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# Effect of supplementary feeding on the social behaviour and distribution patterns of free-ranging southern white rhinoceros

DOI 10.1515/mammalia-2016-0016

Received January 26, 2016; accepted September 30, 2016

**Abstract:** An increasing number of free-ranging southern white rhinos (*Ceratotherium simum* Burchell 1817) live in fenced and intensively managed reserves. They are often kept in small populations and depend on supplementary feeding in the dry season, which can influence their behaviour and distribution. We studied the distribution and social behaviour of free-ranging southern white rhinos in two smaller reserves in South Africa. In the first reserve, the rhinos ( $n=13$ ) were supplementary-fed while in the second one, the rhinos ( $n=8$ ) depended on natural grazing. Following the start of supplementary feeding in the first reserve, the rhinos changed their distribution and concentrated in areas around the feeding places. We observed (79 h of observation) the social behaviour of rhinos at places, where they frequently gathered and the agonistic interactions between them were significantly more frequent at the feeding places (in the first reserve) than at the natural grazing and resting area (in the second reserve). A sufficient number of feeding places and especially their good dispersion could help decrease the agonistic behaviour. Knowledge of the social behaviour of free-ranging rhinos at potentially competitive places in smaller reserves can also be very valuable for better understanding of behaviour of captive animals.

**Keywords:** agonistic behaviour; reserve management; social behaviour; southern white rhinoceros; supplementary feeding.

## Introduction

The southern white rhinoceros (*Ceratotherium simum* Burchell 1817) was once on the brink of extinction (Emslie and Brooks 1999). Due to intensive protection and management measures, its population has grown to approximately 20,000 individuals of which about 93% live in South Africa (Knight 2013). The growth of the wild population has, however, recently slowed down due to a high number of rhinos being poached every year (Knight 2015). Approximately 25% of the free-ranging southern white rhinos in South Africa live in private game reserves (Miliken and Shaw 2012), which significantly contribute to the conservation of the species (Davies-Mostert 2014). Most of these reserves are smaller than 50 km<sup>2</sup> and hold less than 10 rhinos (Castley and Hall-Martin 2003). They are usually fenced and the ungulates are often fed with supplementary food during the dry season to increase population growth (Mysterud 2010).

Predictable distribution of supplementary feeding leads to a significant decrease of home range sizes in free-ranging equids. In addition, the provision of food outside the normal home ranges can decrease the degree of cohesiveness among the animals (Berger 1988). Supplementary feeding has also been shown to influence the social behaviour in a variety of species in captivity including the southern white rhinos (e.g. Schmidt and Sachser 1996, Ganslosser and Brunner 1997, Ganslosser and Dellert 1997, Ganslosser and Thermann 1997, Meister 1997, DeVries et al. 2004, Metrione et al. 2007, Aschwanden et al. 2008). Detailed understanding of rhinoceros behaviour is important for the development of optimal captive and wildlife management (Hutchins and Kreger 2006).

The social behaviour of white rhinos including their agonistic and cohesive (= sociopositive) interactions has been studied in zoological gardens (Mikulica 1991, Meister 1997, Kuneš and Bičík 2001–2002, Swaisgood et al. 2006, Metrione et al. 2007, Cinková and Bičík 2013) and in the wild (Owen-Smith 1971, 1973, 1975). To the best of our knowledge, however, no studies have investigated up until now the influence of supplementary feeding on the social behaviour and distribution of free-ranging rhinos

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living in smaller game reserves. In order to prevent fighting and optimise breeding, it is important to know the impact of such management intervention on the behaviour of the species.

The adult southern white rhinoceros males are territorial while cows, calves and subadults live in groups in overlapping home ranges. The groups are most often formed by an adult female with her calf or a female whose calf had died and 0–6 subadults of both sexes. The groups can also be formed by several subadults without an adult female. The duration of such associations can be from several days to a few years (Owen-Smith 1973, 1975, Shrader and Owen-Smith 2002). White rhinos use a wide repertoire of agonistic and cohesive behaviour to communicate with each other (Owen-Smith 1973, Mikulica 1991, Meister 1997).

Except for adult males, white rhinos do not establish a dominance hierarchy in the wild (Owen-Smith 1973, 1975), which corresponds to the scramble type species as described by van Schaik (1989). He defined two groups of primates according to the feeding conditions as a contest and scramble types and these categories have also been applied to ungulate species. Contest type species access food based on the rank order/dominance system and thus do not increase their aggression [e.g. bongo (*Tragelaphus eurycerus* Ogilbyi 1837): Ganslosser and Brunner 1997, fallow deer (*Dama dama* Linnaeus 1758): Ganslosser and Thermann 1997, plains zebra (*Equus quagga* Boddaert 1785): Ganslosser and Dellert 1997]. Scramble type species [e.g. Asiatic wild ass (*Equus hemionus* Pallas 1775): Ganslosser and Dellert 1997] have no clear rank order which results in food intake per individual proportional to food density. In clumped feeding conditions, the animals will, however, increase their aggressive behaviour due to the lack of any predetermined rank order. Ultimately, competition for resources could cause an increased aggression in the white rhinoceros and the animals might compete for access to resources such as food, water or attractive resting places (Estevez et al. 2007).

The southern white rhinoceros as well as the closely related northern white rhinoceros (*Ceratotherium cottoni* Lydekker 1908, Groves et al. 2010), which belongs to the most endangered species in the world, reproduce very poorly in captivity. Their breeding performance in zoological gardens is much lower (Hermes et al. 2005, Hermes et al. 2006, Swaisgood et al. 2006, Reid et al. 2012) compared to the free-ranging southern white rhinos (Kretzschmar 2002a, Emslie 2008). Social interactions between the captive rhinos including their increased agonistic behaviour have been suggested as one possible reason (Meister 1997, Kuneš and Bičík 2001–2002, Metrione et al. 2007, Cinková and Bičík 2013, Cinková and Policht 2016).

Prolonged or chronic stress, which might result from increased aggression (reviewed by DeVries et al. 2003) can affect the reproduction in mammals (Dobson and Smith 2000, Tilbrook et al. 2000).

We studied the distribution and social behaviour of the free-ranging southern white rhinos in two smaller game reserves in South Africa in order to (1) examine the effect of supplementary feeding on their distribution, and (2) investigate and compare the social behaviour of the rhinos at places, where they gather: at feeding places and at their favourite natural grazing and resting area.

## Materials and methods

### Study sites and animals

The study was conducted in a private game reserve [=private reserve (PR), 91 km<sup>2</sup>] in the Limpopo Province and in the Lichtenburg biodiversity conservation centre [=Lichtenburg centre (LC), 24.5 km<sup>2</sup>] in the North West Province in South Africa from April to August 2008. Both reserves were fenced and housed one adult male and several females with their offspring (PR: n=13, LC: n=8; Table 1). The vegetation in the reserves is classified as a predominantly open woodland in the PR (van Staden 2001) and a rocky highveld grassland in the LC (Bredenkamp and van Rooyen 1996). The climate in these areas is characterised by dry winter (May–September) and wet summer (October–April) (van Staden 2001, North West Province Website 2016). In the dry season, the rhinos in PR were daily given food supplementation (lucerne) at five distinct places in the reserve. The lucerne was offered in separate heaps spread over a large area at each feeding place. All the feeding places except for one were located next to a waterhole and the average distance between two closest feeding places was 1.4 km (Figure 4). In LC, there was no supplementary feeding except for three cases when individual groups were fed with small heaps of lucerne.

### Behavioural observations

Behavioural observations were carried out by IC in the morning and late afternoon at potentially competitive places, where various groups of rhinos often gathered for long periods of time as we wanted to record their frequent meetings. In PR, the rhinos frequently gathered at feeding places and we as well as the local game scouts did not know about any grazing or resting areas, where the rhinos

**Table 1:** Characteristics of the rhinos included in the study and the number of their encounters with different groups.

Sex-age class	Identity	Age (years)	Other members in long-term group	Number of encounters of focal animals with other groups <sup>a</sup>	Observation time (h) <sup>b</sup>
Private reserve (PR)					
Bull	Ali	13		11	7.5 (23.7)
Adult females (AF)	Caroline	29	SF	3	0.6 (2.4)
	Michelle	13	JM	1	2.4 (3.1)
	Mother	29	JM	0	0 (0.4)
	Nicole	13	JM	10	8.0 (24.0)
	Olivia	13	JF, SF, SF	2	0.9 (16.2)
Subadult females (SF)	Belli	6	AF	1	0.3 (2.4)
	Elsabe	3.5	AF, SF, JF	6	3.0 (15.5)
	Natalie	2	AF, SF, JF	3	1.5 (15.5)
Juvenile males (JM)	Alistair	1	AF	0	0 (3.1)
	Mauss	1.5	AF	2	0.1 (0.4)
	Saút	0.5	AF	14	6.4 (24.0)
Juvenile females (JF)	Olga	2	AF, SF, SF	10	5.6 (16.2)
Lichtenburg centre (LC)					
Bull	Bull	22		5	3.6 (10.8)
Adult females (AF)	Cow 1	20	JM	5	8.4 (20.2)
	Cow 3	38		5	4.8 (16.4)
	Cow 6	39		8	9.3 (19.9)
	Cow 8	28		2	1.7 (3.8)
	Cow 11	20		5	4.4 (12.3)
Subadult females (SF)	Subadult	3		1	3.9 (8.8)
Juvenile males (JM)	Calf	0.5	AF	4	6.6 (20.2)

<sup>a</sup>These data include encounters with a bull; all the animals in short-term groups in LC were considered as one group here.

<sup>b</sup>Time of observation of focal animals; data in brackets indicate time for which an animal was present at the study sites and was therefore included in the observations when interacting with a focal animal.

would often gather. The rhinos in LC often gathered near a boma to graze and rest. This area was regularly burned (T. Sikhwihilu, pers. comm.) resulting in a green flush of vegetation, which attracts the herbivores including the rhinos (Mills and Fey 2005). The behavioural observations were therefore conducted at the feeding places in PR and at favourite grazing and resting area of rhinos in LC.

The cohesive and agonistic behaviour of the rhinos was registered using focal animal sampling (Altmann 1974) and the ethogram was adopted from the studies on captive and wild southern and northern white rhinos (Table 2). The focal animal was chosen randomly by drawing lots with names of all the animals present at the study site and the behaviour of the focal animal as well as the behaviour directed by the other animals towards it was recorded. An actor and a recipient of a certain behaviour and the reaction of the recipient were recorded. The rhinos were observed in PR for 36 h (17 observation days) and in LC for 43 h (18 observation days) (Table 1). The observations either continued for as long as the focal animal was present at the study site (in PR) or we switched every 15 min to another animal according to the alphabetical order of their names (in LC).

The interactions between the rhinos were categorised as follows: during encounters between groups, within short-term groups (the animals moved together as one group for some days, but later separated) and within long-term groups (the animals were seen together in >90% of observations). Individuals, who oriented towards one another's movements, tended to stay together and only rarely moved further apart than 25 m were regarded as a group (Owen-Smith 1973). An encounter between groups was defined as a situation when animals from at least two groups met (usually at a distance until 25 m) and it was apparent that they were aware of each other. Encounters of a group with a solitary adult bull were included in encounters between groups. In a few occasions, an actor and/or a recipient of snorts ( $n=52$  in PR,  $n=8$  in LC) could not be identified due to sometimes high number of rhinos at the study sites (the snorts may or may not have been displayed by or directed against the focal animal) and they were therefore not included in the analysis.

The rhinos were categorised into three sex-age classes following Owen-Smith (1973, 1975): adults, subadults and juveniles. Males were regarded as adults at 10–12 years of age when they achieve a socio-sexual maturity and

**Table 2:** The ethogram of white rhinoceros behaviour used in this study (Owen-Smith 1973, Mikulica 1991, Meister 1997, Kuneš and Bičík 2001–2002, Policht et al. 2008).**Category of behaviour**

## Cohesive

1. Rubbing its head (cheek) against another animal
2. Rubbing its head and neck: places neck from the side on the back of a lying rhino and rubs against it
3. Touch and/or rubbing its horn against another animal
4. Leaning its horn against another lying or standing animal
5. Placing its head and neck from the side on the back of partner
6. Touch and/or moving its lips over the skin of another animal
7. Pressing its hind part to another animal in T- or L-posture
8. Placing its head from behind between the hind legs of another standing animal
9. Raising the head of another animal with its posterior horn or its forehead
10. Approaching: an animal approaches and remains in proximity of another rhinoceros; it was only recorded when not affected by another stimulation (e.g. feeding or a human factor)
11. Following another animal
12. Lying side by side<sup>a</sup>: there is a distance up to 1 m between rhinos
13. Standing side by side<sup>a</sup>: there is a distance up to 1 m between rhinos
14. Walking side by side<sup>a</sup>: there is a distance up to 1 m between rhinos
15. Rubbing its side against the side of another animal in passing
16. Contact calling<sup>b</sup>: using calls pant or hic. A series of inhalations and exhalations is emitted when a rhinoceros is isolated from its group and when approaching or staring at other animals
17. Nasonasal meeting<sup>a</sup>: heads up, face to face contact, sometimes allowing noses to meet

## Agonistic

1. Snarl: a loud rasping roar with head thrust forwards, ears laid back and a mouth opened
2. Grunt: a low-frequency vocalisation made with opened mouth and ears laid back
3. Snort: a threat with a nasal exhalation or inhalation
4. Shriek: an intensive shrill sound, reminiscent of the trumpeting of an elephant; made by subordinate bulls or by territorial bulls out of their home territories
5. Gruff squeal: a throaty, rumbling squeal rising in pitch to a tensed cut-off, usually repeated in tenses; made by territorial bulls while chasing after other rhinos
6. Protest turning head and/or body towards the disturbing animal
7. Advancing steps: a few quick steps forward towards another animal
8. Threat with moving head: turns its head aside and suddenly swings it drawing a big bow from side to side
9. Horn prod: a horn prodding gesture made in the direction of recipient
10. Charge: approaches another animal at a rapid trot for a distance of at least several meters (x from advancing steps); it is made silently
11. Clash of horns with another rhinoceros
12. Chase: chases another rhinoceros, which is running away
13. Attack: several successive horn jabbing movements towards the body of a recipient
14. Pressing against another rhinoceros with its body side or with its neck and head

<sup>a</sup>These activities were performed by both animals at the same time so they were included in the behaviour of both participants.

<sup>b</sup>Calls pant and hic described by Owen-Smith (1973) were recorded in one category as they are both used as contact calls. Their acoustic structure is similar and hic can be regarded as an internal part of pant (Cinková and Policht 2016; Policht et al. 2008). Hic is emitted by males when approaching a female, usually in oestrus (Owen-Smith 1973).

become solitary and females at 6.5–7 years of age when their first calf is usually born. The juveniles are driven away by their mothers after the birth of a subsequent calf and the subadult period starts at 2–3 years of age (Owen-Smith 1973, 1975). All interactions, which occurred between two sex-age classes (e.g. were directed from a bull towards a cow or from a cow towards another cow) were included in the analysis. Data where recipients could not be identified were not included as if, for instance, a cow and a subadult were standing close to each other and a

bull approached them, we could not determine which of them he approached (in PR: 1.1% of cohesive interactions and 8.0% of agonistic interactions; in LC: 1.5% of cohesive and 1.2% of agonistic interactions).

### Distribution patterns of the rhinos in PR

We studied the distribution of the rhinos in PR to investigate the influence of supplementary feeding on their

movements. We used a method described by Kretzschmar (2002b) using regular counting of rhino footprints at the waterholes to determine the distribution within a defined area as the waterholes in PR were relatively evenly distributed in the central part of reserve (Figure 4). This method is based on the observation that rhinos usually drink and visit the waterholes once a day or more seldom (Owen-Smith 1973). We chose this method as it best suited the conditions in PR. We could not use, e.g. road transects (see Traill and Bigalke 2006) to investigate the distribution of the rhinos due to the dense vegetation along the roads. We visited all the waterholes in the reserve on a weekly basis and counted all fresh rhino footprints from the previous evening, night or during the sampling day with the help of an experienced game tracker.

The tracks of individual rhinos were identified according to the size of their feet and the individual patterns of lines on their soles (see Alibhai et al. 2008). In addition, cows with calves were also identified by the size of the calf's foot. If the track of the same rhinoceros was found at more than one waterhole, we included only the freshest one. The cow-calf pairs were regarded as one animal because of the dependence of suckling calves on their mothers. Six tracks were not included as their identity was uncertain. The sampling was conducted from 8:00 a.m. to 2:30 p.m. for 4 weeks before and 3 weeks after the beginning of the feeding. The order of the checked waterholes was regularly changed. By using this methodology, we captured the positions of 89% (67–100%) [median (IQR)] of rhinos in the reserve during one sampling day.

## Statistical analysis

We conducted exact non-parametric tests using the IBM SPSS Statistics 20.0 (IBM Corp., Armonk, NY, USA) due to the small sample size (Mundry and Fischer 1998). Alpha level was set at 0.05, and all tests were two-tailed. Data which were used for multiple comparisons were corrected using the Bonferroni adjustments by multiplying p-values by the number of comparisons.

We tested the differences between both reserves in the frequency of agonistic interactions directed from a cow towards a bull or towards another cow during encounters between groups using exact Mann-Whitney U-test. The other sex-age classes were not tested as they only included four or less animals. We pooled the data for the agonistic activities of each individual directed towards all the animals within a certain sex-age class. The differences between sex-age classes in the reactions towards the agonistic behaviour during encounters between groups

in PR were tested by exact Pearson  $\chi^2$ -test. We pooled the reactions of rhinos within a particular sex-age class for each of the four ordinal categories of reactions: (– 2) leaving the place of the interaction (the animal moved away for at least two rhino body lengths, which is approximately 5 m), (– 1) a retreat several steps back, (0) without any reaction or stopping its previous activity and (1) agonistic response. The proportions of reactions between particular sex-age classes were tested with Z-test. The same analysis was not done for LC as the agonistic behaviour was frequently directed only from the cows towards the bull and it was rare between the other sex-age classes.

The distribution of the rhinos was analysed graphically using Map Source 6.15.11 (Garmin Ltd., Southampton, UK). The number of visits of individual rhinos at the waterholes (close/far from a feeding place) per sampling day was compared in each period (before feeding and during the feeding) by exact Wilcoxon sign rank test. The waterholes were considered close to the feeding place if they were situated until 1 km from it. This distance was chosen as the walking speed of a white rhinoceros is on average 3.0–3.8 km/h (Owen-Smith 2013) and we thus regarded 1 km as a very close and easily accessible distance.

## Results

### Companions

The adult bulls were solitary in both reserves. All the females, subadults and juveniles in PR formed long-term groups, which were already together at least several months prior to the start of our study (game scouts in PR, pers. comm.). Three groups consisted of an adult female and her calf, one group of an adult and a subadult female and one group of an adult female, her calf and two subadult females. In LC, only one long-term group was formed by a cow and her calf. The other four cows and the subadult female formed short-term groups of various composition and duration or were rarely observed alone.

### Agonistic behaviour

Agonistic behaviour occurred more often during encounters between groups in PR (86.4% of all observed agonistic interactions) than within long-term groups (13.6%) ( $n=286$  agonistic interactions). We recorded more agonistic activities within short-term groups in LC (60%) than during encounters between groups (40%), and did not observe any

agonistic behaviour within the long-term group (n=80 agonistic interactions). Snort was the most frequently recorded behaviour. Chase was only anecdotally observed in PR when no data were collected on both participants (Figure 1).

The reactions towards the agonistic behaviour during encounters between groups in PR significantly differed across the sex-age classes (exact Pearson  $\chi^2$ -test:  $\chi^2_9 = 69.703$ ,  $p < 0.001$ ) (Figure 2). The most frequent response of all the rhino sex-age classes was “without any reaction or stopping its activity”. “Leaving the place of the interaction” was most frequently recorded in subadults and juveniles. In LC, the bull showed no reaction to the agonistic behaviour of cows in 86.2% of the cases, retreated several steps back in 10.3% and in 3.5% replied with agonistic behaviour (n=29 reactions). There were no differences between the reactions of the bulls in PR and in LC (exact Pearson  $\chi^2$ -test:  $\chi^2_9 = 0.476$ ,  $p = 1$ ).

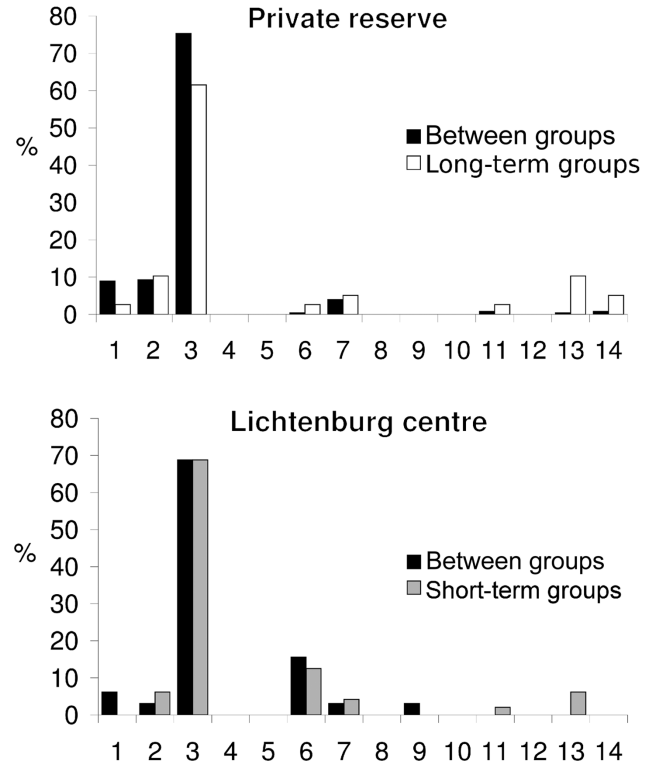
The frequencies of agonistic activities directed during encounters between groups from a cow towards a bull (exact Mann-Whitney U-test:  $U < 0.001$ , Bonferroni corrected  $p = 0.032$ ) or from a cow towards another cow ( $U < 0.001$ , Bonferroni corrected  $p = 0.032$ ) were significantly higher at the feeding places in PR than at the grazing and resting area in LC (Table 3).

## Cohesive behaviour

In PR, cohesive behaviour was very frequently observed within long-term groups (95.4% of all observed cohesive interactions), while it only seldom occurred during encounters between groups (4.6%) (n=1100 cohesive activities). Within long-term groups, cohesive behaviour was the most common in cow-calf pairs (79.1% of all cohesive activities). A similar trend was observed in LC when 63.6% of cohesive activities were recorded within the long-term group, 29.3% within short-term groups and 7.0% during encounters between groups (n=583 activities). No cohesive behaviour was directed from the cows towards the bulls in both reserves and cohesive behaviour between cows from different groups was observed only in LC and rarely (Table 3). Approaching was the most frequently recorded behaviour during encounters between groups. Direct sociopositive contacts such as rubbing head or horn against another animal were seldom observed (Figure 3).

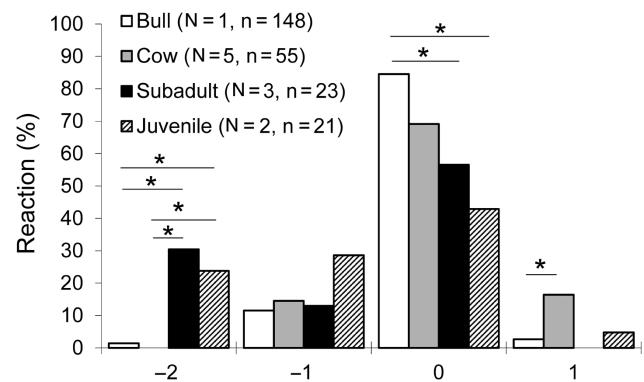
## Distribution patterns of rhinos in PR

The frequency of visits of rhinos at the waterholes before and after the beginning of supplementary feeding did not



**Figure 1:** Proportions of particular agonistic activities recorded during encounters between groups (n=247 displays, t=61.4 h of observation for all the pairs of animals) and within long-term groups (n=39, t=48.3 h) in the private reserve and during encounters between groups (n=32, t=25.3 h) and within short-term groups (n=48, t=29.0 h) in Lichtenburg centre.

Agonistic behaviour: 1. Snarl, 2. Grunt, 3. Snort, 4. Shriek, 5. Gruff squeal, 6. Protest turning head and/or body towards the disturbing animal, 7. Advancing steps, 8. Threat with moving head, 9. Horn prod, 10. Charge, 11. Clash of horns, 12. Chase, 13. Attack, 14. Pressing.



**Figure 2:** Reactions of the recipients to the agonistic behaviour during encounters between groups in the private reserve (PR): (-2) leaving the place of the interaction, (-1) a retreat several steps back, (0) without any reaction or stopping its previous activity and (1) agonistic response. N, The number of animals in particular sex-age class; n, The number of observed reactions. \*Z-test with Bonferroni corrected  $p < 0.05$ .

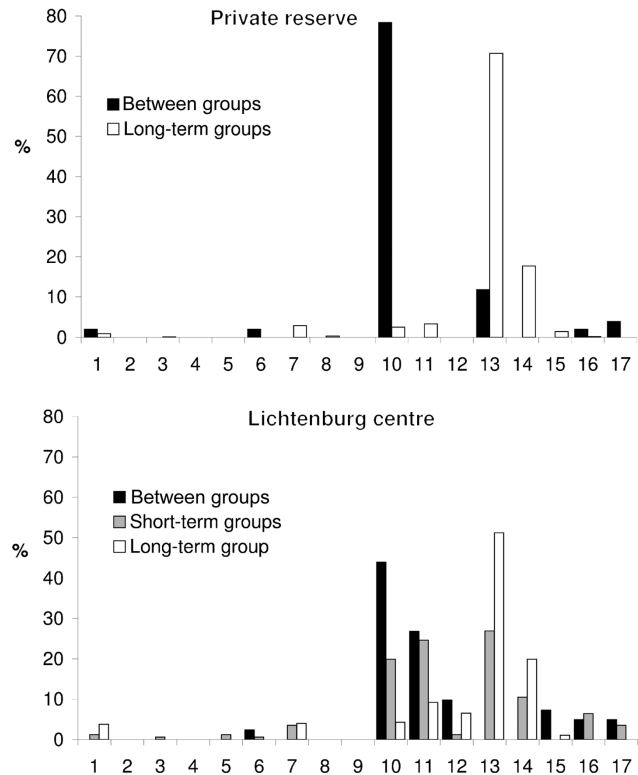
**Table 3:** Agonistic and cohesive interactions during encounters between groups in the private reserve (PR) (at the feeding places) and in Lichtenburg centre (LC) (at the natural grazing and resting area) given in median of frequencies of behaviour per hour of all the animals in particular sex-age class.

	Agonistic behaviour [median (IQR)]		Cohesive behaviour [median (IQR)]	
	PR	LC	PR	LC
Cow → bull	24.8 (8.4–35.8)	1.0 (0–1.3)	0 (0–0)	0 (0–0)
Bull → cow	1.1	0.1	0.5	2.4
Cow → cow	4.1 (2.5–25.8)	0 (0–0)	0 (0–0)	0 (0–0)
Bull → sub	0	0.65	0	0
Sub → bull	0 (0–1.0)	0	0 (0–1.0)	1.3
Bull → juv	0.6	0	0.1	0
Juv → bull	0 (0–0)	0	0 (0–0.6)	0
Cow → sub	2.9 (0–7.9)	–	0 (0–0)	–
Sub → cow	0 (0–0)	–	0 (0–0.4)	–
Cow → juv	0 (0–0.8)	0 (0–0.4)	0 (0–0)	0.4 (0–0.7)
Juv → cow	0 (0–0)	0	0 (0–0)	1.68
Sub → sub	0 (0–0)	–	0 (0–0)	–
Sub → juv	0 (0–1.3)	–	0.6 (0–0.9)	–
Juv → sub	0 (0–0)	–	0 (0–3.9)	–
Juv → juv	0 (0–0)	–	0.1 (0–0.2)	–

differ (exact Wilcoxon signed rank test:  $Z = -0.707$ , Bonferroni corrected  $p = 1$ ). However, the frequency of visits of rhinos at waterholes close to the feeding places (up to a maximum distance of 1 km from a feeding place) was significantly higher during than before feeding ( $Z = -2.459$ , Bonferroni corrected  $p = 0.048$ ). In addition, the frequency of visits of rhinos at waterholes far from the feeding places was significantly higher before than during feeding ( $Z = -2.680$ , Bonferroni corrected  $p = 0.012$ ) (Figure 4).

## Discussion

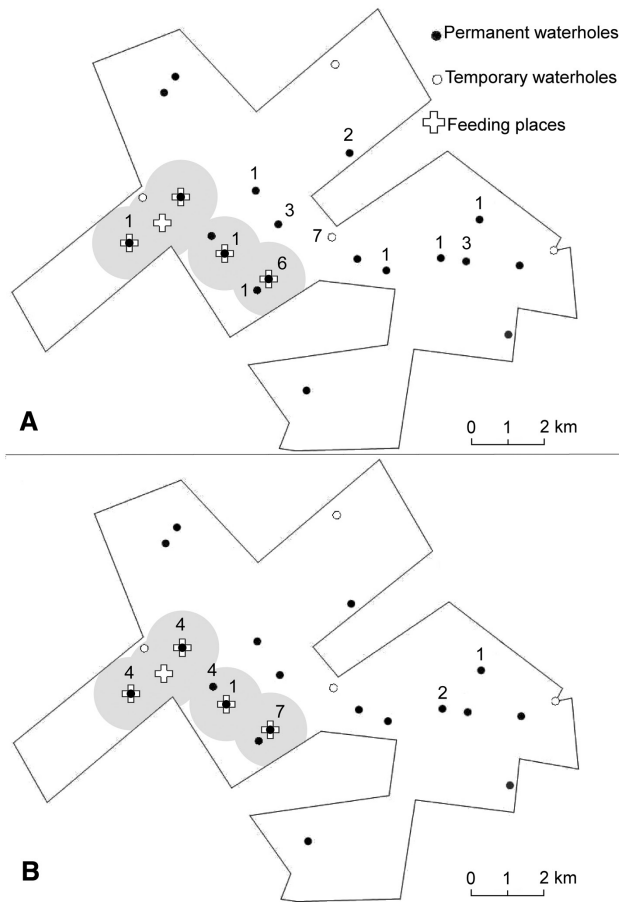
This study reports for the first time the effects of supplementary feeding on the distribution and social behaviour of free-ranging southern white rhinos. We showed that during feeding, rhinos visited waterholes close to the feeding places significantly more frequently than other waterholes as opposed to the time before the feeding had started. This suggests that they changed their distribution following the start of the feeding and preferred areas close to the feeding places. As all the feeding places were located relatively close to each other (the two most distant ones were 4 km apart), various groups of rhinos likely met more frequently, which could increase their agonistic behaviour not only when feeding on supplementary lucerne but also prior to it. For instance, free-ranging



**Figure 3:** Proportions of particular cohesive activities recorded during encounters between groups ( $n = 51$  displays,  $t = 61.4$  h of observation for all the pairs of animals) and within long-term groups ( $n = 1049$ ;  $t = 48.3$  h) in the private reserve and during encounters between groups ( $n = 41$ ,  $t = 25.3$  h) and within short- ( $n = 171$ ,  $t = 29$  h) and long-term groups ( $n = 371$ ,  $t = 15$  h) in Lichtenburg centre. Cohesive behaviour: 1. Rubbing its head, 2. Rubbing its head and neck, 3. Touch and/or rubbing its horn, 4. Leaning its horn, 5. Placing its head and neck, 6. Touch and/or moving its lips, 7. Pressing its hind part, 8. Placing its head from behind, 9. Raising the head, 10. Approaching, 11. Following, 12. Lying side by side, 13. Standing side by side, 14. Walking side by side, 15. Rubbing its side, 16. Contact calling, 17. Nasonasal meeting.

red deer that were hay-supplemented in winter, showed higher aggression than non-supplemented animals not only during the feeding on hay, but also prior to it when feeding on natural vegetation, which might be caused by a high depletion rate and a high predictability of food occurrence at the feeding place (Schmidt et al. 1998).

We compared the agonistic and cohesive behaviour of rhinos at potentially competitive places. The rates of the agonistic interactions directed from a cow towards a bull or towards another cow were significantly higher at the feeding places in PR than at the grazing and resting area in LC. Although other factors such as habitat quality, reserve size or group compositions in each reserve could interfere with our results, the agonistic behaviour was much more frequent in PR than in LC. Owen-Smith (1973)



**Figure 4:** Absolute number of visits of rhinos at the waterholes in the private reserve (A) before ( $n = 28$ ) and (B) during supplementary feeding ( $n = 23$ ).

The grey circles show 1 km radius around the feeding places. Temporary waterholes dried up during the study.

recorded an average rate of 2.3 distance-maintaining threats per hour addressed from a cow towards a bull in the wild which approximately corresponds to the rates of agonistic interactions found in LC (Table 3). Gathering of all the rhinos in one part of the reserve and their higher aggression might be reduced by establishing a sufficient number of feeding places and by ensuring their even distribution. Social behaviour and distribution of the rhinos should be regularly monitored to assess any changes after the start of supplementary feeding.

Captive southern white rhinos increase agonistic encounters and have higher concentrations of stress hormones during clumped than dispersed feeding conditions (corticosterone measured in saliva: Schmidt and Sachser 1996, free cortisol measured in urine: Meister 1997) and a high corticoid variability is connected to acyclicity in females (Carlstead and Brown 2005). Similarly, the

agonistic behaviour in domestic cows decreases and inter-individual distances increase when cows are provided with more feeding space (DeVries et al. 2004). Although the food given to the rhinos in PR was dispersed at the feeding place in many separate heaps, the free-ranging rhinos might be less tolerant of the close proximity of other groups at the feeding place than captive animals, which constantly live in an enclosure of a limited size. The rhinos in our study, however, usually used mild agonistic behaviour such as snort, which can be regarded as a first warning (Owen-Smith 1973, Policht et al. 2008). We observed clash of horns only rarely (Figure 2), while in the study on the captive northern white rhinos, it accounted for 9% of all the agonistic interactions (Cinková and Bičík 2013).

The free-ranging bulls could, nevertheless, become more aggressive at the feeding places towards the youngsters. The bull in PR twice vigorously chased a subadult female and once two subadult females at the feeding places (no data were collected during these interactions on animals, which were involved). He also once attacked a 5-month-old calf, whose mother immediately threatened him. Subadults and juveniles reacted to the agonistic behaviour of others by leaving the place of the interaction (in 30.4% and 23.8% of reactions, respectively) more often than the cows and the bull, which could suggest a development of dominance hierarchy at the feeding places with young animals being submissive.

We observed frequent agonistic interactions between the cows from different groups at the feeding places in PR and some females seemed to be more aggressive than others. The females, however, showed most frequently no reaction or stopped their previous activity. Only 15% of the agonistic activities directed towards them resulted in a retreat several steps back and we did not record leaving the place of the interaction.

A dominance hierarchy among the southern and the northern white rhino females has been reported as a possible contributing factor to their low reproduction in captivity as dominant females might suppress reproduction of subordinates (Mikulica 1991, Mettrione et al. 2007). Several other studies, however, reported that social interactions among the females resemble egalitarian relationships (Meister 1997, Kuneš and Bičík 2001–2002; Swaisgood et al. 2006, Cinková and Bičík 2013) in which resources are shared and the first individual who reaches the resource gets it (Hand 1986). These differences might be influenced by the way of feeding in various zoos with more intensive clumped feeding conditions causing more competitive situations (see also Cinková and Bičík 2013) or potentially also by different group compositions. Social dominance



between the animals requires repeated interactions with the consistent outcome in favour of one animal and often includes a preferential access to resources (Hand 1986). The rhinos in PR were only supplementary-fed for a few months in the dry season, which might not be long enough for a development of dominance hierarchy. The increased agonistic behaviour of the rhinos at the feeding places thus corresponded to the scramble type as defined by van Schaik (1989). However, longer observation hours for all the dyads of females would be necessary for a detailed investigation of females' relationships.

In our study, the rhinos used direct sociopositive contacts by head or horn only rarely. This has also been observed in the wild southern white rhinos (Owen-Smith 1973), but captive southern and northern white rhinos use these behaviours relatively often (Mikulica 1991, Meister 1997, Kuneš and Bičík 2001–2002, Cinková and Bičík 2013). These differences might be a reaction to a restricted space in captivity when the animals are often in permanent visual contact. Similarly, mutual grooming in captive Przewalski horses was more frequent in a herd kept in a smaller enclosure than in a herd living in a larger enclosure (Hogan et al. 1988). In this study, we did not observe any cohesive or play behaviour which would be directed from the cows towards the territorial bulls, but studies on the captive rhinos commonly report it (Meister 1997, Kuneš and Bičík 2001–2002, Swaisgood et al. 2006, Cinková and Bičík 2013). Territorial males in the wild join females for longer periods of time only when they are in oestrus (Owen-Smith 1973), but captive males are often kept with females in one enclosure in almost permanent visual contact on a daily basis. Females could thus partly regard the territorial male as a member of their group, which can change their behaviour.

The basic benefit of group formation in ungulates is the reduction of the predation risk (Jarman 1974). White rhino subadults benefit from group living by familiarisation with novel areas (Shrader and Owen-Smith 2002) and protection from territorial males (Owen-Smith 1973). Adult females do not benefit from group living by being able to reduce their vigilance, and the benefits obtained by subadults and the lack of costs to adult females might be the main drivers of group formation in white rhinos (Shrader et al. 2013). The animals in our study showed the lowest number of agonistic interactions in long-term groups compared to the short-term groups or between groups. In addition, housing captive southern females with a female companion known from adolescence has positive effects on their stress levels (Metrione and Harder 2011). Ultimately, the formation of long-term groups could be beneficial for the rhinos in terms of decreasing their

agonistic behaviour and stress. The duration of associations in rhino groups in our study differed between both reserves and while all the rhinoceros groups in PR were long-term, there was only one long-term group in LC and the other groups were short-term. Small calves of two females in LC died shortly prior to the start of this study and one female was in the last 2 months of pregnancy, which likely affected their behaviour.

Other studies with longer observation hours are necessary to investigate if the frequent agonistic interactions between the rhinos which we observed at the feeding places could significantly raise their stress levels. Such knowledge together with habitat assessments might help wildlife managers make informed decisions about the most suitable frequency and duration of supplementary feeding and about the distribution of feeding places in order to minimise the agonistic interactions between the rhinos. Comparative studies from smaller reserves with various degrees of management interventions can also be very useful for better understanding of the behaviour of captive rhinos.

**Acknowledgements:** We would like to thank the owner of the private game reserve and National Zoological Gardens, South Africa for the permission to undertake this study, personal accommodation and for the financial assistance. We are very grateful to Harold Braack, Antoinette Kotze, Thomas Sikhwivhilu, Wikus Stemmet, Vítězslav Bičík and Norman Owen-Smith for their support and logistical help during our study, and to Petrus for help in the field in the private game reserve. The stay of IC in South Africa was also supported by a mobility grant from the Palacký University. We are grateful to Peter Buss and an anonymous reviewer for valuable comments on the manuscript.

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