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Pilot Investigation of Socio-Spatial Relationships in an Ex Situ White Rhino (*Ceratotherium simum simum*) Bachelor Group

Lara C. Metrione [1,*], Terri L. Roth [2], Yaraila Rodriguez [3] and Elizabeth W. Freeman [4]

[1] South-East Zoo Alliance for Reproduction & Conservation, 581705 White Oak Road, Yulee, FL 32097, USA
[2] Center for Conservation and Research of Endangered Wildlife, Cincinnati Zoo & Botanical Garden, 3400 Vine Street, Cincinnati, OH 45220, USA; terri.roth@cincinnatizoo.org
[3] White Oak Conservation, 581705 White Oak Road, Yulee, FL 32097, USA; yrodriguez@white-oak.org
[4] School of Integrative Studies, George Mason University, 4400 University Drive, MSN 5D3, Fairfax, VA 22030, USA; efreeman@gmu.edu
* Correspondence: lara.metrione@sezarc.com

Abstract: Nonbreeding white rhino bulls are traditionally housed individually in zoos, but space limitations require the exploration of alternative techniques. There are no studies of group-housed bulls, and the feasibility of managing a bachelor group is unknown. Six bulls (two bulls each of 3-, 5-, and 8-yr-olds) in a 3.1 ha enclosure were observed for 30 min each 2×/wk for 20–31 wks. The 3-yr-olds were relocated after the first 20 weeks. Rhino location, nearest neighbor, aggressive behaviors, and dominance interactions were recorded. There was no evidence of habitat spatial segregation. The 3- and 5-yr-olds grouped together by age; 8-yr-olds did not associate as much as younger rhinos. Aggressive vocalizations and physical aggression were infrequent (range 0–1.5/h/bull and 0–1/h/bull, respectively). Eight-year-olds displayed and received aggressive vocalizations the most; three-year-olds displayed and received physical aggression the most. After the 3-yr-olds were removed, the habitat usage and social proximity of the remaining bulls did not change. Aggressive behaviors increased, but vocalizations (range 0.18–3.1/h/bull) remained more frequent than physical aggression (range 0.18–0.73/h/bull). The highest-ranking 8-yr-old engaged in physical altercations the least. The bulls shared space, and the use of vocalizations more than physical aggression deterred injury. These findings indicate that bachelor group management is feasible in a large enclosure with young bulls.

Keywords: behavior; space use; bull; nearest neighbor; aggression; dominance

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1. Introduction

The behavior of wild southern white rhino (*Ceratotherium simum simum*) bulls is well described. Dominant, breeding bulls defend non-overlapping territories but allow subordinate, nonbreeding bulls to live on the same territory [1–5]. Dominant bulls are typically older, larger, and have higher testosterone concentrations than subordinate bulls [4,6]. Most bulls will not become dominant territory holders until they are 12 years of age or older [2], and the reproductive behavior of subordinate bulls is suppressed [2,4,6]. Only dominant bulls mark territory boundaries, using spray-urination, dung-kicking, scraping with the fore- and/or hindlegs, and horn-scraping [2,3]. Subordinate bulls acknowledge territory boundaries and do not cross them [2]. Dominant bulls actively prevent females from leaving their territories, while being careful not to enter an adjacent bull's territory when in pursuit of them [1,2]. Highly ritualized confrontations of advances/retreats and horn-directed behaviors (e.g., scrapings, clashes, and jabbing gestures) reduce the risk of injury when neighboring dominant bulls meet [2,3]. However, some confrontations, particularly during a territory take-over, might be prolonged, more physical, and result in serious injury [2,3]. In contrast, dominant and subordinate bulls accustomed to living on the same territory have been observed grazing and

resting in the same vicinity [2], and approaches by the dominant bull usually are successfully halted by the subordinate bull through space-maintenance vocalizations and head-thrusts [1–3].

Wild female white rhinos do not tolerate companions when they are accompanied by a young calf [2,7]; thus, a cow's older offspring might join with other same- or mixed-sex subadults or adult females [2,7,8]. Therefore, immature, subadult bulls are expected to be observed as part of these pairings or small groups and not solitary. Indeed, subadults do not make unaccompanied excursions out of their home ranges [7], underscoring the importance of sociality among young white rhinos. In managed care, similar companion subgroups within larger breeding herds usually include two or three adult females and/or subadults [9–11].

Because of concerns about the potential for aggression, injury, and mortality, white rhino bulls in managed care typically are not housed together. Previous successful attempts to house male-only groups of which the authors are aware included (a) three half-brothers separated together from their natal herd at weaning and housed together until 4–4.5 years of age; (b) a hand-raised calf (9–18 mo old) with an unrelated bull (3–4 years old); and (c) 8-year-old half-brothers separated together from their natal herd and managed as a pair for the last 4 years. However, there are more bull white rhinos in the North American population than there are spaces available to individually house them in zoological institutions [12], and this problem will be exacerbated by the birth of new male calves from facilities where reproduction is highly successful. As a result, new solutions for managing surplus bulls are needed, and housing bulls together in bachelor groups may offer one option if it does not pose excessive risks to individual wellbeing. Zoological facilities manage bachelor groups of other ungulate species while carefully monitoring aggressive behavior (e.g., *Equus przewalskii* [13]; *Oryx gazella callotis* [14]; *Budorcas taxicolor tibetana* [15]), but it is relatively new territory for rhinos.

Currently, there are no published data on social interactions among white rhino bulls in managed care to provide context for interpreting the potential efficacy of maintaining them in bachelor groups. Animals can behave compatibly or competitively in the same shared space, so documentation of overlapping enclosure space use should be accompanied by additional behavioral observations to assess compatibility [16]. Therefore, this pilot study sought to investigate the behavior of young bulls in an experimental bachelor group by (1) delineating any exclusivity in enclosure use, (2) identifying potential subgroups based on nearest neighbor data, (3) quantifying the frequency of aggressive interactions between individuals, and (4) calculating any dominance hierarchy based on submissive behaviors.

2. Materials and Methods

2.1. Animals

A bachelor white rhino group of six bulls (3 yrs old, n = 2; 5 yrs old, n = 2; 8 yrs old, n = 2; Table 1) was managed in a 3.1 ha habitat at a private facility closed to the public in Florida, USA (81.7427950° W 30.7471514° N). This facility maintains females and subadults in large groups, periodically introducing adult bulls for breeding. Thus, four of the bulls in this study had the same sire (Table 1). The 3-yr-olds lived together in their natal group prior to joining the bachelor group. Bull #3 had prior socialization experience living with the 3-yr-olds for ~14 months when they were calves but had not lived with them for 17 months immediately prior to joining the bachelor group. The 5-yr-olds lived together for one month prior to their introduction to the 8-yr-olds. The 8-yr-olds were imported from the wild at the same time and were housed together for 3.5 years without females and at times with other 3- to 5-yr-old bulls prior to joining this bachelor group.

When this bachelor group was formed, the 8-yr-olds and 5-yr-olds were introduced in the enclosure first and lived there for 16 months. Then, the 3-yr-olds were introduced to the enclosure without other bulls for four days. The 3-yr-olds were introduced to the 5-yr-olds for two weeks before the 8-yr-olds were brought back into the enclosure. Opportunistically, data collection for the study began four months after the bachelor group of six was formed for 20 weeks (11 January–28 May 2021). The 3-yr-olds were transferred to another facility, and observations continued for an additional 11 weeks on the remaining four bulls (4

June–20 August 2021). None of the bulls was considered behaviorally mature based on their young ages, lack of breeding experience, and the lack of routinely observed territorial behaviors (i.e., marking boundaries using spray-urination, dung-kicking, scraping with the fore- and/or hindlegs, and horn-scraping).

Table 1. White rhino bulls observed in a North American zoological facility as a group of six for 20 weeks and then as a group of four for 11 weeks after the youngest bulls were relocated.

Number (DOB)	Age at Time of Study *	Hours Observed for Space Use and Nearest Neighbor	Hours Observed for All Occurrence Behaviors
#1 (est. 1 January 2013)	8.5 years	23.9	7.5
#2 (est. 1 January 2013)	8.5 years	24.5	7.5
#3 † (27 August 2015)	5.8 years	24	7.5
#21 † (24 November 2015)	5.6 years	24.5	7.5
#22 † (21 February 2018)	3.3 years	13.4	2
#30 † (7 February 2018)	3.3 years	13.5	2

* Calculated as of June 2021. † Half-brothers.

Animals were fed 2.7–3.6 kg each of Mazuri® ADF 16 Herbivore Diet (cube) once daily in concrete feeders, 1–2 bales (depending on pasture quality) of coastal hay daily subdivided across the enclosure, and water ad libitum (freely as desired). These rhinos were infrequently manipulated by human intervention: bulls were separated into holding areas once per month for routine health procedures, but dung was removed from middens weekly without the need to move the bulls from the pasture. The bachelor bulls' enclosure was located within the auditory and, likely, olfactory range of female rhinos; it was located within the auditory, olfactory, and visual range of mature, adult bulls. This study was approved by the Institutional Animal Care and Use Committees of the Center for Conservation and Research of Endangered Wildlife (CREW, #22-173) and George Mason University (#1833567-1).

2.2. Behavioral Observations

Focal observations were conducted for 30 min per bull twice weekly, once between 0800 and 1100 h and once between 1300 and 1600 h. Bulls were observed on a rotating schedule so that they were not observed during the same hour every session. Trained observers (n = 2) passed inter-observer reliability tests (≥85%), generating 123.7 h of observation for enclosure use and nearest neighbor analyses. A subset of 34 h of observations by one observer was used for analyses of aggression and dominance. Data were recorded using the ZooMonitor application (https://zoomonitor.org/; Lincoln Park Zoo), which enables animal behavior and location to be recorded during live observations through a customizable user interface that includes a to-scale enclosure map. Location within the enclosure and nearest neighbor including approximate distance (<2 body lengths, >2 body lengths) were recorded instantaneously every 3 min (n = 81.7 h across 28 d for the group of six bulls; n = 42 h across 21 d for the group of four bulls). An abbreviated ethogram was adapted from Owen-Smith [2] and Metrione et al. [10] and included aggressive vocalizations (snort, snarl), non-contact physical aggression (advancing steps, charge), contact physical aggression (horn-to-horn stare, horn prod, horn clash, fight), and submissive behaviors (presenting the side, yielding ground) (Table 2). Continuous recording of all occurrences of aggressive and submissive behaviors, including actor, recipient, and outcome, was utilized (n = 2 h/bull across 4 d for the group of six bulls; n = 5.5 h/bull across 11 d for the group of four bulls). Display of submissive behaviors to another bull was used for calculating the dominance hierarchy in the group of four bulls, detailed below.

Table 2. Ethogram of bull white rhino behaviors monitored at a North American zoological facility.

Behavior	Description
	Aggressive Vocalization
Snort	Nasal inhalation or exhalation
Snarl	A gruff roar, brief or rumbling, made with the mouth open, head thrust back, and ears laid back
	Non-Contact Physical Aggression
Advancing steps	Direct approach at constant speed towards another rhino while head carriage is low
Charge	Rapid advance towards another rhino
	Contact Physical Aggression
Horn-to-horn stare	Primary horns of two rhinos pressed against each other
Horn prod	Abrupt thrust of horn toward another rhino in a jabbing motion
Horn clash	Horn lowered parallel to the ground then hit against recipient's horn
Fight	Multiple attack gestures (horn prods and clashes) made by both opponents
	Submissive
Presenting side	Abruptly turning head or body away from another rhino
Yield ground	Back away, turn to side, or walk off from another rhino

2.3. Spatial Analysis

This study employed the latest methods for integrating ZooMonitor data with Geographic Information System (GIS) software to quantify space use [17]. ZooMonitor's CSV export includes timestamped, unitless x and y coordinates (Space Use Coordinate X and Space Use Coordinate Y). To accurately reference each position with values and units that could be used by ArcGIS® Pro v. 2.9 (Environmental Systems Research Institute Inc., Redlands, CA, USA), the CSV file required modification. A known length of the enclosure was measured, and the endpoints of the length were identified in ZooMonitor's pixel grid coordinate system. These two control points were manually added as a row at the end of the CSV. ArcGIS Pro was then used to transform ZooMonitor data to geographic coordinates. To begin this transformation, the Universal Transverse Mercator (UTM) projection was identified for the enclosure so that horizontal coordinates (x and y) were expressed in meters. A line of the known enclosure length that was used in ZooMonitor was drawn at its corresponding UTM location in ArcGIS Pro using the Create Feature Class tool. The Feature Vertices to Points tool was then used to generate the UTM easting (x) and northing (y) control points at the ends of the line. The enclosure map used in ZooMonitor was georeferenced to the UTM control points to create enclosure boundaries. The ZooMonitor CSV was imported into ArcGIS Pro, and its x- and y-coordinate data were assigned to correspond with UTM x and y coordinates using the XY Table to Point tool. Once both sets of control points of the known enclosure length (in ZooMonitor coordinates and corresponding UTM coordinates) were in the same projection, the ZooMonitor coordinates were georeferenced by establishing two-control links using the Similarity Method in the Transform tool. Points were reviewed, and any points that fell outside the enclosure boundaries were omitted.

Kernel density estimates (KDEs) were calculated in ArcGIS Pro using the Kernel Density tool for all animals for each time period separately (n = 6 bulls together, n = 4 bulls together). The cell size selected was 1 m, with an 8 m search radius (~2 body lengths). The 50% fixed-kernel method was used to define areas where the bulls were most frequently located, and the 95% fixed-kernel method was used to provide a more comprehensive delineation of their space use [18,19]. These KDEs were visually inspected to determine if bulls segregated themselves into exclusive areas, then the amount of overlap in the 50% and 95% KDEs was calculated in ArcGIS Pro for each dyad using the Intersect tool.

2.4. Social Behavior Analysis

Descriptive statistics were used to examine the data. Nearest neighbor relationships and behavior frequencies were calculated separately for the groups of six and four bulls. The strength of nearest neighbor relationships was calculated as the percentage of intervals in which a particular bull was identified as the nearest neighbor to the focal bull and

the percentage of those intervals in which that particular bull was less than or greater than 2 body lengths (~8 m) away. Frequencies of each behavior displayed and received by the focal rhino were also calculated per bull. Frequencies were positively skewed; therefore, median frequencies of each behavior displayed and received were used to summarize data for the bulls grouped by age. Observation hours for all occurrence data were insufficient to calculate a dominance hierarchy for the group of six. However, the dominance hierarchy among the group of 5- and 8-yr-old bulls, after the 3-yr-olds were removed, was calculated based upon the percentages of interactions that resulted in a "win" for each dyad and arranged in a dominance matrix [20]. A bull "won" if the interaction ended with his opponent displaying submissive behavior. In the matrix, values correspond to the percentage of interactions in which the rhino listed on the left of the row dominated the rhino listed above the column, i.e., interactions ended with the rhino listed above the column displaying submissive behavior to the rhino listed on the left of the row. When individuals are correctly arranged from most to least dominant, values in the matrix should increase across rows and decrease down columns [20].

3. Results

3.1. Behavior of Six Bulls

There was no evidence of spatial segregation among the bulls, and all enclosure areas were used by all the bulls (Figure 1). All bulls' 50% and 95% KDEs overlapped with each other (average = 208.4 ± 20.0 m^2 and 1691.8 ± 52.9 m^2, respectively; Table 3). Nearest neighbor relationships were reciprocal between similarly aged bulls, and relationship strength was associated with bull age (Table 4). The youngest bulls were each other's nearest neighbor most frequently (>80%) and were within two body lengths (BLs) of each other ≥93% of that time. The middle-aged bulls were each other's neighbor ≥71% of the time and were within 2 BLs of each other ≥87% of that time. The oldest bulls were each other's nearest neighbor only 31% of the time, though that was still more frequently than they associated with any of the younger bulls (9.6–28.9%). One of the two 8-yr-olds (#1) was the only bull that spent the majority (51.2%) of his time >2 BLs from his preferred nearest neighbor. Excluding #1, the average percentage of time that the bulls spent <2 BLs from their nearest neighbor was 84.7 ± 2.9% (Table 4).

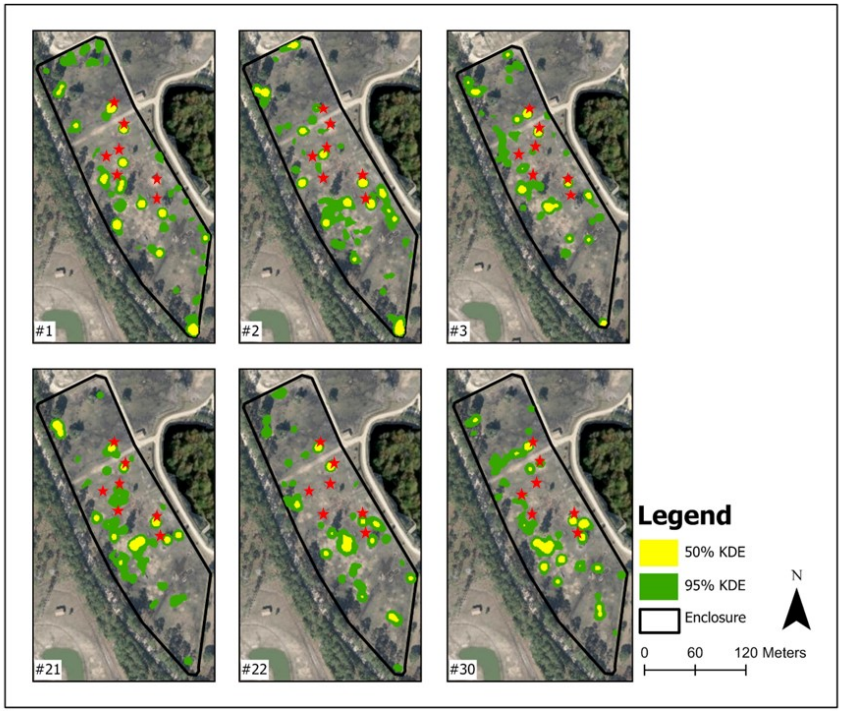

Figure 1. Space use of a 3.1 ha enclosure (outlined in black) at a North American zoological facility by six bull white rhinos from 15 January 2021–28 May 2021 with shelter and feeder locations indicated by red stars.

Table 3. Calculated 50% and 95% kernel density estimates (KDEs; m^2) for each bull and overlap (m^2) in KDE space use for each dyad of bulls in a white rhino bachelor group.

		50% KDE (m^2)			95% KDE (m^2)		
Bull A	**Bull B**	**A—50%**	**B—50%**	**Overlap**	**A—95%**	**B—95%**	**Overlap**
6 Males							
#1	#2	914	979	247	4809	5234	1634
#1	#3	914	750	235	4809	4764	1485
#1	#21	914	731	215	4809	4745	1470
#1	#22	914	831	66	4809	4698	1404
#1	#30	914	610	205	4809	4308	1309
#2	#3	979	750	162	5234	4764	1737
#2	#21	979	731	295	5234	4745	2039
#2	#22	979	831	86	5234	4698	1720
#2	#30	979	610	129	5234	4308	1773
#3	#21	750	731	365	4764	4745	1913
#3	#22	750	831	221	4764	4698	1764
#3	#30	750	610	229	4764	4308	1647
#21	#22	731	831	236	4745	4698	1913
#21	#30	731	610	263	4745	4308	1715
#22	#30	831	610	172	4698	4308	1854
4 Males							
#1	#2	655	1161	100	4252	4107	1574
#1	#3	655	76	0	4252	3418	1402
#1	#21	655	360	68	4252	3140	911
#2	#3	1161	76	66	4107	3418	1300
#2	#21	1161	360	163	4107	3140	1293
#3	#21	76	360	76	3418	3140	1269

Table 4. Percentage of intervals in which each white rhino bull in a bachelor group was identified as the nearest neighbor of the focal bull (preferred associations in bold), and how often that association was within two body lengths.

Focal Bull (Age)	**Neighbor**	**Nearest (%)**	**Within Two Body Lengths (%)**
6 Males			
#1 (8 yo)	**#2**	**31.3**	**48.8**
	#3	13.1	45.7
	#21	22.0	55.9
	#22	21.6	44.8
	#30	11.9	71.9
#2 (8 yo)	**#1**	**31.4**	**65.9**
	#3	9.6	74.1
	#21	11.4	75.0
	#22	28.9	71.6
	#30	18.6	75.0
#3 (5 yo)	#1	5.6	93.3
	#2	4.8	69.2
	#21	**72.6**	**87.2**
	#22	8.1	86.4
	#30	8.9	95.8
#21 (5 yo)	#1	6.5	94.4
	#2	6.5	55.6
	#3	**71.7**	**92.5**
	#22	9.0	100.0
	#30	6.5	88.9
#22 (3 yo)	#1	2.2	50.0
	#2	6.0	93.8
	#3	6.4	94.1
	#21	4.5	100.0
	#30	80.9	93.1
#30 (3 yo)	#1	0.7	100.0
	#2	11.1	93.3
	#3	0.7	100.0
	#21	2.6	71.4
	#22	**84.8**	**96.5**

Table 4. *Cont.*

Focal Bull (Age)	Neighbor	Nearest (%)	Within Two Body Lengths (%)
4 Males			
#1 (8 yo)	#2	34.0	28.2
	#3	**42.1**	**39.8**
	#21	23.9	28.0
#2 (8 yo)	#1	26.7	25.0
	#3	**46.2**	**76.3**
	#21	27.1	56.1
#3 (5 yo)	#1	8.1	88.2
	#2	10.5	86.4
	#21	**81.4**	**86.0**
#21 (5 yo)	#1	2.4	100.0
	#2	13.8	93.1
	#3	**83.8**	**88.6**

Frequencies of displayed and received aggressive vocalizations (range 0.0–1.5/h/bull) and physical aggression (range 0.0–1.0/h/bull) were low, and the median frequency of aggressive vocalizations displayed by the group (0.0 ± 0.58/h) was greater than the median frequency of physical aggression (0.0 ± 0.31/h; Table 5). The oldest bulls displayed and received aggressive vocalizations the most; the youngest bulls displayed and received physical aggression the most (Table 5). The total numbers of non-contact (n = 2) vs. contact (n = 1) physical aggression were similar.

Table 5. Hourly frequencies of aggressive behavior for individual bulls, and median (± SD) hourly frequencies of aggressive behavior for white rhino bull groups/pairs.

	Aggressive Vocalizations		Physical Aggression	
	Actor	Recipient	Actor	Recipient
6 Males				
#1	1.5	1.5	0	0
#2	0	0	0	0
#3	0.5	0	0	0
#21	0	0	0	0
#22	0	0	0	0
#30	0.5	0	1	0.5
4 Males, Ordered by Dominance Rank				
#1	0.55	0.55	0.18	0.18
#3	1.45	0.55	0.55	0.18
#2	3.09	1.09	0.73	0.55
#21	0.18	1.45	0.18	0.36
Social Group				
6 males	0.25 ± 0.58	0.00 ± 0.61	0.00 ± 0.41	0.00 ± 0.20
4 males	1.00 ± 1.30	0.82 ± 0.45	0.36 ± 0.27	0.27 ± 0.17
6 Males Based on Age				
Oldest	0.75 ± 1.06	0.75 ± 1.06	0.00 ± 0.00	0.00 ± 0.00
Middle	0.25 ± 0.35	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Youngest	0.25 ± 0.35	0.00 ± 0.00	0.50 ± 0.71	0.25 ± 0.35
4 Males Based on Age				
Oldest	1.82 ± 1.80	0.82 ± 0.39	0.45 ± 0.39	0.36 ± 0.26
Middle	0.82 ± 0.90	1.00 ± 0.64	0.36 ± 0.26	0.27 ± 0.13

3.2. Behavior of Four Bulls

After the removal of the two youngest bulls, the remaining four bulls continued to use the entire enclosure, especially the northern and central portions, but also the southern tip (Figure 2). There continued to be no evidence of spatial segregation, and overlap of 95% KDEs remained high (average = 1291.5 ± 89.0 m^2; Table 3). Nearest neighbor relationships continued to be reciprocal for the 5-yr-old bulls (Table 4) who continued to spend ≥ 86%

of that time within 2 BLs. Each of the oldest bulls, however, associated more frequently with one of the 5-yr-old bulls than with each other (Table 4). One of the two 8-yr-olds (#1) was the only bull that spent the majority of his time (average = 68.0 ± 3.9%) >2 BLs from his nearest neighbor, whereas the other 8-yr-old (#2) was <2 BLs from his nearest neighbor an average of 52.5 ± 14.9% of the time. Excluding #1, the average percent of time that the bulls spent <2 BLs from their nearest neighbor was 77.7 ± 7.8% (Table 4).

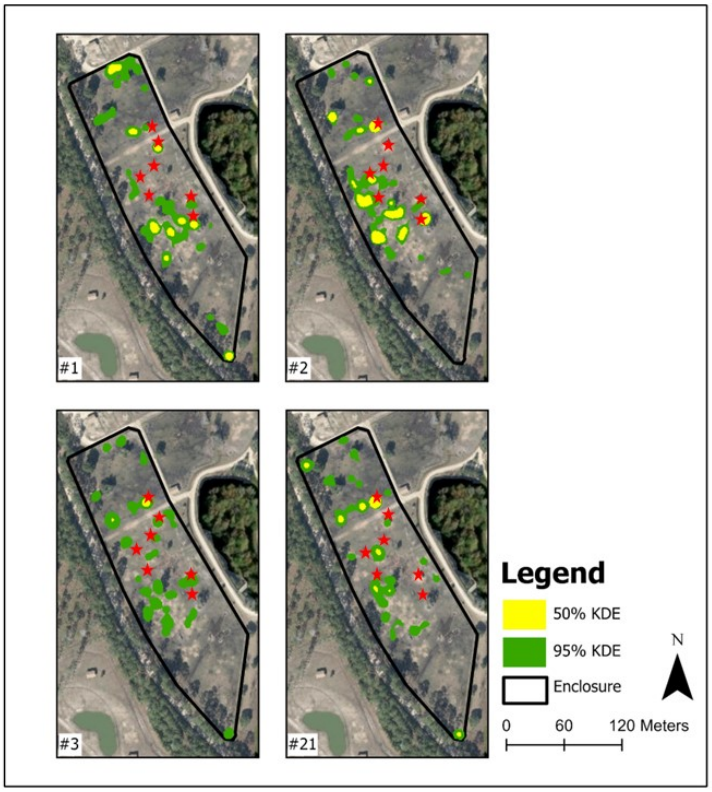

Figure 2. Space use of a 3.1 ha enclosure (outlined in black) at a North American zoological facility by four bull white rhinos from 4 June 2021–20 August 2021 with shelter and feeder locations indicated by red stars.

Frequencies of aggression, displayed and received, were infrequent (vocalizations: range 0.18–3.09/h/bull; physical: range 0.18–0.73/h/bull), but median frequencies of displayed aggressive vocalizations (0.82 ± 0.92/h) and physical aggression (0.27 ± 0.22/h) increased after the youngest bulls were removed (Table 5). The bulls continued to use aggressive vocalizations more than physical aggression (Table 5), and the total occurrences of non-contact physical aggression (n = 8) remained similar to those of contact physical aggression (n = 9).

Interactions of the group of four bulls indicated a dominance hierarchy (Table 6). One 8-yr-old bull (#1) won 100% of interactions with #3 and #21 and therefore was ranked first, but the hierarchy was not strictly linear, and third-ranked #2 won 67% of the interactions with #1. There was no overlap in the 50% KDEs of the first- (#1) and second-ranked (#3) bulls, whereas all other dyads continued to have overlapping space use even in these most frequently used areas (average = 94.5 ± 18.1 m^2; Table 3). On average, the middle-ranked bulls used aggressive vocalizations and physical aggression 6.2× and 3.6× more often, respectively, than the top- and bottom-ranked bulls (Table 5). In fact, vocalizations by the middle-ranking 8-yr-old (#2) and not the top-ranking 8-yr-old (#1) accounted for 80% of the frequency of vocalizations displayed by those older bulls (Table 5). The two lower-ranking bulls received aggressive vocalizations and physical aggression 2.3× and 2.5× more often, respectively, than the two higher-ranking bulls (Table 5).

Table 6. Matrix indicating the possible dominance hierarchy among four bull white rhinos based on the percentage of interactions in which the rhino listed in the column heading displayed submissive behavior to the rhino listed at the row heading.

Bull	#1	#3	#2	#21
#1	x	100	33 †	100
#3	0	x	80	100
#2	67 †	20	x	75
#21	0	0	25	x

† In a linear hierarchy, values should increase across rows and decrease down columns, but those expectations were not met for this dyad of bulls.

4. Discussion

The bachelor group was deemed cohesive based on the lack of spatial segregation and the close associations among the 3- and 5-yr-olds in particular. Pairs or small groups of subadult (single- or mixed-sex) and/or adult females are observed in the wild [2,3,7,8], and the home ranges of those pairs/groups overlap extensively [2,3,21]. Within groups, usually two individuals are close companions that are $\leq$5 m and rarely more than 25 m apart [2]. Consistent with those observations, all the bulls in this study used all portions of the enclosure with no evidence of spatial segregation among them, and the 3- and 5-yr-olds formed subgroups in which the two bulls remained in close proximity to each other. In fact, >1000 m^2 of overlap in 95% KDEs was the norm (mean = 1577 $\pm$ 60.0 m^2), and, with the exception of bull #1 who spent most of his time >2 BLs from other rhinos, bulls showed a preference for close proximity as they were found <2 BLs from their nearest neighbor ~78–85% of the time on average. The observed pairings corresponded to the bulls' prior experience living together before joining the bachelor group. It is possible that the same age-associated close companionships and/or overall cohesiveness of the group might be different in a bachelor group composed of totally unfamiliar bulls. Wild black rhino (*Diceros bicornis*) bulls up to age nine also have overlapping home ranges and form multi-year associations [22]. In that study, bulls over the age of 8 were rarely observed in the core range of similarly aged bulls [22], but the 8-yr-old white rhino bulls in this study had not yet excluded each other from their 50% KDEs and still shared 99.6 m^2 of their most frequently used space. In general, amongst all the bulls, overlapping space use in the central portions of the enclosure likely was promoted by the presence of shade shelters and concrete feeders in that area, which is consistent with findings that wild white rhinos prefer areas close to supplementary feeding locations [23].

A bull attaining maturity might be expected to eventually take on the comparatively more solitary role of a dominant or subordinate adult bull. A higher dominance rank in an 8-yr-old bull was identified based on the outcome of social interactions, and he also distanced himself the most from the others. A second 8-yr-old won a higher percentage of interactions with the first but did not consistently win interactions with the 5-yr-olds, and he spent more time in closer proximity to his nearest neighbor. As these bulls mature, it is possible that enclosure space could continue to be shared because adult dominant bulls allow subordinate bulls to live on the same territory in the wild [1–5] and have been observed to graze and rest in the same vicinity [2]. It was notable that the 50% KDEs of first- and second-ranked bulls did not overlap, although the overlap in their 95% KDEs was among the highest values in the group of four. A recent study including three breeding bulls introduced to an enclosed sanctuary in Uganda found that two of the bulls shared portions of their core range areas [24]. This is in contrast to expectations based on breeding bulls in larger reserves within South Africa and Zimbabwe in which breeding bulls established non-overlapping territories [1–5]. Whether bulls with breeding experience would share enclosure space in a zoo bachelor group is unknown. One limitation of the present case study is that it encompassed a 31-week period rather than several years of bachelor herd management. A longer-term study that explores how behavior and space use change as the

bulls age, mature, and are possibly removed and then reintroduced to the bachelor group following breeding opportunities will provide a rich description of bull social dynamics.

Another limitation of this study was the small number of observation hours. Nonetheless, it was evident that the low frequency of aggressive interactions of any form (vocalization, non-contact and contact physical aggression) observed throughout the study reduced the potential for conflicts that could cause injuries in the bachelor group. Only superficial skin scrapes that required no medical attention were observed on the bulls in this study. Although aggression increased when the youngest bulls were removed, the continued use of aggressive vocalizations more than physical displays might be a strategy to minimize injury. There are sex-specific differences in white rhino vocalization rates, especially for aggressive vocalizations [25], and contact calls differ in quality between territorial and subordinate bulls and encode information about motivation [26]. Vocalizations, therefore, provide honest signals that could deter conflicts between bulls in alignment with their established dominance relationships [26]. Wild subordinate bulls deter attack using space-maintenance vocalizations and head-thrusts while the dominant bull remains silent [1–3]. It was surprising, then, that the highest-ranked bull in the present study used vocalizations more than any other bulls while in the group of six (1.5/h), and the weakest, youngest bulls used physical aggression more often than vocalizations. It is possible these observations could be attributed to the learning process for bull social behavior, and the tolerance of the older and middle-aged bulls could indicate that the youngest bulls' "practice" aggression posed no threat to social status or resource access. Once the youngest bulls were removed, the frequency of vocalizations by the highest-ranked bull decreased, and the greater frequency of both aggressive vocalizations and physical displays overall was attributed to increases in those behaviors by the other three remaining bulls. Social change might be expected to induce disruption, but, as seen with another pachyderm, the hippopotamus (*Hippopotamus amphibius*), undergoing group coalescence as water levels drop, aggression can decrease once social equilibrium is attained [27]. Similarly to this study's observations, hippos rarely utilize physical contact without first using postural and vocal signals [27].

Because dominant bulls in the wild are not challenged for their territory by the subordinate bulls living therein [2,3], aggressive interactions with the dominant bull in a zoo bachelor group might be unlikely once dominance is established. In this study, the highest-ranked bull displayed and received the least physical aggression in the group of four bulls. The second- and third-ranked bulls displayed more aggression while the third- and fourth-ranked bulls received more aggression. Thus, mid- to lower-ranking bulls appear to be important animals to monitor for potential conflict in bachelor groups, particularly as social relationships are being established. Even among these lower-ranking bulls, the tendency to use vocalizations more often than physical displays coupled with the infrequent use of physical aggression altogether suggests that, in a large enclosure with nonbreeding bulls under the age of nine, the level of aggression experienced appears to be low. It is possible that the prior familiarity of some bulls also contributed to the low frequencies of aggression and aided in the establishment of the dominance hierarchy in this group. Although not studied in rhinos, prior contest experience can affect an animal's perception of costs in a future contest [28]. Perhaps allowing young bulls to interact could provide a relatively safer learning opportunity that might avoid more costly interactions in the future.

Attempts to prevent or reduce aggression among animals in managed care can result in solitary housing of individuals, as with most nonbreeding bull rhinos, or pharmacological downregulation of the reproductive axis. The latter method is sometimes unsuccessful in modifying behavior [29,30] and sometimes irreversible [31]. Pharmacological treatments to reduce aggression also can include chemicals intended to impact the nervous system, the effects of which can vary between individuals [32]. Among well-studied laboratory rodents and non-human primates, solitary housing of individuals initially born into social settings but then isolated can result in negative indicators of wellbeing, such as abnormal and anxiety-associated behaviors [33] and immunosuppression either over time [34] or

in response to a subsequent acute stressor [35]. Similarly, in horses (*Equus caballus*), the rhino's closest domestic relative, relocating geldings from more spacious group housing to single housing was associated with indicators of stress, including an increase in the neutrophil-to-lymphocyte ratio, higher plasma cortisol concentrations, development of stereotypical behavior, and display of behaviors associated with contact deprivation, frustration, and apathy [36]. The display of natural social behavior in form, frequency, and function is an important aspect of the behavioral domain in the Five Domains model for animal welfare [37,38] that many zoological institutions have adopted into their wellbeing programs. Rather than solitary housing, allowing appropriate levels of aggression displayed in species-appropriate forms and by age/dominance-appropriate individuals in a group might enhance animal wellbeing by promoting natural social behaviors rather than detract from it due to injuries. Studies on bachelor elephant groups provide good examples (*Loxodonta africana* [39], *Elephas maximus* [40]). In the latter, non-contact aggressive behavior, but not contact aggression, increased during the initial months following the bulls' introduction and then decreased while affiliative behaviors increased in the final months of the study [40]. As in these examples, careful monitoring is essential for interpreting whether the observed aggression is beneficial or detrimental to wellbeing. Group housing is likely only beneficial if the group is compatible and stable [33]. Numerous tools are available for tracking and recording behavior as well as keeper-based ratings of animal welfare to assist managers with interpreting the wellbeing of their animals [41]. Current guidelines note that observation of pacing, excessive running, excessive space-maintenance vocalizations, and diarrhea could be indicative of a rhino in distress [42]. It would be prudent to reconsider group housing if those signs are routinely noted.

Powell et al. [43] contend that ungulates in managed care should experience a net-positive balance of experiences across the lifetime, and thus management practices that allow transitory aggression and competition during life stages where this behavior is an appropriate part of development can be balanced with neutral and positive experiences resulting from the same management practice. Bachelor groups can provide opportunities for social learning, including the proper development of natural fighting displays and skills, and the signals necessary to deter aggression, which can be relevant for future breeding success when males are introduced to a group of females [43]. Other benefits of male socialization can include reduced stereotypical behavior [44], reduced aggressiveness toward humans [45], and reduced magnitude and duration of physiological (e.g., cardiovascular stress measures) and behavioral reactions to husbandry procedures [46]. Social housing also provides opportunities for social play, which is increasingly associated with positive wellbeing due to its psychological benefits to the individual and group [47]. Wild horse stallions not tending harems form bachelor groups [48], but most domestic stallions are singly housed due to fears of aggression and injury [49], similar to bull rhinos. Upon initial exposure to group housing, horse stallions previously housed singly show a higher frequency of aggressive and sparring behavior, but they also show a higher frequency of playing, social grooming, and investigative behavior compared to stallions that were already housed as a group, suggesting there is a built-up motivation for displaying social behavior [50]. Similarly, bull white rhinos might naturally be motivated to engage in social behavior, and solitary housing could deprive them of an outlet for that motivation. Furthermore, in group-housed stallions, mild forms of agonistic interactions, such as displacement and submission, and aggression do not increase when additional stallions are added to the group, suggesting that socialization might facilitate learning of more subtle forms of communication [50]. Thus, beginning to manage bull rhinos in bachelor groups could promote long-term wellbeing through the gradual development of better-socialized bulls as well as bulls that are more resilient to changes in social housing. The findings of this pilot study should be considered preliminary and contextual, but the totality of observations suggest the very low frequencies of aggression observed in this bachelor group likely were balanced by concurrent and future positive benefits of socialization, demonstrated here by spatial evidence of social affiliation, resulting in net-positive wellbeing for the bulls. Future

studies of bachelor bulls should include additional behavioral and physiological indicators of wellbeing.

5. Conclusions

This opportunistic investigation suggests that maintaining white rhino bulls in bachelor groups could be a feasible ex situ management option that is consistent with the natural history of the species and worthy of continued exploration. Wild, subadult bulls often share space and have opportunities to interact [2,3,7,8,21,22], as do adults when dominance is clear and the space is large [1–5,24]. Additionally, current housing recommendations state that white rhino breeding facilities must have space to hold offspring for at least three years after birth to allow sufficient time to find and/or create alternative holding space [42]. Therefore, fulfilling this requirement and providing a more natural existence for bulls at both their natal and new facilities could be promoted by housing them in groups. It is possible that the success of this bachelor group was related to the large size of the enclosure, and bull groups in smaller enclosures might behave differently. The young ages of and previous relationships among the bulls also might have contributed to the group's success. Indeed, two recommendations for reducing aggression among group-housed male laboratory mice (*Mus musculus*) include increasing cage size and grouping the males prior to sexual maturity [51]. Whether group cohesiveness and low rates of aggression would be maintained as bulls in a bachelor group mature is also a key question that remains for future investigation. Additionally, it is unknown if breeding bulls can be rotated in and out of bachelor groups, or if this management strategy is only appropriate for bulls without breeding experience. Regardless, the positive preliminary results reported herein are encouraging, and as bachelor groups become more common with the increasing number of males in managed care, so too will additional opportunities to study white rhino bull social behavior.

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