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Discrimination of familiarity and sex from chemical cues in the dung by wild southern white rhinoceros

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Abstract Communication in rhinos is primarily mediated by the vocal and olfactory signals as they have relatively poor eyesight. White rhinos are the most social of all the rhinoceros species, they defecate at common dungheaps and the adult bulls use dung and urine to mark their territory. Chemical communication may therefore be particularly important in the social interactions of white rhinos, and its knowledge could be very helpful in their management and conservation. However, no studies have investigated up until now the olfactory discrimination in any rhinoceros species in the wild. We have experimentally studied the reactions of the wild southern white rhinos (*Ceratotherium simum*) to the dung of familiar and unfamiliar adult females and adult territorial males. We registered the number of sniffing events, the duration of sniffing and the latency of the vigilance posture from the onset of sniffing. The dung of unfamiliar rhinos was sniffed longer than that of familiar rhinos. The rhinos showed a shorter latency of vigilance posture to the familiar dung of males than that of females. For unfamiliar dung, they displayed a shorter latency of vigilance posture to female than male dung. Our results indicate that the rhinos are able to discriminate the familiarity and sex of conspecifics from the smell of their dung. Olfactory cues could therefore play an important role in the social relationships and spatial organization of the southern white rhinoceros.

Introduction

Olfactory signals have an advantage in that they persist for some period of time in the absence of the depositor and allow the receivers to specifically assess certain parameters of their social environment (Eisenberg and Kleiman 1972). Terrestrial vertebrates perceive olfactory signals via the main olfactory system, which is receptive to volatile signals and through the vomeronasal system, which primarily processes non-volatile pheromones (reviewed by Dulac and Torello 2003). Olfactory signals often play an important role in the communication of ungulates (Grau 1976), which have a well-developed vomeronasal organ (Eisenberg and Kleiman 1972). Vocal and olfactory signals are extremely important for communication in rhinos as they have an excellent sense of hearing and smelling, but relatively poor eyesight (Penny 1987). Cinková and Policht (2014) have recently determined that the contact calls of white rhinos contain information on the individual identity, age class, context and species of the caller (northern versus southern white rhinoceros) and similar information about the signaller may be present in their olfactory cues. Scent-marking behaviours provide honest signals of competitive ability and quality of the signaller to conspecifics in mammals. The receivers assess the signallers by use of

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intrinsic information (for instance, the density of markings or the concentration of hormones), by using memorized information about past opponents and their odours or by scent matching (Gosling and Roberts 2001). According to the scent matching hypothesis, the receiver identifies that an individual is a resource holder and a high-status animal only after meeting it and matching its odour to the receiver's memory of the individual's scent marks (Gosling 1982).

Olfactory cues allowing for the discrimination of individual identity, sex or familiarity in mammals can be contained, for instance, in faeces (horse: Rubenstein and Hack 1992; Krueger and Flauger 2011; domestic cat: Nakabayashi et al. 2012; black rhinoceros: Linklater et al. 2013), urine (giant panda: White et al. 2004; African elephant: Bates et al. 2008; koala: Charlton 2014), body odour (horse: Péron et al. 2014), anogenital gland secretion (brown bear: Jojola et al. 2012) or in a combination of odours from anogenital scent marks, urine, faeces and the pelage (giant panda: Swaisgood et al. 2000). Urine marks can also allow the discrimination of one's own urine from the urine of other familiar conspecifics (domestic dog: Bekoff 2001).

Apart from the pedal glands that have been reported in Indian and Javan rhinos (Cave 1962) and the preputial glands in the white rhinoceros (Cave 1966), rhinos do not have any specialized scent glands. Dung, urine and general body odour thus seem to be the only carriers of scent cues in the white rhinoceros (Owen-Smith 1973). White rhinos defecate at common dungheaps and, when encountering a dungheap, often pause to sniff at dung accumulation for some time (Owen-Smith 1973). The adult females, subadults and juveniles of southern white rhinos live in overlapping home ranges in groups consisting most frequently of two to three individuals (Owen-Smith 1973, 1975; Shrader and Owen-Smith 2002). The adult males are solitary and defend territories, which are exclusive of the territories of other males. They mark their territory, including its boundaries, by kicking movements before and after the defecation to scatter their dung and by spray urination, which is preceded by scrape marking (Owen-Smith 1971, 1973, 1975; Rachlow et al. 1999).

Marking of the territory boundaries is reported more often than marking towards the centre of the territory, which is, however, more usual in very large territories (reviewed by Gosling and Roberts 2001). Kretzschmar et al. (2001) observed that the spray marks of adult southern white rhinoceros males were located closer to the territory border than their dung. Dung might therefore provide more information about the movements of an animal around its territory. In contrast to southern white rhinoceros females, who only rarely scrape their dung after

defecation (Owen-Smith 1973), black rhinoceros females scrape mark more often and the length of the scrapings carries the information about their reproductive state. The length of the scrapings increases in both male and female black rhinos with age (Freeman et al. 2014).

Groves et al. (2010) have recently suggested that two distinct forms of the white rhinoceros should be elevated from the subspecies to the species level, the southern white rhinoceros (*Ceratotherium simum*) and the northern white rhinoceros (*Ceratotherium cottoni*), which has also lately been referred to as the Nile rhinoceros (e.g. Rookmaaker 2011, Rookmaaker and Antoine 2012) following Heller (1913). The population of the northern white rhinoceros presently consists of only seven animals, which makes it one of the most endangered mammals in the world. The numbers of the southern white rhinos are estimated to be 20,424, but poaching for their horn is currently on a rapid increase (Knight 2013).

White rhinos have very low reproductive success in captivity, and both females and males often suffer from reproductive pathologies (Hermes et al. 2005, 2006). Social interactions between the captive rhinos might be one of the possible reasons for the low reproduction (Meister 1997; Swaisgood et al. 2006; Metrione et al. 2007; Cinková and Bičík 2013; Cinková and Policht 2014). White rhinos are the most social out of all the rhinoceros species (see Goddard 1967; Owen-Smith 1973, 1975; Laurie 1982; Penny 1987) and develop a network of social relationships in the wild with their conspecifics inhabiting the same area (Owen-Smith 1973, 1975). This is not available, however, to the rhinos living in the limited environments of zoological gardens. A better understanding of chemical communication in another species with low reproductive success in captivity, the giant panda, has substantially helped improve their breeding programme (Swaisgood et al. 2000, 2003). The use of rhinoceros dung has been suggested as a management tool to help stimulate the reproductive and territorial behaviour of captive rhinos (Fouraker and Wagener 1996) and to assist the management of wild rhinos (Linklater et al. 2006). Linklater et al. (2013) have recently experimentally studied olfactory discrimination in temporarily captive black rhinos. Studies on the olfactory communication of white rhinos, however, remain mainly descriptive and anecdotal.

The aim of this study was to test whether the wild southern white rhinos are able to discriminate familiarity and sex of their conspecifics from the smell of their dung. To our knowledge, no such study has ever been conducted on any rhinoceros species in the wild. Dung is more easily collected than urine, and we tested the reactions of the rhinos to the fresh dung as we were unsure how long possible olfactory cues allowing the discrimination of familiarity and sex could persist in the dung.

Table 1 Characteristics of the test subjects and their inclusion in particular treatments

Subject	Age class	Sex	Donor's familiarity	Donor's sex	Donor's name	Sample number
Shrek	Adult	M	Unfamiliar	F	Labata	1
Sophie	Adult	F	Unfamiliar	F	Mohlaki	2
Susan	Adult	F	Unfamiliar	F	Kedibone	3
Dikgeto[a]	Subadult	M	Unfamiliar	F	Rosy	4
M06[a]	Subadult	M	Unfamiliar	F	Kedibone	5
Henrie[a]	Subadult	M	Unfamiliar	F	Mohlaki	6
Paris	Subadult	F	Unfamiliar	F	Mohlaki	6
Sam	Juvenile	M	Unfamiliar	F	Kedibone	3
Christy	Juvenile	F	Unfamiliar	F	Mohlaki	2
Victor	Adult	M	Familiar	F	Mamasita	7
Rosy	Adult	F	Familiar	F	Sophie	8
Lucy	Adult	F	Familiar	F	Gill	9
Mamasita[a]	Adult	F	Familiar	F	Rosy	10
Alf	Subadult	M	Familiar	F	Nandi	11
Ted	Juvenile	M	Familiar	F	Nandi	11
Rosebud	Juvenile	F	Familiar	F	Mamasita	12
Babs[a]	Juvenile	F	Familiar	F	Rosy	10
Motopi	Adult	M	Unfamiliar	M	Sidney	13
Betty	Adult	F	Unfamiliar	M	Motopi	14
Kedibone	Adult	F	Unfamiliar	M	Victor	15
Dikgeto	Subadult	M	Unfamiliar	M	Victor	16
Nnete	Juvenile	F	Unfamiliar	M	Victor	15
Sidney	Adult	M	Familiar	M	Victor	17
Mamasita	Adult	F	Familiar	M	Victor	18
Rubee	Adult	F	Familiar	M	Shrek	19
M06	Subadult	M	Familiar	M	Victor	20
Henrie	Subadult	M	Familiar	M	Victor	20
Murphy	Juvenile	M	Familiar	M	Shrek	19
Babs	Juvenile	F	Familiar	M	Victor	18

[a] The five animals who were used as a test subject for the second time

Methods

Study area, animals and sample collection

Olfactory communication in the wild southern white rhinos was studied from May–December 2012 in Welgevonden Game Reserve (375 km^2) and in Lapalala Wilderness (360 km^2) situated in the Waterberg Biosphere Reserve in the Limpopo Province, South Africa.

Both reserves are fenced and are situated approximately 50 km apart. The vegetation of both reserves belongs to the savanna biome and is characterized as Waterberg moist mountain bushveld. The annual rainfall in this area varies from 650 to 900 mm, and the altitude ranges from 1,200 to 1,500 m (van Rooyen and Bredenkamp 1996).

We studied the reactions of 24 individually recognizable rhinos to the dung of familiar and unfamiliar adult females and adult territorial males. We included in the study animals of all sex–age classes except for calves younger than 6 months (Table 1). Females were regarded as adults at

6.5–7 years of age when their first calf is usually born and males between 10 and 12 years of age when they achieve socio-sexual maturity and become solitary. The subadult period starts at 2–3 years of age when the juveniles are driven away by their mothers after the birth of a subsequent calf (Owen-Smith 1973, 1975).

The dung used in the experiments was only collected when an adult female or an adult territorial male was observed to defecate, and we were certain about their identity. A 2 kg dung sample was placed into air-tight plastic containers, deep frozen at −20 °C the same day and used in an experiment up to a maximum of 4 months later (four samples were stored at only −5 °C for 5–14 days before being used). Before an experiment, the samples were left for 24 h to unfreeze at room temperature and were used within 12 h after defrosting. We used a total of 20 dung samples from eight adult females and four adult territorial males in the experiments (see Table 1).

The dung used as unfamiliar in Welgevonden Game Reserve was imported from Lapalala Wilderness and vice

versa in order to be certain that the test subject had never come in contact with the donor. Familiar dung was collected from the animals which inhabited the same home range as the test subject. We never used dung from a member of a subject's group as familiar dung. Companions from the same group only rarely move further apart than 25 metres and remain within five metres distance the majority of the time (Owen-Smith 1973). Finding the fresh dung of a companion at a place where the group has just arrived could therefore alter the reactions of the subjects.

Experimental design

The rhinos were followed by car or on foot, and when the animals seemed to be walking in the direction of a dungheap where no fresh dung was present, an experimenter placed a 2 kg dung sample there. The trials were only conducted on dry days to prevent rain from washing away the scent from the samples. The dung was placed more than one rhino body length from the nearest dung pile, and the experimenter then moved away. The distance moved away from the sample differed between the experiments, depended on the structure of the habitat (dense or open), and always allowed a clear view of the study place. The experimenter paid special attention that the rhinos would not see her placing the dung near the dungheap and that the behaviour of the rhinos would not be disturbed in any way. The reactions of the rhinos were video-recorded for 5 min using a Canon Legria HF M31 digital camcorder. Reactions were only counted if the subject was up to a distance of one rhino body length from the sample. All the subjects finished investigating the dung and left the place before the end of the observation period. After an experiment finished, the dung was removed.

In all the successful trials, the dung was approached by the rhinos within 80 min. If no animal approached the sample in a maximum of 90 min, but sometimes sooner, it was removed as the dung beetles usually began removing the dung by this time (the activity of dung beetles and the intensity of dung removal increase with increasing air temperature, see Davis 1996) and we tried to maintain the same amount of samples in all the trials. The trial began when a subject started sniffing the dung as this was the only way we could be sure that the subject was aware of it.

An attempt was made to balance the number of animals of each sex–age class in the treatments. Due to difficulties with data collection, however, it was not possible to include the same number of animals of each sex–age class in each treatment. The inclusion of certain animals in particular treatments was often random as it depended on the availability of unfrozen experimental dung on the particular day. We also did not know which animals we would be able to locate that day. A number of trials were

not successful; the rhinos often did not approach the experimental dung as it was very difficult to predict the exact direction where they were heading so that we could place the dung sample there. Since the adult territorial bulls seemed to react to the dung samples the most intensively (including walking or running around and trying to find the depositor), we included the same number of bulls in each treatment. Adult bulls are territorial (Owen-Smith 1971, 1973, 1975; Rachlow et al. 1999), and there are usually more adult females, subadults and juveniles in the reserves than there are adult bulls. Due to the limited number of bulls at our study sites, we could either include only one bull in each treatment or none. In order to increase the sample size, we included one bull in each treatment.

We only registered the reactions of a maximum of the first two rhinos from the same group who came to sniff the same sample (as long as no rhinoceros urinated or defecated near the sample, which might alter the reactions of others) in order to keep the repetition of the same stimulus to a minimum. Most often, only one or two rhinos came to sniff the sample although in two cases, more animals from the same group arrived (once five and once three animals). Five rhinos were used as a test subject twice (always in two different treatments), and we allowed a mean time of 63 days between the consecutive trials on each of these animals (ranging from 3 days to 4 months) (see Table 1). This approach was the only practical solution to our problem with sample size given the difficulty of collecting these data on wild animals (Wiley 2003). We were careful to assign animal identity and sample number as random factors in statistical analyses following Webster et al. (2012), who were also dealing with a similar problem in a rare and difficult-to-study species when they investigated behavioural responses of African wild dogs to the playback experiments.

Analyses

The video recordings were analysed using the Activities 2.1 computer programme package (Vrba and Donát 1993). We registered the number of sniffing events, the duration of the sniffing and the latency of the vigilance posture from the onset of sniffing which occurred up to a distance of one rhino body length from the sample. Such methods are commonly applied in analyses of olfactory discrimination in other mammals including ungulates (Rubenstein and Hack 1992; White et al. 2004; Krueger and Flauger 2011; Jojola et al. 2012; Nakabayashi et al. 2012; Linklater et al. 2013; Chamaillé-Jammes et al. 2014; Charlton 2014). All the experiments in the field were conducted, and all the video recordings were analysed, by one experimenter (IC) to avoid any inter-observer variation. Sniffing was defined as standing with the head down, above or next to the

sample and with the nose within approximately 20 cm from the sample. Sniffing was often confirmed by a clearly visible movement of the nostrils. The vigilance posture was defined as standing and raising the head, looking and listening; the animal was either scanning the surroundings or had its gaze and ears fixed in a certain direction. If a subject did not assume the vigilance posture, a latency of 5 min was assigned.

All the analyses were performed with IBM SPSS Statistics 20.0 (IBM Corp., Armonk, USA), and we regarded all results with P value <0.05 as statistically significant. We analysed the reactions of the rhinos to the dung samples using linear mixed models with a scaled identity covariance structure and a restricted maximum likelihood estimation (West et al. 2007). This allowed us to test for the influence of the fixed effects of donor familiarity, donor sex and their interaction while accounting for the random effects of animal identity and sample number. To meet the assumptions of the linear mixed model, the variables were Box-Cox transformed (Sokal and Rohlf 2012). The final Hessian matrix of the linear mixed model with the dependent variable latency of the vigilance posture was not positive definite. In such cases, simplification of the model is recommended by removing the random effects which may not be necessary (West et al. 2007). We therefore removed five animals, which were sampled twice (in two different treatments) from the model, and kept only their first reaction to dung sample in the analyses (see Table 1). This allowed us to remove the random effect of animal identity from the model, and the linear mixed model was

then fully completed. The residuals of all the dependent variables (the number of sniffing events, the duration of sniffing and the latency of the vigilance posture) from the linear mixed models were normally distributed (confirmed with Shapiro–Wilk tests), the homogeneity of variances was confirmed by Levene's tests and the distribution of residuals was also checked visually (q–q plots, histograms, boxplots).

Neither the sample number nor the animal identity had any effect on the reactions of the rhinos in the results of the linear mixed models. The reactions of five rhinos, which were included in the study twice in two different treatments, and the reactions of a maximum of two animals, which came to sniff the same sample, could therefore be considered as independent (McGregor et al. 1992), and their inclusion in the model thus proved justified.

Results

The rhinos sniffed the dung of unfamiliar animals longer than that of familiar animals (Fig. 1; LMM: $F_{1,11.66} = 5.228$, $P = 0.042$). The duration of the sniffing did not differ between the female and male dung ($F_{1,5.94} = 0.006$, $P = 0.943$), and there was no influence of the interaction between the donor familiarity and sex on the duration of sniffing ($F_{1,7.73} = 1.200$, $P = 0.306$). The number of sniffing events was similar between the dung of familiar and unfamiliar animals (LMM: $F_{1,15.229} = 1.309$, $P = 0.270$) and between the female and male dung

Fig. 1 Investigation of the dung of unfamiliar and familiar, female and male donors. Data represent mean ± SEM. *$P < 0.05$
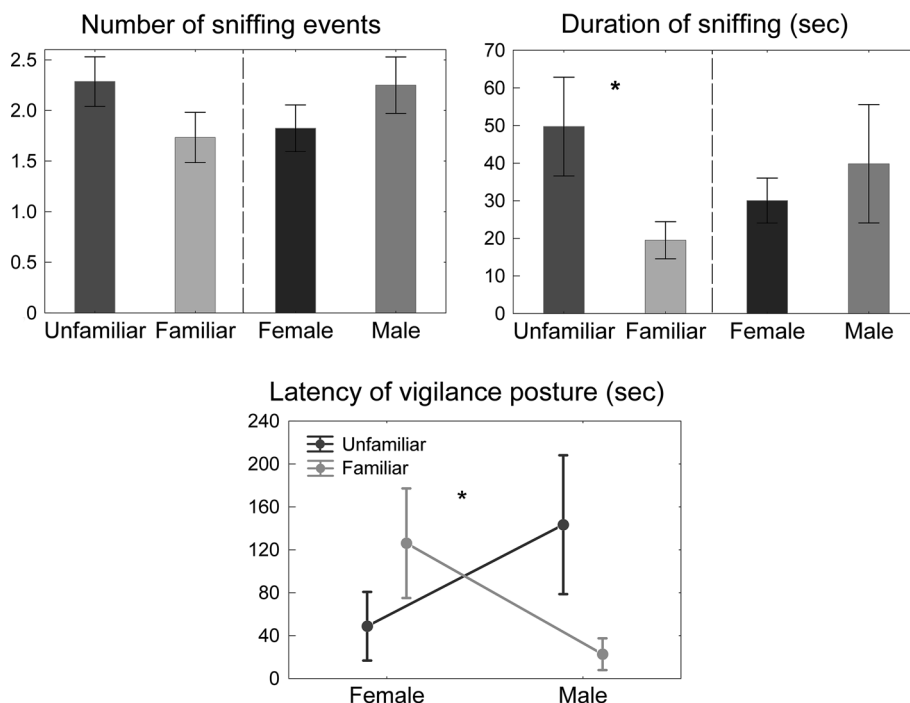
($F_{1,12.879} = 1.202$, $P = 0.293$). There was no influence of the interaction of donor familiarity and sex on the number of sniffing events ($F_{1,14.18} = 1.088$, $P = 0.314$). The latency of the vigilance posture did not differ between the familiar and unfamiliar (LMM: $F_{1,14.75} = 2.023$, $P = 0.176$) and between the female and male dung ($F_{1,14.75} = 0.016$, $P = 0.900$). However, the rhinos displayed a shorter latency of the vigilance posture to the familiar dung of males than that of females. For unfamiliar dung, they showed a shorter latency of the vigilance posture to the female than male dung (interaction donor familiarity*donor sex: $F_{1,14.75} = 5.049$, $P = 0.040$) (see Fig. 1).

Discussion

Our experiments indicate that southern white rhinos are able to discriminate the familiarity and sex of conspecifics from the smell of their dung, and to the best of our knowledge, this is the first such study on any rhinoceros species in the wild. Olfactory signals can persist in the environment for some time, and since the southern white rhinos defecate at common dungheaps (Owen-Smith 1973, 1975), such places could be important sources of information for them. We do not know how long the scent cues allowing for the discrimination of familiarity and sex can persist in white rhinoceros dung. The ability, however, to discriminate such signals in the fresh dung as we present here, could provide the animals with important information about the movements of other rhinos inside their territory or home range. Linklater et al. (2013) studied olfactory communication in temporarily captive wild-caught black rhinos and found that their interest in the dung of conspecifics did not decline with the age of the dung for up to 32 days, with the dung being kept protected from rainfall and direct sunlight. We could therefore predict that the dung of southern white rhinos might retain important chemical information for longer than 1 day, a claim which was supported by our observations of southern white rhinos being interested in older and dry dung.

In our study, the dung of unfamiliar rhinos was sniffed on average more than twice as long as the familiar dung and the differences in the reactions of rhinos to the dung of females and males were shown in the latency of the vigilance posture, which was at the same time dependent on the familiarity of the donor. A shorter vigilance posture to the dung of familiar males compared with the dung of unfamiliar males might be explained by the fact that the rhinos quickly tried to seek out a familiar resident territorial bull as soon as identity could be established, whereas with unfamiliar dung, the rhinos spent time sniffing and attempting to recognize the depositor.

The scent marks are often positioned at places where they can be more easily detected, such as along trails and pathways. In addition, the receiver often benefits from finding scent marks, and in that case, it should actively seek them out (reviewed by Gosling and Roberts 2001). The ability to discriminate the familiarity and sex based on the dung odours can be very important for the social behaviour and spatial organization of the southern white rhinoceros. The territorial bulls often move, for example, in dry seasons to adjacent or more distant territories to seek water (Owen-Smith 1973), and in areas with higher densities of bulls, each territory can be co-inhabited by adult submissive males (Owen-Smith 1971, 1973, 1975; Rachlow et al. 1999). It can therefore be essential for the adult bulls to pay special attention to the scent signals and to distinguish between the dung of familiar submissive males and territorial neighbours and the dung of unknown intruders as well as to recognize the dung of an unknown female walking in their territory. Females and subadults can similarly benefit from discriminating the familiarity and sex from odour cues in dung and register the movements of other groups and of adult bulls inside their home range. Adult territorial bulls can sometimes attack the subadults (Owen-Smith 1973, 1975). After finding the fresh dung of a resident territorial bull, the subadults might avoid confrontation with him by leaving the location as; in such a case, it is likely that the bull is nearby.

Chemical compounds that allow for the discrimination of familiarity or possible individual signature in the dung of southern white rhinos remain to be identified. Research on the vegetation differences between the two study sites was beyond the scope of our study. We believe that the higher interest of rhinos in unfamiliar dung was not triggered by the interest in unknown vegetation since the vegetation of both reserves belongs to the same vegetation type (Waterberg moist mountain bushveld) (van Rooyen and Bredenkamp 1996) and the reserves are only situated 50 km from each other (see "Methods").

Black rhinos can use chemical signals in the dung for identifying individuals and sex–age classes. Although the adult females and males investigate the dung of both sexes similarly overall, there are differences in their reactions towards the dung of subadult males (Linklater et al. 2013). In our study, we pooled the subjects from all sex–age classes because we did not manage to include a sufficient number of animals to be able to test them separately. Nevertheless, it seemed from our experiments that the adult territorial bulls were interested in the experimental dung the most as they also reacted by marking their territory with scrapes and spray urination or by walking or running around and attempting to locate the depositor. Further research should therefore focus on possible differences in

the reactions of females and males to the scent cues of various sex–age classes of rhinos and also on the practical use of olfactory signals in the management and conservation of the white rhinoceros.

Linklater et al. (2006) found that black rhinoceros chemosignals could affect the post-release movements of the animals and they might therefore have a promising use in wildlife management. A knowledge of olfactory communication can also be important for encouraging breeding in mammals, which reproduce poorly in captivity (reviewed by Campbell-Palmer and Rosell 2011). Since the reproductive success of white rhinos is very low in captivity (e.g. Hermes et al. 2005, 2006; Swaisgood et al. 2006), it might be helpful to provide them with additional olfactory stimuli to help simulate the presence of other rhinos and therefore stimulate their social and reproductive behaviour. A knowledge of olfactory communication in southern white rhinos might also help us better understand the communication system of their close relatives, critically endangered northern white rhinos, and increase the chance of their reproduction.

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

Ethical standard The project was approved by the Ethical Commission of the Faculty of Science, Palacký University, and adhered to the "Guidelines for the treatment of animals in behavioural research and teaching" as published by the ASAB (2012). The project complies with the current laws of South Africa and the Czech Republic.

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