

Sex and species recognition by wild male southern white rhinoceros using contact pant calls

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Received: 15 July 2015 / Revised: 24 October 2015 / Accepted: 5 November 2015
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Abstract Recognition of information from acoustic signals is crucial in many animals, and individuals are under selection pressure to discriminate between the signals of conspecifics and heterospecifics or males and females. Here, we first report that rhinos use information encoded in their calls to assess conspecifics and individuals of closely related species. The southern (*Ceratotherium simum*) and critically endangered northern (*C. cottoni*) white rhinos are the most social out of all the rhinoceros species and use a contact call pant. We found that southern white rhino pant calls provide reliable information about the caller's sex, age class and social situation. Playback experiments on wild territorial southern white rhinoceros males revealed that they responded more strongly to the pant calls of conspecific females compared to the calls of other territorial males. This suggests that pant calls are more important form of communication between males and females than between territorial males. Territorial southern males also discriminated between female and territorial male calls of northern species and reacted more intensively to the calls

of northern than southern males. This might be caused by a novelty effect since both species naturally live in allopatry. We conclude that white rhinos can directly benefit from assessing individuals at long distances using vocal cues especially because their eyesight is poor. Pant calls thus likely play a significant role in their social relationships and spatial organization. In addition, better understanding of vocal communication in white rhinos might be helpful in conservation management particularly because of their low reproduction in captivity.

Keywords Southern white rhinoceros · Northern white rhinoceros · Vocal communication · Contact call · Sex recognition · Species recognition

Introduction

Communication is a central mediator of all important social behaviours (McGregor and Peake 2000). Vocal signals mediate agonistic and affiliative interactions between animals and play a crucial role in determining the outcome of intra- and intersexual competition (Owings and Morton 1998). Mammalian vocal signals have been shown to encode information about individual identity, sex, species, age, social situation and motivation of the caller (McComb et al. 2000; Gwilliam et al. 2008; Lemasson et al. 2009; Mathevon et al. 2010; Schneiderová and Policht 2012; Tallet et al. 2013; Cinková and Policht 2014; Pitcher et al. 2014). Discrimination of sex from the vocal signals can allow a receiver to detect a mating partner at longer distance than could be achieved by visual or olfactory cues (Bradbury and Vehrencamp 1998) and therefore increase its mating opportunities (Jones and Siemers 2011). In addition, territorial species could have a higher chance to

Electronic supplementary material The online version of this article (doi:10.1007/s10071-015-0940-7) contains supplementary material, which is available to authorized users.

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detect and deter rivals of the same sex (Galeotti et al. 1997). Contact calls can be particularly important for social communication as they are widely distributed among taxa, facilitate social interactions and group coordination and can allow for a recognition of various kinds of social information including mate recognition (Kondo and Watanabe 2009).

Sensory systems and signals coevolve with species' breeding behaviour and microhabitat choice (Endler 1992). In the context of mate recognition, there is a strong selection pressure to discriminate between the vocal signals of conspecifics and closely related species (Irwin and Price 1999; Braune et al. 2008). Divergence in the signals between different species may be favoured more in sympatry than in allopatry, where the ranges of species do not overlap and where is no risk of heterospecific matings (Ryan and Kime 2003). Discrimination between the conspecific and congeneric heterospecific vocal signals may result in some species from learning, in others be innate (e.g. reviewed by Irwin and Price 1999; Sandoval et al. 2013; Hick et al. 2015). The way that animals respond to conspecific versus heterospecific signals can be complex. The animals should be more likely to react to the heterospecific signals when they are both novel and similar to the signals of conspecifics (Ord and Stamps 2009) and when the costs of incorrectly failing to respond to a conspecific signal are high and the costs of incorrectly responding to a heterospecific signal are low (Bradbury and Vehrencamp 2000).

The northern (*Ceratotherium cottoni*) and southern white rhinos (*C. simum*) are allopatric and have only lately been suggested to be distinct species based on their morphological and genetic differences. The two forms of the white rhinoceros have been separated for over a million years (Groves et al. 2010). The extent of the genetic variation between them is being further investigated (see Knight 2015). The southern species naturally occurs in southern Africa and the northern species (which is also referred to as the Nile rhinoceros) in central Africa (Hillman-Smith et al. 1986). Both species have an excellent sense of hearing and smell, but their eyesight is weak (Penny 1987). The northern and southern white rhinos are the most social out of all the rhinoceros species (Goddard 1967; Owen-Smith 1973, 1975; Laurie 1982; van Gyseghem 1984; Penny 1987; Shrader and Owen-Smith 2002). Adult bulls are territorial, and adult females, calves and subadults live in groups in overlapping home ranges (Owen-Smith 1973, 1975; van Gyseghem 1984). Both species have a large vocal repertoire and use a contact call pant that consists of a series of inhalations and exhalations (Owen-Smith 1973; Policht et al. 2008). The pant call is used by the animals when approaching or greeting another rhinoceros or during separation from their group (Owen-

Smith 1973; Policht et al. 2008; Cinková and Policht 2014) and contains sufficient information for the identification of caller's identity and species. Divergence in pant calls between the northern and southern white rhinos could be caused by an adaptation of the signal structure to different types of habitat in which they naturally live (Cinková and Policht 2014). It is therefore possible that the animals could recognize these signal differences.

Pant calls of the southern white rhinos vary by age class and social situation of the caller (Cinková and Policht 2014); however, it is not known whether their acoustic parameters differ between the females and males and whether possible sex differences depend on the caller's age class and social situation. During the approach of a female, particularly during courtship, adult bulls use a conspicuous type of a contact pant call called the hic (Owen-Smith 1973; Policht et al. 2008), but its acoustic parameters have not been described yet. White rhinos could use pant calls to determine various information about the signaller; however, vocal discrimination has never been studied in any rhinoceros species. It is also not obvious which social conditions may lead to the preference of the rhinos for vocal signalling over the olfactory mode and vice versa, since olfactory communication is also particularly important in the social behaviour of white rhinos. Adult bulls mark their territories with dung and urine (Owen-Smith 1973, 1975; van Gyseghem 1984), and southern white rhinos use dung to determine familiarity and sex of conspecifics (Cinková and Policht 2015).

Although the population of the southern white rhinoceros currently numbers approximately 20,400 individuals, many animals are killed each year by poachers (Knight 2013, 2015). The northern white rhinoceros is currently on the brink of extinction with only four surviving individuals. Both species reproduce poorly in captivity (e.g. Hermes et al. 2005, 2006; Swaisgood et al. 2006), and changes in their social behaviour, a lack of social relationships with conspecifics and communication problems could be contributory factors to this phenomenon (Swaisgood et al. 2006; Metrione et al. 2007; Cinková and Bičík 2013; Cinková and Policht 2014, 2015). Behavioural research has previously been found to significantly aid conservation and help identify and solve problems with breeding of captive populations (Lindburg and Fitch-Snyder 1994; Fisher et al. 2003; Swaisgood et al. 2003).

In the current study, we examined (1) if pant calls of the southern white rhinos convey reliable information about the caller's sex, and if call parameters vary depending on the interaction between sex, age class and social situation of the caller; (2) if wild adult southern white rhinoceros males are able to discriminate sex from the pant calls of conspecifics, if pant calls are an important form of communication in male–female and male–male interactions,

and if responses of males to the conspecific calls differ depending on their social situation; and (3) if wild southern males discriminate sex from the pant calls of closely related northern white rhinos, and if their reactions to the male and female calls of the northern and southern species differ.

Methods

Study sites and animals

Playback experiments on adult territorial southern white rhinoceros males were conducted between June–November 2011 and May–December 2012 in three South African wildlife reserves, Welgevonden Game Reserve (375 km²), Lapalala Wilderness (360 km²) and Mthethomusha Nature Reserve (72 km²). The reserves were fenced, and the rhinoceros populations living there were classified as wild since they lived in large areas, had a natural breeding system and were without routine food supplementation (Emslie and Brooks 1999). There were adult females, juveniles and subadults (including older subadult males aged 6–7 years) in each reserve as well as more than one adult territorial male. The calls of the southern white rhinos were recorded in the reserves mentioned above, in Lichtenburg biodiversity conservation centre (South Africa) and in the zoos at Salzburg, Zlín, Dvůr Králové and Bratislava in 2009–2014. The calls of the northern white rhinos were recorded in the Dvůr Králové zoo in 2009–2012.

Recording procedure

Calls were recorded using a Sennheiser directional microphone ME 67 with K6 powering module, frequency response: 40–20,000 Hz \pm 2.5 db (Sennheiser electronic GmbH & Co. KG, Wedemark, Germany) fitted with a Rycote Softie windshield (Rycote Microphone Windshields Ltd., Gloucestershire, UK) and digital recorders Yamaha Pocketrak C24 (Yamaha Corporation of America, Buena Park, USA) or Marantz PMD 671 (Marantz America, LLC., Mahwah, USA) with a 44.1-kHz sampling rate and 16 bits resolution. The calls were recorded at distances from 2 to 30 m from a calling individual in the following contexts: (1) in visual isolation from other rhinos, and (2) in visual contact with other group members (for females and subadult males) or an adult female (for adult males), at a distance for up to seven rhinoceros body lengths from them. The subadult period starts at 2–3 years of age when a juvenile is chased away by its mother after the birth of a subsequent calf. Females become adult around 7 years of age at first parturition and males between about

10–12 years of age when they attain sociosexual maturity and become solitary (Owen-Smith 1973, 1975).

Acoustic analysis

We could not record calls from a sufficient number of northern white rhinos for the analysis due to their critical conservation status, so their calls were only used in playback experiments. We analysed pant calls (Fig. 1) of 33 southern white rhinos (see Table S1 in Electronic Supplementary Material): ten adult females (five were recorded in isolation, five in visual contact), eight adult males (four were recorded in isolation, four in visual contact), six subadult females (three were recorded in isolation, three in visual contact) and nine subadult males (three were recorded in isolation, six in visual contact). Only calls recorded in good quality with low background noise were included in the analysis.

Since we did not aim to study individual variation in calls and were interested if call parameters change depending on the interaction between the caller's sex, age class and social situation, we only analysed one call from each animal to avoid pseudoreplication (McGregor et al. 1992; see also section Statistical analysis). If more calls from the same individual were recorded, we pseudorandomly selected one of them, as calls from both contexts were available for several animals and we wanted to achieve approximately similar sample sizes in both contexts. We analysed the calls following Cinková and Policht (2014) and selected and computed five temporal parameters and one frequency parameter of calls. We calculated the call duration (sec), the number of elements in the call, the duration of the representative exhalation (sec), the

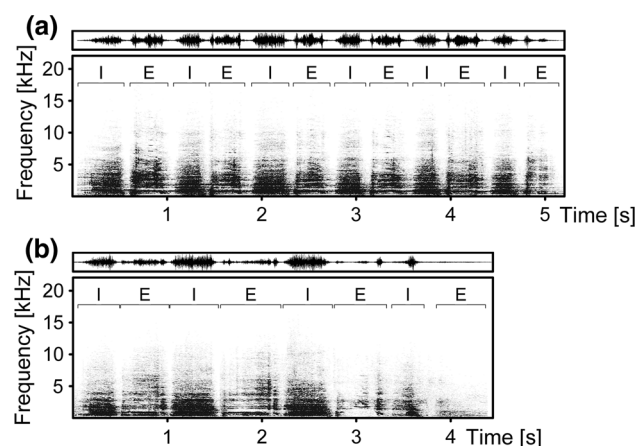


Fig. 1 Representative pant calls of adult female (a) and adult male (b) southern white rhinos recorded in visual isolation from other rhinos. Waveforms (above) and spectrograms (below; spectrogram parameters: FFT length 1024, frame size 100 %, overlap 87.5 % and Hamming window are shown. *I* inhalation, *E* exhalation

order of the longest exhalation in the call and the maximum amplitude of the first global frequency peak (=fp1 amax; relative amplitude) in an inhalation as a measurement of distribution of the frequency amplitude in the spectrum (see also Fischer et al. 2002).

Temporal parameters of calls were computed with Avisoft SAS Lab Pro 5.2.07 (Avisoft Bioacoustics, R. Specht, Berlin, Germany) using the following spectrogram parameters: FFT length 256, frame size 100 %, overlap 50 % and FlatTop window. Particular call elements were classified as inhalations and exhalations and categorized according to their duration: (1) 0.0–0.2 s, (2) 0.21–0.4 s, (3) 0.41–0.8 s and (4) >0.81 s. One representative inhalation and exhalation from the most numerous categories were selected. The spectrograms (FFT length 1024, frame size 100 %, overlap 87.5 %, Hamming window and time resolution 2.9 ms) of the inhalations were then saved as .txt files and analysed using LMA 2008 (developed by Kurt Hammerschmidt; Schrader and Hammerschmidt 1997) to calculate fp1 amax.

Playback experiments

We tested the ability of ten wild adult territorial bulls to discriminate between the pant calls of unfamiliar female and male southern and northern white rhinos. We used playbacks of pant calls of seven subadult (aged ≥ 4 years) and adult female (six captive and one wild) and three adult territorial male (one captive and two wild) southern white rhinos, and the calls of three captive adult female and one adult territorial male northern white rhinos. The calls of southern males and northern male and females were recorded in isolation, and calls of southern females were recorded both in isolation and in visual contact with group members (see Table S2 in Electronic Supplementary Material). Each call was only used once to avoid pseudoreplication (McGregor et al. 1992). Playback stimuli were equalized in terms of root-mean-square amplitude using Avisoft SAS Lab Pro 5.2.07.

We conducted three sets of playback experiments, and each of them consisted of a playback of control sound, female and male pant call. In Experiment 1, we tested if males ($N = 9$) in visual isolation from other rhinos discriminate between the calls of female and male southern white rhinos. In Experiment 2, we studied if males ($N = 6$) in visual contact with a female (in distance from 2 to 7 rhinoceros body lengths from her) react differently to the calls of female and male southern white rhinos. The calls were only played when a female's group consisted of a maximum of three rhinos since a higher number of animals could increase a probability that their behaviour would affect the reaction of the subject males. There were no rhinos from other groups at a study site. Individuals who

oriented towards one another's movements, tended to remain together and only rarely moved further apart than 25 metres were regarded as a group (Owen-Smith 1973). In Experiment 3, we tested if males ($N = 7$) in visual isolation discriminate between the calls of female and male northern white rhinos. We used calls of widespread South African birds as a control: African grey hornbill (*Tockus nasutus*), Swainson's francolin (*Pternistes swainsonii*), pied crow (*Corvus albus*), hadeda ibis (*Bostrychia hagedash*), blacksmith plover (*Vanellus armatus*) and white-faced duck (*Dendrocygna viduata*). There was a mean interval of 11 days between consecutive experiments on one animal, and bulls were exposed to particular experiments in random order (see Table S3 in Electronic Supplementary Material for more information). Pant calls within an experiment were played in random order and were separated by at least 6 min, and the second call was only played when a subject was in a relaxed state again.

The stimuli were broadcast using a GoGen MX381 Barrel digital player (ETA a.s., Prague, Czech Republic) and a custom-built loudspeaker (power output 50 W, frequency response 48–20,000 Hz \pm 3 db) connected to an amplifier (kindly constructed by P. Krchňák and M. Deutschl, Department of Biophysics, Palacký University, Olomouc). The loudspeaker was placed in the vehicle, and the calls were broadcast at a distance of about 15–40 m from the subjects. The rhinos in the study areas were habituated to the presence of the vehicles, and the stimuli were played when a subject was in a relaxed state (i.e. grazing, standing or lying) and not looking in the direction of speaker. Pant calls were broadcast with peak amplitudes at sound pressure level of 85–97 dB (measured at 1 m from the speaker) depending on the distance of rhinos from the speaker (85 dB for 15 m and 97 dB for 40 m), and their volume was equivalent to a naturally panting rhinoceros.

The subject's behaviour was video-recorded using digital camcorder Canon Legria HF M31 (Canon Inc., Tokyo, Japan) for 1 min after the onset of control sound and 5 min after the onset of a pant call. We chose a shorter recording time after the control sound to minimize the possibility that a subject would leave a study site before a pant call was played. Since locating the animals for the study and waiting for the right time to play a call is much more difficult in the wild than, e.g. in controlled settings of zoos, we opted for a higher chance of obtaining the data over equalizing postplayback recording times for the two conditions. We considered 1 min of recording after the control sound sufficient since the animals either reacted to it with a low intensity or did not react at all (see Fig. 3). In 91 % of strong reactions (reactions 5–13) of the subject males to the pant calls (in all three experiments), the approach, running towards the speaker or a female, or walking or running away occurred within 32 s of the onset of

playback. Only in 9 % of strong reactions (=three cases) did the approach start later than 1 min from the onset of playback. It is thus unlikely that if the rhinos reacted strongly to the control sound, they would not show such a reaction in any of the 22 playbacks of control (in all three experiments) until 1 min after its onset.

Behavioural analysis

To quantify male behavioural responses during the experiments, the video recordings were analysed with the computer program package for behavioural studies Activities 2.1 (I. Vrba and P. Donát, 1993) by an experienced observer (IC) blind to the experimental conditions. The reactions to the control sound, female and male pant calls in particular experiments were analysed using the ethological scale, and each individual was scored as one of 13 categories (Table 1). We defined these categories based on the observed reactions of rhinos to the playbacks and ordered them according to their increasing intensity. Ordinal scales such as this have been used in similar studies to monitor changes in behaviour (e.g. Lingle et al. 2007; Policht et al. 2011; Tripovich et al. 2012; Teichroeb et al. 2013). We further analysed only the responses to the pant calls and registered the latency and the duration of the vigilance, looking and turning body towards the speaker and the latency of the approaching, calling with contact call and marking the territory with dung or urine from the onset of playback (see Table 1 for description of these

behaviours). If a certain response did not occur until the end of an experiment, a latency of 300 s was assigned. We also analysed the proportion of time, which the males devoted to grazing, walking/running, standing and lying during the experiments.

Statistical analysis

Statistical analyses were performed with IBM SPSS Statistics 20.0 (IBM Corp., Armonk, USA) and Statistica 12.0 (StatSoft Inc., Tulsa, USA). Alpha level was set at 0.05, and all tests were two-tailed.

We used univariate general linear models (GLM) to test if southern white rhinoceros pant calls differ between the sexes, age classes and contexts. Since we were interested in whether the acoustic parameters of calls vary by these three predictors at the same time, we could not use the general or permuted discriminant function analyses, which serve for the evaluation of one- or two-factorial data sets, respectively (Mundry and Sommer 2007). The call parameters were BoxCox-transformed (Sokal and Rohlf 2012) prior to the analyses to normalize their distribution (confirmed with Shapiro–Wilk tests) and achieve homogeneity of their variances (confirmed by Levene’s tests). Since we conducted five univariate GLM models, we used Bonferroni correction and calculated the Bonferroni *P* critical value by dividing the alpha level by the number of statistical comparisons ($0.05/5 = 0.01$). We only report results that were statistically significant or closely approached significance

Table 1 Ethological scale of male responses to the playback experiments ordered according to their increasing intensity

No.	Reaction
(0)	No reaction
(1)	Vigilance: standing or lying with raised head, gaze fixed or scanning
(2)	Looking: head is raised facing the speaker in an angle equal to or less than 30°
(3)	Turning body towards the speaker in an angle equal to or less than 30°
(4)	Turning body towards the speaker and marking the territory with dung or urine
(5)	Walking or running away from the speaker ^a
(6)	Approaching the speaker or a female
(7)	Approaching the speaker or a female and marking the territory with dung or urine or calling with pant
(8)	Approaching the speaker or a female, marking and calling
(9)	Running towards the speaker or a female
(10)	Running towards the speaker or a female and marking or calling
(11)	Running towards the speaker or a female, marking and calling
(12)	Running towards the speaker, then approaching a female and marking or calling
(13)	Running towards the speaker, then approaching a female and marking and calling

^a This activity was only registered if not influenced by another stimulation as, e.g. walking away from the speaker because the animal started walking towards the waterhole, which was nearby in that direction. Although this reaction is negative and might alternatively be assigned number (−1) in this scale, it is an intensive reaction and we therefore assigned it higher number than, e.g. to no reaction and vigilance. Moreover, we observed this reaction only once (in Experiment 1, see Fig. 3). For comparison, we conducted all the statistical tests in Experiment 1 by assigning number (−1) to this reaction, and the meaning and the interpretation of the results did not change in any way

(for other results, see Table S4 in Electronic Supplementary Material).

Since the males' responses to the playbacks were complex, we analysed them using both the ordinal ethological scale and a principal component analysis (PCA) on behavioural response variables. We used exact nonparametric tests due to the small sample size (Mundry and Fischer 1998). Ethological scores describing the intensity of male responses to the control sound, female and male pant calls in each experiment were compared using the exact Friedman ANOVA. The exact Wilcoxon matched-pairs tests followed by a sequential Bonferroni correction were used for multiple comparisons. Potentially confounding factors (speaker–subject distance, the volume of the playback and the order of the call in an experiment) had no effect on the intensity of reaction of males to the pant calls. Similarly, we found no effect of the caller's population (captive or wild) on the intensity of males' reaction to the calls of southern males and females in Experiments 1 and 2 (see Tables S5 and S6 in Electronic Supplementary Material).

We conducted a PCA with varimax rotation of the behavioural response variables (for rationale, see McGregor 1992) for all three experiments and saved the PC scores using the Bartlett method. We included in the PCAs only those behavioural variables that fulfilled the following criteria. The latency of a behaviour was only included when the behaviour was registered in at least >25 % of reactions in particular experiment. If a behaviour was recorded in all the reactions in an experiment, we used its duration instead of latency since we preferred to include the course of the behaviour of subject males during the whole 5 min of an experiment and not only for the short time until the given behaviour occurred for the first time. This was done to slightly reduce the number of variables used in PCAs as the males' responses were complex and the use of all the variables could result in having an excessive number in the analyses given the small sample sizes. In Experiment 2, the latency of calling with contact call fulfilled our criteria; however, it was only slightly correlated with other behavioural variables and the Kaiser–Meyer–Olkin and Bartlett's criteria for the use of PCA were not fulfilled. We therefore removed it from the analysis. Similarly, we removed the latency of approaching from the PCA in Experiment 3. All the three PCAs then fulfilled Kaiser–Meyer–Olkin and Bartlett's criteria, so their use was justified (McGregor 1992). The latency and the duration of all the behavioural response variables used in PCAs can be found in Fig. S1 in Electronic Supplementary Material.

The scores of the first PC in each experiment were compared using exact Wilcoxon matched-pairs tests. The scores of the second PCs were not tested as in all three

experiments, only one or two variables were strongly correlated with the second PC and the rest of the variables showed a lower correlation ($|r| < 0.45$; see Table 2). The activity of the subject males during the experiments was tested using the exact Friedman ANOVA. The exact Wilcoxon matched-pairs tests followed by a sequential Bonferroni correction were used for multiple comparisons. We only report results that were statistically significant (for other results, see Table S7 in Electronic Supplementary Material).

Results

Sex, age and context differences in pant calls

Males had smaller maximum amplitude of the first global frequency peak (fp1 amax) in an inhalation (GLM: $F_{1,25} = 6.497$, $P = 0.017$) than females, and subadults had shorter call duration ($F_{1,25} = 9.175$, $P = 0.006$) than adults (Fig. 2). There was an interaction between the age class and context in the duration of exhalation ($F_{1,25} = 10.884$, $P = 0.003$). Statistical interactions also indicated differences between the sexes, age classes and contexts in the number of elements in the call ($F_{1,25} = 13.903$, $P = 0.001$), the call duration ($F_{1,25} = 7.977$, $P = 0.009$) and the order of the longest exhalation in the call ($F_{1,25} = 7.887$, $P = 0.01$) (see Fig. 2). Most of these results remained significant after the Bonferroni correction (Bonferroni P critical value = 0.01).

Experiment 1: discrimination between female and male calls of the southern white rhinos by males in isolation

Southern white rhinoceros males in isolation from other rhinos reacted to the control sound, female and male calls of conspecifics with significantly different intensity (exact Friedman ANOVA: $N = 9$, $\chi^2_2 = 14.824$, $P < 0.001$). Their reaction to the female calls was stronger than to the male calls (exact Wilcoxon test: $N = 9$, $Z = -2.673$, Bonferroni corrected $P = 0.012$) (Fig. 3). We included five behavioural variables in PCA. The first PC explained 56 % of the total variance, and higher negative PC1 scores corresponded to the shorter latency of looking, turning body, approaching and marking the territory (Table 2). By comparing PC1 scores, we confirmed that males' reactions to the female calls were stronger than to the male calls (exact Wilcoxon test: $N = 9$, $Z = -2.547$, $P = 0.008$) (Fig. 4). Time devoted by the males to the walking and running after the control sound, male and female calls significantly differed (exact Friedman ANOVA: $N = 9$, $\chi^2_2 = 8.267$, $P = 0.012$) (Fig. 5).

Table 2 Eigenvalues, explained variances and rotated loadings of behavioural variables on the first two factors of the PCAs in Experiments 1, 2 and 3

Behavioural variables	Experiment 1		Experiment 2		Experiment 3	
	SWR calls in isolation		SWR calls in visual contact		NWR calls in isolation	
	PC1	PC2	PC1	PC2	PC1	PC2
L vigilance			0.829	0.373		
D vigilance	-0.025	0.972			-0.592	-0.41
L looking	0.867	-0.222	0.900	0.040		
D looking					0.955	0.011
L turning body	0.955	0.002	0.815	0.226		
D turning body					0.957	0.092
L approaching	0.805	0.399	0.217	0.844		
L calling with contact call					0.405	0.843
L marking the territory	0.693	0.011	0.143	0.864	-0.089	0.855
Eigenvalue	2.79	1.15	2.23	1.65	2.35	1.62
% Variance	55.85	23.08	44.57	33.04	47.03	32.38

SWR southern white rhinoceros, NWR northern white rhinoceros, L latency, D duration

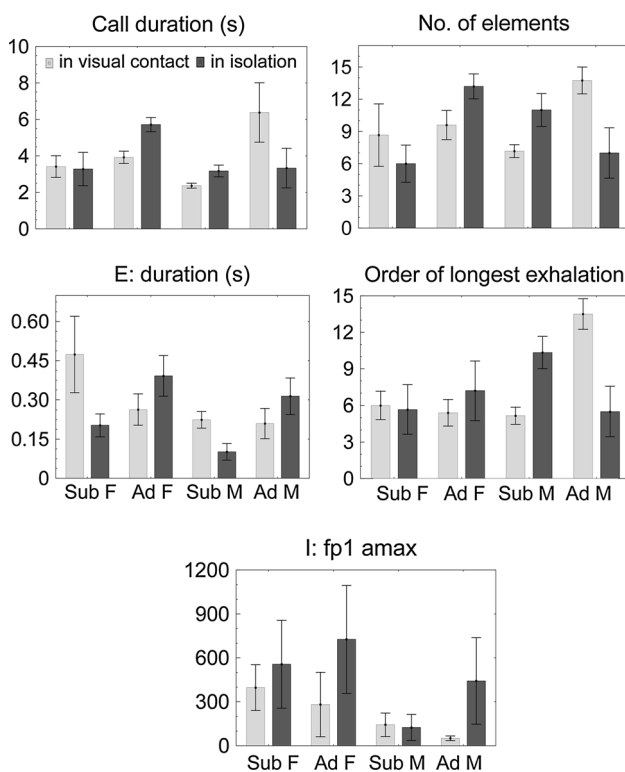


Fig. 2 Acoustic parameters (mean \pm SEM) of southern white rhinoceros pant calls by sex, age class and social situation of the caller. E exhalation, I inhalation, Sub subadult, Ad adult, F female, M male. See “Methods” section for description of acoustic parameters

Experiment 2: discrimination between female and male calls of southern white rhinos by males in visual contact with a female

The differences in the intensity of reaction of males in visual contact with a female to the control sound, female and male southern white rhinoceros calls closely approached significance (exact Friedman ANOVA: $N = 6$, $\chi^2 = 6.333$, $P = 0.052$). The intensity of reaction did not differ between the calls of females and males (exact Wilcoxon test: $N = 6$, $Z = -0.632$, Bonferroni corrected $P = 1$) (Fig. 3). Five behavioural variables were included in the PCA. The first PC explained 45 % of the total variance, and higher negative PC1 scores corresponded to the shorter latency of vigilance, looking and turning body (Table 2). We compared PC1 scores and found that there were no differences between the reactions to the calls of females and males (exact Wilcoxon test: $N = 6$, $Z = -0.524$, $P = 0.688$) (Fig. 4). Time devoted by the males to the walking and running after the control sound, male and female calls did not differ (Fig. 5).

Experiment 3: discrimination between female and male calls of northern white rhinos by southern white rhino males in isolation

The intensity of reaction of the males in isolation from other rhinos to the control sound, female and male northern

Fig. 3 Ethological scale scores of male responses to the playbacks in particular experiments. The intensity of reaction increases on ethological scale from 0 (no reaction) to 13 (running towards the speaker, then approaching a female, marking the territory with dung and urine and calling) (see Table 1 for details). Experiment 1 = calls of southern white rhinos played in visual isolation from other rhinos, 2 = calls of southern white rhinos played in visual contact with a female and 3 = calls of northern white rhinos played in isolation. The connecting lines show responses of individual animals. $**P < 0.05$; $*P < 0.1$

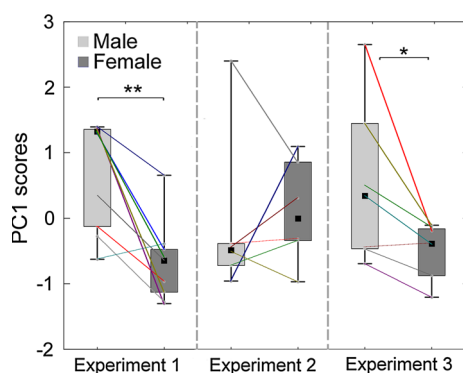
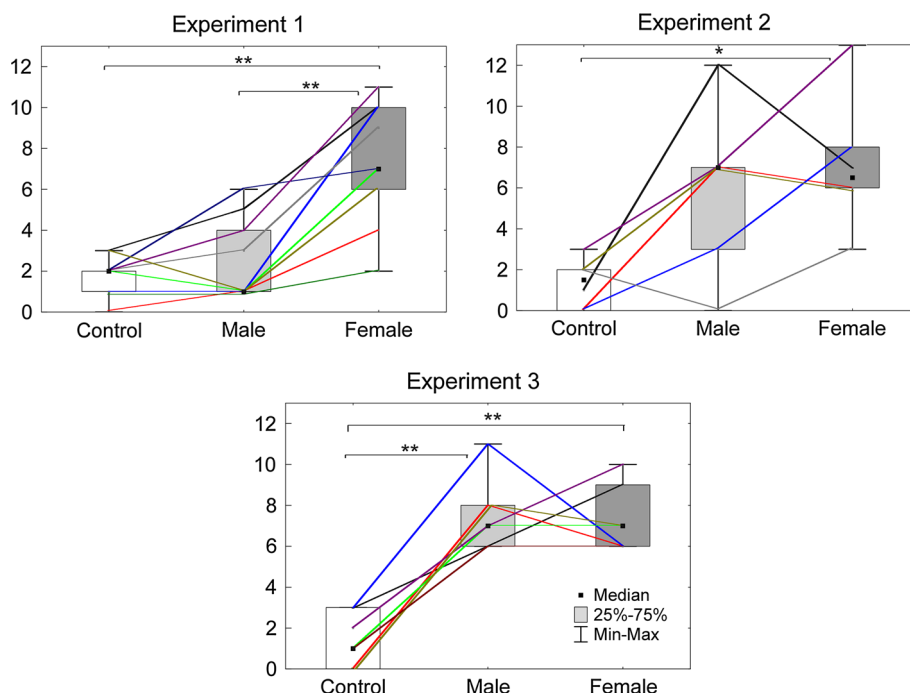


Fig. 4 Principal component 1 scores of the reactions of southern males towards the male and female pant calls in particular experiments. *Experiment 1* calls of southern white rhinos played in isolation, 2 calls of southern white rhinos played in visual contact with a female and 3 calls of northern white rhinos played in isolation. Median 25–75 % \pm min, max values. The connecting lines show responses of individual animals. $**P < 0.01$; $*P < 0.05$

white rhinoceros calls significantly differed (exact Friedman ANOVA: $N = 7$, $\chi^2 = 11.385$, $P = 0.001$). However, males reacted to the female and male calls with the same intensity (exact Wilcoxon test: $N = 7$, ties = 2, $Z = -0.135$, Bonferroni corrected $P = 1$) (Fig. 3). We included five behavioural variables in the PCA, and the first PC explained 47 % of the total variance. Higher negative PC1 scores corresponded to the shorter duration of looking and turning body and the longer duration of vigilance (Table 2). By comparing PC1 scores, we found that the behavioural reactions to the male and female calls differed

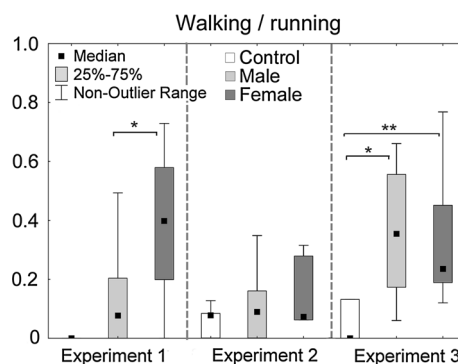


Fig. 5 Proportion of time devoted by the males to the walking and running after the playbacks in particular experiments. *Experiment 1* calls of southern white rhinos played in isolation, 2 calls of southern white rhinos played in visual contact with a female and 3 calls of northern white rhinos played in isolation. $**P < 0.05$; $*P < 0.1$

significantly (exact Wilcoxon test: $N = 7$, $Z = -2.197$, $P = 0.031$) (Fig. 4). Males devoted significantly different time to the walking and running after the control sound, male and female calls (exact Friedman ANOVA: $N = 7$, $\chi^2 = 8.000$, $P = 0.016$) (Fig. 5).

Discussion

This study provides the first evidence of the sex differences in rhinoceros calls and of the ability of rhinos to discriminate information from vocalizations of conspecifics and closely related allopatric species. We analysed the pant

calls of southern white rhinos and found the largest differences between the sexes in the call duration, the number of elements in the call and the order of the longest exhalation in the call, and these parameters depended at the same time on the age class and social situation of the caller. The calls of adult males in isolation were shorter and contained fewer elements than the calls recorded in visual contact (=hic calls, see “Introduction” section), in contrast to the calls of adult females and subadult males which were longer and contained more elements in isolation (see Fig. 2). Longer call duration and higher number of calls per bout have been shown to be associated with increased arousal (chacma baboon: Rendall 2003; giant panda: Charlton et al. 2010), and more frequent repetition of syllables could help other animals locate the caller (Aubin and Jouventin 2002). Adult white rhinoceros males are solitary (Owen-Smith 1973, 1975), and in isolation, they do not have a need to rejoin their group like females and subadults, which could explain the shorter duration of their calls. On the other hand, adult males may experience higher arousal when in visual contact with a female since hic calls are most often uttered when a female is in oestrus (Owen-Smith 1973; Cinková, unpublished data), which could be the reason for the longer duration and the higher number of elements in hic calls. Interestingly, calls of subadult females did not differ in duration between contexts, and the number of elements was highly variable.

The adult southern white rhinoceros males in isolation from other rhinos in Experiment 1 discriminated sex of conspecifics from their contact pant calls and showed a stronger response towards the calls of females than territorial males. This suggests that the pant call is a less important form of communication between territorial males than between males and females and that males are highly motivated to approach a calling female, which is seeking contact. Communication between territorial males may primarily occur via the olfactory signals as different signalers can be preferentially perceived in different communication channels (Endler 1993). The males mark their territories with dung and urine (Owen-Smith 1973) and react intensively to the dung of other territorial males including walking or running around and attempting to find the depositor (Cinková and Policht 2015). Pant calls were therefore probably not selected in the context of territorial male–male communication and are mainly used as a signal for communication between and within groups and thus serving for group cohesion (Owen-Smith 1973) and between adult males and females.

The reactions of the males to the playbacks might have also partly been influenced by relatively low densities of the southern white rhinos at our study sites and by the absence of fully sociosexually mature subordinate males, which could make the importance of status recognition of a

calling male less important. There was, however, more than one adult territorial male in each reserve and also sexually, but not socially mature males of an age of 6–7 years: Southern white rhinoceros males become sexually mature around 6 years of age (e.g. Lindemann 1982; Owen-Smith 1988; Ratajszczak 2000), but social maturity is only achieved at the age 10–12 years, when they become solitary (Owen-Smith 1973, 1975, 1988). Calls of the males may encode information about the caller’s social status (e.g. horses: Rubenstein and Hack 1992; Lemasson et al. 2009), and it has also been suggested that northern white rhinoceros pant calls could differ between adult territorial and subordinate males (Cinková and Policht 2014). Since we only used playbacks of adult territorial male calls, it is unlikely that territorial males would greatly change their reaction depending on the presence or absence of adult subordinate males. They might not react strongly to these calls since they do not want to risk a conflict when it is not necessary (an unknown territorial male has his own territory and might be in another one, e.g. to travel to water). Territorial males might, however, react strongly to the pant calls of adult subordinate males since it could be important to check them and confirm their subordinacy. In addition, in contrast to the hic call, territorial males use pant calls when they are not in visual contact with a female (but when, e.g. seeking a contact with other rhinos) (Owen-Smith 1973; this study). Hic calls could thus elicit a strong reaction of the males since they advertise that the caller accompanies a female and this might be important for the territorial male to check upon.

We did not find any differences in the reactions of bulls in visual contact with a female to the female and male calls of southern white rhinos in Experiment 2. In contrast to the Experiment 1, bulls often approached the speaker or a female in reaction to the pant calls of both sexes and were also calling or marking their territory. We suppose that their reactions were influenced by the presence of a female as the attitude of the animals towards acoustic signals can change depending on the audience (Vignal et al. 2004). Intensities of the reactions of males were variable, particularly to the male calls, which could have been caused by a particular social situation with a female or by a different position of the speaker in relation to a female and a subject male in particular trials. Experiment 2 had the lowest sample size of all three experiments, and a larger sample size would therefore be necessary to determine which factors influence males’ perception of signals in the presence of female.

Bulls in isolation responded strongly to the northern white rhinoceros pant calls in Experiment 3, and the intensity of their reaction on the ethological scale did not differ between the male and female calls. A detailed analysis of behavioural responses using PCA, however,

suggested that males were able to discriminate between the calls of the northern male and females. Bulls in isolation from other rhinos therefore reacted intensively to the female calls of the northern and southern white rhinos and to the calls of the northern male, but their reactions to the conspecific males were weak. This suggests that males may indeed perceive the differences in vocalizations between the male calls of the two species, and since the northern and southern white rhinos are naturally allopatric (Hillman-Smith et al. 1986), discrimination between them cannot result from learning.

We used calls of only one northern white rhinoceros male in Experiment 3, which was the only solution (Wiley 2003) given the critical conservation status of this species when only one male is currently alive. We therefore cannot exclude that his calls did not represent typical northern male calls; however, a detailed acoustic analysis of the northern and southern white rhinoceros pant calls did not show anything specific or unusual about the calls of this male (=male “Súdán”, see Cinková and Policht 2014). The results of the PCA suggested that the subject males differentiated between the calls of the northern male and females and all the males in isolation showed consistently strong reactions towards the calls of the northern male (median reaction on ethological scale = 7), but the reactions to the southern males were consistently lower (median reaction = 1; see Fig. 3).

The role of communicative signals in the recognition between conspecifics and closely related species may be complicated, and animals may show a greater reaction to a heterospecific signal (Ord and Stamps 2009). If the southern white rhinoceros males prefer an olfactory channel for territorial male–male communication (see above) and do not react strongly to the pant calls of conspecific territorial males, a similar vocal signal of a northern male, which contains different and unknown call characteristics, could elicit a strong reaction due to a novelty effect (Tulving and Kroll 1995). The asymmetries in reactions to the female and male calls of the two species could also suggest that the differences between the calls of both sexes are distinct in the northern and southern species, which has also been shown in other closely related mammalian species (e.g. horseshoe bats: Siemers et al. 2005). Playbacks of calls of both white rhinoceros species to the females would be necessary to determine whether there is any indication of reproductive isolation between them based on the vocalizations since female reactions to the male calls are more relevant to assess this (Searcy 1992).

Our results indicate that the pant call is an important signal in the social interactions of white rhinos and that the southern bulls use pant calls to ascertain information about others. Discrimination of sex or species from vocal signals may be especially important for rhinos as their eyesight is

weak (Penny 1987), and vocalizations can allow them to detect and assess other individuals at long distances. If the behavioural mechanisms of the animals are properly understood, they can also be manipulated for conservation and management goals and achieve improved animal welfare (Swaigood 2007). Intensive reactions of the territorial bulls to the pant calls in our study suggest that they can stimulate their social and territorial behaviour. Manipulation of the vocal and olfactory signals (Cinková and Policht 2015) of white rhinos could influence ovarian activity in females and testosterone levels in males as has been shown in other ungulate species (e.g. McComb 1987; Rekwot et al. 2001; Tauck and Berardinelli 2007) and help improve chances for their breeding in captivity and optimize their management.

Acknowledgments We are very thankful to the management and owners of all the wildlife reserves and zoos for kindly allowing IC to conduct field work there. We very much appreciate approval of this project, logistical help and support from the following people from the wildlife reserves: Jonathan Swart, Gerhardt Lorist, André Burger, Shaun McCartney, Anton Walker, Anthony Roberts, Hermann Müller, Elias Mangwane, Lucky Phiri, Louis Loock, Annelize Steyn, Johan Eksteen, Thomas Sikhwivhilu, Thompson Phakalane, Khanyisile Mbatha, and from the zoos: Jochen Lengger, Jiří Hrubý, Ivo Klika, Anton Freivolt, Markéta Horská and Martin Krug. We are very grateful to Vítězslav Bičík, Stanislav Bureš and Norman Owen-Smith for their support of this study and to the rhino keepers in the zoos for their kind assistance. The construction of the speaker by the late Pavel Krchňák and by Martin Deutschl is very much appreciated. IC would also like to express thanks to the wildlife reserves and zoo Dvůr Králové for providing accommodation. Nicolas Mathevon and three anonymous reviewers provided valuable comments, which helped improve the manuscript.

Funding This research was supported by the Internal Grant Agency of the Palacký University in Olomouc PRF 2015-018 and by the mobility grants from the Palacký University to IC.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards Playback experiments and recording of calls for this study were approved by the Ethics and Scientific Committee of the National Zoological Gardens of South Africa (Project P11/03) and adhered to the “Guidelines for the treatment of animals in behavioural research and teaching” as published by the ASAB (2012). The project complies with the current laws of South Africa and the Czech Republic.

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