call
SDF0 [Hz] [a*]	Standard deviation of the fundamental frequency of a call

[a] measured in PRAAT; [b] measured in AVISOFT at the location of maximum and mean amplitude; *only measured for the Grunt; ** only measured for the Grunt and the Hiss.

5.2.4. Statistical analysis

In the first part of the analysis, we investigated the potential of each call type to encode sender identity using the whole data set. Using the Kolmogorov-Smirnov test, we confirmed that the majority of acoustic parameters for the majority of individuals were normally distributed ($P \leq 0.05$). We tested whether the acoustic parameters differed between individuals by calculating a linear mixed model with the acoustic parameter as the dependent variable, the sender as predictor variable, and zoo as a random variable ("nlme" package; Rstudio Team 2018), and tested the effect of the sender using the "anova" function. The random variable zoo was added to account for call adaptations in response to site-specific noise, or similarities based on relatedness of individuals in a given zoo. To control for multiple testing the same null hypothesis, we carried out the Fisher-Omnibus test (Haccou & Meelis, 1994). This test combines the P-values of the different ANOVAs into a single chi-square distributed variable resulting in an overall P-value and thereby in a rejection or acceptance of the null hypothesis. The degree of freedoms represents twice the number of included P-values. Based on the significant parameters in the linear mixed model, we carried out a principal component analysis (PCA) and extracted principal components (PCs) with an eigenvalue higher than 1 to reduce the number of parameters. In that manner, correlating acoustic parameters were represented by the same PC. To investigate whether calls can correctly be classified to the respective individuals, we carried out an independent discriminant function analysis (DFA) based on these PCs using the leave-one-out method for cross validation. To test whether the number of correctly classified calls was significantly higher than expected by chance, we performed a binomial test for each subject and calculated the level of agreement using the kappa test (Scheumann et al., 2007). The level of agreement was defined as follows: Cohen's kappa < 0.00 = poor agreement, 0.00 - 0.20 = slight agreement, 0.21 - 0.40 = fair agreement, 0.41 - 0.60 = moderate agreement, 0.61 - 0.80 = substantial agreement, and 0.81 - 1.00 = almost perfect agreement (Landis & Koch, 1977). To estimate which parameters were important for classification, we investigated the correlation between the DFA function with the PCs and afterwards the correlations of the PCs with the acoustic parameters. Parameters with a loading factor higher than 0.7 were considered as having a strong impact on the respective PC.

In addition, we calculated the potential of individual identity coding (PIC) for each parameter and call type according to Robisson et al. (1993). The PIC tested whether the inter-individual variation of a call type was larger than its intra-individual variation. For the PIC analysis, we calculated the mean ($\mathrm{MEAN}_{\mathrm{Within}}$) and standard deviation ($\mathrm{SD}_{\mathrm{Within}}$) of each subject for each acoustic parameter as well as for the mean ($\mathrm{MEAN}_{\mathrm{Between}}$) and standard deviation ($\mathrm{SD}_{\mathrm{Between}}$) of the whole data set. Using these parameters, we obtained the within-individual ($\mathrm{CI}_{\mathrm{Wi}}$) and between-individual (CI_{B}) coefficients of variation ($\mathrm{CI} = 100*(1+1/4n)*\mathrm{SD}/\mathrm{MEAN}$) where n is the number of calls. Further, we calculated the CI_{W} by averaging the $\mathrm{CI}_{\mathrm{Wi}}$ of all subjects. We determined the PIC for each parameter by calculating the ratio $\mathrm{PIC} = \mathrm{CI}_{\mathrm{B}}/ \mathrm{CI}_{\mathrm{W}}$ (e.g. Bouchet et al., 2012; Ligout et al., 2004). A value of $\mathrm{PIC} > 1$ indicates that this parameter is potentially capable of encoding individuality. Additionally, we calculated the $\mathrm{PIC}_{\mathrm{Overall}}$ as mean of all PIC values across the parameters (Salmi et al., 2014).

In the second part of the analysis, we aimed to compare the level of individual distinctiveness across call types. Since the results of the DFA are affected by the number of individuals included in the analysis (e.g. Beecher, 1989), we balanced our sample and compared the six individuals for which data on all three call types were available. Then, we performed again the discriminant function analysis as described before.

The information capacity criterion (H_{s}) according to Beecher (1989) is based on information theory and calculated in bits. The value 2^{Hs} estimates the number of individuals that can be potentially discriminated based on the considered acoustic parameters of the call. We carried out a one-way ANOVA testing whether the PC scores of the above described principal component analysis differed between individuals. We used the mean squares (MS) of the significant PC components (e.g Beecher, 1989; Bouchet et al., 2013) to calculate the estimates for within-individual variance ($\mathrm{S}^2_{\mathrm{W}} = \mathrm{MS}_{\mathrm{W}}$) and between-individual variance ($\mathrm{S}^2_{\mathrm{B}} = (\mathrm{MS}_{\mathrm{B}} - \mathrm{MS}_{\mathrm{W}})/n_0$ according to Lessells and Boag (1987). Thereby, MS_{B} is the mean square of between-individual variance, MS_{W} is the mean square of within-individual variance and n0 is a coefficient related to the sample size. The value of n_0 is calculated using following formula: $n_0 = [1/(a-1)] \times [\sum_{i=1}^{a} n_i - (\sum_{i=1}^{a} n^2 / \sum_{i=1}^{a} n_i)]$ (a = number of groups; n_i = number of calls in the i^{th} group) and represents the mean sample size per individual. Based on these estimated variances, we calculated the information criterion ($\mathrm{H}_{\mathrm{i}} = \log_2 (\mathrm{S}^2_{\mathrm{T}}/\mathrm{S}^2_{\mathrm{W}})$). The total variance S^2_T was calculated as the sum of $S^2_W + S^2_B$. To estimate the information capacity of a call the information criterions of all significant PCs were summed ($H_s = \sum H_i$).

For the comparison of the level of individual distinctiveness, we also calculated the $PIC_{overall}$ and the H_s for the balanced data set.

5.3. Results

5.3.1. Grunt

The ANOVAs revealed that 21 out of 29 acoustic parameters were significantly different across individuals ($F_{5, 54} \geq 5$, $P \leq 0.040$ and for MINF0, MAXF0, and MEANF0 $_{F5, 36} \geq 4$, $P \leq 0.010$, Fisher-Omnibus test: $\chi 2=281.58$, df = 58, P <0.001; Table 5-4). A PCA based on these significant parameters (except MINF0, MAXF0, and MEANF0, which could not be obtained for all Grunt calls and the other call types) extracted five PCs with an eigenvalue higher than 1 explaining 85% of the variance. An independent DFA based on these five PCs was able to classify 65% of the calls to the respective individual (cross validation: 57%). Significantly more calls were correctly classified than expected by chance for five out of six individuals (binomial test: $P \leq 0.036$). The kappa test resulted in a moderate agreement between the results of the DFA and the observed data (0.56). The DFA calculated five DFs. DF1 and DF2 explained 75% of the variation in the calls. DF1 showed the highest correlation to PC2 (r = -0.604) and DF2 to PC1 (r = 0.732). PC1 showed the highest loading on parameters 50%QUART(mean), 25%QUART(mean), MAX(mean), BAND(mean), and COG ($r \geq 0.810$). PC2 showed the highest loading on parameters 25%QUART(max) and 50%QUART(max) ($r \geq 0.796$). Thus, spectral parameters play a predominant role in encoding sender identity.

Twenty-four of 29 parameters showed a PIC > 1 suggesting a potential for identity coding (Table 5-4).

Table 5-4. Individual differences in the acoustic parameters of the Grunt of the southern white rhinoceros. PIC = potential for individual identity coding, CI_B = between-individual coefficient of variance, CI_W = within-individual coefficient of variance. Bold indicates PIC > 1.0 and P > 0.05; $*F_{5, 36}$.

Parameter	**Descriptive**		**PIC**			**ANOVA**	
	Mean	**SD**	**CI_B**	**CI_W**	**PIC**	**$F_{5, 54}$**	**P**
DUR [s]	1.78	0.97	54.61	54.92	1.0	1.4	0.234
timeMAXPEAK [s]	1.01	0.86	85.59	82.63	1.0	2.3	0.057
VOI [%]	37.46	31.85	85.36	98.20	0.9	4.2	0.003
COG [Hz]	339.12	126.89	37.57	35.28	1.1	5	<0.001
SD [Hz]	294.64	190.43	64.90	48.70	1.3	3.6	0.008
SKE	8.40	5.19	61.98	51.09	1.2	6.9	<0.001
KUR	305.61	433.10	142.31	85.30	1.7	3.2	0.014
F1[Hz]	235.77	57.40	24.45	19.33	1.3	5	<0.001
BDF1 [Hz]	38.61	43.23	112.44	96.66	1.2	0.6	0.713
F2 [Hz]	467.73	73.31	15.74	15.11	1.0	1.0	0.447
BDF2 [Hz]	157.86	187.76	119.44	110.06	1.1	1.8	0.127
HNR	1.60	0.46	29.04	17.00	1.7	9	<0.001
ENTR	0.35	0.12	33.12	28.12	1.2	6	<0.001
MIN(max) [Hz]	89.17	74.61	84.03	43.05	2.0	5.6	<0.001
MAX(max) [Hz]	912.50	487.44	53.64	46.38	1.2	3.1	0.016
BAND(max) [Hz]	816.67	473.83	58.26	50.46	1.2	2.5	0.040
25% QUART(max) [Hz]	257.33	134.57	52.51	36.52	1.4	9	<0.001
50% QUART(max) [Hz]	354.50	156.16	44.23	34.24	1.3	10	<0.001
75% QUART(max) [Hz]	622.17	304.72	49.18	48.23	1.0	2.3	0.056
MIN(mean) [Hz]	80.33	36.17	45.21	29.59	1.5	1.3	0.299
MAX(mean) [Hz]	1168.00	369.80	31.79	24.37	1.3	6	<0.001
BAND(mean) [Hz]	1080.67	372.57	34.62	26.36	1.3	6	<0.001
25% QUART(mean) [Hz]	301.17	87.95	29.33	24.07	1.2	6	<0.001
50% QUART(mean) [Hz]	489.33	149.63	30.71	24.78	1.2	7	<0.001
75% QUART(mean) [Hz]	877.67	489.73	56.03	37.26	1.5	6	<0.001
MINF0 [Hz]	53.43	8.57	16.13	13.47	1.2	4*	0.006
MAXF0 [Hz]	69.21	17.89	26.00	22.90	1.1	4*	0.010
MEANF0 [Hz]	59.92	8.92	14.97	12.42	1.2	6*	<0.001
SDF0 [Hz]	3.99	3.19	80.60	64.65	1.3	0.7*	0.615

5.3.2. Hiss

The ANOVAs revealed that 17 out of 24 parameters were significantly different across individuals ($F_{20, 265} \geq 2.0$, $P \leq 0.030$; Fisher-Omnibus Test: $\chi 2 = 248.10$, df = 48, $P < 0.001$; Table 5-5). A principal component analysis based on these significant parameters extracted five PCs with an eigenvalue higher than 1 explaining 78% of the variance. An independent DFA based on these five PCs was able to classify 26% of the calls to the respective individual (cross validation: 19%). The kappa test revealed a slight agreement (0.20) between the observed data and the classification by the DFA. For 11 out of 21 individuals significantly more calls were correctly classified than expected by chance (binomial test: $P \leq 0.047$). The DFA calculated five DFs. DF1 and DF2 explained 71% of the variation in the calls. DF1 showed the highest correlation to PC2 ($r = 0.627$) and DF2 showed the highest correlation to PC5 ($r = 0.794$). PC2 showed the highest loading on factors SD, ENTR, and MIN(max) ($r \geq |0.701|$).

Seventeen out of these 24 parameters showed a PIC > 1 and thus could potentially be involved in the encoding of individuality (Table 5-5).

Table 5-5. Individual differences in the acoustic parameters of the Hiss of the southern white rhinoceros. PIC = potential for individual identity coding, CI_B = between-individual coefficient of variance, CI_W = within-individual coefficient of variance. Bold indicates PIC > 1.0 and *P* > 0.05.

Parameter	**Descriptive**		**PIC**		**ANOVA**		
	Mean	**SD**	**CI_B**	**CI_W**	**PIC**	**$F_{20, 265}$**	**P**
DUR [s]	0.53	0.24	45.16	33.12	1.4	5	<0.001
timeMAXPEAK [s]	0.23	0.13	57.04	45.57	1.3	3	<0.001
COG [Hz]	785.27	161.41	20.57	17.34	1.2	3	<0.001
SD [Hz]	491.35	213.18	43.42	37.73	1.2	4	<0.001
SKE	5.72	3.47	60.75	45.52	1.3	2	0.008
KUR	121.66	201.59	165.85	87.38	1.9	1	0.401
F1[Hz]	845.30	82.06	9.72	8.06	1.2	4	<0.001
BDF1 [Hz]	233.71	218.80	93.70	78.63	1.2	2	0.057
F2 [Hz]	2214.04	248.56	11.24	9.70	1.2	5	<0.001
BDF2 [Hz]	450.44	331.49	73.66	52.59	1.4	1	0.132
HNR	1.18	0.42	35.64	28.63	1.2	4	<0.001
ENTR	0.71	0.08	11.84	11.41	1.0	2	0.002
MIN(max) [Hz]	261.89	196.21	74.99	70.00	1.1	3	<0.001
MAX(max) [Hz]	1716.40	713.70	41.62	41.50	1.0	1	0.100
BAND(max) [Hz]	1449.27	746.91	51.58	50.02	1.0	2	0.030
25% QUART(max) [Hz]	648.50	210.19	32.44	33.25	1.0	2	0.005
50% QUART(max) [Hz]	832.69	192.72	23.16	22.18	1.0	2	0.001
75% QUART(max) [Hz]	1301.40	465.17	35.77	35.36	1.0	2	0.060
MIN(mean) [Hz]	152.55	121.47	79.69	54.48	1.5	3	<0.001
MAX(mean) [Hz]	2286.33	665.67	29.14	27.90	1.0	1	0.213
BAND(mean) [Hz]	2128.01	690.63	32.48	30.44	1.1	1	0.144
25% QUART(mean) [Hz]	643.53	132.03	20.53	16.39	1.3	7	<0.001
50% QUART(mean) [Hz]	908.43	143.55	15.82	13.11	1.2	3	<0.001
75% QUART(mean) [Hz]	1559.13	482.97	31.00	29.49	1.1	3	<0.001

5.3.3. Snort

The ANOVAs revealed that 16 out of 20 parameters that were measured for Snort vocalizations differed significantly across individuals ($F_{22, 282} \geq 2$, $P \leq 0.028$; Fisher-Omnibus Test: $\chi 2 = 219.20$, df = 40, $P < 0.001$; Table 5-6). The PCA based on these acoustic parameters extracted three PCs with an eigenvalue higher than 1 explaining 77% of the variance. An independent DFA based on these three PCs was able to classify 16% of the calls to the respective individual (cross validation: 14%). The kappa test showed only a slight agreement

(0.11). For 6 out of 23 individuals, significantly more calls were correctly classified than expected by chance (binomial test: $P \leq 0.039$). The DFA calculated three DFs. DF1 and DF2 explained 77% of the variation in the calls. DF1 showed the highest correlation to PC2 ($r = 0.840$), whereas DF2 showed the highest correlation to PC1 ($r = 0.923$). PC1 showed the highest loading on almost all filter-related parameters ($r \geq |0.700|$ for all except MIN(max) and 25%Quart(max)). PC2 showed highest loading on MIN(max) ($r = 0.747$).

All 20 parameters showed a PIC > 1 and could potentially be involved in the encoding of individuality (Table 5-6).

Table 5-6. Individual differences in the acoustic parameters of the Snort of the southern white rhinoceros. PIC = potential for individual identity coding, CI_B = between-individual coefficient of variance, CI_W = within-individual coefficient of variance. Bold indicates PIC > 1.0 and *P* > 0.05.

Parameter	**Descriptive**		**PIC**			**ANOVA**	
	Mean	**SD**	**CI_B**	**CI_W**	**PIC**	**$F_{22, 282}$**	**P**
DUR [s]	0.52	0.18	33.66	29.34	1.2	2	<0.001
timeMAXPEAK [s]	0.17	0.09	54.99	49.30	1.1	2	0.009
COG [Hz]	866.02	395.94	45.76	41.26	1.1	3	<0.001
SD [Hz]	972.70	362.40	37.29	33.40	1.1	3	<0.001
SKE	4.17	2.34	56.09	45.93	1.2	4	<0.001
KUR	33.51	45.14	134.82	91.71	1.5	5	<0.001
HNR	0.82	0.17	21.03	19.97	1.1	1	0.406
ENTR	0.71	0.08	10.48	9.66	1.1	3	<0.001
MIN(max) [Hz]	104.70	97.15	92.86	72.82	1.3	2	0.028
MAX(max) [Hz]	2408.58	1668.55	69.33	66.03	1.1	1	0.117
BAND(max) [Hz]	2299.48	1663.32	72.39	68.93	1.1	1	0.103
25% QUART(max) [Hz]	494.16	320.96	65.00	55.97	1.2	3	<0.001
50% QUART(max) [Hz]	991.39	603.28	60.90	54.81	1.1	2	0.004
75% QUART(max) [Hz]	2286.17	1061.80	46.48	43.30	1.1	3	<0.001
MIN(mean) [Hz]	79.03	41.21	52.19	33.63	1.6	1	0.512
MAX(mean) [Hz]	3667.83	1939.55	52.92	50.16	1.1	2	<0.001
BAND(mean) [Hz]	3583.61	1941.46	54.22	51.45	1.1	2	0.001
25% QUART(mean) [Hz]	613.35	239.37	39.06	32.79	1.2	4	<0.001
50% QUART(mean) [Hz]	1307.84	533.86	40.85	37.75	1.2	3	<0.001
75% QUART(mean) [Hz]	2831.87	939.58	33.21	30.84	1.1	3	<0.001

5.3.4. Comparison of call types

The discriminant function analysis based on a balanced sample of an identical number of individuals per call type (n_{ind} = 6, 5-20 calls per individual; Table 5-7) revealed a classification accuracy of 65% in Grunts (cross validation: 57%), 44% in Hisses (cross validation: 38%), and 30% in Snorts (cross validation: 25%). Thus, classification accuracy decreased from Grunts to Hisses to Snorts. This was supported by the kappa values, which also decreased from 0.56 for Grunts, suggesting moderate agreement, to 0.32 for Hisses, suggesting a fair agreement, to 0.13 for Snorts, reflecting a slight agreement. In addition, the overall PIC and the H_s showed the same pattern. Based on the subject balanced dataset, the $PIC_{Overall}$ and the H_s were lowest for Snorts (PIC = 1.1; Hs = 0.59), intermediate for Hisses (PIC = 1.2; H_s = 0.91), and highest for Grunts (PIC = 1.3, Hs = 2.63; Table 5-7). The values obtained for the balanced data set did not vary much from the total data set for Snorts ($PIC_{Overall}$ = 1.2, H_s = 0.50) and only slightly for Hisses ($PIC_{Overall}$ = 1.2, Hs = 1.25).

Table 5-7. Comparison of the potential for individual identity coding and classification accuracy between the call types Grunt, Hiss, and Snort of the southern white rhinoceros. PIC = potential for individual identity coding, H_s = information criterion, DFA = discriminant function analysis, Total = total data set, Bal. = subject balanced data set, *n* = number of individuals.

		Grunt	**Hiss**		**Snort**	
		Total = Bal. (*n* = 6)	**Total (*n* = 21)**	**Bal. (*n* = 6)**	**Total (*n* = 23)**	**Bal. (*n*= 6)**
Overall PIC		1.3	1.2	1.2	1.2	1.1
H_s		2.63	1.25	0.91	0.50	0.59
No. of PC factors		5	5	4	3	2
DFA	**Original classification [%]**	65	26	44	16	30
	Cross-validation [%]	57	19	38	14	25
	Mean Chance level per individual [%]	< 28%	< 7%	< 19%	< 7%	< 24%
	Kappa-test	0.56	0.20	0.32	0.11	0.13
	Classification category	moderate	slight	fair	slight	slight

5.4. Discussion

All three call types, the Grunt, the Hiss, and the Snort, possessed an acoustic structure capable of encoding individual identity according to their overall PIC (larger than 1) but differed in their acoustic variability and individual distinctiveness (Table 5-7). Based on the calculated information criterion (H_s), the level of individual distinctiveness increased from Snort to Hiss to Grunt. The H_s for the Pant reported by Cinková and Policht (2014b; $H_s = 3.15$) was much higher than the H_s determined for the call types analysed in the present study. Our analysis revealed that the differences in the degree of individual distinctiveness across call types are barely explained by the distance communication hypothesis, partly by the acoustic structure hypothesis, and best by the social function hypothesis.

The present data provide no support for the distance communication hypothesis. Individual distinctiveness was much higher in the Grunt and the Hiss used for short-distance communication than in the Snort that is uttered at variable distances to other individuals (Linn et al., 2018). However, the hypothesis is supported when taking into account the Pant with its high degree of individual distinctiveness, which has been suggested to serve for long-distance communication since this call type has been recorded in situations with conspecifics several hundred meters away (Cinková & Policht, 2014b). The Pant is uttered with the mouth closed (sometimes only the lip is moving due to flehmen during vocalizations; Linn et al., 2018; personal observations) as is the Snort, and sound pressure levels of nasal vocalizations in general are much lower than those of oral sounds due to the fact that in most mammalian species the nasal passages are convoluted and filled with spongy absorbing tissue (Wiley & Richards, 1978). Thus, in African elephants (*Loxodonta Africana*; Stoeger et al., 2012b) and sheep (Sèbe et al., 2010) oral calls are considerably louder than those emitted through the nose or trunk. As vocalizations with low amplitude will not propagate as far as those with high amplitude, it is questionable whether the Pant and the Snort are used for long-distance communication. That the Pant is indeed a low-amplitude call is supported by the difficulties we had to record high quality Pant calls during social interactions. In the present study, we recorded 690 Pant calls. However, due to its low amplitude characteristics, interferences with sounds from animal locomotion or Hisses of female conspecifics, in particular, we were not able to extract a sufficiently large number of calls satisfying our quality criteria. Therefore, we compared our data with the data set published by Cinková and Policht (2014b) who recorded Pant calls from 14 animals in an isolation context, thus obtaining better signal-to-noise ratios.

Our results partly support the acoustic structure hypothesis since the only harmonic call, the Grunt, is more individually distinctive than the Hiss, containing formant-like structures, followed by the noisy Snort. Even though we measured all parameters commonly used in the literature, it could be that other parameters may be better suited to measure individual signatures in Snorts and Hisses. Nevertheless, our findings are in accordance with the assumption that narrow-band harmonic calls are better suited for coding sender identity than broad-band noisy calls (Leliveld et al., 2011; Yin & McCowan, 2004). Thus, the dense energy distribution by the narrow-spaced harmonics favours the projection of formants. However, the Pant showed the highest level of individuality (Cinková & Policht, 2014b) although it has a broad-band acoustic structure without fundamental frequency. The analysis of Cinková and Policht (2014b) showed that sender identity was mainly encoded by temporal parameters such as the duration or the number of elements (Cinková & Policht, 2014b) whereas in our analysis temporal parameters were not important. Although individual differences based on frequency characteristics have been found in various mammals (e.g. Bastian & Schmidt, 2008; Leliveld et al., 2011; Mumm et al., 2014), identity coding based on temporal features has also been described for some species (e.g. Shapiro, 2006, 2010). In calls consisting of bouts of repetitive elements, the number of units per call and thereby the call duration are primarily dependent on individual lung capacity and the control of the air flow speed (Fitch & Hauser, 1995). Individual-specific information based on the variance in temporal features, such as duration or temporal arrangement of frequency elements, has been found in bats (Brown, 1976; Masters et al., 1995) and nonhuman primates (Bouchet et al., 2012; Lemasson et al., 2010). Temporal variation is often related to differences in the arousal state of an animal, which affects the mammalian vocal production mechanism (Kirchhübel et al., 2011). Arousal and anxiety are known to reduce saliva production and to increase muscle tension in mammals (Kirchhübel et al., 2011). In dwarf mongooses (*Helogale parvula*), it was shown that calls emitted during high-arousal situations show less individual variation as compared to calls emitted during low-arousal states (Rubow et al., 2018), whereas in domestic kittens (*Felis catus*) no difference in the level of individual distinctiveness was found between high- and low-arousal contexts (Scheumann et al., 2012). The southern white rhinoceros uttered two call types during aggressive interactions. Hisses acted as a first warning signal, whereas Grunts were a more powerful warning signal indicating a more pronounced motivation to fight (Policht et al., 2008). The Grunts may thus signal a higher level of arousal, yet they exhibited more pronounced individual differences compared to Hisses produced at a lower arousal level.

Our findings best support the social function hypothesis, as the level of individual distinctiveness increases from Snort, to Hiss, to Grunt, to Pant. Thus, the lowest level of individual distinctiveness was found in the Snort, which is often used in non-social situations such as feeding, resting, or locomotion (Linn et al., 2018; Policht et al., 2008). On the other hand, calls with a strong intragroup social function have high levels of acoustic variability, potentially allowing callers to convey a range of individual-specific information. These calls play a major role in affiliative (Pant) and agonistic interactions (Grunt and Hiss) with a specific social partner (Linn et al., 2018; Policht et al., 2008). Individual distinctiveness was highest in Pants functioning as a contact call during socio-positive interactions as compared to Grunts and Hisses uttered during socio-negative interactions. Pants are mainly produced in two distinct social contexts. First, white rhinoceroses emit Pants during social cohesive interactions as a kind of "greeting" when approaching or following a conspecific or a group of individuals (Linn et al., 2018; Policht et al., 2008). Moreover, Pants play an important role in the mating behavior of white rhinoceroses as bulls emit this call during mate guarding and mating encounters (Owen-Smith, 1973; Policht et al., 2008). In both contexts it may be essential for a white rhinoceros to assess the identity of the caller, providing information about physiological and morphological attributes such as body size, dominance rank, or hormonal state. There is strong male-male competition and female mate choice in white rhinoceroses (Kretzschmar et al., 2020) and males use acoustic cues to gather information about rivals (Cinková & Shrader, 2020).

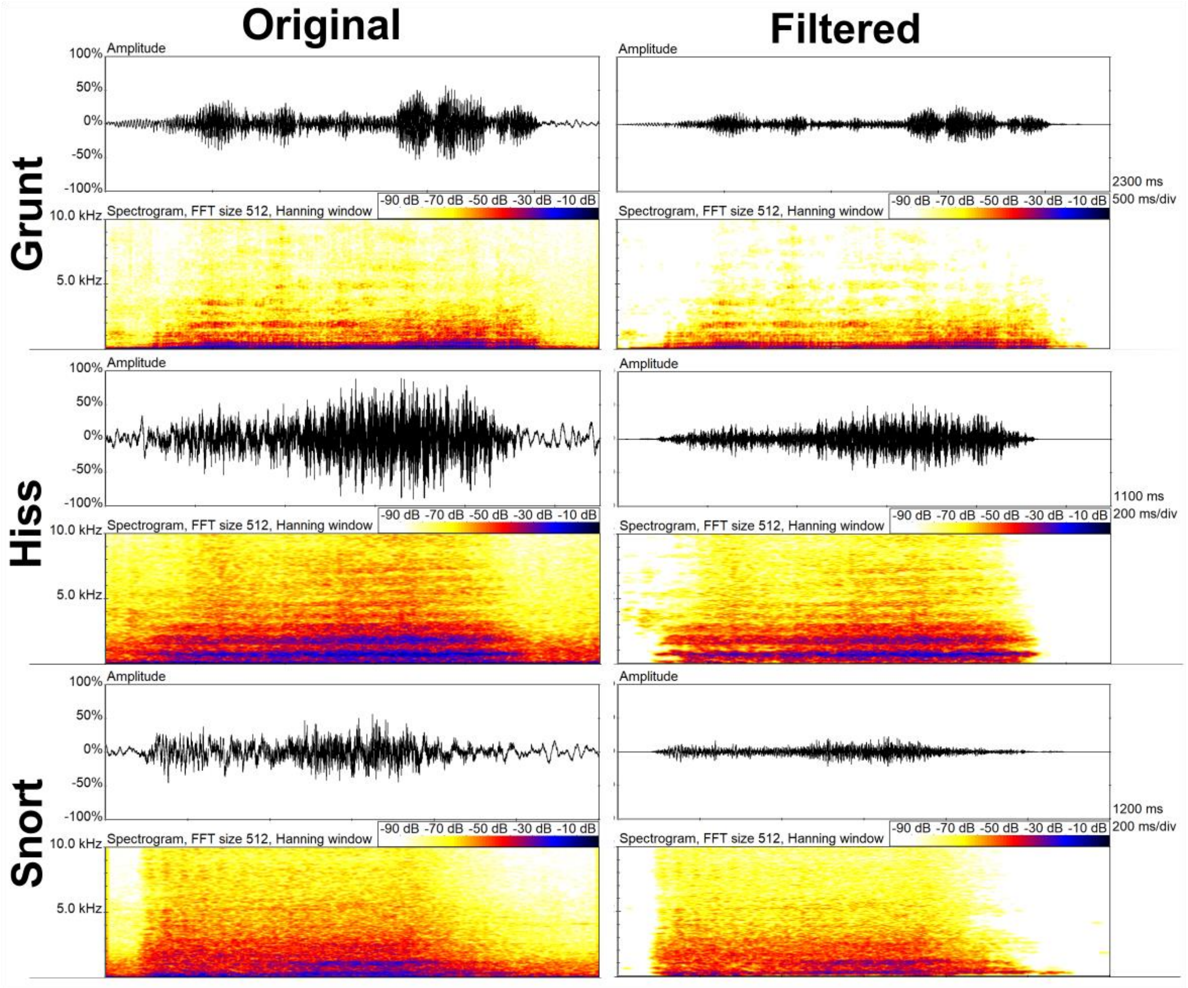
Our finding is in agreement with the expansion of the social function hypothesis by Lemasson and Hausberger (2011) which assumes that individual distinctiveness is higher in calls related to affiliative contexts as compared to calls related to agonistic contexts. Our results agree with other studies showing that individual distinctiveness increases with increasing affiliative social value of a call type (Appendix 5-2; e.g. Ancillotto & Russo, 2016; Bouchet et al., 2013; Lemasson & Hausberger, 2011). Selection may have favoured more individually distinct calls in situations such as social cohesion in which vocal recognition is useful. On the other hand, in situations where context (e.g. aggression) is of greater importance than caller identity, selection will favour the suppression of individual vocal distinctiveness to reduce signal ambiguity and facilitate a rapid response by receivers (Shapiro, 2010). From this point of view, it makes sense that evolution has favoured individual distinctiveness in a contact and mating call, such as the Pant, providing signalers with benefits, but less so in aggressive calls such as the Grunt or the Hiss. Nevertheless, in agonistic contexts it may be important to estimate the potential outcome of an agonistic interaction by assessing the identity of the opponent, which may account for the individual distinctiveness in Grunt calls. For example, in northern elephant seals (*Mirounga angustirostris*), individuals remember the fighting abilities of potential opponents based on individual acoustic signatures (Casey et al., 2015).

Due to the fact that previous studies have used a wide variety of statistical methods to analyse and compare individual distinctiveness in vocalizations of different mammalian species (Appendix 5-2) and that the published results thus may have been influenced by the methods used, we compared the three most prominent methods used in the literature when analysing our data set to compare the level of individual distinctiveness between different call types: discriminant function analysis (DFA), the potential of identity coding (PIC), and the information criterion (H_s). Comparing the results of the DFA based on subject balanced and unbalanced data sets (Table 5-7), we confirmed that the classification accuracy is influenced by the number of individuals included in the analyses (e.g. Beecher, 1989). However, comparing the balanced and the unbalanced data sets, the kappa tests led to similar values, although they resulted in two different classification levels for Hisses (total data set: slight; balanced data set: fair). The overall PIC and the Hs varied only slightly between the balanced and unbalanced data sets (Table 5-7). The kappa test and the Hs provided a similar interpretation for individual distinctiveness. The Hs were below 1 for Snorts and Hiss in the balanced data set, suggesting that only a low number of individuals can be potentially discriminated (Searby et al., 2004), which is in agreement with the slight to fair agreement found by the kappa test. However, the overall PIC was above 1 suggesting a potential for identity coding. Nevertheless, the three measurements showed a comparable trend in the degree of individuality and the information criterion Hs turned out to be a reliable method when comparing different samples across studies as suggested by Beecher (1989) and Bouchet et al. (2013).

Observations made in this study have been carried out on southern white rhinoceroses in a zoo environment, which cannot completely reflect the natural situation. However, as individual signatures are related to the morphology of the individual, especially of the vocal tract, they should be independent from housing conditions or the social environment. Nevertheless, studies on wild southern white rhinoceroses would be important to clarify the role of vocal identity coding in social interactions under natural conditions. Moreover, studies on additional rhinoceros species are needed to clarify the impact of social system on the degree of individual distinctiveness. To date, comparative data are only available for a single species, the solitarily living black rhinoceros (*Diceros bicornis*). Budde and Klump (2003) showed that begging calls of captive adult black rhinoceroses carry individual signatures. Begging calls are often produced toward keepers (personal observation) but due to our limited knowledge on the vocal repertoire of black rhinoceroses the function in conspecific communication is not yet understood. The begging call of the adult black rhinoceros corresponds to Whines produced by infants and subadults of the white rhinoceros. Further research is necessary to clarify whether the different socio-ecological niches, i.e. solitary, forest-dwelling versus semi-social, savanna-living (for discussion see Linn et al., 2018), may account for these differences in vocalization behaviour.

To sum up, our findings for the southern white rhinoceros suggest that the context of social interactions plays a major role in the evolution of individual distinctiveness in vocalizations. However, due to the fact that Grunts and Hisses are emitted in comparable contexts, namely during aggressive interactions, but differ in their acoustic structure and individual distinctiveness, it has to be assumed that not only the type of social interaction but also vocal production mechanisms influence the degree of individuality in different call types. Further, it is still unclear whether conspecifics use the different call types to discriminate and recognize different individuals. Cinková and Policht (2016) showed that southern white rhinoceroses are able to extract information about the sex and the species of the sender when listening to Pant calls. The present data can be used for further playback experiments, which are necessary to gain a clear understanding of the role of individual signatures in the noisy calls of the southern white rhinoceros and its capacity to discriminate between individuals.

5.5. Appendix



Appendix 5-1. Supplementary Data SD1. Original and filtered sonograms of the three call types Grunt, Hiss, and Snort

Appendix 5-2. Overview of studies that investigated individual distinctiveness among different call types within a species (including information on the acoustic structure of the respective call types, the context in which they are given, and typical distance at which they are exchanged) and results for acoustic variability and individual distinctiveness based on the different hypotheses.

Species	**Call type**	**Context**	**Directionality - context**	**Distance**	**Structure**	**Method**	**Result**	**Hypotheses and predictions**		
Reference								**SF[1]**	**DC[2]**	**AS[3]**
PRIMATES										
Western gorilla (*Gorilla gorilla*) Salmi et al., 2014	Grunts	forage, rest, travel	general	close	noisy	PIC, DFA	equal	NO	NO	NO
	Copulation grunt	sexual interaction	directed	close	noisy					
	Hiss grunt	within group aggression	directed - agonistic	close	noisy					
	Scream	escalated within-group aggression	directed - agonistic	close	mixed					
	Hum	foraging	general	intermediate	tonal					
	Hoot series	Isolation, separation	directed	far	tonal					
Chimpanzee (*Pan troglodytes*) Mitani et al., 1996	Pant hoot	group cohesion	directed - affiliative	far	tonal	CV	Pant hoot > Pant grunt	–	YES	YES
	Pant grunt	greeting	directed - affiliative	close	noisy					
Chacma baboon (*Papio hamadryas ursinus*) Rendall et al., 2009	Contact call	Isolation, separation	directed	far	tonal	CV, DFA	Contact call > Distress scream	YES	–	YES
	Distress scream	aggressive interaction to recruit help	directed - agonistic	??	mixed					

Species Reference	Call type	Context	Directionality - context	Distance	Structure	Method	Result	Hypotheses and predictions		
								SF[1]	DC[2]	AS[3]
Rhesus monkey (*Macaca mulatta*) Rendall et al., 1998	Coo	contact	directed	far	tonal	CV, ANOVA	Coo > Grunts > Scream	YES	YES	PART
	Grunt	affiliative interaction	directed - affiliative	close	noisy					
	Scream	aggressive	directed - agonistic	??	mixed					
De Brazza´s monkey (*Cercopithecus neglectus*) Bouchet et al., 2013	Tek+	alarm	general	??	noisy	H_s	ON > Tek+ > Wrr+	PART	–	YES
	Wrr+	aggression	directed - agonistic	??	noisy					
	ON	contact	directed	??	tonal					
Campbell´s monkey (*Cercopithecus campbelli*) Bouchet et al., 2013; Lemasson & Hausberger, 2011	Repetitive rapid chevron (RRC)	aggressive	directed - agonistic	??	mixed	CV, PIC, H_s	CH > SH > ST > RRA > RRC	YES	–	PART
	Repetitive rapid ascending (RRA)	alarm, disturbance	general	??	mixed					
	Single trill (ST)	contact	directed	??	tonal					
	Long single harmonic (SH)	cohesion	directed - affiliative	??	tonal					
	Long low-pitched single harmonic (CH)	affiliative contexts	directed - affiliative	??	mixed					

Species	Call type	Context	Directionality - context	Distance	Structure	Method	Result	Hypotheses and predictions		
Reference								**SF[1]**	**DC[2]**	**AS[3]**
Red-capped mangabey (*Cercocebus torquatus*) Bouchet et al., 2012, 2013	Whoop-Gobble	loud call	general	far	tonal	PIC, H_s	Ro+(uh) = Un+(uh) > Whoop-Gooble = WaHoo > Ti+(uh) = A+(Uh)	YES	NO	NO
	WaHoo	alarm	general	far	mixed					
	Ti+(uh). A+(uh)	food	general	short	mixed					
	un+(uh)	aggression, Hiss	directed - agonistic	short	mixed					
	Ro+(uh)	contact	directed	short	tonal					
Gray mouse lemur (*Microcebus murinus*) Leliveld et al., 2011	Trill	social cohesion	directed - affiliative	far	tonal	DFA+	Trill = Short whistle > Tsak > Grunt	PART	YES	YES
	Short Whistle	general disturbance	general	far	tonal					
	Tsak	aggression	directed - agonistic	close	tonal					
	Grunt	defensive Hiss against predator	general	close	noisy					
CARNIVORA										
Dingo (*Canis dingo*) Déaux et al., 2016	Howl	low arousal	directed	??	tonal	PIC, DFA	Howl > Bark	–	–	YES
	Bark	high arousal	directed	??	noisy					

Species **Reference**	**Call type**	**Context**	**Directionality - context**	**Distance**	**Structure**	**Method**	**Result**	**Hypotheses and predictions**		
								SF[1]	**DC[2]**	**AS[3]**
Dwarf mongoose (*Helogale parvula*) Rubow et al., 2018	Contact call	intragroup social call	directed - affiliative	close	tonal	PIC, DFA+	Isolation call > Contact > Snake call	YES	PART	–
	Snake call	alarm call	general	intermediate	tonal					
	Isolation call	Isolation, separation	directed	far	tonal					
Domestic dog (*Canis familiaris*) Yin & McCowan, 2004	Disturbance bark	disturbance	general	far	noisy	DFA	Isolation bark = Play bark > Disturbance bark	YES	NO	YES
	Isolation bark	isolation	directed	mixed	tonal					
	Play bark	social interaction	directed - affiliative	close	tonal					
Giant otter (*Pteronura brasiliensis*) Mumm et al., 2014	Contact call	social cohesion	directed - affiliative	far	tonal	DFA+	Contact call > Hum	YES	YES	YES
	Hum	group movements	general	close	noisy					
RODENTIA										
African woodland dormouse (*Graphiurus murinus*) Ancillotto & Russo, 2016	Type a	contact	directed	far	tonal	DFA+	Type a > Type d	YES	YES	–
	Type d	aggression	directed - agonistic	close	tonal					

Species **Reference**	**Call type**	**Context**	**Directionality - context**	**Distance**	**Structure**	**Method**	**Result**	**Hypotheses and predictions**		
								SF[1]	**DC[2]**	**AS[3]**
BATS										
Indian false vampire bat (*Megaderma lyra*) Bastian & Schmidt, 2008	Aggression calls	aggression	directed - agonistic	close	noisy	cluster	Response call > Aggression call	–	–	YES
	Response calls	agonistic context	directed - agonistic	close	tonal					

SF = Social function hypothesis, predicts that calls uttered in directed interaction have a higher level of individual distinctiveness than calls uttered in general contexts and that calls uttered in affiliative social context have a higher level of individual distinctiveness than calls uttered agonistic social context; DC = Distance communication hypothesis, predicts that level of individual distinctiveness is highest in call types uttered in far distance, intermediate in call types uttered in intermediate distances and lowest for call types uttered at low distance; AC = Acoustic structure hypothesis, predicts that the level of individual distinctiveness decreased from tonal to noisy calls with harmonic components (mixed) to noisy call types. PIC = potential for individual identity coding, H_s = information criterion, DFA = discriminant function analysis, + = equal number of individuals, CV = coefficient of variance, cluster = cluster analysis, NO = results do not support the hypothesis, YES = results support the hypothesis, PARTLY = results partly support the hypothesis, - = not testable with the data set, ?? = no information available in the paper.

6. GENERAL DISCUSSION: INFORMATION ENCODED IN RHINOCEROS VOCALIZATIONS CONTRIBUTING TO VOCAL COMPLEXITY

In this thesis, I provided further insights into vocal communication of the Southern white rhinoceros, which is said to be the most gregarious of the five rhinoceros species with the most developed social system (e.g. Hutchins & Kreger, 2006). Animals living in a more complex social environment are presumed to exhibit greater complexity in their communication systems with various attributes that can vary in complexity (e.g. Freeberg et al., 2012; Freeberg & Krams, 2015; Krams et al., 2012; Pika, 2017; Sewall, 2015). Two main attributes of the acoustic communication system of the Southern white rhinoceros were investigated: (1) the infant and juvenile vocal repertoire, (2) information on the identity of the sender encoded in vocalizations.

In the following, I will be referring to the results of the study on the infant and juvenile vocal repertoire presented in Chapter 4 to discuss age-class specific vocal repertoires and the relations, homologies, and differences between the infant, the juvenile, and the adult vocal repertoire, as the plasticity of acoustic communication within species constitutes an important aspect in the context of vocal complexity. Additionally, referring to the results of the study on individual distinctiveness presented in Chapter 5, I will discuss the information content of Southern white rhinoceros vocalizations, especially the encoding of indexical information. I will also briefly address the encoding of contextual information by taking into account the results of Study 1 presented in Chapter 4.

Last but not least, I will review and discuss the results of the presented studies in the light the “social complexity hypothesis for communicative complexity” (e.g. Freeberg et al., 2012; Freeberg & Krams, 2015; Krams et al., 2012; Pika, 2017; Sewall, 2015). The complexity of the acoustic communication system of the Southern white rhinoceros will be discussed and compared with that of other rhinoceros species. Thereby, I will take a closer look at further attributes that contribute to the complexity of the communication system of this species and discuss various possible functional relationships between attributes of social and communicative complexity by summarizing the existing literature on rhinoceros vocal communication and by comparing vocal communication but also the socioecology across the family Rhinocerotidae.

6.1. Age-class specific repertoire, openness and variability of the repertoire

The vocal repertoire of the White rhinoceros consists of ten to eleven different call types and contains versatile social vocalizations to mediate social interactions (see Figure 6-1, Table 6-2; Owen-Smith, 1973; Policht et al., 2008). Infant Southern white rhinoceros were vocally active from birth and produced four acoustically distinct call types in four distinct contexts (see Chapter 4, Study 1; Figure 6-1). The Hiss (in Study 1 and previous publications, the Hiss has been termed Threat, but I aim to be consistent in labelling all call types using onomatopoetic labels) occurred during socio-negative interactions, the Pant during cohesive interactions, the Snort in non-social situations such as locomotion or resting, and the Whine during situations of general discomfort such as hunger or isolation. Thereby, the vocal repertoire of infant Southern white rhinoceros contained not only infant-specific vocalizations, namely the Whine, but also vocalizations that correspond in acoustic structure and context to those of adults, namely the Hiss, the Pant, and the Snort. Moreover, even the hand-reared calf emitted these call types and even in the appropriate behavioural context, indicating a strong innate component to the development of vocal production and vocal usage in White rhinoceros.

Infants of various mammalian species have been found to make characteristic vocalizations when distressed, for example, when hungry, in pain, or in the absence of caregivers (e.g. Lingle et al., 2012; Lingle & Riede, 2014; Newman, 2004, 2007). These vocalizations share not only a common motivational state and contextual similarities, but also a basic acoustic structure, a rich harmonic structure with a simple chevron, flat or descending pattern of frequency modulation (e.g. Lingle et al., 2012; Lingle & Riede, 2014; Newman, 2004, 2007). The Whine of Southern white rhinoceros infants is thus one more in a long list of mammalian distress vocalizations, both with regard to context and acoustic structure, adding support to the hypothesis that distress vocalizations are highly-conserved social vocalizations in mammals.

A diverse set of adult vocalizations have been recorded within this thesis (see Figure 6-1) and seven to eight further adult call types have been described in the literature (see Table 6-2; Owen-Smith, 1973; Policht et al., 2008), which infants do not seem to produce (see Chapter 4, Study 1). Most of these call types, however, are used during aggressive interactions, mating or territorial behaviour, behavioural contexts which are not relevant for infants. These findings support the assumption that mammalian vocal repertoires often have specific vocal signals restricted to certain juvenile periods that disappear at a certain age, whereas other signals are restricted to adulthood and do not appear before infants have reached a particular age (e.g.

Baotic et al., 2013; Barros et al., 2011; Stoeger-Horwath et al., 2007). Further studies on different ontogenetic stages and analyses of longitudinal data will be necessary to determine at which point in time White rhinoceros acquire their full adult vocal repertoire. There are only indications, that in adolescent White rhinoceros large parts of the adult vocal repertoire are already developed (Owen-Smith, 1973).

Compared with other mammalian species, White rhinoceros have a small vocal repertoire that show little acoustic modification during development. However, White rhinoceros seem to have the ability to modify contextual usage of calls and to tune use of calls to variations in the social context, including the relationship between caller and receiver. As is the case with many other mammalian species (e.g. Egnor & Hauser, 2004; Seyfarth & Cheney, 2010), contextual usage of some call types changes or rather expands during development, even if call types seem to be fully formed at birth and appear to undergo relatively little modification with regard to structure. As the social environment changes during development, animals must be able to adjust accordingly.

Changes in contextual usage can, for example, be observed for the Pant call of White rhinoceros. This call primarily functions as a kind of contact call during friendly approaches in both infant and adult White rhinoceros (see Chapter 4, Study 1 and Chapter 5, Study 2; Owen-Smith, 1973; Policht et al., 2008; Table 6-2). However, in male adult White rhinoceros this call also acts as a kind of courtship call (Cinková & Policht, 2014; Owen-Smith, 1973; Policht et al., 2008; Owen-Smith, (1973) previously reported a distinct call type and termed this male courtship call Hic. However, Policht et al. (2008) found no substantial difference between male Hic and the pant vocalisation of females). There is, moreover, some evidence that adult Southern white rhinoceros also emit a short high-pitched whine-like call, the Squeak, when being isolated (see Figure 6-1; personal observations; Policht et al., 2008). In addition, adult White rhinoceros males emit modulated tonal calls, the Shriek and the Squeal, comparable to the infant Whine in dominant, mating, and territory behaviour (see Figure 6-1; personal observations, Owen-Smith, 1973). Given the high degree of similarity, with regard to both structure (see Figure 6-1) and partly function, the question arises whether these calls should be considered as one call type and whether the functional differences, but in particular the structural differences, may arise solely through maturational processes. To clarify this hypothesis, further studies including, for example, larger datasets of Squeaks, Shrieks, and Squeals and thus allowing detailed multi-parametric sound analyses, will be necessary.

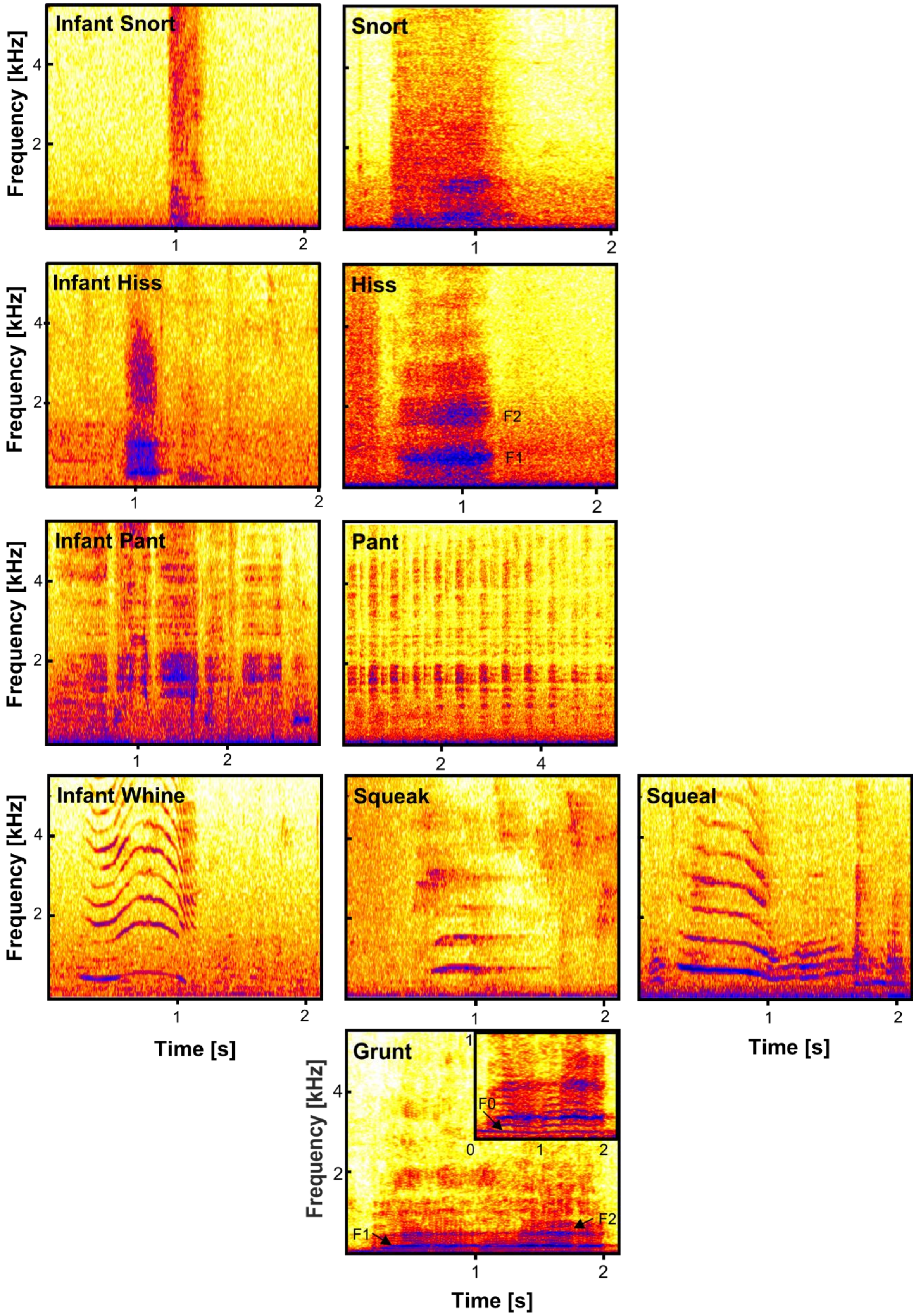


Figure 6-1. Selection of adult and infant call types from the vocal repertoire of the Southern white rhinoceros recorded in different zoos.

In addition to changes in contextual usage, there is considerable flexibility in call usage. Studies of various mammalian species have shown that variation in vocal output depends on a multitude of factors, including the identity of potential listeners and relationship between caller and listeners (e.g. Cheney & Seyfarth, 2018; Elowson & Snowdon, 1994; Snowdon et al., 1997; Seyfarth & Cheney, 2017). For Southern white rhinoceros, differences in call rates for various call types have been observed not only depending on the sex of the caller, but also depending on the sex of potential listeners, the quality of social interactions, and the strength of the social bond between caller and listener (Jenikejew et al., 2020). These differences between constrained call acoustics and more flexible call usage led to the distinction between production learning, which is rare in most mammals, and usage learning, which is common (Janik & Slater, 2000).

6.2. Encoding of indexical and contextual information

Vocalizations which evolve for the purpose of communication are essential for coordinating social interactions. The transmission of the identity to others is important for creating and regulating social relationships that are critical for fitness and survival. The vocal repertoire of the White rhinoceros contains versatile vocalizations to mediate social interactions. Similar to other mammalian species, in the Southern white rhinoceros calls with a strong intragroup social function were characterised by the highest levels of acoustic variability and individual distinctiveness, with the Grunt and the Hiss emitted during agonistic interactions, but in particular calls with high affiliative social values, such as the Pant (see Chapter 5, Study 2; e.g. Ancillotto & Russo, 2016; Bouchet et al., 2013; Lemasson & Hausberger, 2011). These findings support the assumption that the context of social interactions plays a major role in the evolution of individual distinctiveness (e.g. Lemasson & Hausberger, 2011; Snowdon et al., 1997). Selection may have favoured more individually distinct calls in situations in which vocal recognition is useful (e.g. social cohesion). In situations where context is of greater importance (e.g. aggression), selection may have favoured suppression of individual distinctiveness to reduce signal ambiguity (e.g. Ancillotto & Russo, 2016; Bouchet et al., 2013; Lemasson & Hausberger, 2011; Shapiro, 2010). The Pant exhibits not only the highest level of individual distinctiveness, but also provides information about physical characteristics of the caller (e.g. sex, age, subspecies, dominance status; Cinková & Policht, 2014, 2016; Cinková & Shrader, 2020). Pant calls function not only as a contact call during socio-positive interactions, but play also an important role in the mating behaviour of White rhinoceros as males emit this call during mate guarding and mating encounters (Owen-Smith, 1973; Policht et al., 2008). In both contexts it is important to assess the identity of the caller and to gain information about physiological and physical attributes (e.g. dominance rank, fitness, hormonal state) as these information play an important role in mate choice or territorial defence.

Vocalizations have not only the potential to provide information about the caller, but also about the context of the call, including information about the emotional state of the caller and about specific external events or objects. Even if it cannot be excluded that vocalizations of the Southern white rhinoceros have referential quality and transmit specific information to conspecifics, it seems to be more likely that these vocalizations rather reflect the affective or emotional state of the caller. Vocalizations of adult and infant Southern white rhinoceros calls (see Chapter 4, Study 1 and Chapter 5, Study 2) can be predicted in part by the motivation-structural rules of Morton (1977). Hisses, Grunts, and Whines coincided with the predictions. Low frequency, harsh Hisses and Grunts would be assigned to the category aggression. High frequency Whines with a tonal structure would be assigned to the category fearful. However, Pants, for example, contradicted the prediction. Whereas friendly vocalizations should be tonal high frequency calls, Pants of infant and adult Southern white rhinoceros given during cohesive interactions are noisy broad band calls. Discrepancy for friendly vocalizations have also been shown for other mammalian species (e.g. August & Anderson, 1987; Compton et al., 2001; Peters, 2002; Robbins & McCreery, 2003). The extension of the model by Ehret (2006) proposing that aversion should be associated with vocalizations covering a broad frequency range of varying frequency spectrum with noisy component, attraction should be associated with high frequency tonal sounds, whereas cohesion should be associated with low frequency rhythmic vocalizations thus better reflects the relationship between call structure and contextual information in Southern white rhinoceros.

6.3. Vocal complexity in White rhinoceros and other rhinoceros species

The Rhinocerotidae family is an interesting mammalian group in that species exhibit a high diversity not only of ecological adaptations, but also of social systems (see Table 6-1). Thereby, rhinoceros provide a perfect opportunity to consider the relationship between the social and communicative complexity within phylogenetic closely related species.

The White rhinoceros is said to be the most gregarious of the five rhinoceros species with the most developed social system (e.g. Hutchins & Kreger, 2006). The “social complexity hypothesis for communicative complexity” postulates that animals living in a more complex social environment will exhibit greater complexity in their communication systems (e.g. Freeberg et al., 2012; Freeberg & Krams, 2015; Krams et al., 2012; Pika, 2017; Sewall, 2015).

Social complexity can be defined on the basis of various social attributes that can vary in complexity, for example the number of interacting individuals (e.g. group size), the diversity of social roles and relations in social networks, the stability and persistence of relationships, the frequency of interactions among individuals, or the mating and grouping system (see Figure 6-2; e.g. Blumstein & Armitage, 1997b; Bouchet et al., 2013; Freeberg et al., 2012; Freeberg & Krams, 2015; Kappeler, 2019; Krams et al., 2012; Peckre et al., 2019; Pika, 2017; Pollard & Blumstein, 2012). With regard to communicative complexity, various attributes contribute to the complexity of a communication system, such as variation between signal types (e.g. repertoire size, not only in terms of the entire repertoire but also in terms of the repertoire within age classes), but also variation within signal types in terms of the information included in signals (e.g. contextual and indexical information; Figure 6-2; e.g. Blumstein & Armitage, 1997b; Freeberg et al., 2012; Freeberg & Krams, 2015; Pika, 2017; Pollard & Blumstein, 2012).

Table 6-1. Comparison of ecological, social, and communicative attributes of the five rhinoceros species.

		White rhincoeros[1] (*Ceratotherium simum*)	**Black rhinoceros**[2] (*Diceros bicornis*)	**Greater one-horned rhinoceros**[3] (*Rhinoceros unicornis*)	**Javan rhinoceros**[4] (*Rhinoceros sondaicus*)	**Sumatran rhinoceros**[5] (*Dicerorhinus sumatrensis*)
Habitat		Savanna, shrubland, grassland	Wide variety of habitats from desert areas to shrubland and savannas	Forest, grassland, wetlands	Lowland tropical rainforest	Tropical rainforest and montane moss forest
Social attributes	**Social system**	Semi-social	Predominately solitary	Predominately solitary	Solitary	Solitary
	Group size	up to 17 individuals	up to 13 individuals	up to 5 individuals	Very rare	Very rare
	Group structure	Stable bond between mother and calf; females and subadults form long-lasting and temporarily associations; adult bulls live solitarily	Stable bond between mother and calf; temporary and semi-stable associations of females and subadults with partially strong social bonds; adult bulls live solitarily	Stable bond between mother and calf; temporary and semi-stable associations of females and subadults; adult bulls live solitarily	Stable bond between mother and calf; form rarely groups	Stable bond between mother and calf; form rarely groups
	Territorial behaviour	Territoriality; dominant males hold territories with exclusive mating rights, overlap with those of several females; subordinate males tolerated within territories; female territories overlap extensively, no territorial defense	Varies according to habitat type and availability of resources; dominant males hold territories with exclusive mating rights, overlap with those of several females; home ranges of males can overlap; subordinate males tolerated within territories	Some range exclusivity but no true territoriality; breeding males generally territorial, but rely heavily on adopting larger home ranges (seasonal/ habitat changes, home ranges of males can overlap); subordinate males tolerated within territories	n/a	Mating territories not expected

		White rhincoeros[1] (*Ceratotherium simum*)	**Black rhinoceros**[2] (*Diceros bicornis*)	**Greater one-horned rhinoceros**[3] (*Rhinoceros unicornis*)	**Javan rhinoceros**[4] (*Rhinoceros sondaicus*)	**Sumatran rhinoceros**[5] (*Dicerorhinus sumatrensis*)
	Mating system	Polygamous and polyandrous; "Consortship" behaviour; strong male-male competition and female mate choice	Polygamous and polyandrous; "Consortship" behaviour, courtship fights (less violent); male-male competition and female mate choice	Polygamous and polyandrous; "Consortship" behaviour, courtship fights and chases; male-male competition and female mate choice	Polygamous and polyandrous; Courtship fights (less violent)	Polygamous and polyandrous; Courtship fights (less violent)
Communicative attributes	**Acoustic communication**	At least 10-11 different call types used in various non-social and social context have been described (including mating behaviour, mother-offspring interactions, agonistic and affiliative interactions)	At least 6-7 different call types used in various non-social and social context have been described (including mother-offspring interactions, agonistic interactions)	At least 10 different call types used in various non-social and social context have been described (including mating behaviour, mother-offspring interactions, agonistic and affiliative interactions)	n/a	At least 3 different call types have been described (no context information)
		The Pant call contains information on the identity of the sender (individuality, subspecies, age class, sex, dominance status) and on the motivation of the sender	The Begging call contains information on the individual identity of the sender			
		The Snort, the Hiss, and the Grunt have the ability to contain information about the individual identity of the sender				

		White rhincoeros[1] (*Ceratotherium simum*)	**Black rhinoceros**[2] (*Diceros bicornis*)	**Greater one-horned rhinoceros**[3] (*Rhinoceros unicornis*)	**Javan rhinoceros**[4] (*Rhinoceros sondaicus*)	**Sumatran rhinoceros**[5] (*Dicerorhinus sumatrensis*)
		Several call types are already present at birth based on innate mechanisms of vocal production and usage; some call types seem to be restricted to certain juvenile periods or adulthood				

[1] Study 1 of this thesis; Study 2 of this thesis; Cinková & Policht, 2014, 2016; Cinková & Shrader, 2020; Estes, 1991; Kretzschmar et al., 2020; Owen-Smith, 1973, 1975; Pienaar, 1994; Policht et al., 2008; Shrader & Owen-Smith, 2002

[2] Adcock, 1994; Anderson, 2013; Berger & Cunningham, 1998; Budde & Klump, 2003; Cain et al., 2013; Garnier et al., 2001; Goddard, 1966; Guggisberg, 1966; Owen-Smith, 1988; Ritchie, 1963; Schenkel & Schenkel-Hulliger, 1969; personal observations

[3] Hazarika & Saikia, 2010; Laurie, 1978a, b, c, 1982, 1984; Laurie et al., 1983; Tripathi, 2013

[4] Ammann, 1986; Hoogerwerf, 1970

[5] Borner, 1979; Muggenthaler et al., 2003; Muggenthaler & Reinhart, 2003

n/a: no detailed information available

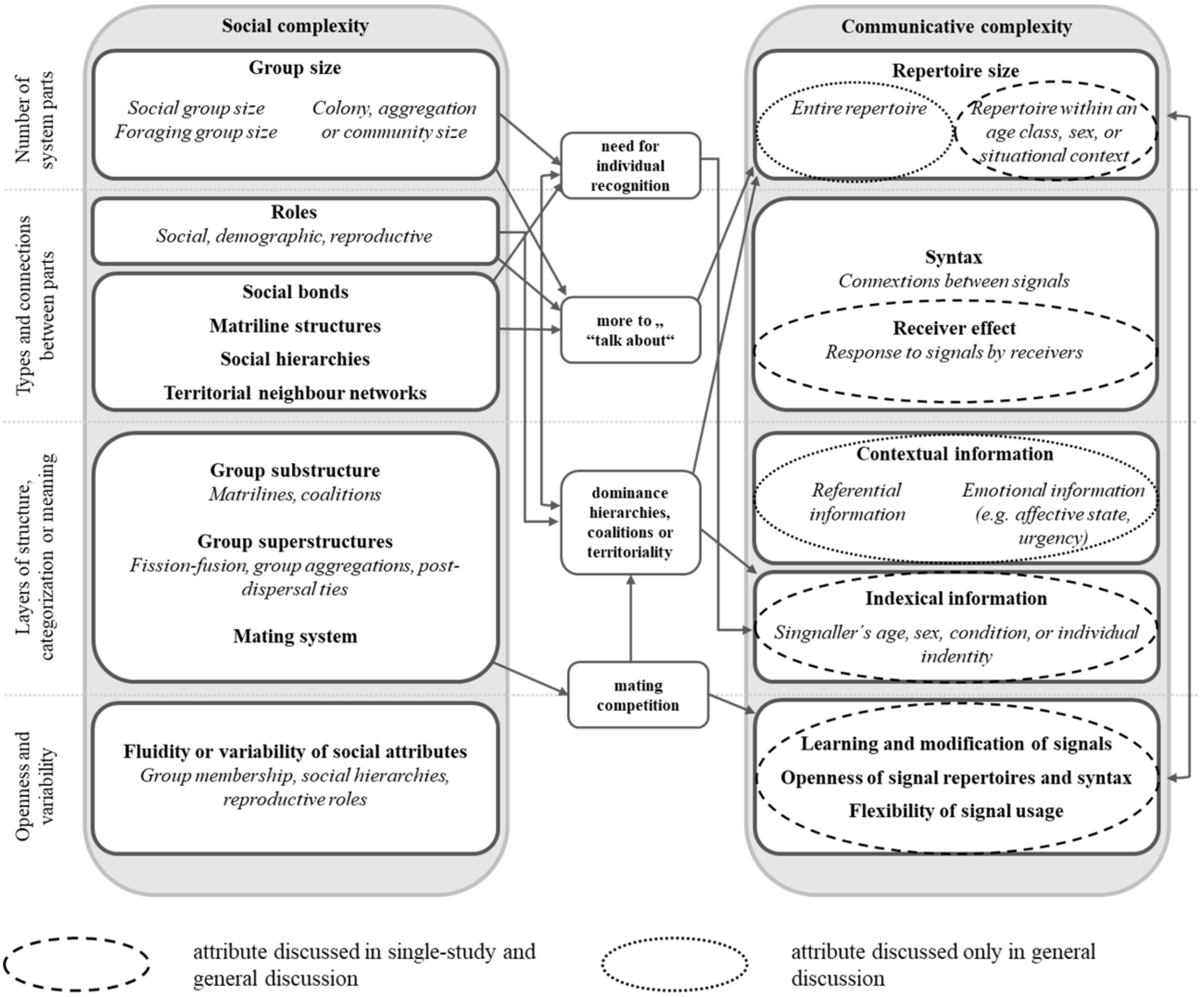


Figure 6-2. A selection of attributes of social and communication systems that can vary in complexity and possible functional relationships. The categories are neither mutually exclusive nor exhaustive. (modified from Pika, 2017; Pollard & Blumstein, 2012)

6.3.1. The vocal repertoire size across rhinoceros species

Even if there are various attributes that contribute to the complexity of a communication system, the vocal repertoire size, defined as the number of call types produced by a species, has been mainly used for assessing vocal complexity within and across species (e.g. Blumstein & Armitage, 1997b; Gustison et al., 2012; McComb & Semple, 2005; Stirling & Thomas, 2003). Evidence is found in various mammalian species that the vocal repertoire size correlates, for example, with the group size of a species (e.g. Bouchet et al., 2013; May-Collado et al., 2007; McComb & Semple, 2005; Pollard & Blumstein, 2011). Comparing the different vocal repertoires across the five rhinoceros species (see Table 6-2) shows an increasing trend in the number of discrete call types from the rather solitary living species to the more gregarious White rhinoceros, but not a linear increase with group size (see Table 6-1). The vocal repertoire of the White rhinoceros, despite being semi-social and living in groups with the largest number of individuals, shows a comparable number of discrete call types as the Greater one-horned rhinoceros, for which much smaller groups have been observed (see Table 6-1). In contrast, for the Black rhinoceros, which seems to form medium-sized associations, less discrete call types have been described. However, it must be acknowledged that for some rhinoceros species only very limited and insufficient data on the vocal repertoire is available or no data at all. Moreover, even though Greater one-horned rhinoceros and Black rhinoceros are generally thought to be predominantly solitary, both species seem also to congregate in either temporary or semi-stable groups, especially of subadults (see Table 6-1; Garnier et al., 2001; Goddard, 1966; Laurie, 1978b; Owen-Smith, 1988; Schenkel & Schenkel-Hulliger, 1969).

Besides group size, other attributes, such as social structure, the number of unique social roles, social bond strength, or the mating system, contribute to the social complexity of a species and correlate with the vocal repertoire size (e.g. Blumstein & Armitage, 1997b; Bouchet et al., 2013; Gustison et al., 2012; McComb & Semple, 2005; Pollard & Blumstein, 2012; Stirling & Thomas, 2003). Variations in these social attributes affect the need for coordination of social activities. As adult males regardless of the species generally tend to be solitary, the localisation of a high-quality mating partners at the right time, for example, should be important for all of the rhinoceros species, whereas for the White rhinoceros coordination of group activities would be another important factor driving vocal complexity. Therefore, it may be more informative to assess the vocal repertoire within a situational context and to consider social attributes such as group structure, social bond strength, and mating system and not just group size.

Even though territorial and mating behaviour are similar across species, there are interspecific differences (see Table 6-1) which might affect the need for communication in this context. Vocalizations are an integral part of the courtship and mating behaviour of all rhinoceros species. However, there are substantial differences between the rhinoceros species especially with regard to the function of vocalizations in mating behaviour. A common behaviour across rhinoceros species is that females emit agonistic vocalizations in response to an approaching male when they are not ready to mate (see Table 6-2; White rhinoceros: Snort, Snarl; Owen-Smith, 1973; Greater one-horned rhinoceros: Snort; Laurie, 1978b; Black rhinoceros: Snort; Schenkel & Schenkel-Hulliger, 1969). Greater one-horned and Sumatran rhinoceros females may announce reproductive condition and location by vocalizations several hours prior to courtship or breeding activity (Laurie, 1978b, 1982a; Zahari et al., 2005). Anecdotal evidence indicates that Sumatran rhinoceros use vocalizations to coordinate courtship and mating behaviour and that females increase vocalization rate (Squeal, Blow) shortly before oestrus (Zahari et al., 2005). In Greater one-horned rhinoceros, the whistling of females attracts bulls that respond with pre-copulatory behaviour, such as prolonged chases (Laurie, 1978b, 1982). Moreover, courtship fights and chases of Greater one-horned rhinoceros are also accompanied by loud vocalizations of the female that often attract further males (Laurie, 1978b, 1982). The male generally squeak-panted during such chases while the female honked or bleated very loudly (Laurie, 1978b, 1982; Tripathi, 2013). It is assumed that such behaviour ensures that the female ultimately mates with the strongest male in the vicinity (Laurie, 1978b, 1982). In contrast, White and Black rhinoceros females do not seem to announce reproductive condition by vocalizations. Vocalizations emitted by the male, however, may play an important role in the coordination of mating behaviour in these species (Owen-Smith, 1973; Policht et al., 2008; personal observations). White rhinoceros males encountering females emit Hic- and/or Pant-calls and even the mating behaviour itself is accompanied by hiccing/panting (Cinková & Shrader, 2020; Owen-Smith, 1973; Policht et al., 2008). These calls contain information about the male´s dominance status and might act as an honest signal for females (Cinková & Shrader, 2020). Moreover, if a female moves towards a boundary region of a male territory, the male blocks the female by moving ahead and emitting Squeals (Owen-Smith, 1973). For the Black rhinoceros there are at least indications that adult males emit Pant/Hic-like calls similar to that of White rhinoceros during mating encounters (personal observations; Figure 6-4).

Differences in the territorial behaviour may also affect call usage and function. In contrast to the Greater one-horned rhinoceros, in which both females and males perform agonistic threat displays including vocalizations (Snorts) to protect their own territory (Hazarika & Saikia, 2010), White rhinoceros vocalizations during agonistic encounters are primarily emitted by the inferior (in terms of physical strength) opponent and should thus rather been interpreted as defensive behaviour. Subordinate males and dominant males while off their own territory, for example when looking for water, show threat displays and vocalize (Snort, Grunt, Roar, Snarl) in response to the presence of dominant resident males and to their approach, whereas the dominant resident male usually just approach to stare silently horn to horn (Owen-Smith, 1973, 1975). However, it has been found, in playback experiments, that territorial White rhinoceros males assess the motivation and dominance status of intruding males by eavesdropping their contact and courtship calls (Cinková & Shrader, 2020). These findings led to the assumption that territorial males are able to determine whether an intruding male just wants to settle into the territory as a subordinate or is looking to challenge the territory holder for ownership of the territory (Cinková & Shrader, 2020).

The different use of vocalizations in mating and territorial behaviour may be related to the differences in habitat and related differences in territorial behaviour and mating behaviour. Greater one-horned rhinoceros rely heavily on adopting larger home ranges that can largely overlap due to rapidly changing habitats and seasonal changes in resource distribution (Laurie, 1978b, 1982). Thus, encounters of territorial males and conflicts on females in oestrus may occur regularly. In contrast, in White rhinoceros dominant males hold territories with exclusive mating rights (Owen-Smith, 1973). Subordinate or territorial males of neighbouring territories may intrude. However, as the intention is only in some cases to challenge the territory holder for ownership of the territory, the assessment of the motivation of the intruder is important to avoid costly fights. Females, on the other hand, living in habitats with low visibility in which males do not hold territories, such as the Greater one-horned rhinoceros, may increase their chances of being mated by advertising readiness for mating with loud vocalizations. Males may increase mating success by following these vocalizations.

As White rhinoceros form not only temporary, but also long-lasting associations, social bond strength is said to be most pronounced in this species. This may influence the proportion of cohesive vocalizations in the vocal repertoire. Call types coordinating cohesive interactions are generally predominantly emitted by females, subadults, and infants (see Table 6-2). Subadults of White rhinoceros may thus coordinate their movements and activities not only by occasional body contact, but also by vocalizations. In this context, vocalizations (Hoarse, Pant) seem to have a proximity-maintaining function (Owen-Smith, 1973, 1975). Moreover, White rhinoceros emit contact calls (Pant) during friendly approaches (Owen-Smith, 1973; Policht et al., 2008). Apart from the White rhinoceros, contact calls have only been described for Greater one-horned rhinoceros and here, in particular, between mother and calves (Moo-Grunt, Table 6-2; Laurie, 1978b).

These findings support the idea that not group size itself but other social attributes are key predictors of how diverse a vocal repertoire is. Pollard and Blumstein (2012) thus suggest that to understand the relationship between these attributes and the vocal repertoire size it is important to ask “what a species has to talk about”. Hence, species with, for example, differentiated relationships, dominance hierarchies, or mating competition should have a more diverse call repertoire.

6.3.2. Age-class specific repertoire, openness and variability of the repertoire across rhinoceros species

When looking at vocal repertoires and the vocal repertoire size, it is important to consider not only the entire repertoire itself, but also the repertoire within specific age classes (see Figure 6-2; e.g. Blumstein & Armitage, 1997b; Freeberg et al., 2012; Freeberg & Krams, 2015; Pika, 2017; Pollard & Blumstein, 2012). Investigating age-class specific vocal repertoires and thereby the openness and variability of a vocal repertoire (e.g. the ability to learn and modify signals, innate mechanism, flexibility in signal usage) provides information on the plasticity of acoustic communication within species which constitutes an important aspect in the context of vocal complexity.

So far there has been little comparative data on the ontogeny and development of acoustic communication in other rhinoceros species (see Table 6-2). For Black rhinoceros infants, one harmonic call type has been described emitted mainly before nursing, comparable in structure and usage with the Whine of White rhinoceros infants (Budde & Klump, 2003). With regard to the Greater one-horned rhinoceros, one predominantly infant-specific call type (Moo-Grunt) has been described emitted by infants towards their mothers, for example, when separated or before suckling (see Figure 6-3; Laurie, 1978b). Even if the context of this infant-specific call is comparable to that of infant-specific calls in White and Black rhinoceros, there are differences with regard to their structure. In contrast to the Black and White rhinoceros infant call, the Moo-Grunt of Greater one-horned rhinoceros infant does not share the characteristic structure of infant distress vocalizations as described for infants of various mammalian species (e.g. Lingle et al., 2012; Lingle & Riede, 2014; Newman, 2004, 2007). It remains unclear why in Greater one-horned rhinoceros different structural infant vocalizations have evolved and which factors have driven this evolution. Environmental conditions might have influenced structural different infant vocalizations. Based on the ‘‘acoustic adaptation hypothesis’’ (Morton, 1975), the general structure of animal vocalizations differs depending on characteristics of the habitat. In general, low frequency vocalizations propagate best in any environment. However, especially in acoustically cluttered environments, such as forests, lower frequencies should be particularly favoured by selection as higher frequencies are more scattered and absorbed by stratified media (e.g. Ey & Fischer, 2009; Nemeth et al., 2001). This might be especially important when considering that Greater one-horned rhinoceros females occasionally leave their calf unattended for short periods while feeding (Bartlett, 1873; Joubert & Eloff, 1971; Laurie, 1978b). Moo-grunt vocalizations might permit localisation and reaggregation of mother and calf especially in dense vegetation.

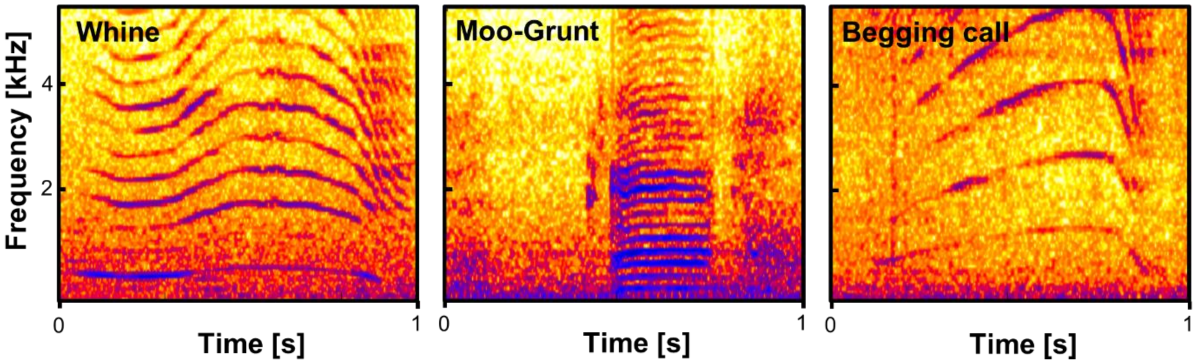


Figure 6-3. Sonograms of Southern white rhinoceros infant Whines (recorded within Study 1), Black rhinoceros infant begging call (© Tembrock, 2008), and Greater one-horned rhinoceros infant Moo-Grunt (© Altmann, n.d.).

With regard to vocal ontogeny, for both the Black and the Greater one-horned rhinoceros no information is available at which time juveniles acquire their full adult vocal repertoire and about the mechanism behind. There are only some indications for the Greater one-horned rhinoceros that infants already produce adult-like vocalizations in comparable contexts (see Table 6-2; Laurie, 1978b). Five of the ten call types have not only been described for adult Greater one-horned rhinoceros, but also for infants (Laurie, 1978b).

Even if infants, at least in White and Greater one-horned rhinoceros, may be able to produce not only infant-specific vocalizations, but also vocalizations that correspond in acoustic structure and context to those of adults, there is some evidence for a certain degree of flexibility and modification regarding call usage, not only in the White rhinoceros, but also in other rhinoceros species. Adult Black rhinoceros emit a harmonic call ("begging call") that corresponds in acoustic structure and context to the distress call of infants (see Table 6-2; Budde & Klump, 2003). There is, however, some evidence that adult Black rhinoceros males may emit these harmonic calls also in the mating context (personal observations, Figure 6-4). Moreover, current observations on Black rhinoceros, show that this rhinoceros species is at least able to learn the relation between a specific acoustic signal and an external event and to react in the appropriate way (Plotz & Linklater, 2020). Black rhinoceros respond to the alarm calls of oxpeckers (*Buphagus erythrorhynchus*) immediately by becoming vigilant and by directing their vigilance downwind and not at the approaching threat (in this case human approach). Similar phenomena of eavesdropping on other species' alarm calls have been described for various mammalian species (e.g. Magrath et al., 2015). It has been assumed, that learning may be essential for recognizing heterospecific alarm calls that varied widely in the acoustic structure from that of conspecifics (e.g. Hauser, 1988; Magrath et al., 2015; Wheeler et al., 2019). This strongly suggests that learning plays an important role in recognizing and responding to heterospecific eavesdropping on alarm calls of oxpeckers by black rhinoceros and that this species is at least able of vocal comprehension learning.

6.3.3. Encoding of indexical information across rhinoceros species

Apart from variation between signal types, i.e. the vocal repertoire size, the complexity of a vocal system may also be associated with variation within signal types in terms of the information included in signals, both contextual (e.g. referential, urgency, affective state) and indexical information (e.g. age, sex, reproductive state, identity; Blumstein & Armitage, 1997b; Freeberg et al., 2012; Freeberg & Krams, 2015; Pika, 2017; Pollard & Blumstein, 2012).

The presence of inter-individual variation in call structure, including information on the identity of the caller, also adds complexity to communicative signals. With increasing group size and more interacting groups members, individuals may benefit from accurately recognizing the sender of a call. Thereby, individual recognition might be especially important in social interactions (e.g. Bouchet et al., 2013). Even if the White rhinoceros seems to be the most gregarious rhinoceros species with the strongest social bonds and largest groupings, one can imagine that for the other rhinoceros species there are also various situations in which it may be essential to assess the identity and quality of the caller based on information about physiological and morphological attributes such as, for example, the body size, the dominance rank, or the hormonal state. Individual discrimination and the assessment of conspecifics might be important for regulating social relationships, for example, to govern cohesion in subadult aggregations of Black and Greater one-horned rhinoceros, even if a socio-positive contact call has only been described for the White rhinoceros so far (see Table 6-2). Physical attributes such as the sex, the body size, or the age of an individual are key determinants of resource holding potential, mate quality, and fighting ability, as these factors can determine the potential outcome of agonistic contests and are positively correlated with reproductive success (Hollister-Smith et al., 2007). It was already shown in recent studies that at least White rhinoceros males use acoustic cues to gather information about rivals (Cinková & Shrader, 2020). However, the use of acoustic cues to obtain information about rivals or potential mates is probably not only important for the White rhinoceros. Evidence suggests that there is a strong male-male competition and female mate choice not only in the White rhinoceros, but also in the Black and the Greater one-horned rhinoceros (Cain et al., 2013; Kretzschmar et al., 2020; Laurie, 1978b). Moreover, there seems to be a positive correlation between male reproductive success and the testosterone level in the Black rhinoceros (Edwards et al., 2015). It is already known that vocalizations also play an important role in the mating behaviour of the other rhinoceros species. Especially in the Greater one-horned rhinoceros, vocalizations are an integral part of the courtship behaviour and are presumed to mediate mate attraction and to ensure that females ultimately mate with the strongest male (see Table 6-2; Laurie, 1982a).

To date, comparative data on individual distinctiveness of vocalizations are unfortunately only available for the Black rhinoceros in which the begging call of captive adult individuals carries individual signatures (see Table 6-2; Budde & Klump, 2003). However, due to our limited knowledge on the vocal repertoire of black rhinoceros the function of this call type in conspecific communication is not yet understood. Captive adult black rhinoceros emit these begging calls, for example, when begging for food (see Table 6-2; Budde & Klump, 2003) and there is some evidence that adult males may emit these harmonic calls also in the mating context (personal observations, Figure 6-4). There are, moreover, indications that adult Black rhinoceros males emit calls structurally similar to that of White rhinoceros Pants in comparable contexts, namely during mate guarding and mating encounters (personal observations; Figure 6-4). This call type is known to be suitable for encoding information about the sender, such as individuality, subspecies, age class, sex, and dominance status, but also about the motivation of the sender in the White rhinoceros (Cinková & Policht, 2014b, 2016; Cinková & Shrader, 2020). It would therefore be not surprising that Black and the Greater one-horned rhinoceros also use acoustic cues to assess the identity of the caller and to obtain information about physiological and morphological attributes such as, for example, the body size, the dominance rank, or the hormonal state. Studies on further call types and further rhinoceros species are needed to clarify the impact of social system on the degree of individual distinctiveness. One should assume that decoding social vocalizations to gather information about conspecifics is highly advantageous for rhinoceros in a diverse set of behavioural contexts, and it is conceivable that more information should be incorporated the higher the uncertainty in their social environment is.

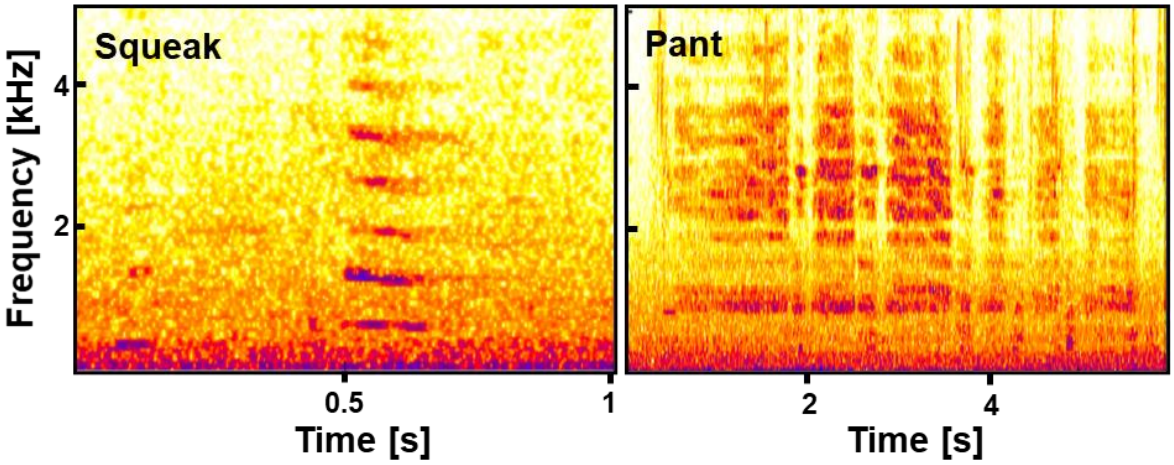


Figure 6-4. Sonograms of Black rhinoceros calls recorded from an adult male in mating context at Hannover Zoo (personal observations; call names have been adopted from the White rhinoceros based on similarities in acoustic structure).

Table 6-2. Comparison of rhinoceros vocal repertoires (no study on the vocal repertoire of the Javan rhinoceros exists).

White rhinoceros				**Black rhinoceros[3]**		**Greater one-horned rhinoceros[4]**		**Sumatran rhinoceros[5]**		**Javan rhinoceros**
Southern white rhinoceros[1]		**Northern white rhinoceros[2]**								
Call type	**Context (sender)**	**Call type**	**Context (sender)**	**Call type**	**Context (sender)**	**Call type**	**Context (sender)**	**Call type**	**Context (sender)**	**Call type/ Context**
Whine	Begging for feeding/ suckling, separation, distress (S, I)	Whine	Foraging (begging for feeding), cohesive interactions (F, S)	Begging call/ Squeak+	Begging for food, distress (A), courtship behaviour (M)	Shriek	Intense agonistic interactions (incl. courtship chases) (M, F)	Eep	(A, I)	n/a
Squeak	Separation, distress (M, S, I)	Squeak	Separation (S)	Juvenile call	Before nursing, distress (I)	Squeak-Pant	Agonistic interactions, warning signal (M, F, S)	Whale	(A, I)	
Squeal	Territorial behaviour, boundary blocking (M)	-	-	Snort	Not obvious (feeding, walking, standing still)	Snort	Diverse contexts, but mainly on the approach of another rhino (M, F, S, I)	Whistle-blow	(A)	
Shriek	Elicited by fear, attack inhibition (M, F, S)	-	-	Hollow snort	Standing still	Honk	Not obvious, but mainly during agonistic interactions (incl. courtship fights) (M, F, S, I)	Blow	Mating behaviour (F)	

White rhinoceros				**Black rhinoceros**[3]		**Greater one-horned rhinoceros**[4]		**Sumatran rhinoceros**[5]		**Javan rhinoceros**
Southern white rhinoceros[1]		**Northern white rhinoceros**[2]								
Call type	**Context (sender)**	**Call type**	**Context (sender)**	**Call type**	**Context (sender)**	**Call type**	**Context (sender)**	**Call type**	**Context (sender)**	**Call type/ Context**
Pant	Contact call, friendly approach (M, F, S, I)	Pant*	Contact call, cohesive interactions, greeting, male courtship call (M, F, S)	Aggressive snort	Before attacking (head held down)	Humph	Fleeing, after brief encounters with other rhinos	Squeal	Mating behaviour (F)	
Hic	Male courtship call (M, S)			Growl	Head held down, no attack followed	Bleat	Agonistic interactions (incl. courtship fights), chasing (M, F, S, I)			
Snort*	Not obvious, but mainly during general activities (M, F, S, I)	Snort	Not obvious, but mainly during foraging (M, F, S)	Pant+	Male courtship call	Roar	Agonistic interactions (incl. courtship fights), chasing (M, F, S, I)			
		Puff	Not obvious, but mainly during foraging (M, F, S)			Moo-Grunt	Activities in proximity of other rhinoceros, contact call between mother and calf (F, S, I)			
Hiss ** (Snort)	Aggressive interactions, first warning (M, F, S, I)	Threat	Aggressive interactions, first warning (M, F, S)			Groan	Agonistic interactions (incl. courtship fights), chasing			

White rhinoceros				**Black rhinoceros**[3]		**Greater one-horned rhinoceros**[4]		**Sumatran rhinoceros**[5]		**Javan rhinoceros**
Southern white rhinoceros[1]		**Northern white rhinoceros**[2]								
Call type	**Context (sender)**	**Call type**	**Context (sender)**	**Call type**	**Context (sender)**	**Call type**	**Context (sender)**	**Call type**	**Context (sender)**	**Call type/ Context**
Snarl*	Aggressive interactions, powerful warning (M, F, S, I)	Grunt	Aggressive interactions, powerful warning (F, S)			Rumble	Diverse contexts, but mainly during non-social activities (M, F, S)			
		Snarl	Aggressive interaction, passive approach, first warning (F)							
Gruff-squeal	Territorial behaviour, chasing (M)	-	-							
Gasp-puff	Response to a sudden fright	-	-							
-	-	Groan	Moan, strenuous exertion							
-	-	Grouch	Foraging and other activities in proximity of other members of the herd (F, S)							

White rhinoceros				**Black rhinoceros**[3]		**Greater one-horned rhinoceros**[4]		**Sumatran rhinoceros**[5]		**Javan rhinoceros**
Southern white rhinoceros[1]		**Northern white rhinoceros**[2]								
Call type	**Context (sender)**	**Call type**	**Context (sender)**	**Call type**	**Context (sender)**	**Call type**	**Context (sender)**	**Call type**	**Context (sender)**	**Call type/ Context**
-	-	Hoarse	Feeding, approach to female (M)							

[1] Owen-Smith, 1973; Study 1 of this thesis; Study 2 of this thesis; personal observations

[2] Policht et al., 2008

[3] Budde & Klump, 2003; personal observations

[4] Laurie, 1978b

[5] Muggenthaler et al., 2003; Muggenthaler & Reinhart, 2003; Zahari et al., 2005

Sender: A, adult; M, adult male; F, adult female; S, subadult; I, infant

* call descriptions for the Southern subspecies (Owen-Smith, 1973; Study 1 of this thesis; Study 2 of this thesis) correspond to different call types for the Northern subspecies (Policht et al., 2008) or vice versa

** in Study 1 of this thesis and previous publications the Hiss has been termed Threat (Policht et al., 2008), but I aim to be consistent in labelling all call types using onomatopoeic labels (probably coincides with the Snort described by Owen-Smith (1973))

\+ call names adopted from the White rhinoceros based on similarities in acoustic structure

n/a: no detailed information available

6.4. Concluding remarks

In this thesis I have presented further piece of the puzzle on vocal communication of the Southern white rhinoceros by focussing on two aspects potentially contributing to the communicative complexity of this species: (1) the vocal repertoire of infants and juveniles and (2) information on the identity of the sender encoded in vocalizations.

Thereby, I found that several call types were already present in new born White rhinoceros, suggesting innate mechanisms of vocal production and usage, but that other call types were restricted to certain juvenile periods or adulthood. With regard to tonal calls, there is a high degree of similarity, in terms of both structure and partly function, when comparing adult and infant calls. Clarification is needed whether the apparent differences may arise through maturational processes. Moreover, there is a certain degree of flexibility during development with regard to call usage and contextual usage. In addition, various call types of the Southern white rhinoceros exhibited an acoustic structure capable of encoding individual identity, but differed in their level of individual distinctiveness. As has already been demonstrated for other species, the context of social interactions, especially affiliative social interactions, may have favoured more individually distinct calls.

It can thus be concluded that, the restricted plasticity and ability to learn and modify vocalizations and the limited openness of the vocal repertoire play only a tangential role in the context of communicative complexity, whereas the potential of encoding information on the sender identity contributes to the complexity of the communication system of the Southern white rhinoceros.

Even if extensive data in the different rhinoceros species is still lacking, variability in vocal communication across these species is evident. Differences in vocal repertoires, including the number of discrete call types, the contextual usage and function, or individual attributes of calls, emphasise that we need to know an animal species, its social organization but also its ecological environment very well to understand what variation in vocalizations means and what factors have favoured this variation. For the different rhinoceros species, social environment and ecological factors may have shaped acoustic communication, in terms of both when to call and how signals look like. However, which specific attributes of social and environmental complexity relate to which attributes of vocal complexity is not easy to determine. Unfortunately, our knowledge about both rhinoceros acoustic communication and socio-ecological behaviour is very limited. It would, therefore, be important to identify attributes of social and ecological environment and how these relate to specific communication attributes, to understand variation in communicative complexity in a given species and this taxonomic group. With regard to acoustic communication this includes identifying specific call types and specific acoustic parameters varying with social and ecological attributes, but also with individual traits, physiological, and phenotypical aspects.

Finally, I should like to say that rhinoceros vocal communication is a highly interesting area of research, not only due to the fact that rhinoceros are one of the largest terrestrial mammals, highly threatened, and fascinating animals, but also in terms of the different socio-ecological niches they inhabit. Rhinoceroses would thus be a promising group to better understand how different socio-ecological adaptations might have effect vocal communication in mammals.

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EDUCATION

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HIGHER EDUCATION

10/2008 - 06/2011	Bachelor of Science Biology at the Ruprecht-Karls-University Heidelberg
06/2011	Graduation Bachelor of Science Title of thesis: Verhalten Asiatischer Elefanten (*Elephas maximus*) in einer Jungbullenherde im Zoo Heidelberg” (Final grade 1.7)
10/2011 - 11/2013	Master of Science Animal Biology and Biomedical Science at the University of Veterinary Medicine Hannover
11/2013	Graduation Master of Science Title of thesis: Mother-offspring communication in grey mouse lemurs (*Microcebus murinus*) during reunions (Final grade 1.2)

11/2013	Beginning of Ph.D. Studies (Dr.rer.nat) at the Institute of Zoology, University of Veterinary Medicine Hannover Title of thesis: What the rhino's voice tells - Information encoded in the vocalizations of Southern White Rhinoceros (*Ceratotherium simum simum*) Under Supervision of PD Dr. Sabine Schmidt and Dr. Marina Scheumann, Institute of Zoology, University of Veterinary Medicine Hannover
04/2014 - 09/2019	Enrollment at the University of Veterinary Medicine Hannover for the Degree of Doctor of Natural Sciences (Dr. rer. nat.)
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10/2012 - 02/2013	Institute of Zoology, University of Veterinary Medicine Hannover - Student assistant
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PUBLICATIONS IN PEER REVIEWED JOURNALS

Linn, S.; Schmidt, S.; Scheumann, M. (2021). Individual distinctiveness across call types of the Southern White Rhinoceros (*Ceratotherium simum simum*). Journal of Mammalogy: 1-7: 10.1093/jmammal/gyab007

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Linn, S.; Scheumann, M. (2019). Difference in individual distinctiveness in noisy calls of white rhinoceros (*Ceratotherium simum simum*). 14th Meeting of the Ethologische Gesellschaft, Hannover, 06.-08.02.2019.

Jenikejew, J.; Chaignon, B.; **Linn, S.**; Scheumann, M. (2019). Interview with a rhino – Functionality of communication calls in the captive Southern white rhinoceros (*Ceratotherium simum simum*). 14th Meeting of the Ethologische Gesellschaft, Hannover, 06.-08.02.2019.

Jenikejew, J.; Chaignon, B.; **Linn, S.**; Scheumann, M. (2018). Interview with a rhino - How vocalisations reflect social interactions in the captive Southern white rhinoceros (*Ceratotherium simum simum*). ASAB winter meeting 2018, Zoological Society of London, London, UK, 06.-07.12.2018.

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Scheumann, M.; **Linn, S.** (2017). First insight into the vocal ontogeny of a large-bodied semi-social mammal, the white rhinoceros. Annual Meeting of the Ethological Society, Bonn, 22.02.-24.02.2017.

Linn, S.; Scheumann, M. (2016). Vocal behavior of infant Southern white rhinoceros: First insights into the call repertoire. 8th ECBB, Vienna, 12.05.-15.05.2016.

Scheumann, M.; **Linn, S.**; Zimmermann, E. (2016). Greeting before entering home: Vocalizations during mother-infant interactions in an infant-parking primate. 8th ECBB, Vienna, 12.05.-15.05.2016.

Linn, S.; Scheumann, M. (2015). First insights into the vocal repertoire of infant Southern white rhinoceros. 10th International Conference on Behaviour, Physiology and Genetics of Wildlife, Berlin, 28.09.-01.10.2015.

Scheumann M.; **Linn S.**; Zimmermann E. (2015). The function of vocal signalling in the mother-infant context of an infant-parking primate. 14. Konferenz der Gesellschaft für Primatologie, Leipzig, 11.02.-13.02.2015

Linn S. (2014). Vocal communication in the Southern White Rhinoceros (*Ceratotherium simum simum*) and the impact of sex hormones. Doktorandentagung der Studienstiftung des Deutschen Volkes, Bonn, 04.11.-07.11.2014