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THE VOCAL REPERTOIRE IN NORTHERN WHITE RHINOCEROS *CERATOTHERIUM SIMUM COTTONI* AS RECORDED IN THE LAST SURVIVING HERD

RICHARD POLICHT[1]*, KRISTINA TOMÁŠOVÁ[2], DANA HOLEČKOVÁ[2]
AND DANIEL FRYNTA[1]

[1]*Department of Zoology, Charles University, Prague, Czech Republic*
[2]*Zoo Dvůr Králové, Dvůr Králové nad Labem, Czech Republic*

ABSTRACT

The Northern White Rhinoceros *Ceratotherium simum cottoni* is a subspecies of the White Rhino that is almost extinct in the wild. We studied the last reproducing herd kept in Zoo Dvur Kralove to describe its vocal repertoire. The calls produced by eight individuals were recorded and analysed as concerned both sound properties and behavioural contexts in which they were emitted. We distinguished 11 calls belonging to four categories: (1) tonal harmonic sounds, (2) puffing sounds, (3) growling sounds, and (4) repetitive sounds. We found an apparent similarity between acoustic parameters of homologous calls recorded in both white rhino subspecies. We further confirmed that the repertoire of white rhino calls is much larger than that reported in other rhino species. We tentatively interpret this finding as an adaptation to increased sociality. Four calls reach the infrasound range; nevertheless, they are probably not used for communication over distance. This is obvious in the case of the *grouch* call, which contains the highest infrasound component. There are, however, other candidates for such a communication function: the repetitive *pant* sound, which is not known in other rhino species. We hypothesise that the repetitions may enhance their audibility in the typical open habitats of white rhinos.

Keywords: rhinoceros, acoustic, signals, vocal repertoire, social behaviour

INTRODUCTION

Despite its large size and wide distribution in the past, surprisingly the Northern White Rhino *Ceratotherium simum cottoni* (Lydekker, 1908) has remained almost unstudied as an African mammal. There are only a few papers devoted to social behaviour of this fascinating creature in the field (e.g., van Gyseghem 1984) or captivity (Mikulica 1991; Kuneš & Bičík 2001-2002). This situation is really alarming in

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*Correspondence: Department of Zoology, Charles University, Viničná 7, CZ-128 44 Prague 2, Czech Republic. E-mail: richard.policht@seznam.cz

face of the current extinction of this animal. During the years 2003-2005, the last wild population of Northern White Rhinos in Garamba National Park in Democratic Republic of Congo was decimated and only four individuals are known to survive (de Merode *et al.* 2005; Hillman Smith & Amube Ndey 2005).

At the time of the study eight individuals including the hybrid female were present at Zoo Dvur Kralove and three at San Diego Wild Animal Park. One male as well as the hybrid female which were included in our study died in 2007. The former zoo is the only institution where they successfully bred. Only 27 individuals of Northern White Rhino have ever been kept in zoos worldwide; 22 of them were wild caught and four captive-born (excluding one hybrid with southern subspecies) at Dvur Kralove (Holečková 2000; Mercado 2004). The herd kept in this zoo probably provides the last opportunity to record social behaviour of the Northern White Rhino.

Pioneering bioacoustic studies in Black Rhino (Budde & Klump 2003) and Sumatran Rhino (Muggenthaler *et al.* 2003) have recently opened previously nearly unexplored (cf. Linklater 2003) field of rhino research. Until now, only a verbal description of white rhino acoustic repertoire has been published (Owen-Smith 1973), however, even this concerns just the nominotypic subspecies, the Southern White Rhino *Ceratotherium simum simum* (Burchell, 1817). It is clearly separated from the Northern subspecies by an almost 2000 km gap between their distinct historical ranges (Owen-Smith 1975), as well as by an independent evolutionary history obvious from 7% divergence of their D-loop sequences (Fernando *et al.* 2006).

White Rhinos of both subspecies exhibit pronounced sociality (Owen-Smith 1973, 1975; Gyseghem 1984; Swaisgood *et al.* 2006) derived from temporary female (mother, aunt) – calf relationships or subadult grouping (sometimes referred as buddy system; Shrader & Owen-Smith 2002), and remarkable preference of open habitats (Estes 1991; Gyseghem 1984; Owen-Smith 1973; Penny 1987). As these characters are unique among extant rhino species, we can expect the emergence of exclusive behavioural adaptations to these conditions. We may predict wider vocal repertoire resulting from more complex social organization and higher representation of repetitive signals, which are advantageous in open habitat due to their resistance to wind turbulences and consequent degradation of the signal (known as the Wiley and Richards hypothesis: Wiley & Richards 1978).

The aim of this paper is: (1) to describe the vocal repertoire of the Northern White Rhino, (2) to validate the classification of recorded sounds using multivariate exploratory statistics, (3) to compare the results with published data concerning other rhino species, (4) to discuss the possible effect of habitat and social system on vocal communication of this species and (5) to compare vocalisations of northern and southern subspecies.

METHODS

Study Site and Subjects

The observations and recordings of Northern White Rhinoceroses were carried out in Zoo Dvur Kralove (East Bohemia, Czech Republic) from November 2004 till July 2006. Three of eight studied animals were wild-caught: Saut (male, 34 years old), Sudan (male, 33) and Nesari (female, 34). The other five animals were zoo-born: Suni (male, 26), Nasi (female, 29), Nabire (female, 23), Najin (female, 17) and Fatu (female, 6). Except Nasi who is a hybrid between the Northern and Southern subspecies, all studied individuals belong to the Northern subspecies *C. s. cottoni*.

Adult rhinos were housed individually in stables except the subadult female Fatu which was kept together with her mother Najin. During the day hours, the females and one male (initially Saut, then Suni) were allowed to freely enter a large open air enclosure (3000m^2). The remaining two males were kept apart with access to separate outdoor enclosures.

The observations of Southern white rhinoceroses (one male and two females) were carried out in Zoo Bratislava (Slovak Republic) in September 2005.

Data Collection

Sound recording was carried out in various situations both in stables and outdoor enclosures. The behavioural context of each sound record was thoroughly recorded.

The animals were recorded using a Sennheiser ME 62 omnidirectional microphone (frequency response 20-20000 Hz ±2.5 dB) and/or Sennheiser ME 67 directional microphone (frequency response 50-20000 Hz ±2.5 dB), both with a K6 powering module. Recordings were captured to the hard disk of a laptop at a sampling rate of 44.1 and 22.05 kHz (16 bit) and stored as individual wave files. Incoming sounds were visualized with the real time spectrogram display and inspected for signal-to-noise ratio, and if the quality was poor sound files were not saved.

The distance between the subject and the microphone ranged between 2 and 20 m. Behavioural data were recorded on a digital camera Canon MVX 250i. Sound recordings and behavioural data were collected simultaneously.

Data Analysis

Recordings were analysed using Avisoft SASLab Pro 4.38 (Specht 2006) software. The 44.1 kHz sampling rate files were changed to 22.05 kHz (using antialiasing filtering) from which the measurements were taken. When searching for infrasound components a 4 kHz sampling rate was chosen to increase frequency resolution to 4 Hz. Sonogram parameters were following: hamming window, FFT-length 1024, frame size 100%, overlap 87.5%. This setting provided a 22 Hz frequency resolution, 5.8 ms time resolution and 28 Hz bandwidth.

Parameters were measured in a combination of manual and automatic procedures. Signal elements were separated manually with the help of an envelope curve and the spectrogram. Next, temporal parameters were computed automatically. These were duration, interval between elements, and distance from start to maximum amplitude. For spectral measurements a one-dimensional function amplitude spectrum (linear) was used. The following parameters were measured with the help of the spectral characteristics function: maximum frequency, minimum frequency, bandwidth, frequency of maximal amplitude (max frequency peak measured on the mean spectrum of the entire spectrogram), 25%, 50% and 75% quartiles (below this frequency is 25%, 50% and 75% of the total energy). When the minimum or maximum frequency was not clearly determined it was taken as an expressive amplitude peak above the background noise. In order to determine minimal frequency of the signal, we decreased the sampling frequency to 4 kHz. In repetitive signals, all the parameters were measured in each sound element. The repetitive call was then divided into three parts consisting of equal number of elements, referred as initial, medial and final segments. The best recorded (according to signal to noise ratio) and fairly representative element of the medial segment was then selected for further analysis. This arbitrary procedure was carried out to avoid fluctuations in breath intensity affecting some call elements, especially those of the initial and final segments. An interval between elements was estimated as the mean value of all such intervals of the given call.

The calls were categorised according to the spectrographic displays to four apparently distinct categories: (1) tonal harmonic calls: (*whine, squeak*); (2) puffing sounds (*puff, snort*, threat); (3) growling sounds (*grunt, snarl, grouch*) including moaning call (*groan*); and (4) repetitive sounds (*pant, hoarse*).

Six call names (*snort, grunt, snarl, whine, squeak* and *pant*) were mostly adopted from Owen-Smith (1973), who distinguished and verbally described 10 calls in the southern subspecies *C. s. simum*. The other four calls (*squeal*, *shriek*, *gruff squeal*, *gasp-puff*) were not found during our study in captive Northern White Rhinoceroses. As discussed below under the Discussion, we also joined "*hic*" and "*pant*". Moreover, we introduced the terms *puff, threat, groan, grouch* and *hoarse* (see Table 1 for the correspondence between the above terms).

The behaviour recorded during the emission of the calls was divided into six categories: (1) cohesive (approach, follow, contact); (2) aggressive (threat, defensive protests and attacks); (3) resting (lying, rest and metabolic needs such as defecation and urination), (4) foraging (feeding activities), (5) separation (a special category covering the situations where an animal was freshly separated from companions and we felt the need to distinguish such situation from the other ones) and (6) other (non-social activities like movement, standing, etc.).

TABLE 1

The comparison of black (after Budde & Klump 2003) and white rhino calls (Owen-Smith 1973, this study). Names of marked calls adopted from Owen-Smith (1973).

black rhino	(after Budde & Klump 2003)		**white rhino**	(this study)
	situation	call	call	situation
tonal sounds:				
	begging for feeding	begging call	*whine	begging for feeding
	–	–	*squeak	separation
puffing sounds:				
	no obvious	snort	*snort	no obvious
	attention	hollow snort	–	–
	aggressive	aggressive snort	–	–
	–	–	threat	first warning
	–	–	puff	no obvious
growling sounds:				
	aggressive	growl	*snarl	aggressive
	–	–	*grunt	powerful warning
	–	–	grouch	foraging and other activities in proximity of other members of the herd
	–	–	groan	moan, body discomfort
repetitive sounds:				
	–	–	*pant	greeting, contact call
	–	–	hoarse	feeding, approach to female

*calls recorded also in southern white rhinoceroses (Owen-Smith 1973), other calls of southern form ("shriek, squeak, squeal, gruff squeal and gasp-puff") were not recorded in this study of northern white rhinoceroses.

Statistical Analysis

In addition to the standard descriptive statistics computed for each call type (Appendices 1-6), we performed a Discriminant Function Analysis (DFA) for each call category. Our aim was to visualise the position of individual calls in a plot of the first canonical axes and to assess the reclassification success. The following 12 variables were used as source data for these multivariate procedures: duration, distance to maximum, frequency of maximum amplitude, lower quartile, median, upper quartile, maximum and minimum frequency, inter quartile range, bandwidth, interval and note duration (the last two variables were included for the analysis of repetitive sounds only). Prior to the analysis, all the variables were log transformed to improve normality of their distribution. Next we excluded highly mutually correlated variables (when $r>0.82$): maximum frequency and upper quartile. *A priori* probabilities of classification were set proportionally to the group sizes. To validate results of discriminant analysis we performed a cross-validation procedure on the basis of the leave-one-out method (SPSS 13.0) and additionally each call was randomly split half-and-half, providing a training set and a test set for each call type. The following classification of one half of the dataset was made, with the discriminant function derived from the other half (Volodina *et al.* 2006). The STATISTICA Analysis System, release 6.0 (StatSoft Inc. 2001) was used for most calculations.

RESULTS

We recorded and analyzed 384 sounds belonging to 11 call types described below and categorized into four distinct categories: tonal calls, puffing sounds, growling sounds and repetitive calls. The backward stepwise DFA resulted in four variables: duration, distance to maximum, minimum frequency and bandwidth. The first two canonical functions had an eigenvalue >1 and described more than 98% of variation. These categories formed distinct clusters when individual calls were plotted in a space of the first two canonical variables (CV1 was correlated with call duration $r=0.82$, CV2 with minimum frequency $r= -0.67$, respectively; (Figure 1). DFA revealed a classification success of 89% (Wilks' lambda = 0.0868) and the cross-validation yielded an average correct assignment of 87% (85.5%; note: the values in the parentheses further refers to results of random half and half split procedure – see under Statistical Analysis).

Puffing sounds were more frequent and consequently most represented in our sample (39.8%), while none of other three categories was considerably underrepresented: growling sounds (23.2%), repetitive sounds (18.8%) and tonal calls (18.2%).

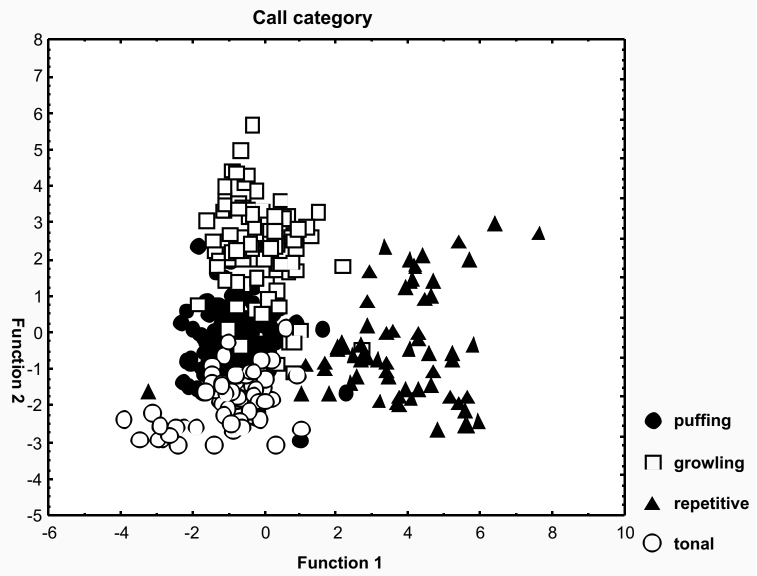

Figure 1. Plot of the first two canonical functions showing separation of call categories.

Two thirds of the analysed calls were emitted during social contexts as aggressive interactions (39%), cohesive behaviour (11%) and recent separation of an individual from the herd (10%). Non social contexts as foraging (27%), moving or standing (5%) or even resting (5%) were markedly less represented. Nevertheless, individual call types and call categories differed considerably in the pattern of behavioural contexts of emissions (Pearson χ2=893.2, P<0.0001, Table 2).

Tonal sounds

Only two tonal harmonic calls were recorded: *whine* and *squeak* (Figure 2-3). They were produced exclusively by the mother (Najin) and her subadult daughter (Fatu). The backward DFA resulted in four variables: duration, frequency of maximum amplitude, minimum frequency and interquartile range. Because only two groups (call types) were present we got only one canonical function. DFA revealed 100% classification success within the category of tonal sounds (Wilks' lambda = 0.167) and cross-validation also assigned 100% (100%) correctly, the *whine* sound being distinctly longer.

Whine (N=2 individuals; n=56 records) is the only melodic sound type we recorded. This vocalisation is harmonic, with modulated frequency and amplitude. It may be more prolonged and sometimes

TABLE 2

Behavioural context of individual call types (%)

	Puffing sounds			**Growling sounds**				**Repetitive**		**Tonal sounds**	
Behaviour	puff	snort	threat	grouch	grunt	snarl	groan	pant	hoarse	whine	squeak
aggressive	0	19	100	0	87	100	0	0	0	0	0
cohesive	13	0	0	4	0	0	0	60	4	17	0
separation	0	4	0	0	0	0	0	40	0	0	100
foraging	58	50	0	63	13	0	0	0	86	77	0
resting	17	12	0	7	0	0	100	0	0	0	0
other	13	15	0	26	0	0	0	0	11	6	0

Behaviour: aggressive (threat, defensive protests and attacks); cohesive (approach, follow, contact); separation (special category covered the situations when the animal was freshly separated from its companions); foraging (feeding activities); resting (lying, rest and metabolic needs such as defecation and urination) and other (non-social actions such as movement, standing, etc.).

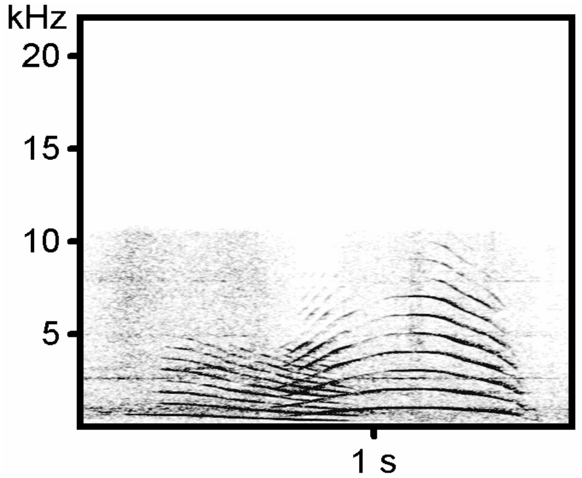

Figure 2. *Whine* spectrogram: a subadult female responds to calling of her mother.

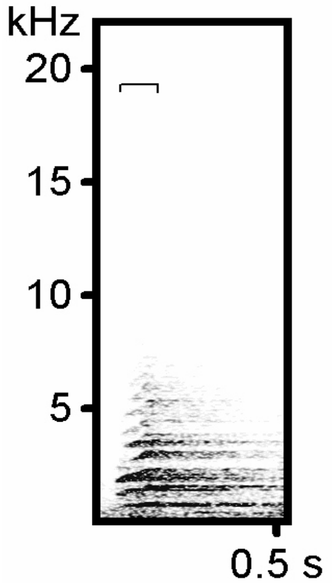

Figure 3. *Squeak* spectrogram: the animal responds to isolation from the group (call duration is marked by a line, sound prolongation (further right) is just a result of reverberation).

arranged in series. *Whine* was emitted most frequently during foraging (70% of records), usually accompanying food begging when feeding adult females block the subadult female from access to food. Sometimes it was recorded in cohesive interactions (14% of records; e.g., approach, standing in a close proximity to each other, another female following the daughter, stabbing of another female by the subadult). The sounds were displayed by the subadult female (91%) or its adult mother (9%).

Squeak (N=1; n=14) is similar to whine, but is a short high-pitched call starting suddenly, reaching its maximal amplitude early, and is finally cut-off abruptly. All cases were recorded after separation of the subadult female (emitter) from her mother and other members of the herd, usually shortly after she lost sight of her mother.

Puffing sounds

These were the most frequent category of calls. We recognised three types: *threat*, *snort* and *puff* (Figure 4-6). All these sounds are made by noisy nasal exhalation or eventually inhalation. The backward stepwise DFA resulted in four variables: median, minimum frequency, inter quartile range and bandwidth. The CV1 discriminating *snort* was correlated with minimal frequency r=-0.82 and bandwidth r=0.70; the CV2 discriminating *puff* with median r=0.56. DFA revealed a 92% classification success (Wilks' lambda = 0.1511) and cross-validation assigned 90.8% (85.7%) correctly.

Threat (N=5; n=101) was emitted exclusively during aggressive interactions (100% of records). It was usually apparently directed to a particular individual (93% of records) and may be viewed as a first warning. When the opponent did not respond, it was followed by growling calls *grunt* and *snarl*, signalling a more pronounced motivation to fight. Most frequently, *threat* was emitted by adult or subadult females (93% of records) as a response to male (Suni) presence (64% of directed threats), i.e., male appearance, approach or proximity; during snarl displays and clashing horns, when backing away, etc. Sometimes, it was recorded also in female-female interactions, e.g., when close feeding, wrestling, hind pressing, blocking, against approaching conspecific. Occasionally, also male (Suni) used threat in response to female attack (7% of records).

Snort (N=6; n=26) was emitted by most individuals, however, the behavioural context of this call was highly variable. It was partly recorded during aggressive interactions e.g., responses to male approach or close feeding, and response to the zoo-park passenger train; 19% of these records were directed to a particular individual, while the remaining records were produced in non social situations without any obvious recipient (e.g., foraging 50% of records).

Puff (N=5; n=26) was also recorded in various contexts including foraging (54%),

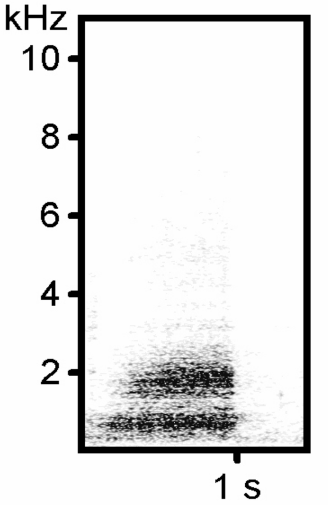

Figure 4. *Threat* spectrogram: sound emitted during an aggressive interaction as a first warning.

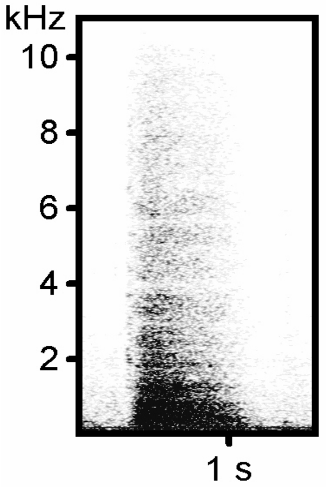

Figure 5. *Puff* spectrogram: no specific behaviour accompanying this call was registered.

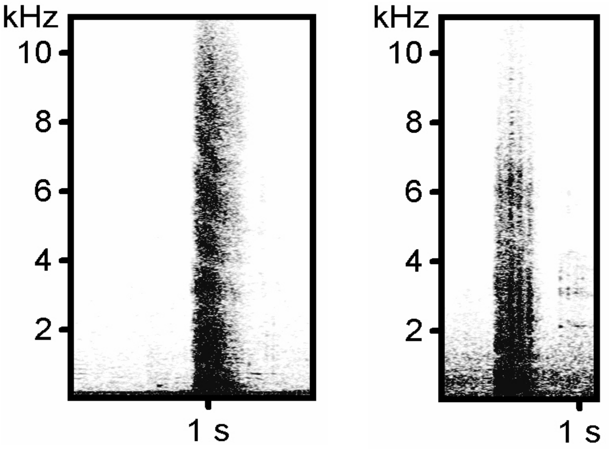

Figure 6. *Snort* spectrograms: different forms of snorts are not accompanied by specific behaviour.

resting (15%), cohesive interactions (12%) and non social situations (12%). Similar to *snorts*, *puffs* were usually not directed to a particular individual.

Growling sounds

This category comprises four similar types of growls, i.e., *grunt*, s*n*arl, *grouch* and *groan* (Figure 8-11). The last mentioned call somewhat differs from the other three ones, and it is categorized as a growling sound more or less casually. The forward stepwise DFA resulted in 7 variables: duration, distance to maximum, lower quartile, median, minimum frequency, inter quartile range and bandwidth. A CV1 clearly discriminating *grouch* and *groan* was correlated with lower quartile

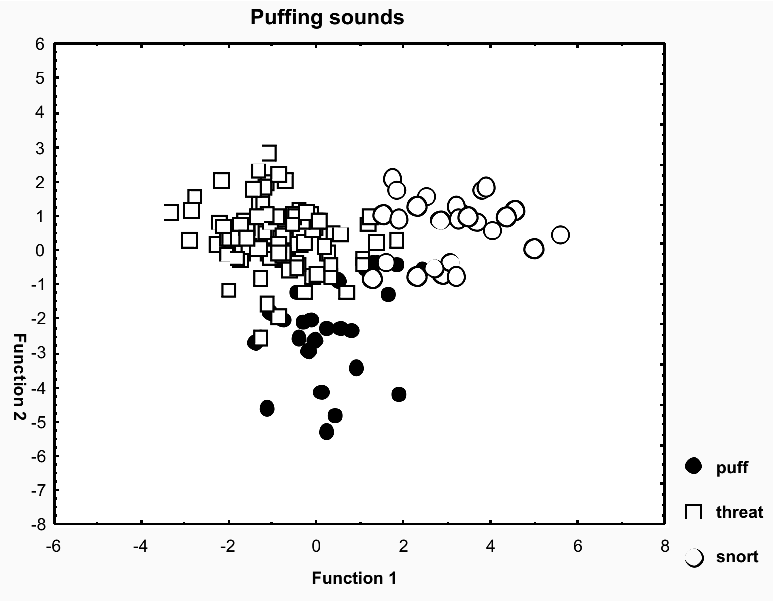

Figure 7. Scores of the first two canonical functions of puffing sounds.

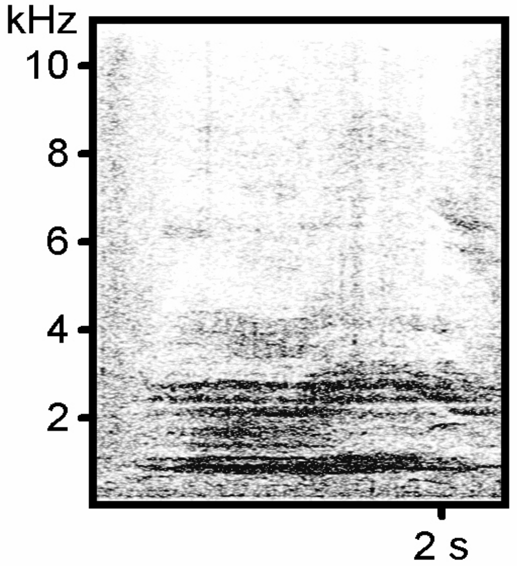

Figure 8. *Groan* spectrogram: the call accompanying defecation, lying down and standing up.

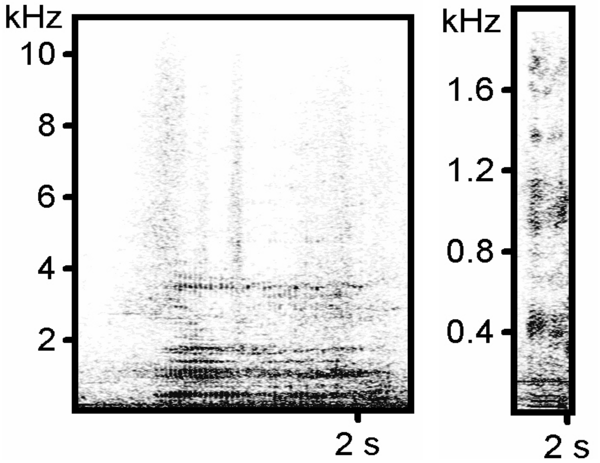

Figure 9. *Grunt* spectrogram (a – sample rate 22,050 Hz; b – sample rate 4,000 Hz): the call emitted in an aggressive context.

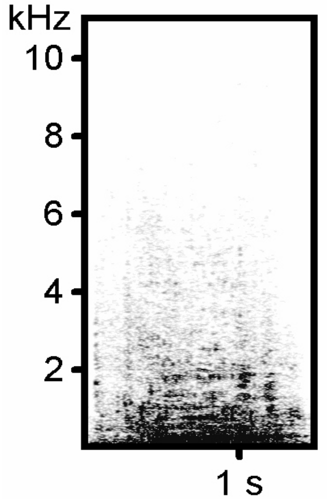

Figure 10. *Snarl* spectrogram: the call is a loud gruff roar accompanying the snarl display.

r=-0.69 and minimum frequency r=-0.55; a CV2 (discriminating *snarl* from *grunt*) with inter quartile range and median r=-0.78, and -0.73, respectively. DFA revealed 91% classification success within the category of growling sounds (Wilks' lambda = 0.0468), (Figure 12). The cross-validation yielded an average correct assignment of 86.5% (88.9%).

Groan (N=4; n=12) is obviously not directed to a specific recipient. It is some kind of moaning accompanying certain forms of strenuous exertion, e.g., defecation, lying down and standing up. No response of any other conspecific to *groan* was recorded.

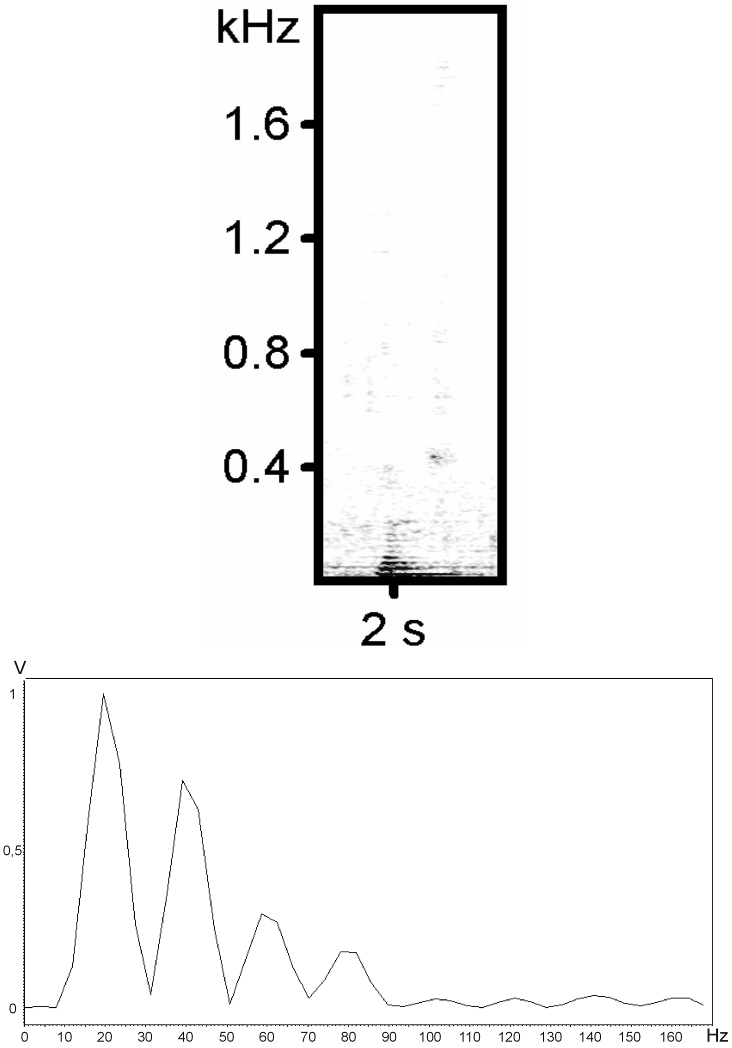

Figure 11. Spectrogram (sample rate 4,000 Hz) and power spectrum of *grouch:* a short calm low frequency sound reaching the infrasound range. In contrast to other growling sounds it is not associated with aggressive interactions.

Grunt (N=5; n=26) is a low frequency vocalization emitted mostly in near aggressive contexts. It was uttered with opened mouth and ears laid back. Its minimum frequency often reached the infrasound range, and we confirmed frequencies as low as 10 Hz. Most frequently it was obviously directed to a particular conspecific (65% of records). 80% of records were emitted during aggressive interactions. It regularly followed a threat which had been missed or ignored by an approaching conspecific. Except in one case the emitter

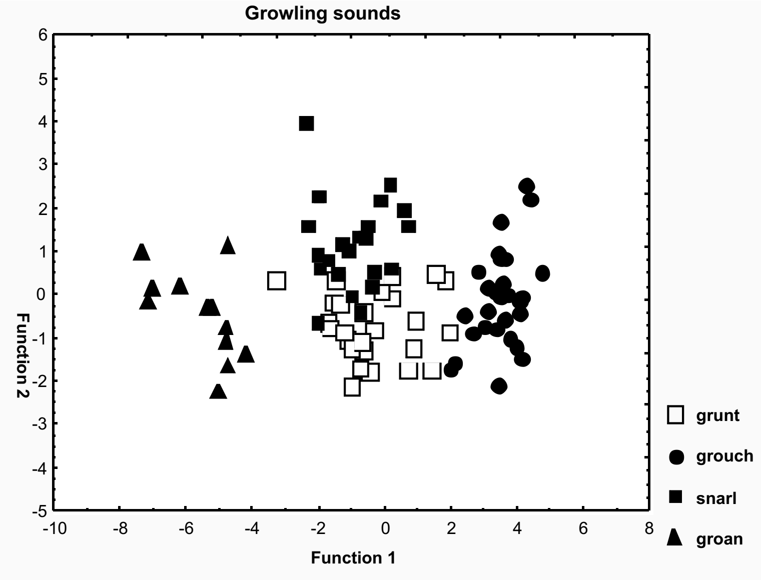

Figure 12. Plot of the first two canonical functions of growling sounds.

was a female (74% of records adult and 23% subadult) responding to an adult male (27%; male approach, investigation of female genital or just feeding in a close proximity, during clashing horns or snarl display of the female), to an adult or subadult female (23% and 15%, respectively; e.g., during close feeding, body wrestling, hind pressing, harassment of the resting individual).

Snarl (N=5; n=23) is a loud gruff roar accompanying a snarl display: ears laid back, head forwards, mouth opened, often protest steps ending in a clash of horns. It is obviously a fully expressed protest to an approaching conspecific. No *snarl* was recorded outside the context of an aggressive interaction as snarl display, clash horns, protest steps, female response to male approach. The vocalising animal was often a female while the recipient was a male (except one male to female and one female to female interactions).

Grouch (N=3; n=28) is a short calm low frequency sound reaching the infrasound range, frequently performed in a series. In contrast to the other growling sounds it is not associated with aggressive interactions and usually (89%) not obviously directed to a particular conspecific. It was produced most often by the adolescent female (Fatu) and her mother (Najin) while feeding (96%), standing, walking, resting, i.e., in situations when these two related individuals or other rhinos were in close proximity to each other.

Repetitive sounds

These sounds are composed of series of wide band elements (syllables) produced at breathing frequency. In exceptional cases such elements may be found as single isolated calls. We recorded two distinct types of repetitive sounds further referred as *pant* and *hoarse* (Figure 13-14). The forward stepwise DFA resulted in 6 variables: call duration, distance to maximum, minimum frequency, interquartile range, interval and note duration. Because only two groups (call types) were present we got only one canonical function. The DFA revealed a 100% classification success within the category of repetitive sounds (Wilks' lambda = 0.01561) and cross-validation revealed 100% (100%) correct assignment as well.

Pant (N=6; n=53) is a sort of air pumping. The series consists on average 13 (from 1 to 44) syllabi, each formed by an exhalation or an inhalation (the former are more audible than the latter ones). The individual elements (syllabi) as well as the intervals between them are shorter than in the *hoarse* call. Ending notes, however, are often prolonged and also reach its maximal amplitude earlier. The call is given with head up, opened mouth and the display is often accompanied by curled tail, which is the emotional manifestation of an eccentric habit similar to those in aggressive interactions. While calling, the animal walked to its companion or gazed intently at them. All *pant* calls were apparently directed to a particular conspecific (usually an adult or subadult female 57% and 41%, respectively). The calling animals were individuals of all kinds (male 32%, adult female 36%, subadult female 32%). Most frequently, this sound was recorded

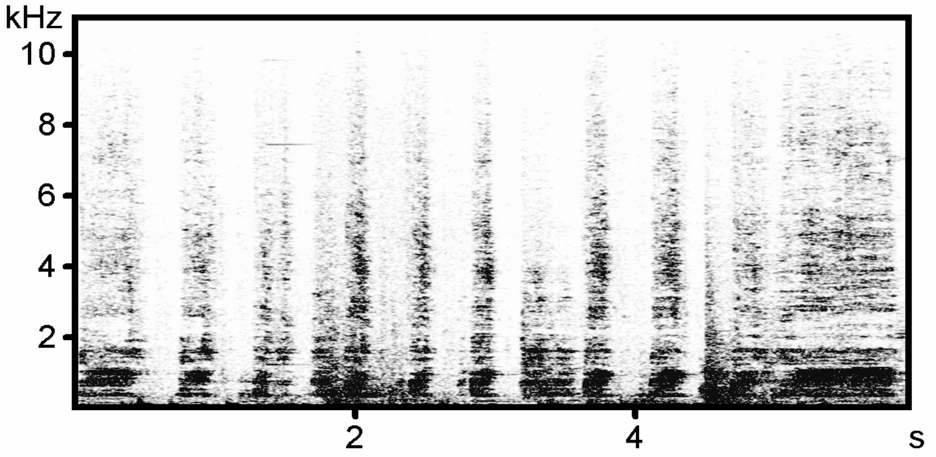

Figure 13. *Pant* recorded during cohesive interactions and in social isolation from the herd

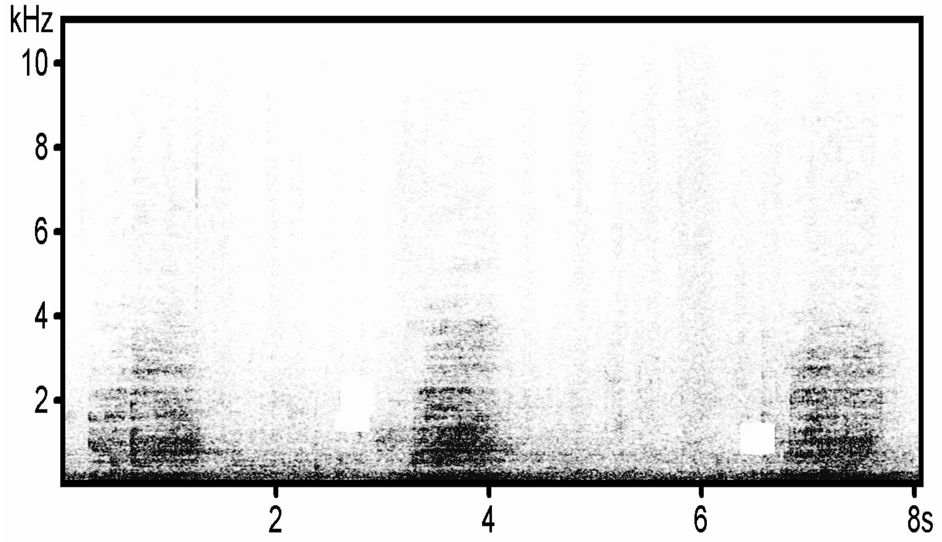

Figure 14. *Hoarse* spectrogram: the sound is a repetitive series of wheezy sounds produced by males.

during cohesive (social investigatory) interactions (60% of records; e.g., approach, follow, facing, greeting: naso-nasal contact, male's olfactory investigation of female faeces and urine, after joining the herd in an enclosure or stable) or following an isolation from the herd (40%, especially between the subadult female and her mother).

We found no substantial difference between male "hic" vocalisation (i.e., wheezy hiccing sound made by courtship of the territorial male while approaching to female) previously reported as a distinct sound type (Owen-Smith 1973, 1975) and *pant* vocalisation of females. Although the female *pant* is usually less intensive, when produced in excited situations (e.g., when a female is separated from the herd) it may closely resemble the male "hic". Therefore, we classed both sound types together as the *pant*. Interestingly enough, even Owen-Smith (1973) explicitly admitted that "hic can be internal part of pant".

Hoarse (N=3; n=19) is a repetitive series of wheezy sounds which has nearly constant rhythm from the beginning to the end and may continue for as long as several minutes (up to 10). *Hoarse* was produced exclusively by males. It was frequently recorded in all three males under study, usually during feeding (86% of records) or other non-social activities. Only 17% of these calls were apparently directed to a particular female.

Comparison of Northern and Southern white rhino calls

We recorded and analyzed 103 sounds of southern white rhinos belonging to four call types: *threat* (n=57), *snort* (n=12), *grunt* (n=21), *snarl* (n=13). When the classification functions discriminating corresponding calls of the northern subspecies were applied to the calls of southern subspecies, we received 93% classification success (75, 85, 95 and 98% for *snort*, *snarl*, *grunt* and *threat*, respectively). As visible from Figure 15, the position of these sounds in the multivariate space largely overlapped those of corresponding calls produced by the northern subspecies. Unfortunately, the limited number of individuals from both subspecies prevented us from performing a more detailed comparison.

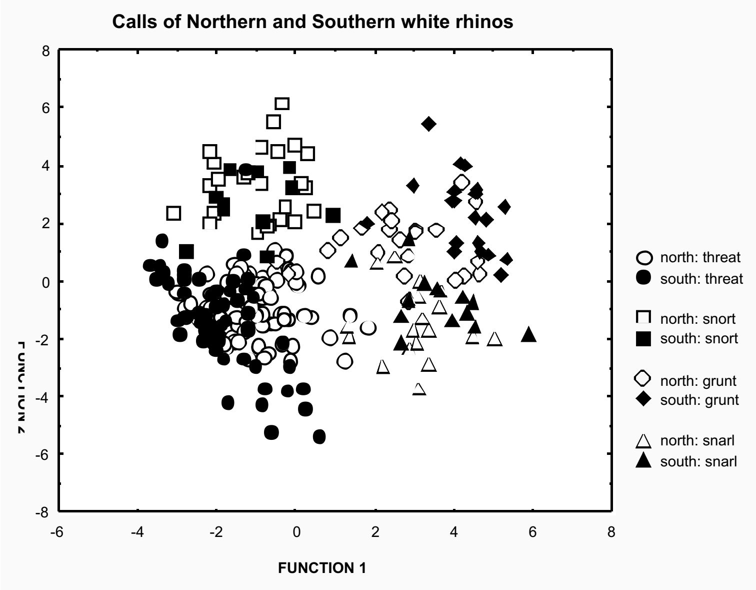

Figure 15. Projection of four calls of Southern White Rhinos into the plain of the first two canonical roots computed for four corresponding calls of Northern White Rhino.

DISCUSSION

The complexity of social organization is probably associated with both frequency and diversity of signalling. As vision plays only a marginal role in rhinos (e.g., Estes 1991), optical signals cannot significantly substitute the acoustic ones even in open habitats. It seems reasonable to expect that a clear tendency to sociality reported repeatedly in white rhinos (Owen-Smith 1973, 1975; Gyseghem 1984; Penny 1987) may enhance the use of acoustic communication channel in these animals. Our results clearly support this hypothesis.

As no quantitative comparative data concerning vocalisation frequency across rhino species are available, we refer to our long-term experience with three rhino species kept in Zoo Dvur Kralove in fully comparable conditions. The comparison leads us to the tentative conclusion that sound production and communication is obviously more expressed in White Rhinoceros *C. simum* than in Black Rhinoceros *Diceros bicornis.* In Zoo Dvur Kralove also Indian Rhinoceros *R. unicornis* vocalize markedly less frequently than *C. simum,* however, it contrasts with some observations under natural conditions (Laurie 1997). Contrary to expectations, even Sumatran Rhinos *Dicerorhinus sumatrensis* use acoustic signals frequently for the specific purpose of parent-offspring communication (von Muggenthaler *et al*. 2003). Nevertheless, in spite of the present habitat of this forest dwelling species, recent ancestors of Sumatran rhinos probably evolved in open habitats as obvious from their phylogenetic affinities (Fernando *et al*. 2006). They are closest extant relatives of extinct Pleistocene rhinos (*Coelodonta*) and thus some of their behavioural traits may reflect their evolutionary past.,

Our results as well as the verbal description of calls produced by *C. s. simum* provided by (Owen-Smith 1973) tentatively suggest that the vocal repertoire of the Southern subspecies of white rhino (*C. s. simum*) resembles that of the Northern subspecies (*C. s. cottoni).* Nevertheless, a thorough quantitative acoustic description of more complete repertoire of sounds uttered by white rhinos of the Southern subspecies is urgently needed to detect eventual subspecific differences.

Owen-Smith (1973) described the following calls: snort, snarl, pant, hic, squeal, shriek, whine, squeak, gruff squeal and gasp-puff. According to our bioacoustic analysis, “snort” contained three different types: “*snort*, *puff* and *threat*”. Similarly, “snarl” involved two different sounds: “*snarl* and *grunt*”. Moreover, we found also “*whine*, *squeak* and *pant*” in the repertoire of northern white rhino. We found no bioacoustic differences between “hic” and “pant” vocalisations, therefore we joined up both calls as “*pant*”. Additionally, we described other calls: “*hoarse*, *grouch* and *groan*”. The remaining calls described by Owen-Smith (1973), that are “shriek, squeak, squeal, gruff squeal and gasp-puff”, were not recorded in our study. The last mentioned “gasp-puff”, which is elicited in situations of sudden fright, seems to respond to our “*snort*”. Because these sounds biacoustically did not differ between situations of fright and other situations, we did not divide these sounds into “gasp-puff” and “snort”.

In *C. s. cottoni* we identified 11 distinct calls. This is more than twice the number reported in *D. bicornis* (five calls, Budde & Klump 2003). Moreover, *C. s. cottoni* produced more calls than *D. bicornis* in three out of four call categories (Table 1). Although the list of calls may be incomplete in both species, a substantial enlargement of the known vocal repertoires is unlikely. This is why the observed difference in vocal repertoire of white and black rhinos seems to be credible. It is the presence of repetitive sounds and wide diversity of growling sounds that is especially apparent in white rhinos. Two growling sounds have an evident function in social communication, signalling an elevated readiness to defensive aggression.

The detailed comparison of vocal repertoires between both sister species of African rhinoceroses revealed that three white rhino calls have obvious homologues in black rhino calls. These are one tonal call (whine = begging), one puffing call (snort) and one growling call (snarl = growl). The former which is not only used in begging, but also as contact call, was reported in other recent rhino species/ subspecies (*C. s. simum*: Owen-Smith 1973; *Dicerorhinus sumatrensis*: von Muggenthaler *et al*. 2003) as well.

On the other hand, the *pant* vocalisation of white rhinos that may be interpreted as a greeting, contact or separation call has no known parallel in any other rhino species. It is highly improbable that such an apparent vocalisation could have been overlooked, as this call is not only loud but also accompanied by distinct behavioural displays.

As the *pant* vocalisation is most probably an apomorphy in white rhino and has an unequivocal function in cohesive social interactions, we may interpret this character as an indirect support for enhanced sociality in this species. Moreover, the *pant* vocalisation consists of numerous repetitions of the elementary syllables and thus may be viewed as an adaptation to a new habitat type. In contrast to black rhino and other recent rhino species, white rhino inhabits open landscapes of grassland savannas. According to Wiley and Richards' hypothesis (Wiley & Richards 1978), irregular fluctuations of amplitude caused by wind turbulences represent the main source of degradation of an acoustic signal in such an open habitat. Therefore, quick repetitions of short syllabics that are easily detectable between wind events may be favoured by selective pressure (Krebs & Davies 1995). The interpretation of living in open-landscape as an apomorphic character is, however, questioned by recent findings concerning *Ceratotherium neumayeri,* the extinct putative ancestor of both black and white rhinos, which suggests rather its intermediary ecological strategy (Geraads 2005).

Some authors speculate about rhino long-distance communication, analogous to the infrasound communication in elephants. Infrasounds were recorded in all four rhino species which are currently kept in captivity (Sumatran, Indian, Black and White; Baskin 1991; Muggenhaler *et al*. 1993). A low frequency moan in black rhinoceros was detectable by geophone at 100 m (O'Connell-Rodwell *et al*. 2001).

Nevertheless, Budde & Klump (2003) found no evidence that any black rhino calls had energy predominantly in the infrasonic range. Moreover, though snarls of white rhinos might be audible 1 km or more away, no rhino was ever seen to be responding to such sounds at a distance (Owen-Smith 1975). Our results confirmed that some white rhino calls (i.e., grouch, grunt, pant and snarl) may reach into the infrasound range. There is, however, no evidence for long-distance communication by these calls. The "*grouch*" has the highest proportion of infrasonic component*,* but this call is emitted by white rhinos usually when the conspecifics are in close proximity.

Penny (1987) hypothesised that the "hic" call (i.e. male call targeted to an oestrous female) might serve for long-distance communication. We agree that this call as well as its female versions that we both refer as "*pant*" call are the best candidates for rhino long-distance communication. These calls are always targeted to a particular conspecific being separated from the caller and their cohesive role is highly probable. The signal role of the infrasound component of any rhino call is, however, uncertain. As recently reported by McComb *et al.* (2003), even in the case of elephants the transmission properties of long-distance calls and hearing abilities of receivers are determined by frequencies of about 100 Hz rather than those below 30 Hz. Thus, the infrasound component of the calls emitted by large animals may be alternatively explained as a by-product of their extreme body size.

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Appendix 1

Descriptive statistics of Northern White Rhino tonal sounds

	Whine N=2, n=56		**Squeak** N=1, n=14	
	Mean	SD	Mean	SD
duration	0.967	0.442	0.133	0.056
dist tomax	0.538	0.423	0.053	0.026
Fmax ampl	1091.411	564.150	1048.000	429.290
quartil 25%	1076.929	417.496	1168.714	323.422
quartil 50%	1576.607	585.817	1863.214	705.068
quartil 75%	2554.018	814.580	2962.429	763.469
F min	631.732	153.744	675.357	110.913
F max	4468.196	1590.879	5219.214	1182.655
bandwidth	3835.304	1530.486	4539.571	1189.236
75-25quartil	1477.089	663.278	1793.714	601.633

(N: number of individuals, n: number of calls analysed, frequency: Hz, duration: s)

Appendix 2

Descriptive statistics of Northern White Rhino puffing sounds

Puff:				**Snort**:			**Threat**:	
N=5, n=26	Mean	SD	N=6, n=26	Mean	SD	N=5, n=101	Mean	SD
duration (all)	0.502	0.172	duration(all)	0.323	0.137	duration(all)	0.561	0.302
disttomax	0.124	0.072	disttomax	0.109	0.078	disttomax	0.305	0.2775
Fmax ampl	376.808	287.465	Fmax ampl	348.938	219.849	Fmax ampl	770.021	297.217
quartil 25%	383.269	161.760	quartil 25%	732.923	252.546	quartil 25%	693.609	176.474
quartil 50%	733.269	290.045	quartil 50%	1720.500	567.989	quartil 50%	1014.890	311.253
quartil 75%	1819.615	855.717	quartil 75%	3558.231	1075.595	quartil 75%	1600.942	451.158
F min	117.538	63.074	F min	64.577	44.431	F min	340.898	166.211
F max	2237.692	1316.158	F max	7966.000	2259.831	F max	2380.569	698.059
bandwidth	2119.731	1325.459	bandwidth	7901.038	2256.263	bandwidth	2039.254	746.720
75q-25q	1436.346	757.632	75q-25quart	2825.308	919.636	75q-25quart	907.333	365.600

(N: number of individuals, n: number of calls analysed, frequency: Hz, duration: s)

Appendix 3

Descriptive statistics of Northern White Rhino groan

N=4, n=12	Mean	SD
duration (all)	1.865	0.978
disttomax	1.189	0.923
Fmax ampl	1048.075	789.248
quartil 25%	934.333	295.809
quartil 50%	1688.083	793.887
quartil 75%	2804.167	1172.328
F min	340.417	257.625
F max	3218.667	2019.642
bandwidth	2878.000	2172.111
75q-25quartil	1869.833	1008.484

(N: number of individuals, n: number of calls analysed, frequency: Hz, duration: s)

Appendix 4

Descriptive statistics of Northern White Rhino growling sounds

Grunt: N=5, n=26	Mean	SD	**Snarl**: N=5, n=23	Mean	SD	**Grouch**: N=3, n=28	Mean	SD
duration(all)	0.979	0.551	duration(all)	1.126	0.6137	duration(all)	0.440	0.168
disttomax	0.594	0.442	disttomax	0.483	0.4048	disttomax	0.263	0.191
Fmax ampl	287.100	393.9	Fmax ampl	231.00	81.936	Fmax ampl	28.179	9.596
quartil 25%	329.650	212.03	quartil 25%	235.93	51.8073	quartil 25%	61.179	25.584
quartil 50%	825.315	311.84	quartil 50%	397.29	157.29	quartil 50%	243.50	192.4
quartil 75%	1600.908	800.34	quartil 75%	723.87	468.7581	quartil 75%	880.57	529.31
F min	41.592	37.098	F min	81.178	53.2209	F min	16.464	3.815
F max	2484.03	997.32	F max	1162.4	747.1888	F max	1641.4	1333.9
bandwidth	2442.04	1002.8	bandwidth	1081.0	764.1756	bandwidth	1624.6	1335.6
75q-25quartil	1271.26	821.27	75q-25quart	487.94	429.9169	75q-25quart	819.39	515.69

(N: number of individuals, n: number of calls analysed, frequency: Hz, duration: s)

Appendix 5

Descriptive statistics of Northern White Rhino repetitive sounds

Pant:			**Hoarse**:		
N=6, n=53	Mean	SD	N=3, n=19	Mean	SD
nu.note	13.451	8.577	nu.note	9.000	7.654
duration (all)	6.300	4.409	duration(all)	26.207	18.315
duration (note)	0.272	0.120	duration(note)	1.057	0.248
interval (mean)	0.575	0.302	interval(mean)	3.574	0.623
disttomax	0.132	0.111	disttomax	0.773	0.290
Fmax ampl	1154.3	670.2	Fmax ampl	1016.213	834.880
quartil 25%	932.509	368.039	quartil 25%	763.068	640.302
quartil 50%	1575.28	586.631	quartil 50%	1265.942	652.947
quartil 75%	2478.53	1044.297	quartil 75%	2070.874	923.747
F min	300.528	263.402	F min	416.484	424.274
F max	4393.47	2026.253	F max	3654.858	1520.850
bandwidth	4092.47	2070.980	bandwidth	3238.189	1607.970
75quart-25quart.	1546.02	889.533	75q-25quartil	1307.805	685.587

(N: number of individuals, n: number of calls analysed, frequency: Hz, duration: s)

Appendix 6

Correlations of individual factors with canonical roots

category	**puffing**		**growling**		**tonal**		**repetitive**	
	Root 1	Root 2	Root 1	Root 2	Root 1	Root 2	Root 1	Root 1
dist to max	-0.06	0.12			-0.16	-0.29		-0.29
F max ampl							0.01	
quartil 25%					-0.69	0.27		
quartil 50%			0.37	0.56	-0.42	-0.73		
F min	-0.06	-0.67	-0.82	0.36	-0.55	0.37	0.06	-0.15
bandwidth	0.09	-0.36	0.70	0.35	-0.01	-0.42		
75-25 quart			0.58	-0.05	-0.10	-0.78	0.09	0.01
call duration	0.82	-0.04			-0.31	0.12	-0.85	-0.33
note duration								-0.68
interval								-0.78

Appendix 7

Descriptive statistics of Southern White Rhino calls

	N=3 **Threat**: n=57		N=3 **Snort**: n=12		N=3 **Grunt**: n=21		N=3 **Snarl**: n=13	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
duration	0.422	0.239	0.379	0.210	0.855	0.644	1.148	0.414
disttomax	0.204	0.157	0.119	0.075	0.513	0.479	0.680	0.428
Fmax ampl	760.616	143.189	608.333	588.963	27.905	12.555	194.538	66.407
quartil 25%	733.860	98.726	709.917	379.313	87.538	52.363	191.592	34.114
quartil 50%	1049.044	359.101	1492.083	610.876	475.867	283.163	297.931	92.797
quartil 75%	1763.161	570.660	2802.667	861.549	1265.924	287.899	706.954	181.688
F min	504.460	153.318	90.417	70.384	20.129	10.482	42.038	20.433
F max	2466.944	1174.577	6419.417	1281.017	2704.824	873.945	1959.062	1041.523
bandwidth	1961.988	1244.555	6328.333	1292.771	2684.157	873.811	1916.846	1037.675
75q-25quartil	1029.302	517.903	2092.750	569.899	1178.386	268.921	515.362	169.182

(N: number of individuals, n: number of calls analysed, frequency: Hz, duration: s)