

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

Ivana Cinková^{a, b, *}, Adrian M. Shrader^{a, c}

^a School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa

^b Department of Zoology and Laboratory of Ornithology, Faculty of Science, Palacký University Olomouc, Czech Republic

^c Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

ARTICLE INFO

Article history:

Received 5 November 2019

Initial acceptance 16 December 2019

Final acceptance 17 April 2020

MS number 19-00737R

Keywords:

dominance status

motivation

subordinate

territoriality

vocal communication

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 anoestrous 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 trials revealed that territorial males differentiated between the calls of subordinate and other territorial males, showing a shorter latency to 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 probably pose the lowest risk to the resident male in terms of fighting ability. In contrast, the reactions of the territorial males to 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.

© 2020 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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 a male's body size (red deer, *Cervus elaphus*: Reby & McComb, 2003), age (chacma baboon, *Papio cynocephalus ursinus*: Fischer, Hammerschmidt, Cheney, & Seyfarth, 2002) and dominance status (e.g. feral horse, *Equus caballus*: Rubenstein & Hack, 1992; chacma baboon: Kitchen, Seyfarth, Fischer, & Cheney, 2003; fallow

deer, *Dama dama*: Vannoni & McElligott, 2008; spotted hyaena, *Crocuta crocuta*: Mathevon, Koralek, Weldele, Glickman, & Theunissen, 2010; crested macaque, *Macaca nigra*: Neumann, Assahad, Hammerschmidt, Perwitasari-Farajallah, & Engelhardt, 2010). The ability to obtain this information from a male's calls may allow females to quickly assess the quality of the male (Georgiev, Muehlenbein, Prall, Thompson, & Maestriperi, 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-

* Correspondence: I. Cinková, Department of Zoology and Laboratory of Ornithology, Faculty of Science, Palacký University, Olomouc, 771 46, Czech Republic.

E-mail address: ivanacinkova@centrum.cz (I. Cinková).

Smith, 1973, 1975; Shrader & Owen-Smith, 2002). Territorial males communicate their dominance status by marking their territory with dung and urine (Marneweck, Jürgens & Shrader, 2017a, 2018a; Owen-Smith, 1973). However, although olfactory signals can remain in the environment for a long time (Eisenberg & Kleiman, 1972; but see ; Marneweck, Jürgens & Shrader, 2017b, 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, Tomášová, Holečková, & Frynta, 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 (Briefer, 2012; McElligott & Hayden, 1999). 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, Charron, Courcoul, & Rodier, 2011). In other species, males vocalize towards females and competing males during the breeding season (red deer: Reby, Hewison, Izquierdo, & Pépin, 2001; sika deer, *Cervus nippon nippon*: Wyman, Locatelli, Charlton, & Reby, 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 (Ellis et al., 2011; McComb, 1987).

Adult southern white rhino males use a 'hic' call when approaching a female, mainly during courtship. This courtship hic call is a variation of the contact pant call (nonreproductive), which adult males may use when they become visually isolated from a female that they are following (Cinková & Policht, 2016; Policht et al., 2008). Thus, hic calls help indicate the motivation of the male (i.e. reproduction). Although these two calls are most often used in the situations mentioned above, intermediate sounds between pant and hic calls can sometimes be heard in intermediate contexts (e.g. when a bull loses 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, personal 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 hic calls increases with time and during the last few hours before copulation, the male calls intensively and repeatedly tries to mount the female. Since territorial males are usually the only ones to have access to oestrous 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 (Marneweck et al., 2018a; Owen-Smith, 1973). These intrusions may simply be males looking for water, where intruding males either avoid the territory holder or, if confronted, they act submissively, which leads to the confrontation being brief and nonaggressive. However, in some instances these intrusions may lead to the territory 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, Bishop, Crawford, Schmidt-Küntzel, & Stratford, 2012), thus reducing the territorial male's reproductive output.

Territorial males may detect intruders via their olfactory signals at middens (also called dung heaps; 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 and interacts with a female, 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 whether they signal the male's dominance status (territorial or subordinate) and motivation (contact calling towards an anoestrous 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 their behaviours would depend 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 regard to the contact calls of subordinate males, we predicted that territorial males would 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 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 they randomly met while trespassing to reach a water source (Owen-Smith, 1973). Thus, we expected territorial males to react most 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 km² 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 trials with wild free-ranging territorial southern white rhino males. Individual males were identified by features such as variation in horn size and shape, body size, hairiness of ears and tails, and tears and notches in ears. In the playbacks, and for the acoustic analyses, we used the calls recorded in HiP and also 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 & Policht, 2016). Males were regarded as adult from about 10–12

years of age when they attain sociosexual 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 \pm 2.5 db (Sennheiser electronic GmbH & Co. KG, Wedemark, Germany) fitted with a Rycote Softie windshield (Rycote Microphone Windshields Ltd., Stroud, U.K.), and digital recorders Olympus LS-100 (Olympus Corporation, Tokyo, Japan) and Yamaha Pocketrak C24 (Yamaha Corporation of America, Buena Park, CA, U.S.A.) with a 44.1 kHz sampling rate and 16 bits resolution. The calls were recorded 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 oestrous 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 anoestrous female they were following but with which they lost 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). For the calls previously recorded by I.C. in other wildlife reserves and zoological gardens the same recording equipment and procedures were used (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, Appendix Tables A1 and A2). We were unable to record courtship hic calls from subordinate males as they rarely have access to oestrous 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.

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 s; (2) 0.21–0.4 s; (3) 0.41–0.8 s; (4) >0.81 s. Since exhalations and inhalations vary in structure according to their duration (see Cinková & Policht, 2014, 2016), this helps to categorize 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. We calculated entropy and the harmonic-to-noise ratio (both measured at maximum amplitude of element), the number of elements (inhalations and exhalations) in each call, the proportion of inhalations in the call out of all call elements and, owing to the high prevalence in courtship calls, the proportion of inhalations in category 1 (0–0.2 s)

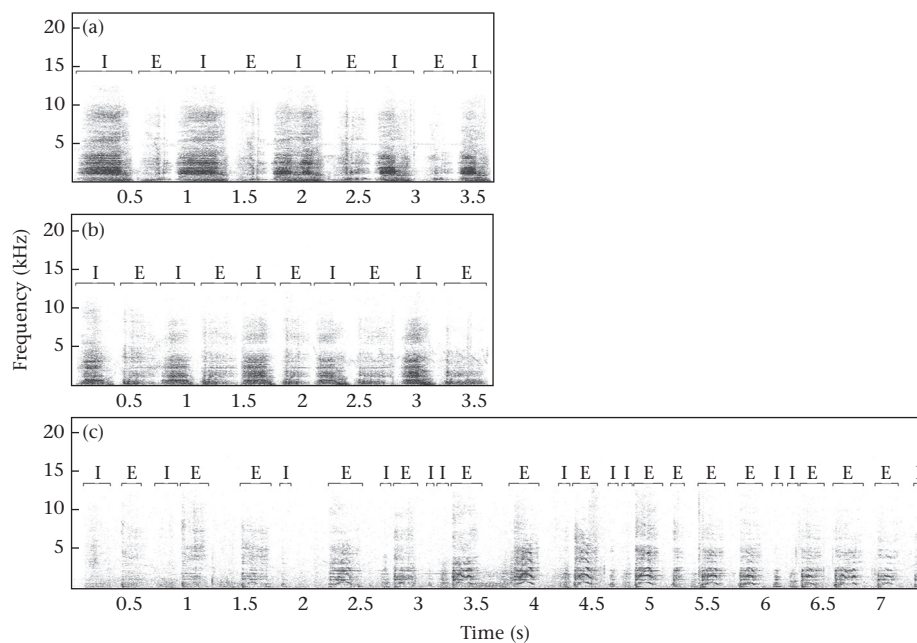


Figure 1. Representative spectrograms of (a) a contact pant call of a subordinate male, (b) a contact pant call of a territorial male and (c) a courtship hic call of a territorial male. The contact and courtship calls of the territorial males are from the same individual to eliminate interindividual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

in the call out of all inhalations. We then saved the spectrograms as .txt files and analysed them using LMA 2015 (developed by K. Hammerschmidt, German Primate Center, Göttingen, Germany), 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 their importance for discriminating between groups (see also [Schrader & Hammerschmidt, 1997](#)).

Playback Trials

To determine whether territorial southern white rhinoceros males discriminate between the contact and courtship calls of territorial males and contact calls of subordinate males, we conducted playbacks on 21 territorial males in HiP. Twelve of these males were exposed to more than one type of these three stimuli ([Appendix 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 male and there was an interval 74 ± 18 days (mean \pm SE) between consecutive playback trials on the same male. We used a territorial call of the emerald-spotted wood dove, *Turtur chalcospilos*, and a contact call of the southern ground hornbill, *Bucorvus leadbeateri*, as controls as they represented neutral sounds for the rhinos, regularly heard in the local soundscape.

In total, we conducted 51 playback trials using four different stimuli (eight trials with a control, 16 using contact calls of six territorial males, 14 using courtship calls of five territorial males and 13 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 at least 8 km from the territory of the subject male. Territory sizes of males in HiP range from 0.75 to 2.6 km² and, normally, territorial males rarely leave their territory except when forced to go to the closest water source during the dry season ([Owen-Smith, 1973](#)). Thus, it is unlikely that the calls of individuals that 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 their duration and number of elements (see Results; [Cinková & Policht, 2016](#)) as these depend 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, personal observations). To account for this, we calculated the mean duration and confidence interval of our recordings (13.4 s; range 11.2–15.0 s) using 38 hic calls from various males. Then, to help control for behavioural variation linked to call duration, we limited the calls we used to those in which the duration was 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 s. However, we did not cut these calls to exactly 13.4 s 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 durations 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, Blankenship, Dawes, & Holekamp, 2010](#); [Benson-Amram, Heinen, Dryer, & Holekamp, 2011](#); [Cinková & Policht, 2016](#)). We targeted rhinos 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 a playback 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 \pm 3 dB) connected to an amplifier (constructed by P. Krchňák and M. Deuschl, 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 levels of 89–96 dB (measured at 1 m from the speaker) depending on the distance of rhinos from the speaker (89 dB for ca. 15 m and 96 dB for ca. 35 m). This is based on the inverse square law of sound transmission through air, with a 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 3 min after each stimulus was played. The order in which the stimuli were played to individual males was random but depended on the availability of specific stimuli. As we were recording some of the calls that we used for playbacks while the playback trials were being carried out, not all the calls were available at the start of the study.

Behavioural Analysis

To quantify male behavioural responses during the playbacks, 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 those to 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 the subject male displayed it within 60 s of 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 3 min after the playback.

Since the intensity of the reactions to the contact and courtship calls differed significantly from that to 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 the body was turned towards the speaker, the duration of walking and running (any movement in general) and the latency to approach the speaker within 3 min of the onset of playback (see [Table 1](#) for descriptions of these behaviours). We recorded the duration of any walking and running instead of the duration of an approach since the latter was generally only short

Table 1
Ethological scale of male responses to the playbacks ordered according to their increasing intensity (following Cinková & 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 at an angle equal to or less than 30°
(3)	Turning body towards the speaker at 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
(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

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

and males then often continued walking or running in the surrounding area, probably searching for the intruder. If we only measured the duration of approach, all this information would be lost. Moreover, we played calls 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 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 a playback trial, a latency of 180 s was assigned. Although the subject males also sometimes reacted with a 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 in only 14% and marking the territory in 46% of reactions).

A second observer (A.M.S.) who was blind to the experimental condition analysed 20% of the videos, to assess interobserver reliability. Spearman rank correlations showed that all analysed behaviours were comparable between observers (duration of looking towards the speaker: $r_s = 0.933$, $P < 0.001$; duration that the body was turned towards the speaker: $r_s = 0.917$, $P = 0.001$; duration of walking and running: $r_s = 0.983$, $P < 0.001$; latency to approach the speaker: $r_s = 0.983$, $P < 0.001$).

Statistical Analysis

To examine the probability of correctly assigning the calls 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 for call type (Appendix Table A4). The parameters were Box–Cox 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. We used exact Mann–Whitney U tests to test the first discriminant scores of both DFAs. To test whether the parameters resulting from the final DFAs differ statistically depending on the dominance status of the male and call type, we also 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 regard to the proportion of inhalations in a call (see Results). Since a courtship call is a special type of 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 regard 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 were recorded in visual isolation, 14 in visual contact with group members; see Cinková and Policht (2016) for details of the animals).

To determine whether the intensity of the males' reactions to the control calls differed to the reactions to the rhino calls, we used a 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 were tested for all four types of stimuli; see Appendix Table A3). Since the data were ordinal and included repeated measures, we could not use a generalized linear mixed model (GLMM) for the analysis. The reactions of males to the control calls differed significantly from those 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 data set (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 the 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 among the rotated components more evenly than before rotation (see Jolliffe, 2002). Before the analysis, the variables were Box–Cox 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 GLMM and included PC scores with a 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. Post hoc 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 because we did not test the reactions of males to the courtship calls of subordinate males (we did not manage to record these calls as subordinate males only rarely have access to an oestrous female, see above), and (2) we tried to run a trial analysis with two fixed effects, but 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, Welch, & Galecki, 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, NY, U.S.A.). The Box–Cox transformations were done using Statistica 13.4.0.14 (TIBCO Software Inc., Palo Alto, CA, U.S.A.). 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 Status and Motivation on Males' Calls

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:

$U < 0.001$, $N_1 = 9$, $N_2 = 6$, $P < 0.001$). Territorial males had more elements and a lower proportion of inhalations in each call and a higher proportion of inhalations in category 1 (0.0–0.2 s) in their courtship call than 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 calls made in isolation and calls made in visual contact with group members (Mann–Whitney U test: $U = 64.5$, $N_1 = 11$, $N_2 = 14$, $P = 0.479$).

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: $U < 0.001$, $N_1 = 13$, $N_2 = 8$, $P < 0.001$). A key difference between the contact calls of territorial and subordinate males was that territorial males had a significantly higher minimum frequency of the second distribution of frequency amplitude in an inhalation (Table 3; see Appendix Fig. A1 for power spectra of contact pant calls of territorial and subordinate males).

Males' Behavioural Reactions during Playbacks

The intensity of the reactions of males to the control sound, territorial contact, territorial courtship and subordinate contact calls differed significantly (exact Friedman test: $\chi^2_3 = 15.689$, $N = 8$, $P < 0.001$; Fig. 2). Specifically, compared to the control, males reacted more intensively to the territorial contact call (exact Wilcoxon signed-ranks test: $Z = -2.536$, $P = 0.048$), the territorial courtship call ($Z = -2.527$, $P = 0.048$) and the subordinate contact call ($Z = -2.546$, $P = 0.048$). 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.

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 Appendix 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 approach the speaker, or they did not approach at all, and spent less time walking

Table 2
Differences in call parameters depending on the call type (motivation) of males

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)	6.0 (3.4–6.8)	<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 s) in call	0.00 (0.00–0.33)	0.66 (0.50–0.83)	5.5	0.03

The parameters are shown in the order they were included by the DFA model. 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 the 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) \times location], df1maloc = location of the maximum frequency of the first dominant frequency band [(1/duration) \times location], IQR = interquartile range. Significant differences after sequential Bonferroni correction are indicated in bold.

Table 3
Differences in call parameters depending on the dominance status of males

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 – pftmean (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 s) in call	0.00 (0.00–0.00)	0.00 (0.00–0.13)	50.5	1

The parameters are shown in the order they were included by the DFA model. 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, pftmean = 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. IQR = interquartile range. Significant differences after sequential Bonferroni correction are indicated in bold.

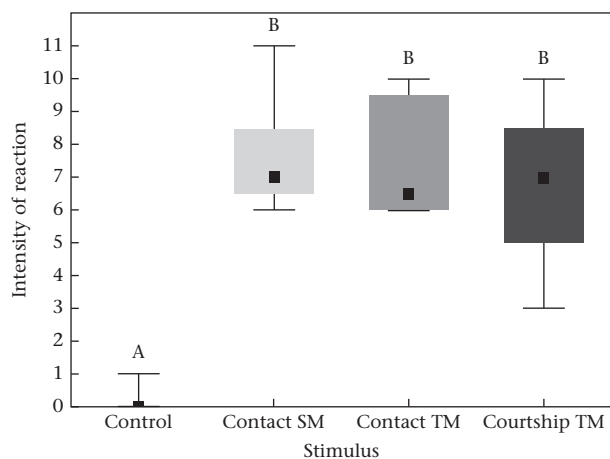


Figure 2. Intensity of reaction of males to the playbacks of the control (i.e. bird calls), the contact call of a subordinate male (Contact SM), the contact call of a territorial male (Contact TM) and the courtship call of a territorial male (Courtship TM). Only eight males tested for all four types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

or running around (Fig. 3). The PC1 scores of males' reactions to the three types of playback 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

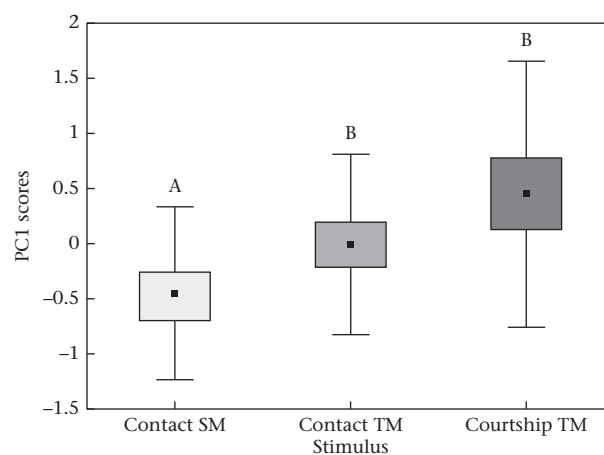


Figure 3. Principal component 1 scores of the reactions of males to the playbacks of the contact call of a subordinate male (Contact SM), the contact call of a territorial male (Contact TM) and the courtship call of a territorial male (Courtship TM). The mean is indicated by the black square, the box represents the standard error and the whiskers show standard deviations. Different letters indicate significantly distinct groups.

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 to 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, they showed the longest latency to approach and spent the longest time with their body turned and looking towards the speaker after the playback of a territorial courtship call (Appendix Fig. A2).

Table 4
Loading factors of behavioural variables on the first and second factor of the principal component analysis

Variable	PC1	PC2
Duration of looking towards the speaker	0.63	0.69
Duration that 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

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 playbacks 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 males 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 an 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: 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, although why is unclear (Neumann et al., 2010). Vocal parameters can be affected by vocal effort or the motivational state of an animal (Fischer, Kitchen, Seyfarth, & Cheney, 2004) or reflect certain features of the calling male such as his body size (Charlton, Zhihe, & Snyder, 2009) or testosterone levels (Charlton, Swaisgood, Zhihe, & Snyder, 2012). In white rhinos, testosterone levels are significantly higher in territorial than subordinate males (Rachlow, Berkeley, & Berger, 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 (Cinková & Policht, 2016; Owen-Smith, 1973). Yet, these calls are longer 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, in contrast, pant calls are longer when individuals are visually isolated from group members (Cinková & Policht, 2016). We found that courtship hic calls of males contain significantly fewer inhalations than exhalations and a greater proportion of shorter inhalations than contact pant calls. In addition, we confirmed that this feature is specific to male courtship calls. Moreover, inhalations in courtship calls are sometimes 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 that 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 territory 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 induce females' oestrus or provide females with information about the quality of a male. Similarly, the roaring of red deer stags during the 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, Charlton,

Locatelli, & McComb, 2010). In future studies, it would be interesting to examine whether courtship calls influence the initiation of oestrus in white rhino females and to compare the courtship calls of various males to assess interindividual 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 territory holder for ownership of the territory, (2) on his way to water or (3) looking for a new home range within which to nonaggressively settle into as a subordinate (Owen-Smith, 1973). It is thus likely to be 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 to the calls of subordinate males compared to the calls of dominant males has been observed in other mammals including feral horses (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 than territorial males. This might explain why the males in our study spent less time trying to assess the situation by looking at and turning towards the speaker in reaction to subordinate contact calls.

Territory holders responded less to the contact calls of trespassing territorial males than to subordinate males, perhaps because the former are generally not looking to take over a territory. Moreover, in many cases, confrontations between trespassing territorial males and territory holders result in the trespasser acting submissively and 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.

Nevertheless, the weaker responses to the courtship calls of trespassing territorial males than 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 we recorded were in between the mean reactions to the courtship territorial and subordinate contact calls (see Appendix 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 territory 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 probably enables them to gather more information about the situation and the intruder. Most 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: Reby et al., 2005) and quality (gelada, *Theropithecus gelada*: Benítez, Pappano, Beehner, & Bergman, 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 territory holders (which were in visual isolation from other rhinos) in our study reacted to the contact pant calls of trespassing territorial males in comparison to subordinate males, their reactions were generally more intense (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 those 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. This is when a response is influenced by the presence of other individuals and/or the composition of the audience (see Vignal, Mathevon, & Mottin, 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 for security reasons) it is possible that the territorial males in our study reacted more intensely to the calls of other territorial males as there was a greater probability of other rhinos being in the surrounding area. In addition, we found an overall significant effect of a male's identity on his reactions. We observed that some males generally spent more time walking around after the playback of another male, while others generally spent more time looking or turned towards the speaker. This could have been influenced by various factors that we could not control such as the density of the rhinos in the area, the age of the male or how long he had held 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. Territory 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.

Acknowledgments

We thank Ezemvelo KwaZulu-Natal Wildlife (EKZNW) for permission to work in Hluhluwe-iMfolozi Park and Dave Druce and Jed Bird (EKZNW) for logistical support during our study. This research was supported by the National Research Foundation (Grant to A.M.S: 114622) and a donation from Mark McCann. I.C. was supported by the Department of Zoology, Palacký University Olomouc and the Internal Grant Agency of Palacký University Olomouc (IGA_PrF_2017_023, IGA_PrF_2018_026). We are thankful to Stanislav Bureš (Palacký University Olomouc) for his support of this study. Two anonymous referees provided valuable comments, which helped to improve the manuscript.

References

Benítez, M. E., Pappano, D. J., Beehner, J. C., & Bergman, T. J. (2017). Evidence for mutual assessment in a wild primate. *Scientific Reports*, 7, 2952.

- Benson-Amram, S., Heinen, V. K., Dryer, S. L., & Holekamp, K. E. (2011). Numerical assessment and individual call discrimination by wild spotted hyenas, *Crocuta crocuta*. *Animal Behaviour*, 82, 743–752.
- Briefer, E. F. (2012). Vocal expression of emotions in mammals: Mechanisms of production and evidence. *Journal of Zoology*, 288, 1–20.
- Charlton, B. D., Swaisgood, R. R., Zhihe, Z., & Snyder, R. J. (2012). Giant pandas attend to androgen-related variation in male bleats. *Behavioral Ecology and Sociobiology*, 66, 969–974.
- Charlton, B. D., Zhihe, Z., & Snyder, R. J. (2009). The information content of giant panda, *Ailuropoda melanoleuca*, bleats: Acoustic cues to sex, age and size. *Animal Behaviour*, 78, 893–898.
- Cinková, I., & Policht, R. (2014). Contact calls of the northern and southern white rhinoceros allow for individual and species identification. *PLoS One*, 9, e98475.
- Cinková, I., & Policht, R. (2016). Sex and species recognition by wild male southern white rhinoceros using contact pant calls. *Animal Cognition*, 19, 375–386.
- Dubost, G., Charron, F., Courcou, A., & Rodier, A. (2011). Social organization in the Chinese water deer, *Hydropotes inermis*. *Acta Theriologica*, 56, 189–198.
- Eisenberg, J. F., & Kleiman, D. G. (1972). Olfactory communication in mammals. *Annual Review of Ecology and Systematics*, 3, 1–32.
- Ellis, W., Bercovitch, F., FitzGibbon, S., Roe, P., Wimmer, J., Melzer, A., et al. (2011). Koala bellows and their association with the spatial dynamics of free-ranging koalas. *Behavioral Ecology*, 22, 372–377.
- Endler, J. A. (1993). Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society, Series B, Biological Sciences*, 340, 215–225.
- Fischer, J., Hammerschmidt, K., Cheney, D. L., & Seyfarth, R. M. (2002). Acoustic features of male baboon loud calls: Influences of context, age, and individuality. *Journal of the Acoustical Society of America*, 111, 1465–1474.
- Fischer, J., Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: Acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*, 56, 140–148.
- Georgiev, A. V., Muehlenbein, M. P., Prall, S. P., Thompson, M. E., & Maestripieri, D. (2015). Male quality, dominance rank, and mating success in free-ranging rhesus macaques. *Behavioral Ecology*, 26, 763–772.
- Guerier, A. S., Bishop, J. M., Crawford, S. J., Schmidt-Küntzel, A., & Stratford, K. J. (2012). Parentage analysis in a managed free ranging population of southern white rhinoceros: Genetic diversity, pedigrees and management. *Conservation Genetics*, 13, 811–822.
- Hayes, S. A., Kumar, A., Costa, D. P., Mellinger, D. K., Harvey, J. T., Southall, B. L., et al. (2004). Evaluating the function of the male harbour seal, *Phoca vitulina*, roar through playback experiments. *Animal Behaviour*, 67, 1133–1139.
- Jolliffe, I. T. (2002). *Principal component analysis* (2nd ed.). New York, NY: Springer-Verlag.
- Kitchen, D. M., Seyfarth, R. M., Fischer, J., & Cheney, D. L. (2003). Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology*, 53, 374–384.
- Marneweck, C., Jürgens, A., & Shrader, A. M. (2017a). Dung odours signal sex, age, territorial and oestrous state in white rhinos. *Proceedings of the Royal Society: Biological Sciences*, 284, 20162376.
- Marneweck, C., Jürgens, A., & Shrader, A. M. (2017b). Temporal variation of white rhino dung odours. *Journal of Chemical Ecology*, 43, 955–965.
- Marneweck, C., Jürgens, A., & Shrader, A. M. (2018a). The role of middens in white rhino olfactory communication. *Animal Behaviour*, 140, 7–18.
- Marneweck, C., Jürgens, A., & Shrader, A. M. (2018b). Ritualised dung kicking by white rhino males amplifies olfactory signals but reduces odour duration. *Journal of Chemical Ecology*, 44, 875–885.
- Mathevon, N., Koralek, A., Weldele, M., Glickman, S. E., & Theunissen, F. E. (2010). What the hyena's laugh tells: Sex, age, dominance and individual signature in the giggling call of *Crocuta crocuta*. *BMC Ecology*, 10, 9.
- McComb, K. (1987). Roaring by red deer stags advances the date of estrus in hinds. *Nature*, 330, 648–649.
- McElligott, A. G., & Hayden, T. J. (1999). Context-related vocalization rates of fallow bucks, *Dama dama*. *Animal Behaviour*, 58, 1095–1104.
- McGregor, P. K. (1992). Quantifying responses to playback: One, many, or composite multivariate measures? In P. K. McGregor (Ed.), *Playback and studies of animal communication* (pp. 79–95). New York, NY: Plenum.
- McGregor, P. K., Catchpole, C. K., Dabelsteen, T., Falls, J. B., Fusani, L., Gerhard, C., et al. (1992). Design of playback experiments: The thornbridge Hall NATO ARW consensus. In P. K. McGregor (Ed.), *Playback and studies of animal communication* (pp. 1–9). New York, NY: Plenum.
- McGregor, P. K., & Peake, T. M. (2000). Communication networks: Social environments for receiving and signalling behaviour. *Acta Ethologica*, 2, 71–81.
- Mundry, R., & Sommer, C. (2007). Discriminant function analysis with non-independent data: Consequences and an alternative. *Animal Behaviour*, 74, 965–976.
- Neumann, C., Assahad, G., Hammerschmidt, K., Perwitasari-Farajallah, D., & Engelhardt, A. (2010). Loud calls in male crested macaques, *Macaca nigra*: A signal of dominance in a tolerant species. *Animal Behaviour*, 79, 187–193.
- Owen-Smith, N. (1971). Territoriality in the white rhinoceros (*Ceratotherium simum*) Burchell. *Nature*, 231, 294–296.
- Owen-Smith, R. N. (1973). *The behavioral ecology of the white rhinoceros*. Ph.D. thesis. Madison, WI: Wisconsin University.
- Owen-Smith, R. N. (1975). The social ethology of the white rhinoceros *Ceratotherium simum* (Burchell 1817*). *Zeitschrift für Tierpsychologie*, 38, 337–384.

- Policht, R., Tomášová, K., Holečková, D., & Frynta, D. (2008). The vocal repertoire in northern white rhinoceros (*Ceratotherium simum cottoni*) as recorded in the last surviving herd. *Bioacoustics*, 18, 69–96.
- Preuschoft, S., & van Schaik, C. P. (2000). Dominance and communication: Conflict management in various social settings. In F. Aureli, & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 77–105). Berkeley, CA: University of California Press.
- Rachlow, J. L., Berkeley, E. V., & Berger, J. (1998). Correlates of male mating strategies in white rhinos (*Ceratotherium simum*). *Journal of Mammalogy*, 79, 1317–1324.
- Reby, D., Charlton, B. D., Locatelli, Y., & McComb, K. (2010). Oestrous red deer hinds prefer male roars with higher fundamental frequencies. *Proceedings of the Royal Society: Biological Sciences*, 277, 2747–2753.
- Reby, D., Hewison, M., Izquierdo, M., & Pépin, D. (2001). Red deer (*Cervus elaphus*) hinds discriminate between the roars of their current harem-holder stag and those of neighbouring stags. *Ethology*, 107, 951–959.
- Reby, D., & McComb, K. (2003). Anatomical constraints generate honesty: Acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour*, 65, 519–530.
- Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W. T., & Clutton-Brock, T. (2005). Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proceedings of the Royal Society: Biological Sciences*, 272, 941–947.
- Rohwer, S. (1982). The evolution of reliable and unreliable badges of fighting ability. *American Zoologist*, 22, 531–546.
- Rubenstein, D. I., & Hack, M. A. (1992). Horse signals: The sounds and scents of fury. *Evolutionary Ecology*, 6, 254–260.
- Ryan, M. J. (1990). Signals, species, and sexual selection. *American Scientist*, 78, 46–52.
- Schrader, L., & Hammerschmidt, K. (1997). Computer-aided analysis of acoustic parameters in animal vocalisations: A multi-parametric approach. *Bioacoustics*, 7, 247–265.
- Shrader, A. M., & Owen-Smith, N. (2002). The role of companionship in the dispersal of white rhinos (*Ceratotherium simum*). *Behavioral Ecology and Sociobiology*, 52, 255–261.
- Snowdon, C. T. (2004). Sexual selection and communication. In P. M. Kappeler, & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp. 57–70). Cambridge, U.K.: Cambridge University Press.
- Sokal, R. R., & Rohlf, F. J. (2012). *Biometry. The principles and practice of statistics in biological research*. New York, NY: W. H. Freeman.
- Vannoni, E., & McElligott, A. G. (2008). Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males. *PLoS One*, 3(9), e3113.
- Vignal, C., Mathevon, N., & Mottin, S. (2004). Audience drives male songbird response to partner's voice. *Nature*, 430, 448–451.
- Waser, P. M., & Brown, C. H. (1984). Is there a "sound window" for primate communication? *Behavioral Ecology and Sociobiology*, 15, 73–76.
- Watts, H. E., Blankenship, L. M., Dawes, S. E., & Holekamp, K. E. (2010). Responses of spotted hyenas to lions reflect individual differences in behavior. *Ethology*, 116, 1199–1209.
- West, B. T., Welch, K. B., & Galecki, A. T. (2007). *Linear mixed models: a practical guide using statistical software*. Boca Raton, FL: Chapman and Hall.
- Wyman, M. T., Locatelli, Y., Charlton, B. D., & Reby, D. (2014). No preference in female sika deer conspecific over heterospecific male sexual calls in a mate choice context. *Journal of Zoology*, 293, 92–99.

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
Pamir	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 that had just achieved adulthood and was around 10–12 years of age), middle (a fully grown, mature individual) and old (an animal with traits indicative of old age 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 that had just achieved adulthood and was around 10–12 years of age), middle (a fully grown, mature individual) and old (an animal with traits indicative of old age such as a large posterior horn and wrinkled appearance) (following Owen-Smith, 1973).

Table A3

Playbacks with particular males and intensities of their reactions to the playbacks on an increasing ordinal scale from 0 (no reaction) to 11 (running towards the speaker and marking and calling) (see Table 1 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 entered in the forward stepwise discriminant function analyses (for status and call type)

Variable	Description	Status		Call type	
No el.	No. of elements (inhalations and exhalations) 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 s) in the call out of all inhalations	Entered		Entered	
Entropy(max)	Quantifies the pureness of sound. It is the ratio 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 first DFA (Hz)	I	E	I	E
Q1end	End frequency of the first DFA (Hz)	I			
Q1max	Maximum frequency of the first DFA (Hz)	I			E
Q1min	Minimum frequency of the first DFA (Hz)	I		I	
Q1mean	Mean frequency of the first DFA (Hz)	I		I	
Q1med	Median frequency of the first DFA (Hz)		E		
Q1maloc	Location of the maximum frequency of the first DFA ((1/duration)×location)	I	E	I	E
Q2st	Start frequency of the second DFA (Hz)	I			
Q2end	End frequency of the second DFA (Hz)	I		I	
Q2max	Maximum frequency of the second DFA (Hz)	I			
Q2min	Minimum frequency of the second DFA (Hz)	I			
Q2mean	Mean frequency of the second DFA (Hz)	I	E		
Q2maloc	Location of the maximum frequency of the second DFA ((1/duration)*location)	I	E	I	E
Q3st	Start frequency of the third DFA (Hz)	I	E	I	
Q3min	Minimum frequency of the third DFA (Hz)	I		I	
Q3med	Median frequency of the third DFA (Hz)	I			
Q3maloc	Location of the maximum frequency of the third 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 first DFB (Hz)	I			
Df1min	Minimum frequency of the first DFB (Hz)	I	E	I	E
Df1mean	Mean frequency of the first DFB (Hz)	I	E	I	E
Df1med	Median frequency of the first DFB (Hz)		E		E
Df1chfre	No. of changes between original and floating average curve LM of the first DFB	I	E	I	E
Df1chmea	Mean deviation LM of the first DFB (Hz)	I	E	I	
Df1chmax	Maximum deviation LM of the first DFB (Hz)	I			
Df1pr	Percentage of time segments where a first DFB could be found	I		I	
Df1maloc	Location of the maximum frequency of the first DFB ((1/duration)×location)	I	E	I	E
Df1miloc	Location of the minimum frequency of the first DFB ((1/duration)×location)	I	E	I	E
Df1trfak	Factor of linear trend of the first ^t DFB (global modulation)	I	E	I	E
Df1fretr	Alternation frequency between first DFB and linear trend	I	E	I	E

(continued on next page)

Table A4 (continued)

Variable	Description	Status	Call type	
Df2max	Maximum frequency of the second DFB (Hz)	I		
Df2mean	Mean frequency of the second DFB (Hz)	I	E	I E
Df2pr	Percentage of time segments where a second DFB could be found	I	E	E
Df3mean	Mean frequency of the third DFB (Hz)			I
Df3med	Median frequency of the third DFB (Hz)			I
Df3pr	Percentage of time segments where a third DFB could be found			I
Diffmax	Maximum difference between first and second DFB (Hz)	I	E	I E
Diffmean	Minimum difference between first and second DFB (Hz)	I	E	I E
Diffremax	Maximum number of DFBs	I	E	I
Ampratio1	Amplitude ratio between first and second DFB	I	E	I E
Ampratio2	Amplitude ratio between first and third DFB	I	E	
Ampratio3	Amplitude ratio between second and third DFB	I	E	I E
F1mean	Mean frequency of the first GFP (Hz)	I		I
F2mean	Mean frequency of the second GFP (Hz)	I		
F1wst	Start frequency of the first GFP (Hz)	I	E	I
F1wend	End frequency of first GFP (Hz)	I	E	I
F1wmax	Maximum frequency of first GFP range (Hz)	I	E	
F1wmin	Minimum frequency of first GFP range (Hz)	I	E	E
F1wmean	Mean frequency of the first GFP (Hz)			E
F1wmed	Median frequency of the first GFP (Hz)		E	
Fp1max	Maximum frequency of the first GFP (Hz)	I		
Fp1amax	Maximum amplitude of the first 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

We indicate whether a variable was measured in an inhalation (I) and/or an exhalation (E). DFA = distribution of frequency amplitude, DFB = dominant frequency band, LM = local modulation, P = global frequency peak.

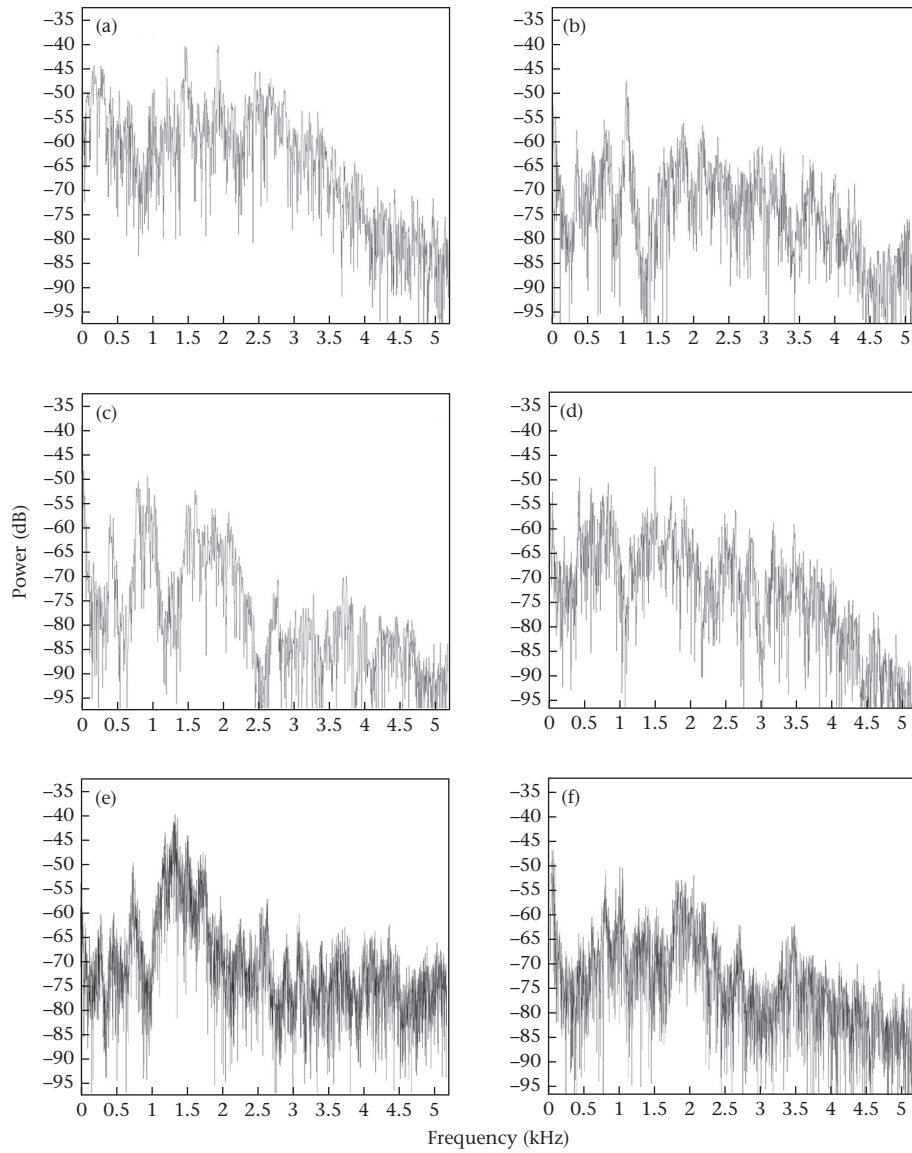


Figure A1. Power spectra (logarithmic) of contact pant calls of territorial and subordinate males: (a) subordinate (male Funani), (b) subordinate (Sibongiseni), (c) subordinate (Bhekezizwe), (d) territorial (male Bongo), (e) territorial (Bhekumbuso), (f) territorial (Sakhile). First 5 kHz of the inhalations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

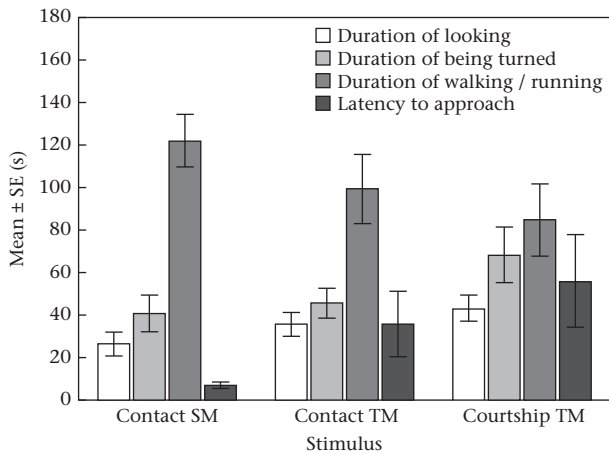


Figure A2. Behavioural reactions of the territorial males to the playbacks of the contact call of a subordinate male (Contact SM), the contact call of a territorial male (Contact TM) and the courtship call of a territorial male (Courtship TM).