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Individuality, species-specific features, and female discrimination of male southern white rhinoceros courtship calls

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Abstract

Male vocalizations associated with courtship can play a key role in mate selection. They may help females obtain information about males' quality and identity and/or may contain species-specific properties that help prevent interspecies breeding. Despite vocalizations being a prominent part of the courtship of white rhinos, the role that they play in white rhino breeding behaviour has not been extensively studied. Both southern (SWR) and critically endangered northern white rhino (NWR) males intensively vocalize during courtship with hic calls. We examined these calls and found that call properties differed between NWR and SWR males. In addition, we found that individual SWR males could be identified with a high degree of accuracy using their hic calls and that the signature information capacity in hic calls would allow females to individually recognize about 11 adult males living in or moving through their home-ranges, which may help with mate selection. Then, we conducted playback experiments with wild anoestrus SWR females. The females discriminated between the NWR and SWR hic calls and between the SWR hic and SWR pant calls. However, we only found differences in the latency of observed behaviours, not in their duration or in the intensity of females' reaction. This might suggest that females which are not in oestrus are not highly responsive to a male's motivation (i.e., seeking contact or mating), but are more interested in assessing his dominance status or familiarity. Ultimately, our results indicate that courtship hic calls encode information which might help females choose mating partners.

Keywords Vocal communication · Southern white rhino · Northern white rhino · Individuality · Species differences · Female mate choice

Introduction

Recognition is required for almost all social interactions and can allow animals to obtain a wide range of information, including an individual's species, motivation (e.g., breeding), and identity (Tibbetts and Dale 2007). The motivational state of an animal (such as in the context of reproduction, or when seeking and maintaining contact between individuals) can affect the acoustic structure of vocalizations and, therefore, inform the receivers of the signaller's intentions (McElligott and Hayden 1999; Briefer 2012). While contact calls can act as a greeting, maintain group cohesion, and help reunite separated individuals (Kondo and Watanabe 2009), signals that are specific for particular species in the context of reproduction can function as a pre-zygotic (premating) isolating mechanism and allow individuals to identify and locate appropriate mates. In addition, if being recognizable improves mating success, sexual selection can favour individuals who actively broadcast information about their identity (Tibbetts and Dale 2007). If females prefer mating with familiar males, individually distinct vocalizations in association with previous experience may increase the reproductive success of particular males (Reby et al. 1998).

The southern white rhinoceros (SWR) (*Ceratotherium simum*) and the critically endangered northern white rhinoceros (NWR) (*Ceratotherium cottoni*) have a wide vocal repertoire and males intensively vocalize towards females during courtship (Owen-Smith 1973; Policht et al. 2008).

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Adult NWR and SWR males are territorial, while subadults, adult females, and calves live in groups in home-ranges that overlap (Owen-Smith 1973; van Gyseghem 1984; Shrader and Owen-Smith 2002). Female home ranges are much larger than males' territories and can encompass 6–7 of them (Owen-Smith 1973). However, although there can be a skew in reproductive success among various territorial males, it is not known which factors influence females to preferentially mate with particular males (Kretzschmar et al. 2020). A male accompanies a female moving within his territory for up to 20 days before she comes into oestrus. During this time, he occasionally approaches her while giving a courtship hic call. For the last few hours prior to copulation, the male repeatedly calls and tries to mount the female (Owen-Smith 1973).

Although male hic calls form an important part of courtship in white rhinos, it is still unknown which information may be encoded in these calls and if this information might assist females with mate choice. Previous research has focused on various information encoded in white rhino contact pant calls (Cinková and Policht 2014, 2016; Cinková and Shrader 2020) and found that SWR and NWR pant calls contain information on the individual identity and species of the caller (Cinková and Policht 2014). The adult males' hic call, as well as their contact pant call, is a nasal call which is emitted with a closed mouth and consists of a series of intensive inhalations and exhalations. Adult males may use a contact pant call when they lose visual contact with a female that they are following (Policht et al. 2008; Cinková and Policht 2014, 2016). Information about individual identity has recently also been found in SWR agonistic grunt calls. However, the level of individual distinctiveness was significantly lower than in pant calls (Linn et al. 2021).

The NWR and SWR are allopatric with the SWR naturally occurring in southern Africa and the NWR (also called the Nile rhinoceros) in central Africa (Hillman-Smith et al. 1986). There is an ongoing scientific debate on whether the NWR and SWR should be treated as subspecies or as separate species (Groves et al. 2010, 2017; Knight 2011; Moodley et al. 2018). A genetic divergence between the NWR and SWR indicates a separation time of over a million years (Groves et al. 2010).

While SWR numbers are between 17,000 and 19,000 individuals in the wild (Emslie et al. 2019), there are only two aging NWR females left on the planet who are no longer capable of carrying a pregnancy to term. As such, the NWR is on the verge of extinction. Researchers are in the process of trying to rescue the NWR by novel stem cell and assisted reproduction technologies using tissue samples and fibroblast cell lines from 13 individuals that have been kept in captivity (Saragusty et al. 2016). In vitro fertilization can be carried out using pure NWR embryos, but the strategy also includes possible creation of hybrid NWR x SWR embryos.

If this happens, the embryos will be transferred into surrogate SWR mothers. Future plans for saving the NWR genes also consider the possibility of natural hybridization between the NWR and SWR (Knight 2011; Saragusty et al. 2016). It is thus essential to better understand their breeding behaviour and possible behavioural differences between the NWR and SWR.

In this study, we first investigated if there are acoustic differences between the courtship hic calls of the NWR and SWR males. Then, we studied if the hic calls of territorial SWR males encode information on the male's identity and calculated information criterion (Hs) to compare our data with the results of Cinková and Policht (2014) on pant calls. Hic calls that are emitted when a male approaches an oestrus female can be distinguished with 100% accuracy from the contact pant calls. Compared to pant calls, hic calls are significantly longer, contain significantly more exhalations than inhalations, and the inhalations are shorter than in pant calls (Cinková and Shrader 2020). Cinková and Shrader (2020) hypothesized that the emphasis on the repetition of exhalations in hic calls may be due to exhalations containing important information about the male for the oestrus female. Pant calls encode information about the individual identity of the caller (Cinková and Policht 2014) and since males use them when they are seeking to re-establish contact with a female (Owen-Smith 1973; Cinková and Policht 2016; Cinková and Shrader 2020), individual recognition can be important in such situations. Hic calls are emitted by males when they can see and are approaching a female, and therefore, there might be a stronger selection pressure for the information about the quality of the male in hic calls rather than his identity. However, identity cues in males' courtship hic calls could be especially favoured if females preferably mate with known males within whose territories they spend a lot of their time. We were thus interested if SWR hic calls may contain stronger information about the individual identity of the caller than pant calls and in which call parameters this information may be encoded.

Since territorial males primarily direct both pant and hic calls towards females (Owen-Smith 1973), females as intended receivers should benefit the most from discriminating various information about the caller. Previous studies only assessed the reactions of territorial SWR males towards these calls (Cinková and Policht 2016; Cinková and Shrader 2020), so we first investigated if adult anoestrus SWR females distinguish between the hic calls of NWR and SWR males. Knowledge about the responses of SWR females to the conspecific/heterospecific courtship signals could give us better insight into whether there might be any behavioural barriers in reproduction between the SWR and NWR. Then, we studied if the females react differently to the pant and hic calls of conspecific SWR males. We are aware that it would be preferable to conduct these experiments

with oestrus females, as this would ensure that they were receptive and likely making mate choice decisions. However, logistically it proved to be too difficult as females in the wild usually only come into oestrus about 27–30 months after falling pregnant (Owen-Smith 1973). In addition, conducting these experiments in zoological gardens was not ideal as captive white rhino females often cycle erratically or not at all (Hermes et al. 2006).

Methods

Study site and animals

We conducted the study in Hluhluwe-iMfolozi Park (HiP; 960 km^2), South Africa from March 2017 to July 2018, in November 2018, and February, June, September and November 2019. In the first part of the study, we recorded hic and pant calls of adult territorial SWR males. Then, we carried out playback trials with wild anoestrus adult SWR females. We considered males as adult from when they attain socio-sexual maturity and become solitary (i.e., 10–12 years of age). Territorial males mark their territory by spray urinating preceded by scrape marking and by kicking their dung after defecation (Owen-Smith 1973; Marneweck et al. 2018). Females become adult when their first calf is usually born (i.e., 6.5–7 years of age). Since an adult male may follow a female for ca. 20 days before she comes into oestrus (Owen-Smith 1973), we considered all females which were not accompanied by a male as anoestrus. We did not determine the oestrus state of the females by faecal hormone analysis as the females were not fitted with radio-transmitters, thus it was logistically impossible to regularly monitor and collect dung from the 45 free-ranging females included in the study. All females in our study were adult and were accompanied by a calf and/or a subadult. We did not conduct a playback trial if the female's group consisted of more than three animals, since this would increase the probability that the reaction of other group members to the playback would influence the reaction of the female. Individuals were identified by tears and notches in ears, their horn size and shape, hairiness of ears and tails, and their body size. In addition, females were also identified by the size and sex of their calf.

For the acoustic analyses and in the playback trials, we used calls recorded during this study in HiP, and calls of territorial SWR males previously recorded by I.C. in Welgevonden Game Reserve, Mthethomusha Nature Reserve (both South Africa), Zoo Dvur Kralove, and Zoo Zlin (both Czech Republic) (see Cinková and Policht 2016). The calls of three territorial NWR males were recorded by I.C. and by Richard Policht (Czech University of Life Sciences Prague) in the Zoo Dvur Kralove between 2005 and 2009.

Recording procedure

We recorded the hic and pant calls 5–25 m from a calling male from a vehicle or on foot. We used a directional Sennheiser microphone ME 67 with K6 powering module (frequency response: 40–20,000 Hz ± 2.5 db; Sennheiser electronic GmbH & Co. KG, Wedemark, Germany) equipped 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. We recorded the pant calls when a male was visually isolated from other rhinos, and the hic calls when the male approached an oestrus female. To obtain the pant calls, we recorded when a male naturally called towards an anoestrus female, or we played back a recording of a pant call and then recorded the male's response. We ensured that we recorded hic calls during courtship and oestrus by keying off the behaviours of the males and females. Specifically, we looked for squirt urinating by the female, and the male closely following, placing his head on the female's hindquarters, mounting her, and trying to copulate (Owen-Smith 1973). The calls from the other reserves and zoological gardens were recorded using the same procedures and equipment (in addition, some of these calls were also recorded with a digital recorder Marantz PMD 671).

Acoustic analysis

We examined the hic calls of three territorial NWR males and six territorial SWR males to study the differences in call parameters between them. We only included one call from each male in the analysis to avoid pseudoreplication (McGregor et al. 1992) as although we recorded a varying number of calls from particular males, we only had one recording of a hic call from one of the three NWR males. Thus, we could not analyse all the recorded calls per individual using permuted discriminant function analysis (DFA), which controls for the multiple use of the same subject. This is because the data used for the calculation of the discriminant functions in permuted DFA should be balanced with regard to the number of replicates included per subject, which we did not have. Thus, the permuted DFA only includes a number of calls per subject which is equal to the lowest number of calls available from any subject (Mundry and Sommer 2007). If we had more than one recording from an individual, we selected high-quality calls with low background noise and randomly chose one call from them.

To analyse the individual differences in hic calls of territorial SWR males, we compared 45 calls from five males (see Table 2). We recorded the calls for each male either on different days or if some of them were recorded on the

same day, we used calls from different recordings, since calls from the same sequence could be more similar in their acoustic structure than calls from different sequences. Unfortunately, due to the small number of recorded hic calls from the three NWR males, we were unable to run a similar analysis for them.

The calls were analysed following Cinková and Policht (2014, 2016) and Cinková and Shrader (2020) using Avisoft SAS Lab Pro 5.2.12 (Avisoft Bioacoustics, R. Specht, Berlin, Germany). We examined the spectrograms of the hic calls (spectrogram parameters: Fast Fourier Transform (FFT) length 1024, frame size 100%, overlap 87.5%, Hamming window, time resolution 2.9 ms) and classified the call elements in each call as either inhalations or exhalations. Inhalations and exhalations vary in structure according to their duration (see Cinková and Policht 2014, 2016) and were, therefore, divided into four categories which helped to classify the call elements of each call: (1) 0.0–0.2 s, (2) 0.21–0.4 s, (3) 0.41–0.8 s, and (4) > 0.81 s. For each call, we calculated the number of elements (inhalations and exhalations), the duration of the longest and shortest inhalation and exhalation, the proportion of inhalations out of all call elements, proportion of inhalations in category 1 (0–0.2 s) out of all inhalations, and the proportion of exhalations in category 1 (0–0.2 s) out of all exhalations.

Since hic calls are repetitive signals, we chose only one inhalation and one exhalation from each call to measure the spectral parameters. These were selected using the duration categories described above. The most frequent duration category of inhalations in each call was identified and one intensive, well-recorded representative element was chosen from that category and was then used in the analysis. The same was done for the exhalations in each call. We analysed the spectrograms of these inhalations and exhalations and calculated their duration (sec), the distance from the start to the location of maximum amplitude (sec), 25%, 50% and 75% quartiles (below these frequencies is 25%, 50% and 75% of the total energy; Hz), the frequency of maximum amplitude (Hz), the entropy (allows to quantify the randomness of the sound) and the harmonic-to-noise ratio (the ratio of harmonic to nonharmonic energy). The frequency parameters and the ratios were measured at maximum amplitude of an element and at mean spectrum of entire element. The spectrograms were then saved as.txt files and analysed using LMA 2015 (developed by Kurt Hammerschmidt), which describes dynamics of a call by calculating many frequency and temporal parameters. Programme LMA was specifically developed for the analysis of complex vocalizations including noisy and atonal calls (Schrader and Hammerschmidt 1997). By computing many acoustic parameters, we could describe complex acoustic patterns without assuming the importance of the different parameters to discriminate between groups (see also Schrader and Hammerschmidt 1997).

Playback experiments

To determine if adult anoestrus SWR females discriminate between the control and the pant calls of territorial SWR males, hic calls of territorial SWR males, and hic calls of territorial NWR males, we conducted playback experiments on 45 females in HiP. In 11 of these playback trials, we used the control, nine were with the hic calls of three territorial NWR males, 10 with the hic calls of five territorial SWR males, and 15 were with the pant calls of seven territorial SWR males. For controls, we used the contact call of a southern ground hornbill (*Bucorvus leadbeateri*) and the territorial call of the emerald spotted wood dove (*Turtur chalcospilos*). These bird species were common in HiP and their calls thus represented neutral sounds for the rhinos. We only played one playback to each of the females and only used each recording of an individual male once to avoid pseudoreplication (McGregor et al. 1992). In addition, we controlled for possible recognition of familiarity by exposing the females to the calls of unfamiliar territorial males. We did this by playing HiP females calls of males from other reserves, or of HiP males whose territories did not overlap with females' home ranges. We were able to ensure this, as we regularly recorded the different study animals in particular locations. Thus, we had a good idea of which individuals we found in the different areas. Territory sizes of males in HiP range from 0.75 to 2.6 km^2 and average home-range sizes of females are 11.6 km^2 (Owen-Smith 1973). Thus, we limited our use of the calls of males to females whose closest known locations were at least 12 km apart.

All the females in our study were accompanied by a calf with an estimated age up to around 2.5 years except for one female, who was only accompanied by a subadult male of about 4 years of age. We suspect that she was either too old to have another calf and her 4-year-old son, therefore, stayed with her or she lost her new calf and was, therefore, joined by a subadult male, who was probably unrelated, but might also have been her previous calf. To keep the conditions for all the playback trials similar, a subject female's calf was not separated from her for more than one rhino body length when a playback was played. Before we played a playback, we made sure that there were no other rhinos than the subject female's group in the visible area surrounding the place of a trial.

The duration and number of elements of white rhino hic calls can vary, as these depend on the distance from which the male starts to approach the female (Cinková and Policht 2016; Cinková and Shrader 2020). As a male often calls for the full distance he travels, the farther away he is from the female, the longer the call. However, when a male

approaches, a female may use agonistic calls and behaviours towards him, which could stop the male from approaching and thus limit the duration and number of elements of the call (I. Cinková, unpublished observations). As such, we pooled our recordings of 38 hic calls from three SWR males and 14 hic calls from three NWR males which were available at the start of the playback trials and after we confirmed normality of their distribution, we calculated the mean duration ± CI for SWR hic calls (13.4 s; range 11.2–15.0 s) and NWR hic calls (13.0 s; range 9.9–16.1 s). Then, to help control for behavioural variations which might be caused by call duration, we limited the calls we used to those in which the durations were within the confidence interval range. If the calls were longer than this, we either cut the start or end of a call, removing the section with the worst recording quality such that the call duration was close to the mean. Yet, we did not cut the calls at exactly the mean as this may have resulted in elements being cut part way. By maintaining the durations of the cut calls within the natural variance, and not cutting the call elements part way, we are confident that the cropped calls sounded natural to the rhinos. Contrary to the hic calls, the variability of the duration and number of elements in pant calls is low (Cinková and Policht 2014, 2016; Cinková and Shrader 2020) and we thus used the original recordings of these calls. Finally, we limited the duration of the control sounds to match the mean duration of the hic calls while not cutting any of the call elements part way.

We played the calls from an open window of a vehicle (following Watts et al. 2010; Benson-Amram et al. 2011; Cinková and Policht 2016; Cinková and Shrader 2020) 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) with an amplifier (kindly constructed by M. Deutschl and P. Krchňák, Department of Biophysics, Palacký University Olomouc). We targeted females that were turned laterally to the speaker, grazing or standing, and were between 15 and 35 m from the vehicle. We equalized the playback stimuli in terms of root mean square amplitude using Avisoft SAS Lab Pro 5.2.12. Since sound pressure level drops 6 dB with each doubling of distance from the sound source (i.e., the inverse square law of sound transmission) (see Waser and Brown 1984), we broadcast the calls with the peak amplitudes at sound pressure level between 89 and 96 dB (measured at 1 m from the speaker) (i.e., 89 dB for ~ 15 m and 96 dB for ~ 35 m). This resulted in the sound pressure level being approximately the same for all the females, irrespective of their distance to the speaker. Moreover, these adjustments resulted in the call volume being the same as a naturally calling rhino.

After each stimulus was played back, we video recorded the behaviour of the females for 3 min. Although the order in which particular stimuli were played to females was generally random, not all the calls were available at the start of the study as we continued to record and obtain calls after the study started. As such, the calls that we used depended on which recordings were available.

Behavioural analysis

The video recordings of the females' reactions to the playbacks were analysed by an experienced observer (I.C.) blind to the experimental conditions (i.e., the videos were muted when being analysed). This research was part of a long-term study and the playback trials were conducted over a period of over two and half years. In addition, the data were analysed about a year after the data collection ended. We used programme Activities 2.1 (developed by Vrba and Donat 1993) and first analysed the intensity of the immediate reaction of the females within 60 s from the onset of the playback to assess the variability of their reactions and to determine whether the immediate reactions to the pant and hic calls differed from control calls. We used ordinal ethological scale and each reaction was scored as one of seven categories (adjusted following Cinková and Policht 2016; Cinková and Shrader 2020; Table 1).

As the intensity of immediate reactions in response to the pant and hic calls differed from the control (see "Results"), we limited our analysis to the responses to the pant and hic calls. We recorded the latency to the first reaction to the playback (using all reactions described in Table 1), which was either routine vigilance or looking or intense vigilance or looking. This allowed us to quantify how fast the females responded to a playback without comparing particular reactions. Then, we recorded the most frequently observed intense reactions (= reactions numbered three and higher in Table 1), intense vigilance (i.e., standing with raised head, feeding stopped, gaze fixed or scanning; the position of the eyes is at the level of or above the height of the skin fold over the base of the animal's foreleg) and intense looking (i.e., head raised facing the speaker at an angle equal to or less than 30°; the position of the eyes is at the level of or above the height of the skin fold over the base of the animal's foreleg), which were observed in 85.3 and 73.5% of the females' reactions, respectively. We recorded the latency and duration of these behaviours within 3 min from the onset of playback. To avoid having highly censored data (when none of these behaviours occurred during the trial), we combined these behaviours into two variables: the latency of intense vigilance and looking (= the latency until one of these behaviours occurred), and the duration of intense vigilance and looking (= the sum of total duration of both behaviours). In two trials, none of these behaviours were observed before the end of the trial and we thus assigned a latency of 180 s to them. We previously assessed the interobserver reliability for these behaviours in a similar playback study (see Cinková

Table 1 Female responses to the playback trials ordered according to their increasing intensity (adjusted following Cinková and Policht 2016; Cinková and Shrader 2020)

No.	Reaction
(0)	No reaction
(1)	Routine vigilance: standing with slightly raised head, feeding stopped, gaze fixed or scanning. The position of the eyes is below the height at which the skin fold over the base of the animal's foreleg is
(2)	Routine looking: head is slightly raised facing the speaker in an angle equal to or less than 30°. The position of the eyes is below the height at which the skin fold over the base of the animal's foreleg is
(3)	Intense vigilance: standing with raised head, feeding stopped, gaze fixed or scanning. The position of the eyes is at the level of or above the height at which the skin fold over the base of the animal's foreleg is
(4)	Intense looking: head is raised facing the speaker in an angle equal to or less than 30°. The position of the eyes is at the level of or above the height at which the skin fold over the base of the animal's foreleg is
(5)	Turning body towards the speaker in an angle equal to or less than 30° while also routinely looking
(6)	Turning body towards the speaker in an angle equal to or less than 30° while also intensely looking
(7)	Approaching the speaker

and Shrader 2020) and Spearman correlation ranks showed high correlations between observers with $r_S > 0.9$.

Statistical analysis

To examine the probability with which the hic calls could be correctly assigned to NWR or SWR males and to an individual (for SWR males), we carried out two forward stepwise DFAs. We checked all the variables computed in Avisoft and LMA and excluded those that had zero variation. Then, we conducted Box–Cox transformation, which resulted in most of the variables achieving normality. The DFA is robust with respect to violation of assumptions of multivariate normality and of homogeneity of covariance matrices (Brown and Wicker 2000). Pairwise correlations between variables were checked and only one from a highly correlated pair ($r \geq 0.85$) was kept in the analyses. This process resulted in 81 variables remaining for the analysis of differences between the NWR and SWR males and 116 for the analysis of differences between individuals (Supplementary Table S1). Using a forward stepwise DFA, we could find call parameters which differed between the NWR and SWR males and between individual SWR without making any prior assumptions and expectations about what parameters should differ (Mundry and Sommer 2007).

The DFA model for the differences between the NWR and SWR males included five parameters. To meet the requirement of DFA of the number of parameters needing to be smaller than the number of objects in the class with smallest sample size (Mundry and Sommer 2007), we ran the final DFA with the first two parameters as the analysis included three calls of NWR males and six calls of SWR males. We then ran the DFA for differences between individual SWR males, and since eight parameters were included by the model, we only used the first four in the final model as two of the males contributed only five calls to the analysis. We

then validated classification results of DFAs using the leave-one-out cross-validation procedure. Exact Mann–Whitney U test was used to test if the first discriminant scores of NWR and SWR hic calls differed. Since the call parameters did not comply with the assumptions for parametric t test (Sokal and Rohlf 2012), we used exact Mann–Whitney U tests (on non-transformed data) with sequential Bonferroni correction to test whether the parameters resulting from the final DFA statistically differed between the NWR and SWR males.

We described the signature information capacity in hic calls of SWR males following Beecher (1989). We did this as it allows for a comparison of the signature information content in the calls across the different species and sample sizes (Beecher 1989). In addition, it has been recommended as a reliable method to quantify individual identity in calls, which gives us the maximum number of individuals that could be discriminated using a set of acoustic parameters (Linhart et al. 2019). Information capacity (H_S) in vocalizations is calculated in bits (Beecher 1989). To estimate the number of individuals that can potentially be discriminated based on the call parameters considered, one can use the value 2^{HS} (Beecher 1982). Following Arnold and Wilkinson (2011) and Carter et al. (2012), we extracted principal components (PCs) with Eigenvalue > 1 using varimax rotation and the four call parameters which were previously included in DFA for differences between individuals. Using the Bartlett method, we saved the PC scores and then obtained the variance component estimate (VCE) of the random factor individual for each retained PC using the ANOVA method, which is robust to departures from the normality assumptions. To estimate the percentage of variance contributed by the random factor, the VCE for each factor was weighted by the percentage variance explained by its corresponding PC. We then calculated the total signature information capacity for inter-individual differences (SB^2) and within-individual differences (=unexplained variation in calls) (SW^2) from the

VCEs. The total variance (ST^2) is calculated as the sum of SB^2 and SW^2. We then summed the information in each PC ($H_i = \log_2 (ST/SW)$) to calculate the total information capacity in the call ($H_S = \Sigma H_i$) and the repeatability of each PC ($SB^2/(SB^2 + SW^2)$)) (Beecher 1989; Arnold and Wilkinson 2011; Carter et al. 2012).

To determine whether the intensity of the females' reactions towards the control and various male calls differed, we used the nonparametric Kruskal–Wallis test on the behaviour scores assigned, since the data were ordinal. Then, we conducted Mann–Whitney U tests with a sequential Bonferroni correction for pairwise comparisons. The reactions of females to the control calls significantly differed from the reactions to all the male calls, and since median reaction to the control calls was no reaction (see "Results"), we omitted the control from further analyses.

To examine if the females discriminated between different types of male calls, we first tested the latency to the first reaction and the latency of intense vigilance and looking. These two variables were not highly correlated (Spearman's correlation coefficient: $r_S = 0.568$). Since the data were positively skewed, we conducted a generalized linear model (GLM) using gamma distribution with log link function. To determine the differences in the duration of intense vigilance and looking of females in reaction to the playbacks, we used GLM with Tweedie distribution and identity link function, since the data were positively skewed and contained two zero values. Call type (NWR hic, SWR hic, SWR pant) was included in the models as a factor. When post-hoc pairwise comparisons were conducted, we applied sequential Bonferroni correction.

All analyses were performed with IBM SPSS Statistics 20.0.0 (IBM Corp., Armonk, USA). Alpha level was set at 0.05 and all tests were two-tailed.

Results

Differences between the courtship hic calls of the southern and northern white rhino males

The courtship hic calls of NWR males consisted of 37 (27–60) elements (median (IQR)), had 0.25 (0.07–0.32) proportion of inhalations in call and 0.73 (0.67–1) proportion of short inhalations (category 1: 0–0.2 s) out of all inhalations in the call. The courtship hic calls of SWR males consisted of 60 (34–68) elements (median (IQR)), had 0.29 (0.32–0.33) proportion of inhalations in call and 0.66 (0.50–0.83) proportion of short inhalations (category 1: 0–0.2 s) out of all inhalations in the call (Fig. 1).

The two call parameters included in the DFA (minimum frequency of the third distribution of frequency amplitude in an inhalation and 75% quartile measured at the mean spectrum of entire exhalation (= below this frequency is 75% of the total energy)) allowed us to assign 100% of male hic calls (100% cross-validated) correctly as NWR or SWR (Wilks' $\lambda = 0.103$, df = 2, $\chi^2 = 13.640$, $p = 0.001$). The first discriminant scores of the NWR and SWR hic calls significantly differed (exact Mann–Whitney U test: $U < 0.001$, $n_1 = 3$, $n_2 = 6$, $p = 0.024$). Hic calls of NWR males had lower minimum frequency of the third distribution of frequency amplitude in an inhalation (median (IQR): 302 (129–1640) Hz) than hic calls of SWR males (2028 (1942–2373) Hz) (exact Mann–Whitney U test: $U < 0.001$, $p = 0.048$). In contrast, the 75% quartile of an exhalation did not differ between the hic calls of NWR (median (IQR): 2670 (2620–5030) Hz) and SWR males (2580 (1850–3230) Hz) ($U = 6.000$, $p = 0.439$).

Information on individuality in southern white rhino male courtship hic calls

The four call parameters included in the DFA allowed us to assign 95.6% of calls (93.3% cross-validated) to a particular male ($N = 5$ males, $n = 45$ calls, Wilks' lambda = 0.001, $p < 0.001$) (Table 2, Fig. 2). The first three discriminant functions with Eigenvalue > 1 explained 98.6% of the variability (Table 3). Using the same four call parameters, we extracted two principal components with Eigenvalue > 1, which accounted for 90.6% of the total variance in calls. From this variation, 86.7% was explained by differences between individuals. Using this model, we calculated the signature information in the SWR males' hic calls, which was 3.52 bits with a mean repeatability of PCs 0.89. This would allow for a discrimination of 11.5 individual males based on the call parameters used.

Females' reactions to the males' courtship hic and contact pant calls

The intensity of the reactions of females to the control sound, NWR hic, SWR hic, and SWR pant calls of males differed significantly (Kruskal–Wallis test: $\chi^2_3 = 19.876$, $n = 45$, $p < 0.001$; Fig. 3). When compared to the control, females reacted more intensively to the NWR male hic call (Mann–Whitney U test: $U = 6.000$, $n_1 = 11$, $n_2 = 9$, $p < 0.006$), the SWR male hic call ($U = 7.500$, $n_1 = 11$, $n_2 = 10$, $p < 0.006$) and the SWR male pant call ($U = 11.000$, $n_1 = 11$, $n_2 = 15$, $p < 0.006$). The intensity of the females' reaction to the NWR hic and SWR hic calls ($U = 38.500$, $n_1 = 9$, $n_2 = 10$, $p = 1$), NWR hic and SWR pant calls ($U = 57.500$, $n_1 = 9$, $n_2 = 15$, $p = 1$) and SWR hic and pant calls ($U = 75.000$, $n_1 = 10$, $n_2 = 15$, $p = 1$) did not differ.

Latency to the first reaction to the playback was significantly affected by the type of male's call such that females displayed the first reaction faster to the NWR hic and SWR
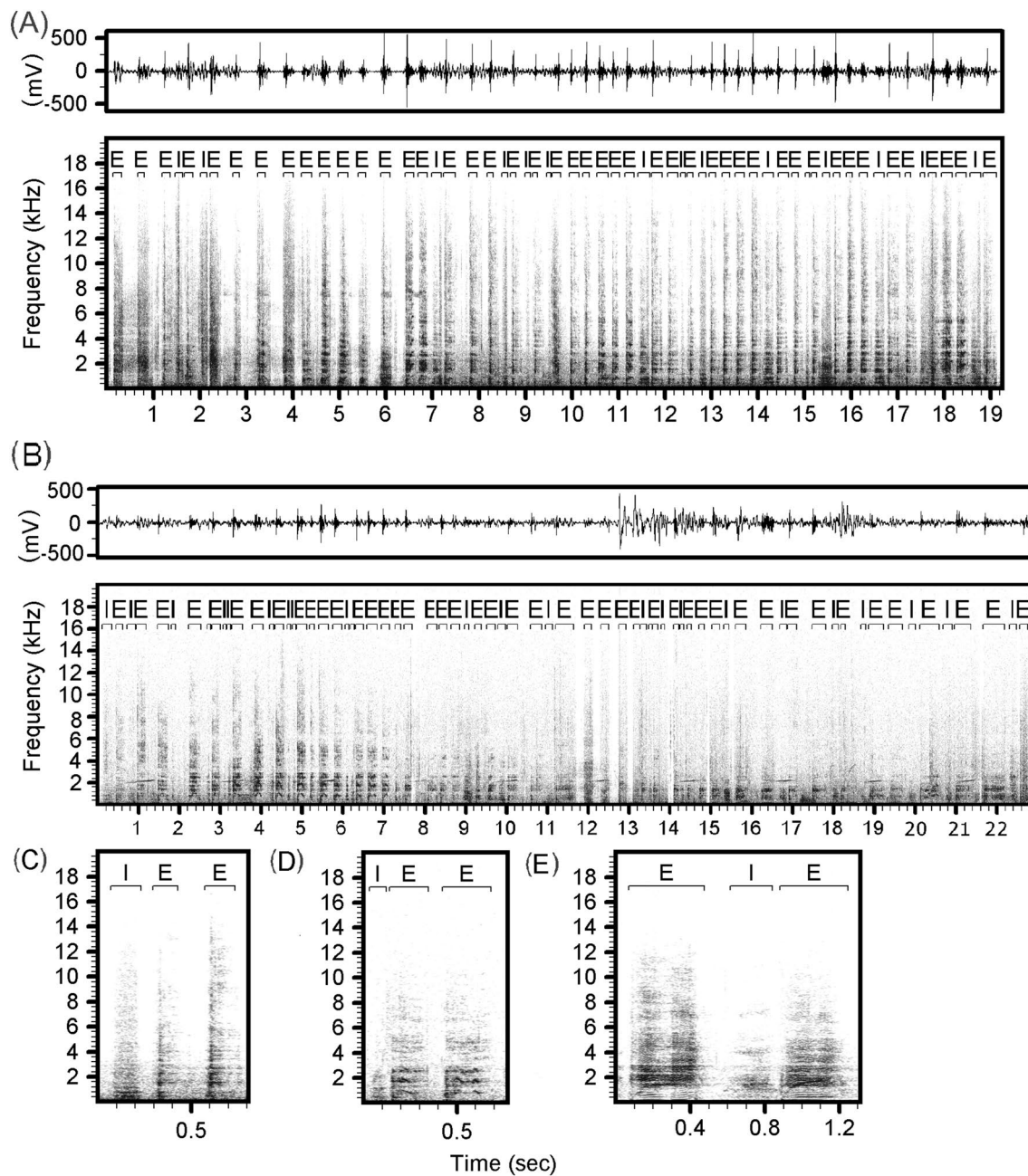
Fig. 1 Spectrograms and waveforms of adult territorial male courtship hic calls **A** entire call of northern white rhino Súdán, **B** entire call of southern white rhino Bongo, and spectrograms showing a detailed structure of the exhalations and inhalations of particular males **C** northern white rhino Súdán, **D** southern white rhino Bongo, **E** southern white rhino Themba. Inhalations **I**, exhalations **E** are shown. Spectrogram parameters: FFT length 1024, frame size 100%, Hamming window, overlap 50% (in graphs **A** and **B**) or 87.5% (in graphs **C**, **D**, **E**)

pant than to the SWR hic call. Moreover, the latency of intense vigilance and looking of females was shorter in reaction to the SWR hic and NWR hic than to SWR pant call. Nevertheless, there was no difference in the duration of intense vigilance and looking in reaction of females to the playbacks (Table 4, Fig. 4).

Discussion

Both northern and southern white rhino males use a conspicuous hic call during courtship (Owen-Smith 1973; Cinková and Policht 2016; Cinková and Shrader 2020).

Table 2 Classification success of courtship hic calls of adult territorial southern white rhino males in discriminant function analysis

Male ID	Location	N of calls contributed	% Correctly classified	% Correctly classified cross-validated
Bongo	Hluhluwe-iMfolozi Park	5	100	80
Natal	Dvur Kralove Zoo	7	85.7	85.7
Sontuli	Hluhluwe-iMfolozi Park	8	87.5	87.5
Themba	Mthethomusha Nature Reserve	20	100	100
Victor	Welgevonden Game Reserve	5	100	100
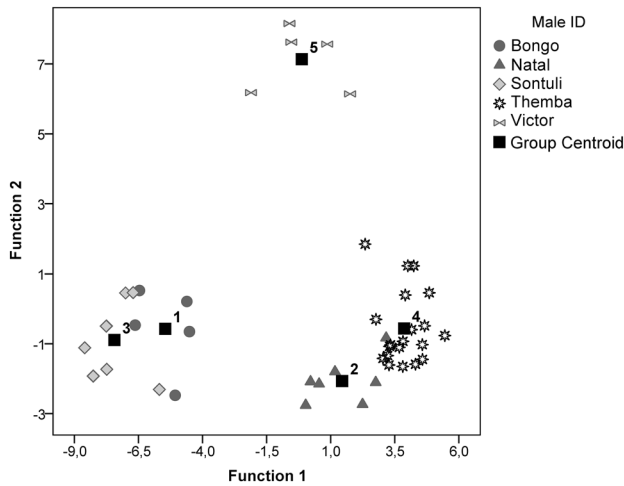
Fig. 2 Vocal individuality in courtship hic calls of adult territorial southern white rhino males. The plot displays the first two canonical discriminant functions with the centroid values of courtship calls for each male

However, the role that this call plays in white rhino breeding behaviour has not yet been extensively studied, nor is it clear whether the hic call encodes information about the calling male, which might assist females with mate choice. We analysed the hic calls and conducted playback experiments with females and found that hic calls differ between the SWR and NWR males. Moreover, our results demonstrate that hic calls of SWR males were individually distinct, with a high level of correct classification in DFA. Playback experiments indicated that wild anoestrus SWR females were able to recognize some differences between the courtship hic calls and contact pant calls of conspecific males and between the hic calls of SWR and NWR males. However, the females only showed differences in reaction to these calls in the latency to the first reaction and in the latency of intense vigilance and looking. We did not find any differences in the intensity of reaction or in the duration of intense vigilance and looking, which might indicate that it is not essential for anoestrus females to strongly distinguish between these calls. However, they may well discriminate between them and show stronger differences in reaction between pant and hic and between hic calls of SWR and NWR only when they are in oestrus. This, however, requires further research.

If there is a benefit to being accurately identified, signallers would be expected to actively broadcast their identity with distinctive cues (Tibbetts and Dale 2007). In a previous study (Cinková and Shrader 2020), we found that courtship hic calls in comparison to contact pant calls contain a larger proportion of exhalations than inhalations and that the inhalations are shorter in hic calls. We hypothesised that the reason for increased repetition of exhalations in hic calls might be that they contain information on the quality

Table 3 Mean ± SE of four acoustic variables entered into the DFA for individual differences in courtship hic calls of southern white rhino males

Variable	Description	Mean ± SE	Discriminant functions		
			1	2	3
E—quart25(mean)	25% quartile (measured at mean spectrum of entire element)	1064 ± 104.0	0.824	0.157	− 0.501
E—q3med	Median frequency of the third distribution of frequency amplitude (Hz)	4743 ± 321.1	0.429	0.683	0.499
E—f1wmed	Median frequency of the first global frequency peak (Hz)	2391 ± 226.1	0.057	0.424	− 0.338
E—ranmean	Mean frequency range (Hz)	4360 ± 611.6	0.572	− 0.377	0.180
Eigenvalue			22.62	7.47	1.37
% of variance			70.9	23.4	4.3
Cumulative %			70.9	94.3	98.6

DFA structure matrices show the pooled within group correlations between discriminating variables, and standardized canonical discriminant functions with Eigenvalues > 1
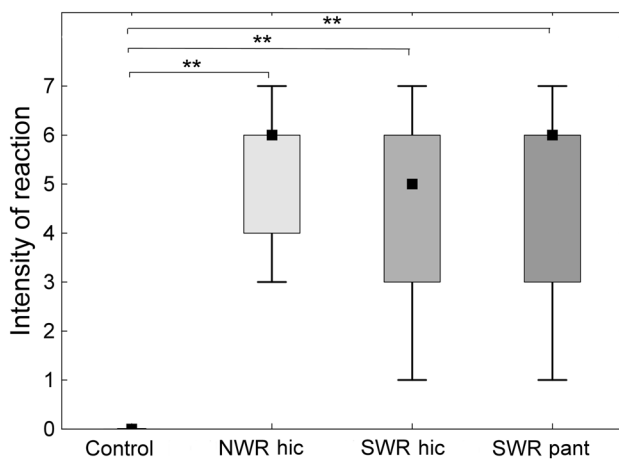
Fig. 3 Intensity of reaction of females 60 s from the onset of the playback of a control (i.e., bird calls), northern white rhino courtship hic call (NWR hic), southern white rhino courtship hic call (SWR hic) and southern white rhino contact pant call (SWR pant). The intensity of reaction increases on ethological scale from 0 (no reaction) to 7 (approaching the speaker) (see Table 1 for details). Median is indicated by the black square, box represents 25–75% quartile range and the whiskers show non-outlier range. **$p < 0.01$

Table 4 Results of statistical tests examining the differences in the reactions of southern white rhino females to the playbacks of southern (SWR) and northern (NWR) white rhino male courtship hic and contact pant calls

Variable	Test statistic	p value
Latency to the first reaction	$\chi_2^2 = 14.594$	**0.001**
Stimulus	$\chi_2^2 = 16.591$	**<0.001**
SWR hic vs SWR pant		**0.003**
SWR hic vs NWR hic		**0.008**
SWR pant vs NWR hic		0.695
Latency of intense vigilance and looking	$\chi_2^2 = 17.650$	**<0.001**
Stimulus	$\chi_2^2 = 23.527$	**<0.001**
SWR hic vs SWR pant		**0.016**
SWR hic vs NWR hic		0.302
SWR pant vs NWR hic		**0.008**
Duration of intense vigilance and looking	$\chi_2^2 = 3.817$	0.148
Stimulus	$\chi_2^2 = 4.648$	0.098

Significant differences are in bold

of the male, and/or stimulate the female into oestrus. The results from this study show that exhalations in hic calls indeed encode important information about the vocalizing male, since DFA included four frequency parameters of exhalations as the most important parameters for recognition among individual males. On the contrary, individual differences in SWR pant calls were previously described to be mediated mainly through the temporal parameters of calls, including call duration, number of elements in the call,

and temporal characteristics of inhalations and exhalations in the call (Cinková and Policht 2014).

Individual distinctiveness in vocalizations can vary within the same species depending on the call type and is to some extent influenced by the acoustic structure and context of calls (Leliveld et al. 2011; Linn et al. 2021). The information about the individual identity which we found in SWR male courtship hic calls is somewhat greater than that which was previously found in white rhino contact pant calls. Identity cues in contact calls can be important for the (1) recognition of group members when they get out of sight or when establishing a contact after a short separation, (2) identification of some members of other groups which share the same home-range, and (3) recognition of territorial or subordinate males in whose territories or home-ranges rhinos spend most of their time. The total information capacity in SWR pant calls was found to be 3.15 bits based on the call parameters used, which allows for a recognition of approximately nine individuals (calculations included acoustic differences between sexes so this includes both males and females) (Cinková and Policht 2014). In our study, we determined that the total information capacity in SWR male hic calls was 3.52 bits and thus enables for a discrimination of 11.5 individual males. Somewhat greater information capacity in hic calls than in pant calls may indicate a greater need for correct identification of males during courtship. For example, since the home ranges of SWR females can encompass six to seven male territories and within each of these territories, there can be up to three adult subordinate males (Owen-Smith 1973), being able to correctly identify individuals might help females to distinguish a preferred mating partner from other familiar males or from unknown trespassing males.

Although SWR males intensively associate with females only shortly before they come into oestrus and females freely move across the territories of various males, females spend about 50% of the wet season in one or two adjacent territories (Owen-Smith 1973). It has been shown that there can be a skew in mating success among various territorial males and that many females could be monogamous (Kretzschmar et al. 2020). White et al. (2007) found that the preferential use of male territories by wild SWR females was significantly correlated with total grassland area in the territories and their study also indicated that females most likely mated with males in whose territories they spend most of the time. This would emphasize the need of females to use reliable cues, including acoustic ones in courtship hic calls, to recognize the owner of the preferred territory. Nevertheless, to determine if SWR females use cues encoded in hic calls to individually identify males and assess their quality and suitability as a mating partner, further research is required.

In our study, calls of two of the males from HiP clustered together in DFA for individual differences between males
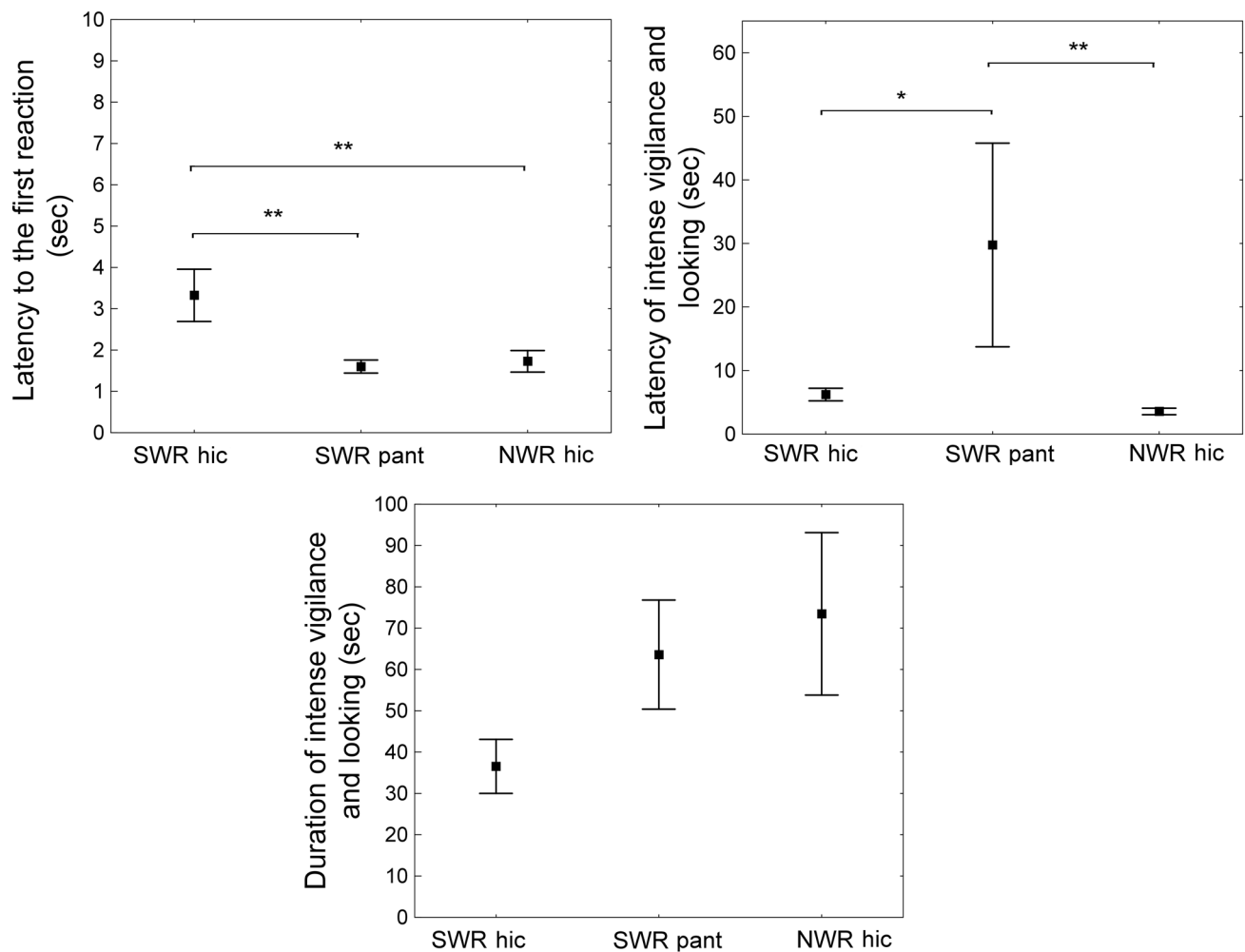
Fig. 4 Latencies and duration of reactions of females to the playbacks of northern white rhino courtship hic call (NWR hic), southern white rhino courtship hic call (SWR hic) and southern white rhino contact pant call (SWR pant). The data are shown as mean ± SE. Asterisks indicate significant differences between groups: **$p < 0.01$, *$p < 0.05$

(see Fig. 2). We cannot exclude that males from the same population might have similar calls. However, calls of two other males from different distant locations also clustered together. It is thus possible that this is a coincidence as calls of some individuals may naturally be more similar than calls of other individuals.

Different responses to conspecific and heterospecific signals should especially be important in the context of courtship as mistakes in mate choice can result in wasted reproductive investment for females (Ord and Stamps 2009). In various species, communication signals can serve as a pre-zygotic isolating mechanism preventing hybridization between closely related species (Bradbury and Vehrencamp 1998). However, species-specific mating calls in naturally allopatric species may not provide a solid barrier between them and thus they could be capable of hybridization when introduced in the same areas. This may be due to the fact that there is no need for the animals to discriminate between

the signals of conspecifics and signals of a closely related species when they do not share the same range. The differences in calls between them can thus rather be a consequence of divergent sexual selection pressures deriving from geographic isolation and improved environmental propagation (Wyman et al. 2011, 2014). As the distribution ranges of NWR and SWR have been separated within recorded history by ca. 2000 km (Hillman-Smith et al. 1986), it is unlikely that they would be familiar with the differences in each other's calls.

As the last male NWR died in 2018, and the remaining two females cannot carry young to term, the NWR can only be saved from extinction by in vitro fertilization followed by the transfer of the embryo into a surrogate SWR mother. Since the conservation strategy for the NWR does not only consider creating pure NWR embryos, but also hybrid embryos between the NWR and SWR and future plans also consider possible natural hybridization between

them (Knight 2011; Saragusty et al. 2016), research into their vocal behaviour and courtship calls might help to reveal any potential behavioural barriers in interbreeding between the NWR and SWR. In our study, we were able to assign 100% of courtship hic calls correctly as NWR or SWR male. Moreover, anoestrus SWR females in our study showed some differences in reaction to the NWR and SWR males when their latency to the first reaction was shorter to the NWR hic calls. Similar calls of an allopatric species, which, however, contain novel characteristics, could elicit a quicker response than familiar conspecific calls (Tulving and Kroll 1995; Ord and Stamps 2009). If a pure NWR male is born via in vitro fertilization in the future and later socialized with SWR females, our results provide a valuable insight suggesting that the differences in hic calls between the SWR and NWR males might potentially lead to a reduction in likelihood of natural hybridization between the NWR and SWR. The vast majority of mammals produce only innate vocalizations which are evoked by sexual cues or emotional state and are not learned through cultural experience or through vocal practice (Nieder and Mooney 2019). Thus, it is highly likely that the acoustic structure of the courtship hic calls is also innate and, therefore, would not be modified by learning if a NWR male would grow up with SWR. However, further research involving SWR and NWR females in oestrus would be required to determine whether the differences in courtship hic calls might provide a barrier in hybridization between the SWR and NWR when they are brought together.

In our study, the latency of the first reaction of SWR females was shorter to SWR contact pant calls than to SWR courtship hic calls. On the contrary, their latency of intense vigilance and looking was shorter to SWR hic calls than pant calls. This result shows that while the females first quickly attended to the playback of male contact pant call, this reaction usually only included routine vigilance or looking, and the females were not interested to immediately pay more attention to the call with intense vigilance or looking like they did with courtship hic calls. However, there were no differences in the intensity of reaction or in duration of intense vigilance and looking, which can indicate that females which are not in an oestrus state may not attend intensively to a male's motivation (trying to establish contact or wanting to mate) but rather may be interested in assessing his familiarity and identity, dominance status (territorial or subordinate), or his quality.

In our study, except for one female who was in a group with a 4-year-old subadult male, each female was accompanied by her young calf until about 2.5 years of age. Since mothers are protective of their calves (Owen-Smith 1973), it might be possible that cows with younger calves could be more attentive to some vocalizations of an unknown adult male nearby due to a possible increased need to protect the calf against him. In addition, once a female's calf

is around 1 year of age, she usually comes into oestrus and falls pregnant, while the current calf continues to accompany her until the new one is born (Owen-Smith 1973). It might thus also be possible that the reproductive phase of the female (lactation anoestrus/cycling/pregnant) can play a role in her attentiveness to vocalizations of males. However, our sample size was small and unbalanced with regards to various age-groups of calves accompanying their mothers, which prevented us from making any detailed comparisons and conclusions.

Breeding behaviour of white rhinos has not been studied extensively, and thus all the factors which may influence females to preferentially mate with particular territorial males are not known (White et al. 2007; Kretzschmar et al. 2020). A majority of free-ranging white rhinos are kept in fenced protected areas and more information about their behaviour during courtship and breeding would help to properly manage their populations. In addition, behavioural research can help pinpoint and resolve problems with breeding of captive populations (Lindburg and Fitch-Snyder 1994). The southern and northern white rhinos have very low rate of reproduction in captivity (Hermes et al. 2005, 2006) and the reasons for this are still not fully understood. Vocal displays form a prominent part of white rhino courtship and the role of vocalisations in mate choice and possibly in stimulating females' oestrus should thus be properly established.

Declarations

ABS (2017) guidelines for the treatment of animals in behavioural research and teaching.

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