WILEY
InterScience®
DISCOVER SOMETHING GREAT

RESEARCH ARTICLE

Social and Spatial Relationships in Captive Southern White Rhinoceros (*Ceratotherium simum simum*)

Lara C. Metrione,[1,2]* Linda M. Penfold,[1] and George H. Waring[2]

[1]*White Oak Conservation Center, Yulee, Florida*
[2]*Department of Zoology, Southern Illinois University, Carbondale, Illinois*

Although critical to the conservation of white rhinoceros, captive breeding has proven challenging because of the poor and irregular reproductive health of many captive rhinos, and social interactions may play a significant role. This research investigated the social and spatial relationships of two captive groups of southern white rhinoceros (*Ceratotherium simum simum*) by examining the frequency of companion changes, the number of space maintenance vocalizations made per hour by each reproductively mature female, and dominant/subordinate interactions. The observed captive rhinos did not change their companionships during the study. They exhibited space maintenance vocalizations and display greater than once per hour, particularly when feeding. Females housed with four calves on $0.033 \, \text{km}^2$ exhibited space maintenance vocalizations more frequently ($X \pm \text{SE} = 6.19 \pm 0.199/\text{hr}$) than females housed with one calf and more space ($0.06 \, \text{km}^2$, $X \pm \text{SE} = 0.55 \pm 0.182/\text{hr}$) and females housed without calves and more space ($0.65 \, \text{km}^2$, $X \pm \text{SE} = 1.90 \pm 0.086/\text{hr}$). Wider separation of food piles and of females with young calves is suggested to reduce the interpreted spatial stress. The presence of a large number of rhinos in restricted captive space resulted in the formation of herds with dominance hierarchies that were enforced during competition for food and shade. The most subordinate rhino in each of the herds exhibited unusual behaviors such as dung-kicking and nonestrus urine squirting, and neither has ever reproduced. Suppression of subordinate rhinos might lead to social stress that could negatively impact reproductive success. Zoo Biol 26:487–502, 2007. © 2007 Wiley-Liss, Inc.

Keywords: social behavior; vocalizations; companionship; dominance; reproduction

INTRODUCTION

The southern white rhinoceros (*Ceratotherium simum simum*), once nearing extinction, now boasts a population of about 11,000 individuals. However, they breed poorly in captivity with the exception of a few successful institutions, and estrous cycles are often irregular or absent [Radcliffe et al., 1997; Patton et al., 1999; Brown et al., 2001; Graham et al., 2001; Hermes et al., 2006]. Previous research suggests that social interactions could impact reproductive cycles and breeding in these animals. For example, estrous cyclicity and mating may require exposure to an unfamiliar sexually mature male as captive white rhino females kept with the same male their entire life did not come into estrus or did not mate until given access to a novel male [Reece, 1993; Bertschinger, 1994; Pienaar, 1994; Patton et al., 1999; Brown et al., 2001].

Free-ranging female and adolescent southern white rhinoceros are social with up to six individuals in a group [Owen-Smith, 1973, 1975; Shrader and Owen-Smith, 2002], though usually only two are close companions [Owen-Smith, 1973; Hillman-Smith, 1987; Shrader and Owen-Smith, 2002]. Associations between free-ranging individuals frequently last less than a month, particularly those that involve adolescents, but some may persist for lengthy periods of time [Owen-Smith, 1973, 1975; Shrader and Owen-Smith, 2002]. Owing to lack of space and other logistics, it is possible that captive females and adolescents do not change companions monthly.

Despite their social tendencies, Owen-Smith [1973, 1975] observed various vocalizations and displays by wild southern white rhinoceros that served to increase and maintain interindividual distance, and comparatively fewer facilitated advancement (Appendix A). Space maintenance vocalizations included the "snort" and "snarl" [Owen-Smith, 1973, 1975]. In the wild, because the nearest rhinos are most often close companions, space maintenance vocalizations are usually asserted less than once per hour [Owen-Smith, 1973]. Owen-Smith [1973] also observed that wild white rhino cows with small infants were more likely than other cows to direct space maintenance vocalizations at approaching rhinos. In this study it was predicted that captive females are spatially stressed. Here, spatial stress is defined as unrest, which is the result of another animal being located too near the affected animal and is indicated by the emittance of space maintenance vocalizations more frequently than once per hour. It was further predicted that females with calves that cannot move away from the group exhibit a greater frequency of space maintenance vocalizations than those who can move away or who are not accompanied by a calf. Captive white rhinos were studied at two sites with differences in enclosure size and group structure allowing for comparisons.

METHODS

Animals

Two groups of southern white rhinoceros were observed by L. C. Metrione. Group A (Table 1) was observed at a private institution, White Oak Conservation Center, Yulee, Florida (30°N38′ 81°W36′), for 12 weeks (May–August 2004), and group B (Table 1) was observed at a public institution, the Wilds, Cumberland, Ohio (39°N51′ 81°W39′), for 9 weeks (August–October 2004).

TABLE 1. Composition of the white rhinoceros groups studied at White Oak Conservation Center (May–August 2004) and the Wilds (Aug–October 2004)

Rhino ID	Age	Sex	Status	Wild-caught
Group A: White Oak Conservation Center				
Linda[^]	Adult-16	Female	Reproductive	Yes
Luke[^]	Juvenile-1.5	Male	Prepubertal	No
Kit′	Adult-7	Female	Reproductive	Yes
K.C.′	Juvenile-1.5	Male	Prepubertal	No
Kathy[γ]	Adult-16	Female	Reproductive	Yes
Maggie[γ]	Juvenile-1.5	Female	Prepubertal	No
Natalie[φ]	Adult-14	Female	Reproductive	Yes
Tony[φ]	Juvenile-1.5	Male	Prepubertal	No
Lucy[φ]	Adolescent-3	Female	Near puberty	No
Helen[φ]	Adult-12	Female	Nonreproductive	Yes
Bernard	Adult-14	Male	Reproductive	Yes
Group B: the Wilds				
Half-Ear[♦]	Adult-33	Female	Postreproductive	Yes
Notch[♦]	Adult-33	Female	Postreproductive	Yes
Mamma[*]	Adult-36	Female	Postreproductive	Yes
Julie[*]	Adult-11	Female	Pregnant	No
Maggie[*]	Adult-9	Female	Pregnant	No
Longhorn[†]	Adult-33	Female	Postreproductive	Yes
Karla[†]	Adult-19	Female	Nonreproductive	No
Tex	Adult-10	Male	Reproductive	No
Bubba	Adult-18	Male	Reproductive	No
Group B′: the Wilds				
Mamma[*]	Adult-36	Female	Postreproductive	Yes
Julie[*]	Adult-11	Female	Pregnant	No
Maggie[♠]	Adult-9	Female	Lactating	No
Zenzele[♠]	Calf-<1 month	Female	Pre-pubertal	No

Owing to the birth of a calf, group B needed to be split, resulting in the formation of a second group at the Wilds, group B′. Companions are indicated by matching symbols.

Group A's pasture (0.033 km²) was mowed twice monthly, dung piles were cleaned weekly, feeding slabs were cleaned daily, and the rhinos were separated into five corral areas for approximately 2 hr during weekly blood collections. They were fed 7.26 kg of Mazuri ADF-16 cubes (Purina Mills Inc., 505N. Indiana) daily per rhino in the evening on five adjacent, linearly arranged feeding slabs located in the corral areas, accessible from the pasture and from one to the next. In the pasture in morning and on the slabs in the evening, 4.54–5.44 kg of coastal Bermuda-grass hay was also fed twice daily per rhino. Water was provided ad libitum.

Neither group B nor their pasture (0.65 km²) was managed as intensively, and multiple hoofstock species were kept in the same enclosure. The rhinos were fed once daily with 3.63 or 4.54 kg for females and males, respectively, of Mazuri ADF-25 pellets (Purina Mills Inc.) and approximately 1.5 kg of orchard grass/timothy hay per rhino. Water was provided ad libitum. Twenty-four days into the study, rhinos in group B were moved to a different enclosure for 1 day when the males were switched and two females were permanently removed. A calf was born 3 weeks before the end

of the study, and all rhinos except the mother and calf were moved to an adjacent enclosure ($0.51\,km^2$) for 1 week at the end of which the mother and calf were moved to a breeding enclosure ($0.06\,km^2$). The remaining members of group B returned to the original enclosure. Five days later, two adult females from group B were moved to the breeding enclosure with the mother and calf, forming group B′.

Behavioral Observations

Observations of group A were made from a golf cart that could be maneuvered around the enclosure's perimeter. Observations of group B were made from a truck within the pasture. The vehicles, to which the rhinos became accustomed quickly and paid little attention, were positioned as close as possible to the majority of the rhinos (∼2–300 m at White Oak and ∼2–1,660 m at the Wilds). Animals were observed for 8–9 hr/day, 5–7 days/week, with a 1-hr break midday when the rhinos were inactive. Once group B′ was formed, this and group B were each observed for 4 hr/day (evenly divided between the morning and afternoon to prevent bias). Seven days of observation for a continuous 9 hr, conducted initially and periodically throughout the study, were used to determine and confirm that the rhinos were mostly inactive during the midday hours, and no vocalizations occurred during that time.

A previously published ethogram of wild southern white rhinoceros behavior [Owen-Smith, 1973, 1975] was used to identify behaviors and vocalizations (Appendix A). All observations of those behaviors were recorded on field data sheets under the 15-min time block in which they occurred [Owen-Smith, 1973]. Adult rhino activity and nearest neighbors (used to determine the frequency of companion changes) were recorded using scan sampling technique [Altmann, 1974] every 15 min.

Although associations change little during 15 min, this interval was convenient for recording all audible vocalizations made by adult rhinos throughout the observation period. Snorts and snarls were interpreted as space maintenance vocalizations [Owen-Smith, 1973, 1975]. When snorts were made with each breath, a pause needed to occur before a subsequent vocalization was scored. Snarls, which require an increased effort, had an inherent pause in between. Estrus consort was defined as periods during which a male approached a female approximately every 15 min making a "hiccing" vocalization [Owen-Smith, 1973, 1975], smelled her vagina and the squirted urine, chin-rested, and made mounting and breeding attempts. Space maintenance vocalizations made by the female to the male during estrus consort were recorded, but they were distinguished from vocalizations made outside of consort relationships when the data were analyzed. When a vocalization could not be definitively assigned to the rhino from which it came, it was recorded as unidentified.

The following behaviors were interpreted as acts of subordination: backing away, presenting the side, and yielding (the termination of an approach or the relinquishing of ground or food). A running tally of the number of times in which one rhino acted in subordination to another or in which there was a "draw" was maintained.

Statistical Analysis

A zero was recorded for time during which there were no data collected (as during the midday break) based on the 7 days of full observation when

no vocalizations were recorded during that break. Owing to the nature of the hypothesis, it was better to record a zero and be conservative than to eliminate those hours from the data set, which would bias the mean to a higher number of vocalizations per hour. When a particular rhino was not visible in group B for a full hour, that hour was not counted in the final vocalization analysis for that particular rhino. The mean number of vocalizations made per hour per female was calculated, and a separate mean was recalculated using the number of vocalizations made per hour excluding those made in the context of an estrus consort relationship. The number of vocalizations per hour per female was compared between females at each site using the nonparametric Kruskal–Wallis method for nonparametric data. To compare the number of vocalizations per hour per female between groups, the nonparametric Kruskal–Wallis method and Dunn's method were used. These tests were carried out using SAS 9.1 software (SAS Institute Inc., 2002–2003) and SigmaStat 3.0 software (SPSS Inc., 2003).

The percent of encounters between two rhinos that resulted in acts of subordination was calculated for all possible pairs except mother and calf [(No. in subordination/(No. in subordination+No. in dominance+No. draws)) × 100]. These values were entered into a dominance matrix. Two aspects were considered when creating the overall dominance hierarchy for each group: (1) the percentage of times that a rhino acted in subordination to or dominated another (organized in the matrices) and (2) the number of rhinos dominating a particular rhino versus the number of rhinos it dominated, illustrated by dominance diagrams. Each time the group structure changed in groups B and B′, a new tally of dominance/subordinate interactions was begun.

RESULTS

Companionships

Companionships did not change during the study (Table 1). All but one of the adult females in group A had calves that were their companions. An unrelated adult and adolescent accompanied a female–calf pair. This quartet was broken apart only temporarily during the 1–2-day periods when either of the adults were in estrus consort with the male. When seeking shade or feeding, it was common for more than one subgroup (a mother–calf pair or the quartet) to huddle under one pavilion or at one feed slab. In group B, the females had one or two adult companions. These companionships did not change when rhinos were removed or added to the group except when one of the females had a calf, after which she no longer accompanied her companions.

Vocalizations

Of the 23,158 space maintenance vocalizations recorded during 603 observation hours for group A, 3.55% (822) were unidentified. Of the 5,791 space maintenance vocalizations recorded during 495 observation hours for groups B and B′, 1.50% (87) was unidentified. The single feeding and more widespread distribution of feed piles allowed for better discrimination of vocalizations at the Wilds. When many rhinos vocalized at once, it was possible that vocalizations were missed or a particular rhino drowned out the voice of another.

In group A, space maintenance vocalizations were directed to other adults, the adolescent, and sometimes an unrelated calf. Because the male engaged in estrus consort relationships six times, discrimination of vocalizations during those associations from others needed to be made. During feeding, there was constant competition as the rhinos moved around their food. It was noted that the more widespread the distribution of the morning hay in the pasture, the fewer confrontations there were, and hence fewer space maintenance vocalizations. During the day while grazing or resting, the rhinos were spread-out around the enclosure and vocalizations were minimal. In the evening, there were usually two cow–calf pairs per feed slab initially. The subordinate adult cow within the quartet and the male ate alone at the last feed slabs. Eventually, the feed slabs at the beginning of the line were depleted of food, and the rhinos then competed for food at the last slabs, thus increasing the number of vocalizations (Fig. 1). The male made space maintenance vocalizations when defending his food.

In groups B and B', space maintenance vocalizations were rarely directed at a companion except during feeding (data not shown). Rather, they were directed at females from other subgroups, the male, or sometimes other species. None of the females was engaged in estrus consort relationships. Depending on their distribution when the keepers entered the pasture, these rhinos were either fed in a line along the road or in their separate companion subgroups. When all of group B was fed in the same area, competition was intense. As the size of group B decreased and when companion subgroups were fed separately from each other, the number of space maintenance vocalizations remained at lower frequencies similar
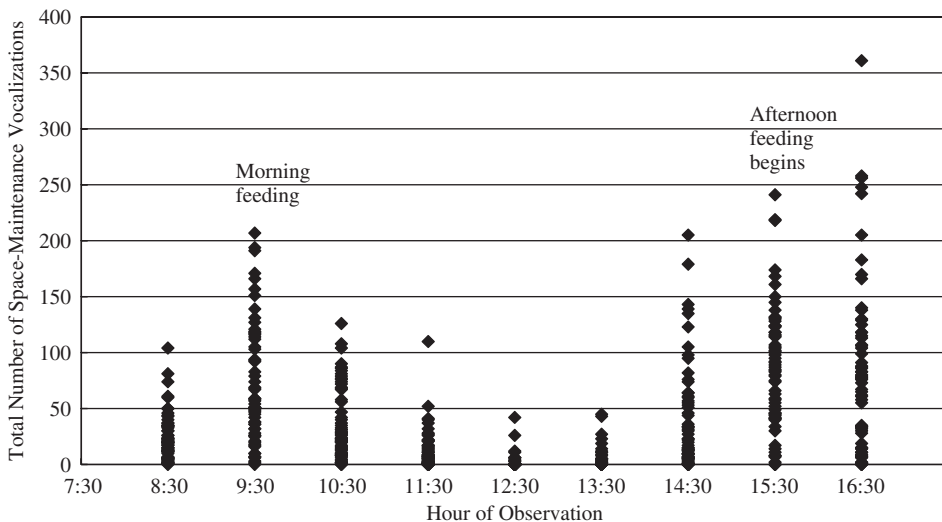

Fig. 1. Total number of space maintenance vocalizations made per day per hour (represented by each point) by adult female white rhinos in group A (White Oak) relative to the observation time period from 7 : 30 to 16 : 30 over the course of 12 weeks (May–August 2004). A majority of the vocalizations occurred during the daily feeding times. In the mornings, the group was fed hay in the pasture area while in the evenings the group was fed on feed-slabs in more restricted corral areas.

to nonfeeding times. Both males made space maintenance vocalizations during feeding.

Captive females at both White Oak and the Wilds had mean numbers of space maintenance vocalizations greater than one per hour (Table 2), occurring predominantly during feeding or when the rhinos had to compete for limited shade. In group A, the number of space maintenance vocalizations per hour excluding estrus consort vocalizations (as not all females were likewise engaged) was different between females (Kruskal–Wallis test: H11 = 71.2702, 4 d.f., $P < 0.0001$). The mean number of vocalizations made per hour per female including those made during estrus consort relationships was slightly higher than the means when calculated excluding vocalizations made during estrus consort relationships: during estrus consort, mean space maintenance vocalizations increased from 3.18 to 3.21/hr (range 0–49), from 6.38 to 6.95/hr (range 0–69), and from 7.43 to 8.14/hr (range 0–99) for the three mated females. The mean number of space maintenance vocalizations per hour in groups B and B′ together was also different between females (Kruskal–Wallis test: H11 = 28.8696, 6 d.f., $P < 0.0001$).

There was a significant difference in the number of vocalizations made by each adult female per hour between the three groups (Kruskal–Wallis test: H11 = 410.569, 2 d.f., $P < 0.001$). Excluding estrus consort vocalizations, females in group A, living in $0.03 \, km^2$ with four calves, vocalized significantly more than those in group B ($X \pm SE = 1.90 \pm 0.086$/hr, Dunn's method: $Q = 17.120$, $P < 0.05$) living in $0.65 \, km^2$ with no calves and those in group B′ ($X \pm SE = 0.55 \pm 0.182$/hr, Dunn's method: $Q = 8.697$, $P < 0.05$) living in $0.06 \, km^2$ with one calf. The new mother's mean number of space maintenance vocalizations dropped from 2.95/hr when she was in group B to 1.36/hr (a total of 45 during 33 hr of observation) when she was with group B′.

TABLE 2. Vocalization averages/hour, standard error (SE), and range of vocalizations/hour for adult female white rhinoceros in groups A, B, and B′ excluding those made during estrus consort

Rhino	Mean no. vocalizations/hr $\pm$ SE	Range
Group A (White Oak)		
Kathy	11.15 ± 0.767	0–129
Kit	7.60 ± 0.501	0–70
Linda	7.43 ± 0.498	0–99
Natalie	6.38 ± 0.408	0–61
Helen	3.18 ± 0.247	0–49
All females	6.19 ± 0.199	0–129
Groups B and B′ (the Wilds)		
Maggie	2.95 ± 0.303	0–36
Karla	2.82 ± 0.284	0–42
Longhorn	2.63 ± 0.264	0–40
Mamma	2.00 ± 0.215	0–51
Half-Ear	1.73 ± 0.303	0–39
Notch	1.56 ± 0.256	0–22
Julie	1.07 ± 0.136	0–32
All females	1.84 ± 0.083	0–51

Group A

	Linda	Kit	Kathy	Natalie	Helen
Linda	0	17	19	21	76
Kit	13	0	11	28	46
Kathy	4	9	0	28	62
Natalie	8	11	6	0	74
Helen	3	5	2	1	0

	Natalie	Tony	Helen	Lucy
Natalie	0	NA	74	97
Tony	0	0	69	74
Helen	1	25	0	42
Lucy	0	8	31	0

a

Group B

All females, prior to birth of calf

	Half-Ear	Notch	Longhorn	Maggie	Julie	Mamma	Karla
Half-Ear	0	71	63	44	50	76	69
Notch	6	0	56	38	38	48	31
Longhorn	6	28	0	23	40	25	71
Maggie	44	18	23	0	23	56	48
Julie	25	31	27	54	0	8	53
Mamma	19	38	0	20	90	0	33
Karla	15	25	13	16	33	33	0

b

Group B

Without Half-Ear and Notch, prior to birth of calf

	Longhorn	Karla	Maggie	Julie	Mamma
Longhorn	0	66	26	83	71
Karla	14	0	27	30	100
Maggie	19	27	0	19	50
Julie	17	10	70	0	13
Mamma	14	0	44	81	0

c

Group B

Without Half-Ear, Notch, and Maggie

	Longhorn	Mamma	Karla	Julie
Longhorn	0	73	94	92
Mamma	27	0	29	96
Karla	6	71	0	36
Julie	8	4	36	0

d

Fig. 2.   Dominance matrices for groups A and B. The winners of the interactions are listed vertically whereas losers are listed horizontally. Numbers are equal to the percent of the total number of dominance/subordinate interactions that occurred between the pair. For example, in group B, Half-Ear was dominant over Notch 71% of the time, whereas Notch was dominant over Half-Ear only 6% of the time. Thirty-three percent of the time their interactions resulted in a "draw."

Group B

All females, including interactions with Maggie after birth of calf

	Half-Ear	Notch	Longhorn	Maggie	Julie	Mamma	Karla
Half-Ear	0	71	63	44	50	76	69
Notch	6	0	56	38	38	48	31
Longhorn	6	28	0	24	67	64	78
Maggie	44	18	24	0	43	59	43
Julie	25	31	18	44	0	9	36
Mamma	19	38	18	26	88	0	30
Karla	15	25	10	20	33	47	0

e

Group B

All females, excluding interactions with Maggie after birth of calf

	Half-Ear	Notch	Longhorn	Maggie	Julie	Mamma	Karla
Half-Ear	0	71	63	44	50	76	69
Notch	6	0	56	38	38	48	31
Longhorn	6	28	0	25	67	64	78
Maggie	44	18	20	0	21	53	39
Julie	25	31	18	62	0	9	36
Mamma	19	38	18	32	88	0	30
Karla	15	25	10	21	33	47	0

f

Fig. 2.   Continued.

Dominance/Subordinate Interactions

A majority of confrontations occurred during feeding. Although a particular rhino was generally dominant over another, the lack of completely asymmetric outcomes between pairs accounts for the high number of dominance reversals that appear below the diagonal in the dominance matrices (Fig. 2a–f). The dominance diagrams (see Fig. 3a and b for examples) constructed for each group and each phase of group B were useful for clarification of the hierarchies. Dominance diagrams for phases of group B showed some intransitive (circular) relationships, suggesting that the hierarchies in that group were not strictly linear. There seemed to be no pattern relating the mean number of space maintenance vocalizations made by a female and that female's level of dominance.

The dominance hierarchy (beginning with alpha rank) in group A was as follows: Linda→Kit→Kathy→Natalie→Helen (Figs. 2a and 3a). The dominance hierarchy within the quartet was as follows: Natalie→Helen→Lucy (Fig. 2a).

Within companionships in group B, one companion, usually the elder, was dominant over another. Once her calf was born, one female became dominant over a companion to whom she previously had been subordinate. Although a few relationships were intransitive (see Fig. 3b for examples), the overall trend in dominance for group B when all seven females were initially present is described here in a linear format for ease of understanding: Half-Ear→Notch→Longhorn→Maggie→Julie→Mamma→Karla (Figs. 2b and 3b). The group B hierarchies after
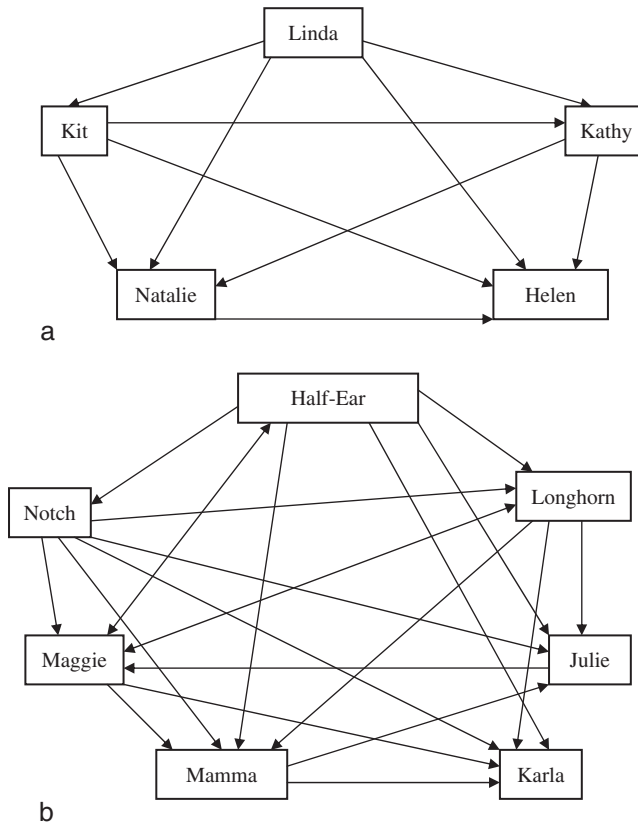
Fig. 3.   Diagrams depicting dominance in the groups of rhinos based on the percentages shown in Figs. 2a–f. The dominant animal is at the origin of the arrow, and the subordinate animal is at the head of the arrow. Ties are depicted by a double-headed arrow.

the removal of two rhinos (Fig. 2c) and after the removal of the new mother (Fig. 2d) were based on a small number of observations due to the short duration of those group compositions, therefore the validity of those hierarchies is questionable. The hierarchy was recalculated to include all interactions over the 9-week observation period, including those with Maggie once she had her calf, creating a larger data set. The resulting hierarchy was as follows: Half-Ear→Notch→Longhorn→Maggie→Julie→Mamma→Karla (Fig. 2e). The structure of the hierarchy did not change if it was constructed excluding interactions with Maggie once her calf was born (Fig. 2f).

DISCUSSION

This study showed that these captive white rhino females did not change companions monthly. Frequencies of space maintenance vocalizations greater than 1 per hour were recorded, particularly during feeding and particularly by females who had both calves and limited space. A linear dominance hierarchy and a

dominance hierarchy with a few intransitive relationships were evident in both captive groups and were best demonstrated during competition for food and shade.

The group sizes observed were consistent with those of wild white rhino companions (2–6 rhinos) [Owen-Smith, 1973; Pienaar, 1994; Shrader and Owen-Smith, 2002]. A free-ranging female with a young calf would not be expected to join with another rhino [Owen-Smith, 1973]; however with older calves, an additional companion might be allowed to join as seen in the quartet. In contrast to the average 1-month companionships observed in the wild [Owen-Smith, 1973; Pienaar, 1994; Shrader and Owen-Smith, 2002], captive females' companionships remained stable throughout observation (2–3 months), though one rhino did separate herself from her companions before and after parturition. The presence of only one adolescent in the study probably contributed to the infrequency of companion changes. The mother–calf companionships in group A contributed to the infrequency of companion changes at that location. Shrader and Owen-Smith (2002) suggested that companionships in the wild provide a way for adolescents to gain exposure to new areas or act as a social guard against territorial males. In captivity, companionships might provide social guarding from aggression by more dominant females. Low-ranking rhinos, such as Helen and Karla, formed companionships with more dominant rhinos. This would also contribute to the stability of the companionships. Another possibility is that in captive situations where many rhinos are kept together, interactions may be sufficiently diverse and frequent to minimize boredom with a particular adolescent or adult companion, alleviating the need to change companions.

In contrast to wild white rhinos, the captive rhinos in this study made space maintenance vocalizations greater than once per hour, and this outcome suggests that the rhinos at these two sites were spatially stressed relative to their wild counterparts. Considering that the home range for a wild pair or group is $7.2–45.2 \, km^2$ [Owen-Smith, 1973, 1975; Pienaar, 1994; Shrader and Owen-Smith, 2002], it is logical that these captive females felt crowded as they came in hourly contact with other subgroups. It was noted that fewer vocalizations were heard between companions than between rhinos from different subgroups, and this would explain why fewer vocalizations were recorded in the wild.

Although wild cow groups move separately, Owen-Smith [1973] observed "some degree of attraction" between them: the average space between the cow groups was just over half the value expected from a random distribution. Interestingly, whereas the rhinos in group A spread out around their $0.033 \, km^2$ pasture during the day, the rhinos in group B often remained within a $\sim 0.20 \, km^2$ area despite the opportunity to disperse further. Vocalizations remained low relative to feeding times, however, because the rhinos were resting or grazing in subgroups (separated by $>25 \, m$). This suggests that the interpreted spatial stress is mainly a result of the closer proximity of and resource competition among the rhinos during feeding or when seeking shade rather than insufficient enclosure size for those $\geq 0.033 \, km^2$. The finding of greater space maintenance vocalizations and spatial stress during feeding in the study is supported by another study that found corticosterone concentrations in male and female white rhinos were elevated 17–54% above the animals' mean concentrations when hay was provided in clumps [Schmidt and Sachser, 2000]. From an animal management perspective, a majority of the spatial stress could be decreased by increasing interindividual distance during feeding

rather than by constructing larger enclosures. Whereas Owen-Smith [1973] found that territorial males generally did not make space maintenance vocalizations during confrontations on their territory, males in this study made snorts and snarls when defending their food.

The significantly greater frequency of space maintenance vocalizations in group A compared with groups B and B′ supports the hypothesis that females with calves that could not move away from the group exhibited a greater frequency of space maintenance vocalizations than those without calves and those who had a calf but also had more space. This suggests that females with calves are more likely to be spatially stressed in dense captive arrangements. The smaller pasture size (0.033 vs. 0.65 km^2 or 0.06 km^2), spatially restricted feed slabs, and twice daily feeding directly contributed to the inability of the females in group A to move away from each other relative to females in groups B and B′. It is possible that the cows' vocalizations were used to preempt or halt an advance on their calf and were not in response to spatial infringement, but one could argue that the intended result of the vocalization remains the same. Although the interpreted spatial stress did not apparently impact reproduction in these groups, as 6/12 females produced offspring, one survey study found that total enclosure area was significantly positively correlated with black rhinoceros' (*Diceros bicornis*) breeding success [Carlstead et al., 1999b].

Importantly, Maggie (group B) was able to and did separate herself from all other rhinos ∼20 hr before parturition. This is consistent with wild females that seek dense brush in areas not frequented by other rhinos a day or less before parturition [Owen-Smith, 1973]. The nearest rhinos at the time of parturition were a minimum of 140 m away. However, after ∼1 hr the calf drew the attention of two rhinos, one of which tossed the calf into the air with her primary horn. Although this calf was uninjured, clearly it is within a cow's best interest to remain secluded while her calf is most vulnerable. The separation distances Maggie maintained in group B′, based on the limited and decreased frequency of space maintenance vocalizations relative to when she was in group B, allowed her to avoid excessive spatial stress.

In the wild, Owen-Smith [1973] observed that several groups sometimes came together at a resting area or moved together due to some disturbance "giving the false appearance of belonging to the same large 'herd'" but found that those alliances were only transient. Restricted space and management of the captive groups in this study, however, has created a herd consisting of companion subgroups at each location. The social structure of this herd in which the animals interact hourly has resulted in a stable dominance hierarchy that has not been documented in wild populations. Owen-Smith [1973] suggested that characterizing dominance relationships has little meaning in wild white rhino groups because competitive situations do not arise, but such situations certainly do arise in captivity, particularly with regard to food and shade in these observed groups, as evidenced by the increased incidence of space maintenance vocalizations.

Ganslosser and Brunner [1997] applied Wrangham's [1980] and Van Schaik's [1989] ecological and social primate models to ungulates whereby feeders searching for clumped food should form female-bonded groups within which exist "contest" conditions and access is determined by a dominance system. This situation can be applied to the groups in this study. In group A, the reevaluation of the

hierarchy was carried out as females competed for the first feed slab, occupied by the more dominant females. The male and a subordinate female usually occupied the last feed slabs. Confrontations occurred as the more dominant females moved down the line of slabs, and the male and subordinate female would move back to the first slabs for scraps. In groups B and B′, the hierarchy was also reconfirmed daily, though slightly less obvious because feeding was often more spread out. Incidently, there was no apparent pattern between the order of rhinos in the domiance hierarchy and their mean number of space maintenance vocalizations or their ages.

Most interesting about the hierarchies was the most subordinate animals. Helen (group A) rarely attempted to challenge the other females, made the fewest space maintenance vocalizations, and quickly made a subordinate gesture when challenged. Also behaviorally different from the other females, Helen was the only female observed in the study to kick her dung each time she defecated. Although observations of cows occasionally and weakly kicking their dung are documented [Owen-Smith, 1973], habitual dung-kicking at dung piles is a behavior that has only been recorded for territorial males [Owen-Smith, 1971, 1973; Rachlow, 1997; Rachlow et al., 1998].

The least dominant female in group B, Karla, was also observed to behave differently than the other females. First, one of the males would charge at her from a distance and engage her in a confrontation from which he would not yield, as he usually did with the other females, until Karla's companion aided her defense. Second, she constantly squirted urine, even after having emptied her bladder in stream-urination. The squirt was not the dribble-squirt exhibited by females only during estrus, but powerful squirts, usually two at a time, resembling the spray-urination used exclusively by territorial males [Owen-Smith, 1973, 1975].

As a submissive display, bachelor and immature male zebra will adopt the posture and facial expression of an estrus female to dampen aggression by a dominant male [Estes, 1991]. In general, the observed female rhinos were very intolerant of the males, so behaving more like a male by dung-kicking or urine-squirting would seem counter-productive if the intent was to reduce aggression by other females. If Karla's squirting was meant to mimic estrus squirting though she was not in estrus, this would serve to attract the male, but she already had difficulty preventing him from attacking her and was never receptive to the advances. The male behaviors displayed by these two females, then, were probably not carried out to deter aggression. Rather, the abnormal behaviors might contribute to their suppression by other group members.

Helen cycled and copulated during the course of this study and in years past [Steele, personal communication]. Similarly, Karla cycled and copulated in years past, including just 1 year before this study [Clawson and Wickham, personal communication]. Neither female has ever been confirmed to be pregnant. What may be significant is that two females from two different herds had different behaviors from the other females in their herd, including male-like behaviors, were at the bottom of the dominance hierarchies, and also have not reproduced. A survey study conducted on black rhinos found that greater amounts of aggressiveness and assertiveness contributed positively to a female's chances of breeding [Carlstead et al., 1999a]. Perhaps dominance over other females in groups of white rhinos plays a role in determining their reproductive success. Alternatively, chronic

psychological stress can cause infertility by the actions of glucocorticoids in mammals [Boonstra et al., 1998]. Carlstead and Brown [2005] found that noncycling female rhinos had more variable corticoid concentrations. Observations of this study suggest that constant suppression by members of the herd could be a significant source of social stress resulting in physiological responses that impair reproduction. For this study, social stress is defined as unrest characterized by abnormal behaviors, where "normal" is characterized as the typically observed displays and interactions recorded in the wild by Owen-Smith [1973], and caused by suppression by more dominant animals. It would be interesting if subordinate female rhinos who experience reproductive difficulty could be considered for relocation to a site where they may be able to become more dominant and potentially reproductive.

CONCLUSIONS

1. When they are kept in large groups with few adolescents, captive white rhino females did not change companions as often as they do in the wild.
2. Increased vocalizations were recorded, particularly during feeding, likely indicating spatial stress. This can be managed by wider separation of food piles.
3. Females with calves made vocalizations more than those without calves to maintain greater separation distances, and a female nearing parturition required seclusion from her companions.
4. Unseen in the wild, dominance hierarchies developed in large groups of captive white rhinos likely as a result of the induced herd social structure and competition for resources.
5. The most subordinate females in two different groups exhibited male-like behaviors and failed to produce offspring even though they seemed to cycle normally and/or copulated. This could be the result of social stress.

ACKNOWLEDGMENTS

Appendix A
Ethogram of wild southern white rhinoceros behaviors [Owen-Smith, 1973] (see Table A1).

TABLE A1.

Behavior or vocalization	Purpose	Description
Snort (vocalization)	Mild "keep-away" warning	Nasal exhalation or inhalation
Snarl (vocalization)	More powerful distance-increasing tool	A gruff roar, brief or rumbling, made with the mouth open, head thrust back, and ears laid back
Pant (vocalization)	Contact seeking or maintaining call	A chesty exhalation or inhalation
Hic (vocalization)	Signifies bull's intent to court	Repetitive wheezy exhalations with a throb produced at the beginning of each inhalation
Squeal (vocalization)	Signifies the actions of the bull (toward a cow) are in the context of territory boundary blocking	High pitched then falling off; may become a singing wail
Shriek (vocalization)	Attack inhibiting	Intense/shrill; ears thrust back, head thrust forward
Whine (vocalization)	Calf seeking udder or adolescents moving back toward companions	A thin, mewing tone that rises and falls in pitch
Squeak (vocalization)	Distress signal used by calves	Abrupt and high pitched
Gruff squeal (vocalization)	Emphasizes presence of bull	Throaty, rumbling squeal
Gasp-puff (vocalization)	Response to sudden fright	Sudden inhalation or exhalation
Pinning ears back	Distance increasing display	Ears laid back, usually coupled with head thrust and snort or snarl
Advancing steps	More powerful distance-increasing effect than a snarl or snort alone	Actor steps quickly toward the recipient and simultaneously gives a snarl, snort, or shriek
Horn prod	Ritualized attack movement	Head lowered followed by upward jabbing movement
Horn clash	Gesture to repel encroachment	Horn lowered parallel to the ground then hit sideways against horn of the recipient
Charge	Intimidation display	Rapid advance
Head flings	Play invitation and indication of excitement	Head swung up and down rapidly
Presenting the side	Act of appeasement	Turning head away from other rhino
Horn against horn stare	Intimidation display	Horns of two bulls pressed together with heads raised and ears forward
Horn wiping	Assertion of presence/status	Sideways, twisting movements of the horn on the ground
Scraping	May be related to the deposition of scent marks	Hindlegs or forelegs dragged with nail pressed against the ground
Tail curled	Associated with situations of general autonomic stimulation	Curling of tail may be held or repeated
Nasonasal meeting	Potentially for individual identification	Movements slow and relaxed eventually allowing noses to meet
Attack	To drive recipient away	Horn jabbing movements directed toward body of recipient
Fight	Opponents attempting to drive each other away	Attack gestures made by both opponents
Acceptance of tactile contact	To strengthen bonds	Expression of a close bond through nonaggressive physical contact
Urine/dung smelling	Identification	Smelling of urine or dung; may be followed by flehmen
Smelling of vagina	Estrus identification, courtship	Bull smells cow's vaginal area; may be followed by flehmen
Chin resting	Courtship	Bull rests his head on the rump or back of the cow
Mounting	Breeding	Bull straddles cow's back with forelegs while standing on hindlegs; may or may not be preceded by erection

REFERENCES

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–265.

Bertschinger HJ. 1994. Reproduction in black and white rhinos: a review. In: Penzhorn BL, Kriek NJ, editors. Rhinos as game ranch animals. Proceedings of a symposium. Onderstepoort, Republic of South Africa: South African Veterinary Association. p 115–161.

Boonstra R, Hik D, Singleton GR, Tinnikov A. 1998. The impact of predator-induced stress on the snowshoe hare cycle. Ecol Monogr 79: 371–394.

Brown JL, Bellem AC, Fouraker M, Wildt DE, Roth TL. 2001. Comparative analysis of gonadal and adrenal activity in the black and white rhinoceros in North America by noninvasive endocrine monitoring. Zoo Biol 20:463–486.

Carlstead K, Mellen J, Kleiman DG. 1999a. Black rhinoceros (*Diceros bicornis*) in US zoos: I. Individual behavior profiles and their relationship to breeding success. Zoo Biol 18:17–34.

Carlstead K, Fraser J, Bennett C, Kleiman DG. 1999b. Black rhinoceros (*Diceros bicornis*) in US zoos: II. Behavior, breeding success, and mortality in relation to housing facilities. Zoo Biol 18:35–52.

Carlstead K, Brown JL. 2005. Relationships between patterns of fecal corticoid excretion and behavior, reproduction, and environmental factors in captive black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros. Zoo Biol 24:215–232.

Estes RD. 1991. Zebras, asses, and horses. In: Estes RD, editor. The behavior guide to African mammals. Berkeley, CA: University of California Press. p 235–248.

Ganslosser U, Brunner C. 1997. Influence of food distribution on behavior in captive bongos, *Taurotragus euryceros*: an experimental investigation. Zoo Biol 16:237–245.

Graham L, Schwarzenberger F, Möstl E, Galama W, Savage A. 2001. A versatile enzyme immunoassay for the determination of progestogens in feces and serum. Zoo Biol 20:227–236.

Hermes R, Hildebrandt TB, Walzer C, Göritz F, Patton ML, Silinski S, Anderson MJ, Reid CE, Wibbelt G, Tomasova K, Schwarzenberger F. 2006. The effect of long non-reproductive periods on the genital health in captive female white rhinoceros (*Ceratotherium simum simum*, *C.s. cottoni*). Theriogenology 65:1492–1515.

Hillman-Smith K. 1987. Northern white rhinos in Garamba National Park. Pachyderm 9:19–22.

Owen-Smith RN. 1971. Territoriality in the white rhinoceros (*Ceratotherium simum*) Burchell. Nature 231:294–296.

Owen-Smith RN. 1973. The behavioural ecology of the white rhinoceros. Dissertation, University of Wisconsin, Madison.

Owen-Smith RN. 1975. The social ethology of the white rhinoceros *Ceratotherium simum*. Z Tierpsychol 38:337–384.

Patton ML, Swaisgood RR, Czekala NM, White AM, Fetter GA, Montagne JP, Rieches RG, Lance VA. 1999. Reproductive cycle length and pregnancy in the southern white rhinoceros (*Ceratotherium simum simum*) as determined by fecal pregnane analysis and observations of mating behavior. Zoo Biol 18: 111–127.

Pienaar D. 1994. Social organization and behaviour of the white rhinoceros. In: Penzhorn BL, Kriek NJ, editors. Rhinos as game ranch animals. Proceedings of a symposium. Onderstepoort, Republic of South Africa: South African Veterinary Association. p 87–92.

Rachlow JL. 1997. Demography, behavior, and conservation of white rhinos. Dissertation, University of Nevada, Reno.

Rachlow JL, Berkeley E, Berger J. 1998. Correlates of male mating strategies in white rhinos (*Ceratotherium simum*). J Mammal 79: 1317–1324.

Radcliffe RW, Czekala NM, Osofsky SA. 1997. Combined serial ultrasonography and fecal progestin analysis for reproductive evaluation of the female white rhinoceros (*Ceratotherium simum simum*): preliminary results. Zoo Biol 16: 445–456.

Reece RW. 1993. Rhinoceros SSP programs in North America: an overview. In: Ryder OA, editor. Rhinoceros biology and conservation. Proceedings of an international conference. San Diego, CA: Zoological Society of San Diego. p 294–295.

SAS Institute Inc. 2002–2003. SAS 9.1. Cary, NC, USA.

Schmidt C, Sachser N. 2000. Effects of food dispersal, translocation and panic on salivary corticosterone concentrations in the white rhinoceros. In: Lechner-Doll M, editor. Physiology and ethology of wild and zoo animals. Proceedings of the third international symposium. Berlin, Germany: Leibniz Institute for Zoo and Wildlife Research. p 113.

Shrader AM, Owen-Smith N. 2002. The role of companionship in the dispersal of white rhinoceros (*Ceratotherium simum*). Behav Ecol Sociobiol 52:255–261.

SPSS Inc. 2003. SigmaStat 3.0. Chicago, IL, USA.

VanSchaik CP. 1989. The ecology of social relationships amongst female primates. In: Standen V, Foley FA, editors. Comparative socioecology. Oxford, England: Blackwell Scientific. p 195–218.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. Behaviour 75: 262–300.