Rival assessment by territorial southern white rhinoceros males via eavesdropping on the contact and courtship calls

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Highlights

- Contact calls of adult southern white rhino males signal their dominance status.
- There is an emphasis on the repetition of exhalations in males' courtship calls.
- Males discriminate between the calls of subordinate and territorial males.
- Eavesdropping on intruders' calls can help males to better defend their territory.

ABSTRACT

Eavesdropping on vocal signals allows animals to gather information about conspecifics. For males, eavesdropping can be a low-risk method for determining the dominance status (e.g. territorial or subordinate) and motivation (e.g. mate seeking) of rivals. Adult southern white rhino males (*Ceratotherium simum*) are territorial and in addition to other vocalizations, use contact and courtship calls when communicating with females. Although male territories are exclusive, the owners may tolerate up to three resident subordinate males. However, rival males sometimes intrude. Moreover, these intrusions may lead to rivals interacting with females. We investigated whether territorial males eavesdrop on vocal signals directed towards females by intruding males to determine their dominance status (territorial or subordinate) and motivation (contact calling an anoestrus female or approaching a female in oestrus during courtship). To do this, we first recorded and analysed contact and courtship calls of adult southern white rhino males and determined that these calls signal the males' dominance status and motivation. Playback experiments revealed that territorial males differentiated between the calls of subordinate and other territorial males, showing shorter latency of approach and longer searching behaviour (i.e. walking and running) after the playback of a subordinate's call. The reason for this response could be that the intruding subordinate male might be looking to challenge the territorial male for his territory. However, subordinates likely pose the lowest risk to the resident male in terms of fighting ability. In contrast, the reactions of the territorial males towards the calls of other territorial males suggest that the presence and not the motivation of an intruding male was the most important factor influencing the male's reaction. We conclude that territorial males eavesdrop on the acoustic signals of trespassing males to gather information about these rivals, which can help them to better defend their territory.

Keywords: dominance status, motivation, subordinate, territoriality, vocal communication

INTRODUCTION

A key benefit of vocalizations is that they transfer information quickly and can travel over great distances (Endler, 1993). While many vocal signals are apparently directed to specific individuals, they can be available to other potential receivers through eavesdropping (McGregor & Peake, 2000). Moreover, a wide range of information can be encoded in vocalizations beyond the specific signal. For example, vocalizations can carry information about male´s body size (red deer (*Cervus elaphus*): Reby & McComb, 2003), age (chacma baboon (*Papio cynocephalus ursinus*): Fischer et al., 2002), and dominance status (e.g. feral horse (*Equus caballus*): Rubenstein & Hack, 1992; chacma baboon (*Papio cynocephalus ursinus*): Kitchen et al., 2003; fallow deer (*Dama dama*): Vannoni & McElligott, 2008; spotted hyena (*Crocuta crocuta*): Mathevon et al., 2010; crested macaque (*Macaca nigra*): Neumann et al., 2010). The ability to obtain this information from a male’s calls may allow females to quickly assess the quality of the male (Georgiev et al., 2015). Males, however, may benefit by being able to determine the fighting ability of the calling male and thus the risk they may face if they challenge him (Rohwer, 1982).

Adult southern white rhino (*Ceratotherium simum*) males are territorial yet each territory can be co-inhabited by up to three subordinate adult males. These subordinates do not challenge the territorial male for his territory, but also do not help with the territory defence (Owen-Smith, 1973). In contrast, females, juveniles, and subadults live in groups in overlapping home ranges (Owen-Smith, 1973, 1975; Shrader & Owen-Smith, 2002). Territorial males communicate their dominance status via marking their territory with dung and urine (Owen-Smith, 1973; Marneweck et al., 2017a, Marneweck et al., 2018a). However, although olfactory signals can remain in the environment for a long time (Eisenberg & Kleiman, 1972; yet see Marneweck et al., 2017b; Marneweck et al., 2018b), they tend to be transmitted slowly (Endler, 1993).

In addition to using olfactory communication, white rhinos have a wide vocal repertoire (Owen-Smith, 1973). As part of this repertoire, white rhinos use a contact pant call, which consists of a series of intensive inhalations and exhalations. This call is used by all sex-age classes when approaching or greeting another individual, or when an individual is visually isolated from other rhinos (Owen-Smith ,1973; Policht et al., 2008; Cinková & Policht, 2014, 2016). Pant calls carry information about the sex, individual identity, species, age-class, and social situation of the caller (Cinková & Policht 2014, 2016). As such, the ability to discriminate the dominance status of a male from his vocal signals would allow other males to react accordingly when a direct encounter is likely.

Motivational state or arousal (such as in the context of reproduction) of an animal can affect the acoustic structure of vocalizations (McElligott & Hayden, 1999; Briefer, 2012). Levels of arousal are often encoded in vocal parameters such as calling rate, call duration, or amplitude (Briefer, 2012). In some species, males use such reproductive courtship calls to attract females from a distance (frogs: Ryan, 1990; koala (*Phascolarctos cinereus*): Ellis et al., 2011), or when approaching and sniffing a female (Chinese water deer (*Hydropotes inermis*): Dubost et al., 2011). In other species, males vocalize towards competing males and towards females during breeding season (red deer (*Cervus elaphus*): Reby et al., 2001; sika deer (*Cervus nippon nippon*): Wyman et al., 2014). Such calls indicate the male's motivation (i.e. reproduction) and may also serve to stimulate the female or help induce the female's oestrus (McComb, 1987; Ellis et al., 2011).

For adult southern white rhino males, they use a 'hic' call when approaching a female, mainly during courtship. This courtship hic call is a variation of the contact pant call (non-reproductive), which adult males may use when they become visually isolated from a female that they are following (Policht et al., 2008; Cinková & Policht, 2016). Thus, 'hic' calls help indicate the motivation of the male (i.e. reproduction). Although these two calls are most often used in situations mentioned above, intermediate sounds between pant and hic calls can sometimes be heard in intermediate contexts (e.g. when a bull loses a visual contact with a female, he starts panting towards her, but as soon as he sees her, his calling can gradually change to hic; Owen-Smith, 1973; I. Cinková, unpublished observations). A male accompanies a female for up to 20 days before she comes into oestrus and occasionally approaches her while calling with a courtship hic call. The frequency of hiccing increases with time and during the last few hours before copulation, the male intensively calls and repeatedly tries to mount the female. Since territorial males generally are the only ones to have access to oestrus females, hic calls are seldom used by subordinate or adolescent males (Owen-Smith, 1973).

Despite white rhino males maintaining exclusive territories, holders and subordinate males of neighbouring or nearby territories, or newcomers to the area may intrude (Owen-Smith, 1973; Marneweck et al., 2018a). These intrusions may simply be males looking for water, where intruding males either avoid the territory holder, or if confronted, they act submissive, which leads to the confrontation being brief and non-aggressive. However, in some instances these intrusions may lead to the territorial holder being challenged for his territory, which can lead to fights (Owen-Smith, 1973). Moreover, sneaky copulations by other males may occur inside the owner's territory (Guerier et al., 2012), thus reducing the territorial male's reproductive output.

Territorial males may detect intruders via their olfactory signals at middens (also called dungheaps) (Owen-Smith, 1973; Marneweck et al., 2018a). However, eavesdropping on their acoustic signals may prove to be a better way to detect an intruder when he is close. If an intruding male meets a female and interacts with her, he can contact call towards her or if he happens to encounter a female in oestrus, he can start courting her which includes calling with courtship hic calls. Since males defend their territories against rivals (Owen-Smith, 1971), we expected that it would be essential for territorial males to listen and react to the calls of other males trespassing inside their territory and discriminate the dominance status (i.e. territorial or subordinate) and motivation (e.g. calling towards a female in oestrus) of the trespasser. To examine this, we first analysed the contact pant calls and courtship hic calls of territorial and subordinate males to determine if they signal the male's dominance status (territorial or subordinate) and motivation (contact calling towards an anoestrus female or approaching a female in oestrus during courtship). After that, we investigated how territorial males reacted when they heard an unknown intruding adult male inside their territory calling towards a female, and what strategies these territorial males used when a direct encounter with an intruder may be close. We predicted that territorial males would direct their behaviours differently depending on the dominance status and motivation of the intruder. The recognition of these characteristics from vocal cues would allow territorial males to determine at a large distance, at little cost and with no risk, whether aggressive interactions were required (McGregor & Peake, 2000).

With regards to the contact calls of subordinate males, we predicted that territorial males would want to confront the subordinates to confirm their intentions as they may be looking to take over the territory. However, subordinates could also just be looking for a territory where to stay and settle as resident subordinates (Owen-Smith, 1973). Although intruding territorial males may pose a threat to the resident male, they have their own territory and may only contact call towards a female which they randomly met while trespassing to reach a water source (Owen-Smith, 1973). Thus, we expected territorial males to exhibit the strongest reaction to the courtship hic call of a trespassing territorial male as it meant that an intruding male was in the company of an oestrus female and might therefore represent the highest threat to the territory holder due to stolen breeding opportunities.

METHODS

Study site and animals

The study was conducted in the 960 km^2 Hluhluwe-iMfolozi Park (HiP), South Africa during March 2017 to July 2018, November 2018 and February 2019. The study comprised two parts. First, we recorded contact pant calls and courtship hic calls of adult territorial and subordinate males. Second, we conducted playback experiments with wild free-ranging territorial southern white rhino males. Individual males were identified by features such as variations in horn size and shape, body size, hairiness of ears and tails, and tears and notches in ears. In the playback experiments, and for the acoustic analyses, we used the calls recorded in HiP and also used calls of territorial males previously recorded by I.C. in Welgevonden Game Reserve, Lapalala Wilderness, Mthethomusha Nature Reserve (all South Africa), Zoo Dvur Kralove, and Zoo Zlin (both Czech Republic) (see Cinková and Policht 2016). Males were regarded as adult from about 10–12 years of age when they attain socio-sexual maturity and become solitary (Owen-Smith, 1973, 1975).

Recording procedure

We recorded the different calls in HiP when following the rhinos in a vehicle or on foot using a Sennheiser directional microphone ME 67 with K6 powering module, frequency response: 40–20 000 Hz ± 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 Olympus LS-100 (Olympus Corporation, Tokyo, Japan) and Yamaha Pocketrak C24 (Yamaha Corporation of America, Buena Park, USA) with a 44.1 kHz sampling rate and 16 bits resolution. The calls were recorded at distances from 5–25 m from a calling male in the following contexts: (1) contact pant calls in visual isolation from other rhinos, and (2) courtship hic calls while approaching an oestrus female. We recorded the contact calls when territorial and subordinate males either replied to a playback of a contact pant call or when they naturally called towards an anoestrus female which they were following but with which they lost a visual contact (e.g. a female moved off while the male was grazing, which resulted in the two being separated. The male then contact called the female while starting to look for her). To ensure that the hic calls were recorded during courtship and oestrus, we confirmed oestrus using behavioural indicators, namely when a female was squirt urinating, and a male was continuously following her, placing his head on her rump, mounting her, and trying to copulate (see Owen-Smith, 1973). The calls previously recorded by I.C. in other wildlife reserves and zoological gardens were recorded using the same recording equipment and procedures (see Cinková & Policht, 2016).

Acoustic analysis

We analysed the contact pant calls of 13 territorial males and eight subordinate males to study the influence of males' dominance status on their call parameters. To analyse the differences between territorial male call types, we compared courtship calls of six males and contact calls of nine males (Fig. 1, Table A1 and A2). We were unable to record courtship hic calls from subordinate males as they rarely have access to oestrus females (Owen-Smith, 1973). To avoid pseudoreplication, each male contributed only one call in each analysis (McGregor et al., 1992). If more than one call was available from a specific male, we chose the highest quality recording with the lowest background noise.

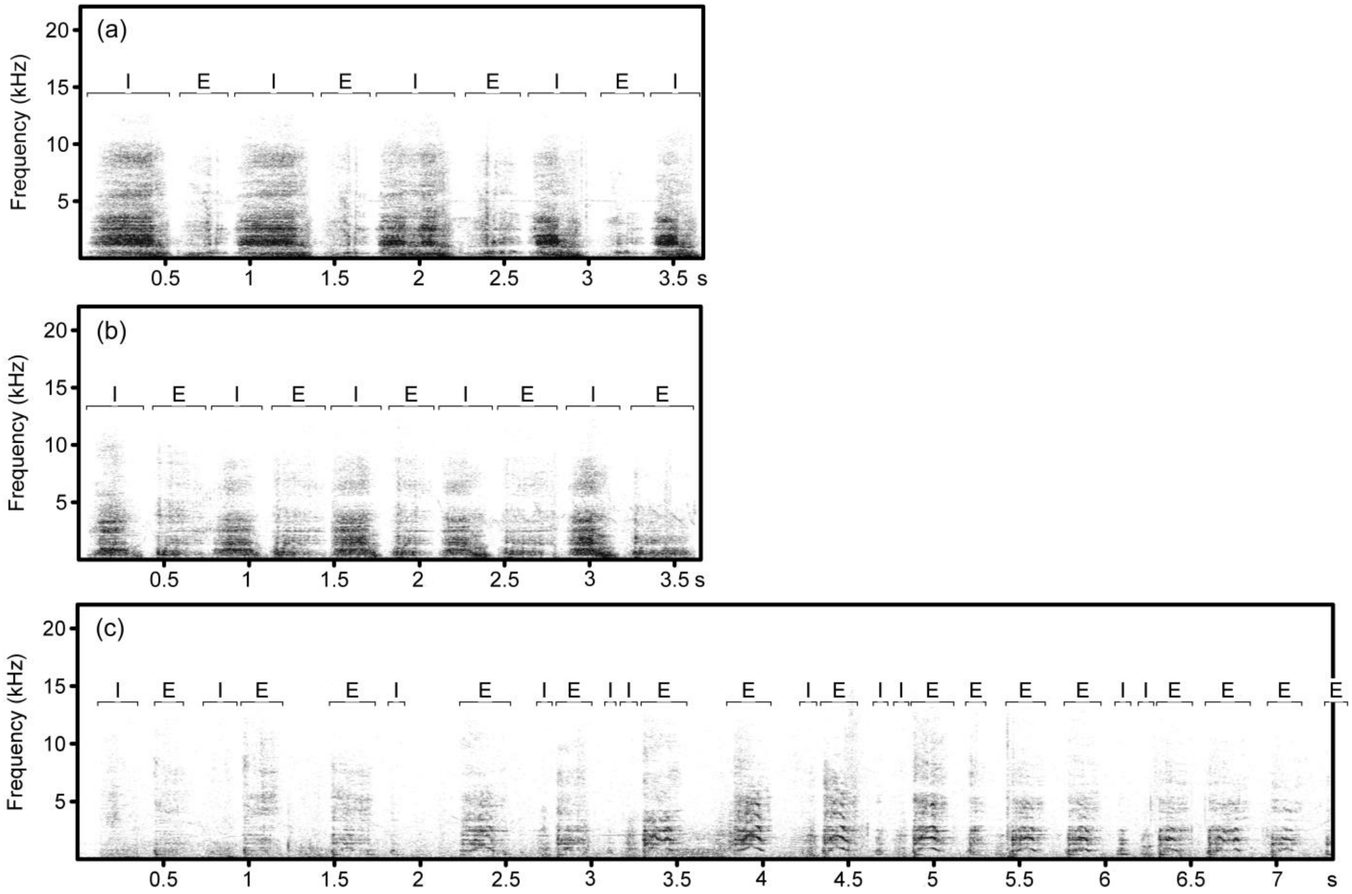

Figure 1. Representative spectrograms of (a) contact pant call of a subordinate male, (b) contact pant call of a territorial male, and (c) courtship hic call of a territorial male. The contact and courtship calls of the territorial males are from the same individual to eliminate inter-individual differences and thus show the differences between the call types. The graph shows only the first 7.5 sec of the courtship call, but its full duration is 22.6 sec. The contact calls are shown in full duration as recorded. Inhalations (I), exhalations (E) are indicated. Spectrogram parameters: FFT length 1024, frame size 100%, overlap 87.5%, Hamming window.

We analysed the calls following Cinková and Policht (2014, 2016). As pant calls are repetitive signals, we only selected certain elements of the calls to measure the spectral parameters. The call elements in each call were classified as either inhalations or exhalations, which could easily be determined by listening to the call recordings and could also be seen when the animal was vocalizing. The inhalations and exhalations were categorized according to their duration using Avisoft SAS Lab Pro 5.2.12 (Avisoft Bioacoustics, R. Specht, Berlin, Germany). This gave us four duration categories: (1) 0.0–0.2 sec, (2) 0.21–0.4 sec, (3) 0.41–0.8 sec, (4) >0.81 sec. Since exhalations and inhalations vary in structure according to their duration (see Cinková & Policht 2014, 2016), this helps to categorise the call elements of each call. We classified the most important exhalations and inhalations of each call as those that were most frequent (using the duration categories) in each call. We then selected one intensive, well-recorded representative inhalation and exhalation from that duration category to be used in the analysis.

The spectrograms of these inhalations and exhalations were analysed using the following spectrogram parameters: Fast Fourier Transform (FFT) length 1024, frame size 100%, overlap 87.5%, Hamming window, time resolution 2.9 ms, and we calculated entropy and harmonic-to-noise ratio (both measured at maximum amplitude of element). Based on the inspection of these spectrograms of contact and courtship calls, we also computed the number of elements (inhalations and exhalations) in each call, proportion of inhalations in the call out of all call elements, and due to the high prevalence in courtship calls, the proportion of inhalations in category 1 (0–0.2 sec) in the call out of all inhalations. We then saved the spectrograms as .txt files and analysed them using LMA 2015 (developed by Kurt Hammerschmidt), which computes many parameters describing the frequency and time dynamics of a call (see Schrader & Hammerschmidt, 1997). We included many acoustic parameters as it allowed a comprehensive description of complex acoustic patterns, without any assumptions about the importance of any of the parameters for discrimination between groups (see also Schrader & Hammerschmidt, 1997).

Playback experiments

To determine if territorial southern white rhinoceros males discriminate between the contact calls of territorial males, courtship calls of territorial males, and contact calls of subordinate males, we conducted playback experiments on 21 territorial males in HiP. Twelve of these males were exposed to more than one type of these three stimuli (Table A3). Males were identified as territorial if they exhibited territorial behaviour such as urine spraying and dung kicking before and after defecation (Owen-Smith, 1973). Only one call per day was played to a particular male and there was an interval 74 ± 18 days (mean ± SE) between consecutive playback experiments on the same male. We used a territorial call of emerald spotted wood dove and a contact call of southern ground hornbill as controls as they represented neutral sounds for the rhinos as they regularly were heard in the local soundscape.

In total, we conducted 51 playback trials using four different stimuli (8 trials with control, 16 trials using contact calls of six territorial males, 14 using courtship calls of five territorial males, and 13 trials using contact calls of five subordinate males). To control for possible recognition of familiarity, we exposed individuals to calls of unfamiliar males to simulate unknown intruders. Specifically, we exposed HiP males to calls from males in other reserves, or to other HiP males whose territories or home-ranges were a minimum of eight km from the territory of the subject male. Territory sizes of males in HiP range from 0.75–2.6 km^2 and under normal occasions, territorial males rarely leave their territory except when forced to make an excursion to the closest water source during the dry season (Owen-Smith, 1973). Thus, it is unlikely that the calls of individuals which we recorded and played back would be known to the subject males.

Except for one recording of a courtship hic call, which we used twice, we limited the use of each recording to a single playback to avoid pseudoreplication (McGregor et al., 1992). Courtship calls can vary in terms of their duration and number of elements (see results, Cinková & Policht, 2016) as it depends on the distance from which the male starts to approach the female. Specifically, if a male approaches from far away, he tends to call for a long time (i.e. over the full distance he travels). In contrast, females may stop a male from approaching using agonistic calls and behaviours, which would then limit the duration and number of elements of the calls (I. Cinková, unpublished observations). To account for this, we calculated the mean duration ± CI of our recordings (13.4 sec; range 11.2 to 15.0 sec) using 38 hic calls from various males. Then, to help control for behavioural variations linked to call duration, we limited the calls we used to ones in which the durations were within the confidence interval range. For calls that were longer than this, we cut the call such that the duration was close to the mean of 13.4 sec. However, we did not cut these calls to exactly 13.4 sec as we did not want any elements to be cut part way. To reduce call durations, we cut either the start or end of a call, removing the section with the worst recording quality. As the call elements were not cut and the duration of the calls were within natural variance, it is unlikely that the cropped calls would sound unnatural to the rhinos.

In contrast to the courtship calls, the variability of the contact calls in terms of their duration and number of elements is low (see results, Cinková & Policht, 2014, 2016). Thus, we used the original recordings of these calls. Finally, we limited the duration of the control sounds to correspond to the mean duration of the courtship calls. As with the courtship calls, we did not cut any of the elements of these calls part way.

For each of the trials, we played the different calls from a speaker facing out of an open window of a vehicle (following Watts et al., 2010; Benson-Amram et al., 2011; Cinková &

Policht, 2016). We targeted rhinos between 15–35 m from the vehicle that were in a relaxed state (i.e. grazing, standing, or resting), and were turned laterally to the speaker and thus not looking in its direction. We only conducted the experiment when we could not detect any other rhinos around as this could influence the reaction of the subject male. The stimuli were broadcast using a Transcend MP710 MP3 Player (Transcend Information Inc., Taipei, Taiwan) and a custom-built loudspeaker (power output 50 W, frequency response 48–20 000 Hz ± 3db) connected to an amplifier (kindly constructed by P. Krchňák and M. Deutschl, Department of Biophysics, Palacký University Olomouc). Playback stimuli were equalized in terms of root mean square amplitude using Avisoft SAS Lab Pro 5.2.12 and broadcast with peak amplitudes at sound pressure level of 89–96 dB (measured at 1 m from the speaker) depending on the distance of rhinos from the speaker (89 dB for ~15 m and 96 dB for ~35 m). This is based on the inverse square law of sound transmission through air, with sound pressure level drop of 6 dB with each doubling of distance from the sound source (see Waser & Brown, 1984). The sound pressure level was thus approximately the same for all males listening to the playbacks independent of their distance from the sound source. The volume of all the playbacks was equivalent to a naturally calling rhinoceros. The behaviour of the males was video recorded for three minutes after each stimulus was played back. The order in which particular stimuli were played to individual males was random but depended on the availability of specific stimuli. Specifically, we were recording some of the calls which we used for playbacks while the playback experiment study was being carried out. Thus, not all the calls were available at the start of the study.

Behavioural analysis

To quantify male behavioural responses during the experiments, the video recordings were analysed using Activities 2.1 (developed by Vrba & Donát, 1993) by an experienced observer (I.C.) blind to the experimental conditions. We first analysed the intensity of reaction of the males using the ordinal ethological scale to assess the variability of males' reactions and determine whether the reactions to the contact and courtship calls differed from control calls. Each reaction was scored as one of 11 categories following Cinková and Policht (2016) (Table 1). We only scored a behaviour as vigilance, looking or turning body if these reactions were displayed by the subject male within 60 sec from the onset of the playback. We did this to link these behaviours directly to the playback and not to a random event naturally occurring within the three minutes after the playback.

Table 1

Ethological scale of male responses to the playback experiments ordered according to their increasing intensity (following Cinková and Policht, 2016)

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*
(6)	Approaching the speaker
(7)	Approaching the speaker and marking the territory with dung or urine or calling with pant
(8)	Approaching the speaker, marking and calling
(9)	Running towards the speaker
(10)	Running towards the speaker and marking or calling
(11)	Running towards the speaker, marking and calling

* Walking or running away from the speaker was not recorded in this study.

Since the intensity of the reactions towards the contact and courtship calls differed significantly from the controls (see results), we further analysed only the responses to the contact and courtship calls and registered the duration of looking towards the speaker, the duration that their body was turned towards the speaker, the duration of walking and running (any movement in general), and the latency of approach towards the speaker within three minutes from the onset of playback (see Table 1 for description of these behaviours). We measured the duration of any walking and running instead of duration of an approach since an approach towards the speaker was generally only short and males then often continued walking or running in the surrounding area and likely searching for the intruder. If we only measured the duration of an approach, all this information would be lost. Moreover, we played playbacks when the males were in a relaxed state (e.g. grazing or resting) so we minimized the possibility that the males would randomly walk after the playback just by continuing their previous activity. The behaviours which we recorded were not mutually exclusive (i.e. when a male was walking and looking towards the speaker at the same time, both behaviours were recorded). If an approach did not occur until the end of an experiment, a latency of 180 sec was assigned. Although the subject males also sometimes reacted with calling with contact call or marking the territory with dung or urine, we did not further analyse these behaviours as they only occurred infrequently and randomly (we registered calling only in 14% of reactions and marking the territory in 46% of reactions).

Twenty percent of the videos were then analysed by a second observer (A.M.S.) who was blind to the experimental condition, to assess interobserver reliability. Spearman rank correlations showed that all analysed behaviours were comparable between observers (duration of looking towards the speaker: $R = 0.933$, $P < 0.001$; duration that their body was turned towards the speaker: $R = 0.917$, $P = 0.001$; duration of walking and running: $R = 0.983$, $P < 0.001$; latency of approach towards the speaker: $R = 0.983$, $P < 0.001$).

Statistical analysis

To examine the probability with which the calls could be correctly assigned to a status (territorial versus subordinate) and type (contact versus courtship), we conducted two forward stepwise discriminant function analyses (DFA). All the variables computed in Avisoft and LMA were checked and those that had zero variation were excluded. We checked for pairwise correlations between variables and only one from a highly correlated pair ($r > 0.85$) was kept in the analyses. After this, 105 variables remained for status and 80 variables for call type (Table A4). The parameters were BoxCox transformed to improve normality of their distribution. We entered parameters into the two DFAs, for status and for call type. The requirement for DFA is that the number of parameters included by the model should be smaller than the number of objects in the smallest class of objects otherwise DFA tends to overestimate discriminability (Mundry & Sommer, 2007). Since the DFA model included nine parameters for call type, we picked the first five and ran the final DFA with them, as the number of objects in the smallest class of objects was six (the analysis included six courtship calls and nine contact calls). The DFA model for status included only five parameters so the requirement on the number of parameters was fulfilled (the analysis included eight contact calls of subordinate males and 13 of territorial males). Classification results of DFAs were then validated using the leave-one out cross-validation procedure. Exact Mann-Whitney U-test was used to test the first discriminant scores of both DFAs. To test whether the parameters resulting from the final DFAs statistically differ depending on the dominance status of the male and call type, we used exact Mann-Whitney U-tests since our call parameters did not comply with the assumptions for parametric statistical models (Sokal & Rohlf, 2012). For their high ability to describe the characteristics of calls, we also tested the three temporal parameters computed in Avisoft (see above). The resulting p-values were corrected for multiple comparisons using a sequential Bonferroni procedure.

We found significant differences between the courtship hic and contact pant calls of males with regards to the proportion of inhalations in a call (see results). Since a courtship call is a special type of a contact call made by males when in visual contact with a female, we were interested whether the contact calls of other rhino sex age-classes also differ with regards to the proportion of inhalations depending on the social situation of the caller (i.e. whether the caller is in visual contact with group members or in visual isolation from other rhinos). To explore this, we used a Mann-Whitney U-test to examine the contact pant calls of 25 rhinos (adult females, subadult females, and subadult males) previously recorded by I.C. (11 of them were recorded in visual isolation, 14 in visual contact; see Cinková and Policht (2016) for the details about the animals).

To determine whether the intensity of the males' reactions towards the control calls differed to the reactions to the rhino calls, we used nonparametric exact Friedman ANOVA on the behaviour scores assigned followed by exact Wilcoxon-paired tests with a sequential Bonferroni correction. This only allowed us to include complete observations in the analysis (i.e. only eight males which were tested for all four types of stimuli; see Table A3). Since the data were ordinal and included repeated measures, we could not use generalized linear mixed model for the analysis. The reactions of males to the control calls significantly differed from the reactions to all the rhino calls. As males did not react at all or only reacted to the control calls with a low intensity (see results), we omitted the control calls from further analyses as these data would strongly skew our dataset (i.e. large number of zero values in the data) and further analysis would not be possible.

Finally, we used principal component analysis (PCA) to analyse the four behavioural responses to the contact and courtship calls and extracted the principal components (PC) with eigenvalue > 1 using the Bartlett method (for rationale of using PCA, see McGregor, 1992). We did not employ rotation as the unrotated solution was satisfactory, showed high loading factors on PC1 for all our behavioural responses, and explained the data well. One of main drawbacks of rotation is that by applying it, information about the nature of any really dominant components can be lost as although the total variance explained remains unchanged, it is redistributed amongst the rotated components more evenly than before rotation (see Jolliffe, 2002). Before the analysis, the variables were BoxCox transformed (Sokal & Rohlf, 2012). Since the data did not comply with the assumption of homogeneity of variances of residuals for the use of a linear mixed model, we used a generalized linear mixed model and included PC scores with normal distribution as a target variable, stimulus (contact subordinate call, contact territorial call, courtship territorial call) as a fixed effect and male identity with scaled identity covariance type as a random effect. Posthoc pairwise comparisons were conducted using sequential Bonferroni adjustments. We only included one fixed effect (stimulus) and not two fixed effects (dominance status and call type) as, (1) the analysis would be unbalanced due to the fact that we did not test the reactions of males to the courtship calls of subordinate males (the reason is that we did not manage to record these calls as subordinate males only rarely have an access to an oestrus female, see above), and (2) we tried to run a trial analysis with two fixed effects, however, the final Hessian matrix of the model was not positive definite and the model thus could not be run. In such cases, simplification of the model is recommended (West et al. 2007). By including only one fixed effect (stimulus), the model was simplified and successfully run.

All analyses were performed with IBM SPSS Statistics 20.0.0 (IBM Corp., Armonk, USA). The BoxCox transformations were done using Statistica 13.4.0.14 (TIBCO Software Inc., CA, USA). Alpha level was set at 0.05 and all tests were two-tailed.

Ethical note

All experimental procedures were approved by the Animal Ethics Committee of University of KwaZulu-Natal and given the reference number AREC/001/017. This work followed the ASAB/ABS guidelines for the treatment of animals in behavioural research and teaching.

RESULTS

Effect of a dominance status and motivation on the calls of males

The five call parameters included in the DFA allowed us to assign 100% of courtship and contact calls of territorial males (100% cross-validated) to the correct call type (Wilks' lambda = 0.027, $P < 0.001$). Moreover, the first discriminant scores of the courtship and contact calls were significantly different (exact Mann-Whitney U-test: $N_1 = 9$, $N_2 = 6$, $U < 0.001$, $P < 0.001$). Territorial males had a greater number of elements in each call, a lower proportion of inhalations in call and a higher proportion of inhalations in category 1 (0.0–0.2 sec) in their courtship call compared to their contact call (Table 2). In contrast, the proportion of inhalations in the contact pant calls of adult females, subadult females, and subadult males did not differ between the calls emitted in isolation and calls emitted in visual contact with other rhinos (Mann-Whitney U-test: $N_1 = 11$, $N_2 = 14$, $U = 64.5$, $P = 0.479$).

Table 2

Differences in call parameters depending on the call type (motivation) of males. The parameters are shown in order how they were included by the DFA model

No.	Variable	**Territorial: contact call** (median (IQR); N=9)	**Territorial: courtship call** (median (IQR); N=6)	***U***	***P***
1.	No. of elements in call	6.0 (5.0–9.0)	60 (34–68)	<0.1	**<0.007**
2.	E - hnr (max)	36 (32–36)	29 (27–36)	14.0	0.53
3.	E - df1fretr	16 (15–18)	14.5 (9.7–16.7)	20.0	0.91
4.	E - df1miloc	0.94 (0.85–1.00)	0.47 (0.27–1.00)	14.0	0.37
5.	I - df1maloc	0.25 (0.08–0.64)	0.32 (0.07–0.89)	26.0	0.96
	Proportion of inhalations in call	0.50 (0.50–0.60)	0.33 (0.29–0.44)	1.5	**0.006**
	Proportion of inhalations in category 1 (0.0–0.2 sec) in call	0.00 (0.00–0.33)	0.66 (0.50–0.83)	5.5	**0.03**

I = parameter computed in an inhalation, E = parameter computed in an exhalation, hnr (max) = the ratio of harmonic to nonharmonic energy (measured at the maximum amplitude of element), df1fretr = alternation frequency between first dominant frequency band and linear trend, df1miloc = location of the minimum frequency of the first dominant frequency band [(1/duration) * location], df1maloc = location of the maximum frequency of the first dominant frequency band [(1/duration) * location]. Significant differences after sequential Bonferroni correction are indicated in bold.

The DFA model for status included five call parameters and 100% of contact calls (100% cross-validated) were correctly assigned to a territorial or subordinate male (Wilks' lambda = 0.13, $P < 0.001$). The differences between the first discriminant scores of the territorial and subordinate contact calls were significant (exact Mann-Whitney U-test: $N_1 = 13$, $N_2 = 8$, $U < 0.001$, $P < 0.001$). A key difference between the contact calls of territorial males and subordinate males was that territorial males had significantly higher minimum frequency of the second distribution of frequency amplitude in an inhalation (Table 3; see Fig. A1 for power spectra of contact pant calls of territorial and subordinate males).

Table 3

Differences in call parameters depending on the dominance status of males. The parameters are shown in order how they were included by the DFA model

No.	Variable	**Territorial: contact call** (median (IQR); N=13)	**Subordinate: contact call** (median (IQR); N=8)	***U***	***P***
1.	I - q2min (Hz)	1251 (992–1553)	259 (86–820)	14.5	**0.04**
2.	I – pfmed (Hz)	1079 (820–1467)	734 (43–1640)	44.0	1
3.	I – pftrmean (Hz)	349 (279–370)	455 (296–648)	37.5	1
4.	I - pfmaloc	0.74 (0.56–0.90)	0.55 (0.11–0.65)	30.0	0.82
5.	I - pfmiloc	0.11 (0.06–1.00)	0.29 (0.03–0.82)	48.0	1
	No. of elements in call	8.0 (5.0–10.0)	10.0 (7.0–13.5)	34.5	1
	Proportion of inhalations in call	0.50 (0.50–0.60)	0.50 (0.50–0.52)	51.0	0.97
	Proportion of inhalations in category 1 (0.0-0.2 sec) in call	0.00 (0.00–0.00)	0.00 (0.00–0.13)	50.5	1

I = parameter computed in an inhalation, E = parameter computed in an exhalation, q2min = minimum frequency of the second distribution of frequency amplitude (where the distribution of frequency amplitude describes the energy distribution in the sound), pfmed = median peak frequency, pftrmean = mean deviation between peak frequency and linear trend, pfmaloc = location of the maximum peak frequency [(1/duration) * location], pfmiloc = location of the minimum peak frequency. Significant differences after sequential Bonferroni correction are indicated in bold.

Males' behavioural reactions during the playback experiments

The intensity of the reactions of males to the control sound, territorial contact, territorial courtship, and subordinate contact calls differed significantly (exact Friedman Test: $N = 8$, $\chi2 = 15.689$, $df = 3$, $P < 0.001$; Fig. 2). Specifically, males reacted more intensively to the territorial contact call than to the control (exact Wilcoxon Signed Ranks Test: $Z = -2.536$, $P = 0.048$), to the territorial courtship call than to the control ($Z = -2.527$, $P = 0.048$), and to the subordinate contact call than to the control ($Z = -2.546$, $P = 0.048$). There were no differences in the intensity of reaction of males to the courtship territorial and contact territorial calls ($Z = - 0.426$, $P = 1$), courtship territorial and contact subordinate calls ($Z = -0.742$, $P = 1$) and contact territorial and contact subordinate calls ($Z = -0.135$, $P = 1$). The median reaction to all the male calls was to approach the speaker and mark with dung or urine, or call with a pant.

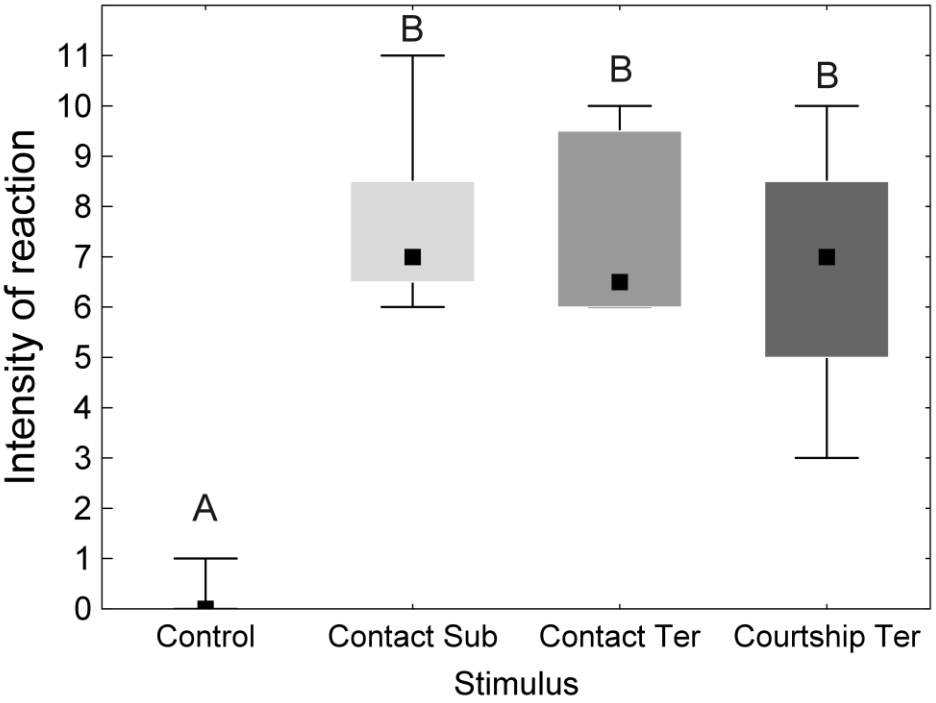

Figure 2. Intensity of reaction of males towards the playbacks of the control (i.e. bird calls), contact call of a territorial male (Contact Ter), courtship call of a territorial male (Courtship Ter) and contact call of a subordinate male (Contact Sub). Only eight males which were tested for all four types of stimuli were included in the analysis. The intensity of reaction increases on ethological scale from 0 (no reaction) to 11 (running towards the speaker, and marking and calling) (see Table 1 for details). Median is indicated by the black square, box represents 25–75% quartile range, the whiskers show minimum-maximum values. Different letters indicate significantly distinct groups.

Territorial males reacted to 100% of contact calls of subordinate males intensively (i.e. with reaction 6–11; Table 1) whereas to the calls of territorial males, their reactions were more variable. The males reacted intensively to 87.5% of contact calls of territorial males and 71.4% of courtship calls of territorial males (see Table A3). We entered four behavioural variables into the PCA. Two PCs with Eigenvalue > 1 were extracted (Table 4). The first PC explained 54.5% of the total variance (see Table 4). High PC1 scores indicated that males spent a long time looking and being turned towards the speaker, and that it took them longer to start approaching the speaker, or they did not approach at all, and spent short time walking or running around (Fig. 3). The PC1 scores of males' reactions towards the three types of playbacks of male calls differed significantly (GLMM: $F_{2,13} = 8.628$, $P = 0.004$; see Fig. 3). There was a significant effect of the random factor individual identity on males' reactions (estimate + $SE = 0.52+0.21$, $Z = 2.51$, $P = 0.012$). Pairwise comparisons showed differences between the territorial males' reactions to the contact calls of subordinates and territorial courtship calls (estimate + $SE = -1.01+0.33$, $t = -3.08$, $P = 0.027$), and between the subordinate contact and territorial contact calls (estimate + $SE = -0.36+0.12$, $t = -2.98$, $P = 0.027$). In contrast, the differences in the territorial males' reactions to the territorial courtship and territorial contact calls were not significant (estimate + $SE = 0.65+0.34$, $t = 1.89$, $P = 0.078$). The second PC explained 30.9% of the total variance (see Table 4). High PC2 scores indicated that males spent a long time looking and being turned towards the speaker and a long time walking or running around, and that they showed a short latency to approach the speaker. However, the PC2 scores (mean ± SE) of males' reactions towards the territorial contact (-0.09±0.35), subordinate contact (-0.09±0.19), and territorial courtship (0.18±0.19) calls did not differ (GLMM: $F_{2,17} = 0.798$, $P = 0.466$).

Behaviourally, the territorial males always approached the speaker after a playback of a subordinate male's contact call and spent the greatest amount of time walking or running. In contrast, the territorial males showed the longest latency of approach and spent the longest time with their body turned and looking towards the speaker after the playback of a territorial courtship call (Fig. A2).

Table 4

Loading factors of behavioural variables on the first and second factor of principal component analysis

Variable	**PC1**	**PC2**
Duration of looking towards the speaker	0.63	0.69
Duration that their body was turned towards the speaker	0.81	0.44
Duration of walking/running	-0.74	0.55
Latency to approach the speaker	0.76	-0.52
Eigenvalue	2.18	1.23
% total variance explained	54.48	30.86

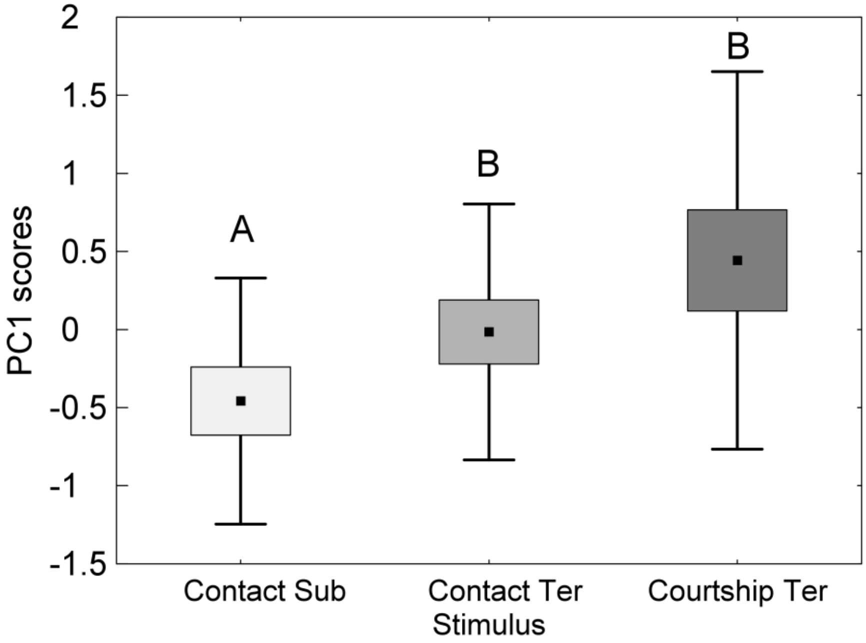

Figure 3. Principal component 1 scores of the reactions of males towards the playbacks of the contact call of a subordinate male (Contact Sub), contact call of a territorial male (Contact Ter) and courtship call of a territorial male (Courtship Ter). Mean is indicated by the black square, box represents standard error, the whiskers show standard deviation. Different letters indicate significantly distinct groups.

DISCUSSION

The results of our study revealed that the calls of southern white rhino males encode information about their dominance status (territory holder, subordinate) and motivation (contact or courtship call). Moreover, the playback experiments indicated that territorial males were able to determine the difference between courtship calls of territorial males and contact calls of subordinate males, and between the contact calls of territorial and subordinate males. In contrast, the males did not react differently to the contact and courtship calls of other territorial males suggesting that the presence, and not the motivation of an intruding male, was the most important factor influencing the male's reaction. Thus, by eavesdropping on the calls of trespassing males, territorial holders are able to obtain key information about these trespassers and react accordingly.

Contact calls of territorial males in our study showed patterns of more energy distributed in higher frequencies (i.e. they had higher values of minimum frequency of the second distribution of frequency amplitude in an inhalation) than contact calls of subordinate males. Such vocal status indicators could prevent contests between males based on already established dominance system (Preuschoft & van Schaik, 2000). The influence of social status on the calls of males has also been found in crested macaques (*Macaca nigra*). Specifically, in social situations high-ranking males use calls with more energy in high frequencies (i.e. their frequency amplitudes across the spectrum are higher) compared to low-ranking males. However, the reason for this is unclear (Neumann et al., 2010). Vocal parameters can be affected by vocal effort, the motivational state of an animal (Fischer et al., 2004), or reflect a certain physiological features of the calling male like his body size (Charlton et al., 2009) or testosterone levels (Charlton et al., 2012). In white rhinos, testosterone levels are significantly higher in territorial males compared to subordinate males (Rachlow et al., 1998). Thus, these differences may play a key role in creating the differences in the contact pant calls that we recorded. However, little is known about the relationship between the distribution of frequency amplitude in calls and testosterone levels, and thus this area should be further explored. Nevertheless, since contact calls of adult southern white rhino males are predominantly directed towards females (Owen-Smith, 1973; Cinková & Policht, 2014, 2016), the information about the male's dominance status within the call might act as an honest signal for females.

White rhino hic and pant calls are repetitive calls consisting of a series of inhalations and exhalations (Owen-Smith, 1973; Cinková & Policht, 2016). Yet, these calls have a longer duration when an individual is in a high state of arousal. For adult males, this is when they are in the company of a female compared to when they are in visual isolation from other rhinos. For other rhino sex-age classes, on the contrary, pant calls are longer when individuals are visually isolated from group members than when they are in visual contact with them (Cinková & Policht, 2016). We found that courtship hic calls of males contain significantly less inhalations than exhalations, and contain a greater proportion of shorter inhalations than contact pant calls. In addition, we confirmed that this feature is only specific to male courtship calls. Moreover, inhalations in courtship calls are sometimes very quiet, while the exhalations often have a clearer structure than exhalations in contact calls, which seem to be noisier (see Fig. 1). The main function of inhalations in courtship calls could thus be to allow males to continue calling and repeat exhalations while getting enough air.

Snowdon (2004) suggested that signals which are a result of sexual selection should be sexually dimorphic and allow individuals to identify the dominance status of the signaller. White rhino courtship hic calls are only produced by males, mostly by territorial holders. In addition, since hic calls have a similar structure to the contact pant calls, they might also encode information on the dominance status of the male in their acoustic parameters. Moreover, the emphasis on repetition of exhalations, which we found in the courtship hic calls, might serve to stimulate or help induce females' oestrus or provide females with information about the quality of a male. Similarly, roaring of red deer stags during breeding season advances oestrus in hinds (McComb, 1987) and hinds make mating decisions based on the vocal characteristics of the roars of stags that indicate their high reproductive success (Reby et al., 2010). In future studies, it would be interesting to examine if courtship calls have an influence on the initiation of oestrus in white rhino females and to compare the courtship calls of various males to assess inter-individual differences and then link these differences to each male's breeding success.

We tested the hypothesis that southern white rhino males assess each other by their calls and use this information to decide on how to respond. In response to the contact calls of intruding subordinates, territorial males reacted more dramatically in that they always approached the speaker and spent the longest time walking and running and thus searching for this intruder, than they did to the calls of an intruding territorial male. There are a number of reasons why a subordinate male may intrude into a territory, including that he may be: 1) looking to challenge the territorial holder for ownership of the territory, 2) on his way to water, or 3) looking for a new home-range within which to non-aggressively settle into as a subordinate (Owen-Smith, 1973). It is thus likely important for the resident territorial male to find the intruding subordinate and confirm his intentions. A similar pattern of more dramatic responses from dominant males towards the calls of subordinate males compared to the calls of dominant males has been observed in other mammals including feral horses (*Equus caballus*) (Rubenstein & Hack, 1992) and harbour seals (*Phoca vitulina*) (Hayes et al., 2004). It is possible that the reason for this is similar in all these species. In addition, subordinate males may pose a lower risk in terms of their fighting abilities in comparison to territorial males. This might explain why the males in our study spent less time trying to assess the situation by looking and being turned with their body towards the speaker in reaction to subordinate contact calls.

Generally weaker responses of the territorial holders to the contact calls of trespassing territorial males compared to subordinate males could be that trespassing territorial males are generally not looking to take over a territory. Moreover, in many cases, confrontations between trespassing territorial males and territorial holders result in the trespasser acting submissive thus avoiding aggressive interactions (Owen-Smith, 1973). This may suggest that there is less urgency in responding to the contact calls of a trespassing territorial male, as they tend to pose little threat, compared to a subordinate male which may be looking to challenge for the territory.

Yet, the weaker responses of the territorial holders to the courtship calls of trespassing territorial males in comparison to the contact calls of subordinate males are perplexing. White rhinos establish territories to secure exclusive breeding opportunities with females (Owen-Smith, 1973). As a result, the courtship calls of a trespassing territorial male would indicate that the territory holder is missing out on a breeding opportunity. In response to a courtship call of an intruding territorial male, territorial males spent the longest time turned and looking towards the speaker, and they showed the longest latency to approach the speaker. In addition, the means of all four behavioural reactions to the territorial contact calls which we recorded were in-between the mean reactions to the courtship territorial and subordinate contact calls (see Fig. A2). However, the reactions of the territorial males to the contact and courtship calls of trespassing territorial males did not differ significantly. This suggests that the territorial holders were not strongly affected by the motivation (type of call) of a territorial trespasser, but rather by the simple fact that the rival territorial male was calling from inside their territory.

Since the costs of an aggressive encounter with an intruding territorial male might be high, as territorial males are generally large and have to be good fighters to have a territory (Owen-Smith, 1973), the territory holder might first want to gather more information and try to assess the situation before reacting intensively. Our results tend to support this as we observed that the males spent more time turned and looking towards the speaker after they heard calls of territorial males in comparison to contact calls of subordinate males. This likely enables them to gather more information about the situation and the intruder. A majority of territorial males then approached and searched for the intruding territorial male. The reason why some did not, might have been due to the vocal parameters of the calls we used for playbacks, which reflected certain physical characteristics of the caller not assessed in our study. Indeed, males of other mammalian species use the vocalizations of an opponent to assess his body size (red deer (*Cervus elaphus*): Reby et al., 2005) and quality (gelada (*Theropithecus gelada*): Benítez et al., 2017) in relation to theirs or to assess his current androgen levels (giant panda (*Ailuropoda melanoleuca*): Charlton et al., 2012) and they modify their reaction accordingly. However, understanding these impacts on the behaviour of southern white rhino males would require further study.

Despite the perceived lower intensity with which the territorial holders (that were in visual isolation from other rhinos) in our study reacted towards the contact pant calls of trespassing territorial males in comparison to subordinate males, the reactions to the territorial contact calls in our study were generally higher (median reaction was approaching and marking the territory or calling) than those recorded by Cinková and Policht (2016) (median reaction was vigilance). Yet, the reactions we recorded tend to correspond to the reactions to territorial contact calls recorded by Cinková and Policht (2016) when territorial males were in the company of an adult female, which they ascribed to the audience effect. The audience effect is when a response of a receiver is influenced by the presence of other individuals and/or the composition of the audience (see Vignal et al., 2004). As the white rhino density in our study site was several times higher than that of Cinková and Policht (2016) (exact values not provided due to security reasons) it is possible that the territorial males in our study reacted more intensively to the calls of other territorial males as there was a greater probability of other rhinos being in a surrounding area. In addition, we found an overall significant effect of a males' identity on their reactions. We observed that some males spent generally more time walking around after the playback of another male, while others spend generally more time looking or being turned with their body towards the speaker. This could have been influenced by various factors which we could not control such as the density of the rhinos in the area, the age of the male, or the time for which he was holding his territory.

Ultimately, our results suggest that white rhino territory holders can obtain key information about trespassing individuals by eavesdropping on their acoustic signals, thus allowing them to react accordingly. Territorial holders therefore obtain another source of information with which they can assess the intention of trespassers and thus better defend their territory and increase their breeding potential.

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Appendix

Table A1

Recordings of contact pant calls of territorial and subordinate males

Male ID	Location	Age	Status
Kashka	Zoo Zlin	Young	Territorial
Dikgopeng	Lapalala Wilderness	Young	Territorial
Pamír	Zoo Dvur Kralove	Young	Territorial
Lwandle	Hluhluwe-iMfolozi Park	Middle	Territorial
Sakhile	Hluhluwe-iMfolozi Park	Middle	Territorial
Bhekumbuso	Hluhluwe-iMfolozi Park	Middle	Territorial
Themba II.	Hluhluwe-iMfolozi Park	Middle	Territorial
Bafana	Hluhluwe-iMfolozi Park	Middle	Territorial
Khwezi	Hluhluwe-iMfolozi Park	Middle	Territorial
Wandile	Hluhluwe-iMfolozi Park	Middle	Territorial
Bongo	Hluhluwe-iMfolozi Park	Middle	Territorial
Victor	Welgevonden Game Reserve	Middle	Territorial
Natal	Zoo Dvur Kralove	Old	Territorial
Funani	Hluhluwe-iMfolozi Park	Old	Subordinate
Siphiwe	Hluhluwe-iMfolozi Park	Old	Subordinate
Sibongiseni	Hluhluwe-iMfolozi Park	Old	Subordinate
Uluthando	Hluhluwe-iMfolozi Park	Young	Subordinate
Bhekizizwe	Hluhluwe-iMfolozi Park	Young	Subordinate
Sfiso	Hluhluwe-iMfolozi Park	Middle	Subordinate
Gatsha	Hluhluwe-iMfolozi Park	Young	Subordinate
Zithulele	Hluhluwe-iMfolozi Park	Young	Subordinate

Age of the males: Young (a male which just achieved adulthood and was around 10–12 years of age), Middle (a fully grown, mature individual), and Old (an animal showing an older age from key traits such as a large posterior horn and wrinkled appearance) (following Owen-Smith, 1973).

Table A2

Recordings of territorial male contact pant and courtship hic calls

Male ID	Location	Age	Call contributed
Kashka	Zoo Zlin	Young	Contact pant call
Dikgopeng	Lapalala Wilderness	Young	Contact pant call
Lwandle	Hluhluwe-iMfolozi Park	Middle	Contact pant call
Sakhile	Hluhluwe-iMfolozi Park	Middle	Contact pant call
Bhekumbuso	Hluhluwe-iMfolozi Park	Middle	Contact pant call
Themba II.	Hluhluwe-iMfolozi Park	Middle	Contact pant call
Bafana	Hluhluwe-iMfolozi Park	Middle	Contact pant call
Khwezi	Hluhluwe-iMfolozi Park	Middle	Contact pant call
Wandile	Hluhluwe-iMfolozi Park	Middle	Contact pant call
Natal	Zoo Dvur Kralove	Old	Courtship hic call
Pamir	Zoo Dvur Kralove	Young	Courtship hic call
Victor	Welgevonden Game Reserve	Middle	Courtship hic call
Themba I.	Mthethomusha Nature Reserve	Middle	Courtship hic call
Bongo	Hluhluwe-iMfolozi Park	Middle	Courtship hic call
Sontuli	Hluhluwe-iMfolozi Park	Middle	Courtship hic call

Age of the males: Young (a male which just achieved adulthood and was around 10–12 years of age), Middle (a fully grown, mature individual), and Old (an animal showing an older age from key traits such as a large posterior horn and wrinkled appearance) (following Owen-Smith, 1973).

Table A3

Playback experiments with particular males and intensities of their reactions to the playbacks on increasing ordinal ethological scale from 0 (no reaction) to 11 (running towards the speaker and marking and calling) (see Table 1 in main text for details)

Male ID	**Control**	**Subordinate Male Contact Pant Call**	**Territorial Male Contact Pant Call**	**Territorial Male Courtship Hic Call**
Bafana	0	10	10	3
Bongo	0	11	7	8
Lwandle	1	7	6	7
Seme	0	7	9	7
Shaka	0	6	6	7
Sontuli	0	7	6	3
Sthenjwa	0	6	6	9
Themba	0	7	10	10
Msizi	-	-	-	3
Thando	-	-	2	-
Mpilo	-	9	-	-
Smiso	-	6	7	7
Thulani	-	-	-	6
Nkosiyabo	-	-	-	3
Vusumuzi	-	7	7	-
Lwazi	-	6	3	-
Khwezi	-	11	6	6
Bandile	-	-	-	10
Bheka	-	-	7	-
Delani	-	-	7	-
Dube	-	-	6	-

Table A4

Variables which were entered into the forward stepwise discriminant function analyses (for status and call type). We indicate if a variable which was entered, was measured in an inhalation (I) and/or an exhalation (E)

Variable	Description of a variable	Status		Call type	
No el.	Number of elements (inhalations and exhalation) in call	Entered		Entered	
Proportion I	Proportion of inhalations in the call out of all call elements	Entered		Entered	
I - cat.1-%	Proportion of inhalations in category 1 (0–0.2 sec) in the call out of all inhalations	Entered		Entered	
Entropy(max)	Quantifies the pureness of sound. It is the ration of the geometric mean to the arithmetic mean of the spectrum (measured at maximum amplitude of element)	I		I	
Hnr(max)	The ratio of harmonic to nonharmonic energy (measured at maximum amplitude of element)	I	E	I	E
Q1st	Start frequency of the 1st DFA [Hz]	I	E	I	E
Q1end	End frequency of the 1st DFA [Hz]	I			
Q1max	Maximum frequency of the 1st DFA [Hz]	I			E
Q1min	Minimum frequency of the 1st DFA [Hz]	I		I	
Q1mean	Mean frequency of the 1st DFA [Hz]	I		I	
Q1med	Median frequency of the 1st DFA [Hz]		E		
Q1maloc	Location of the maximum frequency of the 1st DFA [(1/duration)*location]	I	E	I	E
Q2st	Start frequency of the 2nd DFA [Hz]	I			
Q2end	End frequency of the 2nd DFA [Hz]	I		I	
Q2max	Maximum frequency of the 2nd DFA [Hz]	I			
Q2min	Minimum frequency of the 2nd DFA [Hz]	I			

Q2mean	Mean frequency of the 2nd DFA [Hz]	I	E		
Q2maloc	Location of the maximum frequency of the 2nd DFA [(1/duration)*location]	I	E	I	E
Q3st	Start frequency of the 3rd DFA [Hz]	I	E	I	
Q3min	Minimum frequency of the 3rd DFA [Hz]	I		I	
Q3med	Median frequency of the 3rd DFA [Hz]	I			
Q3maloc	Location of the maximum frequency of the 3rd DFA [(1/duration)*location]	I	E	I	E
Df1st	Start frequency of the first DFB [Hz]	I			
Df1end	End frequency of the first DFB [Hz]	I		I	
Df1max	Maximum frequency of the 1st DFB [Hz]	I			
Df1min	Minimum frequency of the 1st DFB [Hz]	I	E	I	E
Df1mean	Mean frequency of the 1st DFB [Hz]	I	E	I	E
Df1med	Median frequency of the 1st DFB [Hz]		E		E
Df1chfre	Number of changes between original and floating average curve LM of the 1st DFB	I	E	I	E
Df1chmea	Mean deviation LM of the 1st DFB [Hz]	I	E	I	
Df1chmax	Maximum deviation LM of the 1st DFB [Hz]	I			
Df1pr	Percent of time segments where a 1st DFB could be found (%)	I		I	
Df1maloc	Location of the maximum frequency of the 1st DFB [(1/duration)*location]	I	E	I	E
Df1miloc	Location of the minimum frequency of the 1st DFB [(1/duration)*location]	I	E	I	E
Df1trfak	Factor of linear trend of the 1st DFB (global modulation)	I	E	I	E
Df1fretr	Alternation frequency between 1st DFB and linear trend	I	E	I	E
Df2max	Maximum frequency of the 2nd DFB [Hz]	I			
Df2mean	Mean frequency of the 2nd DFB [Hz]	I	E	I	E

Df2pr	Percent of time segments where a second DFB could be found (%)	I	E		E
Df3mean	Mean frequency of the 3rd DFB [Hz]			I	
Df3med	Median frequency of the 3rd DFB [Hz]			I	
Df3pr	Percent of time segments where a 3rd DFB could be found (%)			I	
Diffmax	Maximum difference between 1st and 2nd DFB [Hz]	I	E	I	E
Diffmean	Minimum difference between 1st and 2nd DFB [Hz]	I	E	I	E
Diffremax	Maximum number of DFB’s	I	E	I	
Ampratio1	Amplitude ratio between 1st and 2nd DFB	I	E	I	E
Ampratio2	Amplitude ratio between 1st and 3rd DFB	I	E		
Ampratio3	Amplitude ratio between 2nd and 3rd DFB	I	E	I	E
F1mean	Mean frequency of the 1st GFP [Hz]	I		I	
F2mean	Mean frequency of the 2nd GFP [Hz]	I			
F1wst	Start frequency of the 1st GFP [Hz]	I	E	I	
F1wend	End frequency of 1st GFP [Hz]	I	E	I	
F1wmax	Maximum frequency of 1st GFP range [Hz]	I	E		
F1wmin	Minimum frequency of 1st GFP range [Hz]	I	E		E
F1wmean	Mean frequency of the 1st GFP [Hz]				E
F1wmed	Median frequency of the 1st GFP [Hz]		E		
Fp1max	Maximum frequency of the 1st GFP [Hz]	I			
Fp1amax	Maximum amplitude of the 1st GFP (relative amplitude)	I	E	I	
F2pr	Percentage of time segments where a second GFP could be found (%)	I	E		
Ranmax	Maximum frequency range [Hz]	I	E		E
Ranmean	Mean frequency range [Hz]			I	
Pfmin	Minimum peak frequency [Hz]		E	I	E

Pfmed	Median peak frequency [Hz]	I			
Pftotmax	Frequency of the total maximum amplitude [Hz]			I	E
Pftotmin	Frequency of the total minimum amplitude [Hz]	I			
Pfmaloc	Location of the maximum peak frequency [(1/duration)*location]	I	E	I	E
Pfmiloc	Location of the minimum peak frequency [(1/duration)*location]	I	E	I	E
Pfjump	Maximum difference between successive peak frequencies [Hz]			I	
Pftrfak	Factor of linear trend of peak frequency (global modulation)	I	E	I	
Pftrfre	Alternation frequency between peak frequency and linear trend	I	E	I	E
Pftrmean	Mean deviation between peak frequency and linear trend [Hz]	I		I	
Pftrmax	Maximum deviation between peak frequency and linear trend [Hz]	I			
Csmaxd	Standard deviation of correlation coefficient of successive time segments	I		I	
Csmaloc	Location of maximum correlation coefficient of successive time segments [(1/duration)*location]	I	E	I	E
Disturb	Percentage of disturbed time segments (%)	I	E	I	E
Tonal	Percentage of tonal time segments (%)		E		E

I = inhalation, E = exhalation, DFA = distribution of frequency amplitude, DFB = dominant frequency band, LM = local modulation, P = global frequency peak

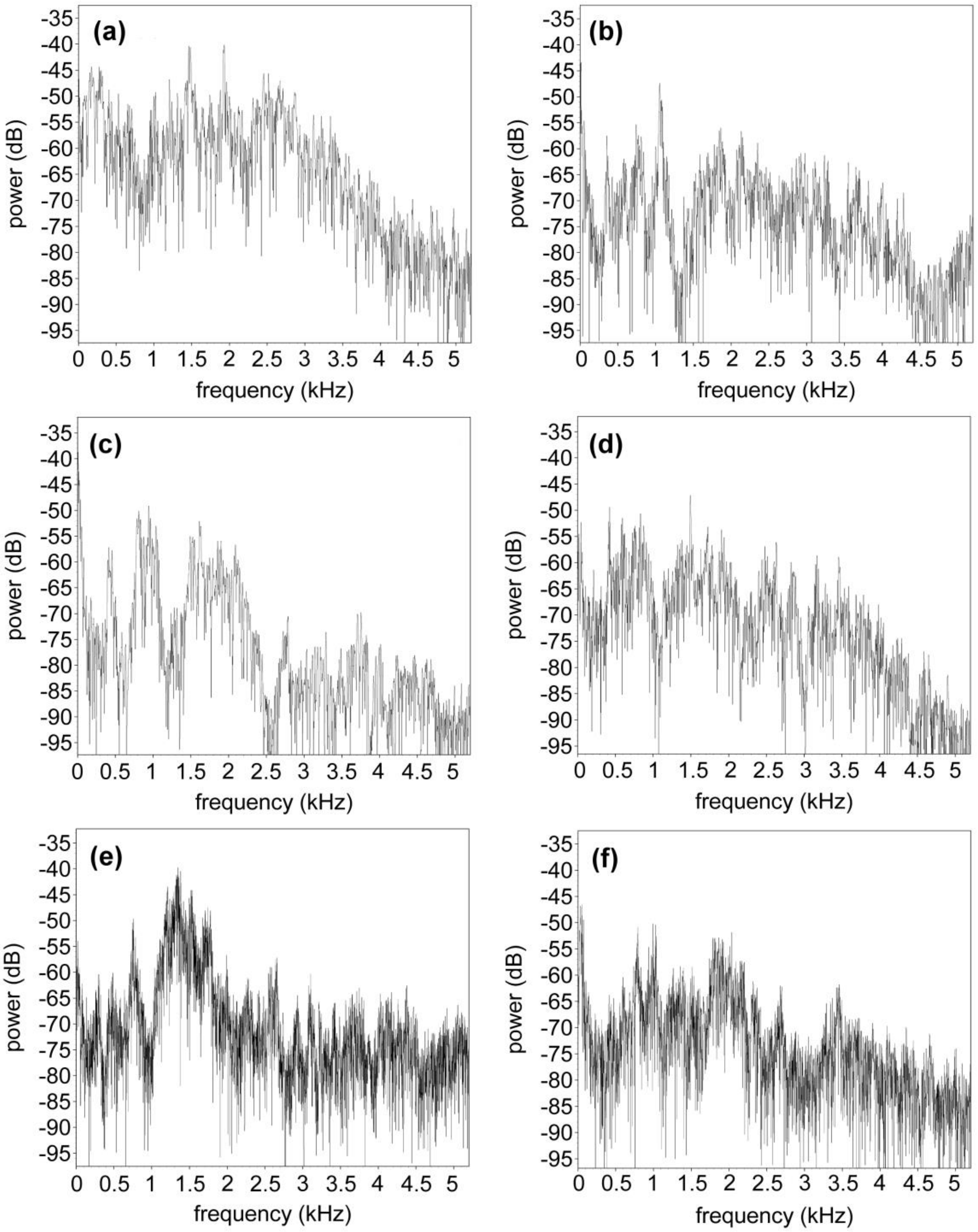

Figure A1. Power spectra (logarithmic) of contact pant calls of territorial and subordinate males: (a) subordinate (male Funani), (b) subordinate (Sibongiseni), (c) subordinate (Bhekizizwe), (d) territorial (male Bongo), (e) territorial (Bhekumbuso), (f) territorial (Sakhile). First 5 kHz of the inhalations are shown. See Table A1 for detailed information about particular males.

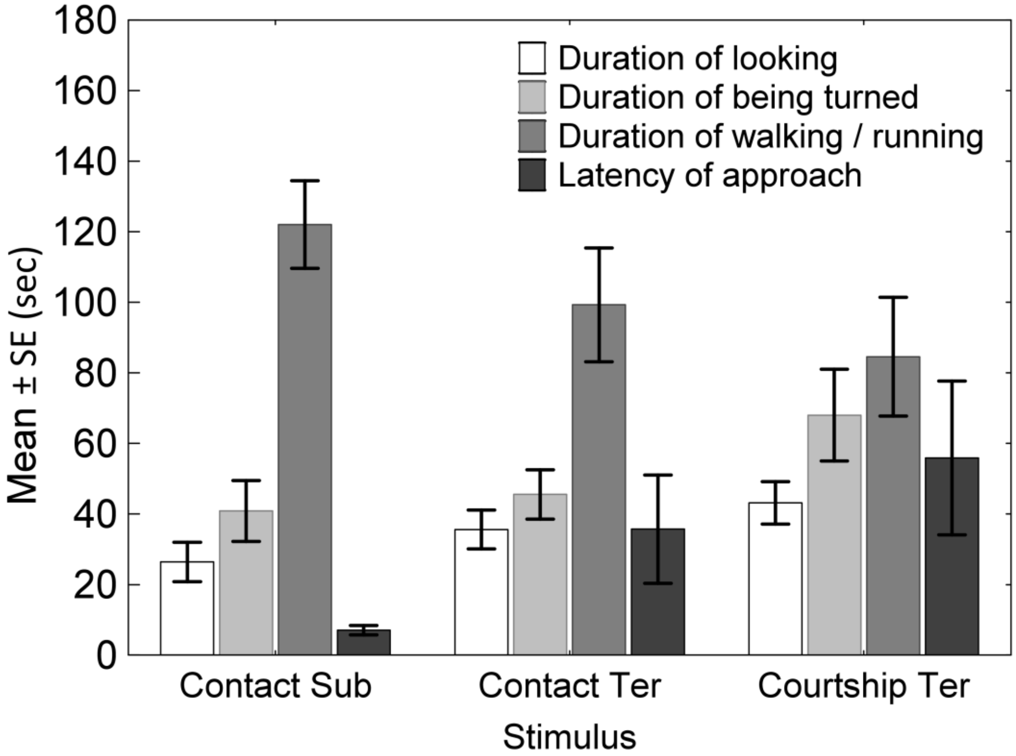

Figure A2. Behavioural reactions of the territorial males towards the playbacks of the contact call of a subordinate male (Contact Sub), contact call of a territorial male (Contact Ter) and the courtship call of a territorial male (Courtship Ter).