

Exploring the behaviors and social preferences of a large, multigenerational herd of zoo-housed southern white rhinoceros (*Ceratotherium simum simum*)

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Abstract

The zoo-housed southern white rhinoceros (SWR) population is of special concern due to their lack of consistent breeding success. An enhanced understanding of SWR social preferences could better inform management planning by promoting natural social relationships, which can positively affect their well-being. The large, multigeneration herd housed at the North Carolina Zoo provides an ideal opportunity to examine rhino sociality across different ages, kin types, and social groupings. Eight female rhinos' social and nonsocial behaviors were recorded from November 2020 through June 2021 across 242 h. Activity budget analyses revealed strong seasonal and temporal variations in grazing and resting behaviors, with no stereotypic behaviors recorded. Bond strength calculations suggested that each female maintained strong social bonds with one to two partners. Beyond mother–nursing calf bonds, we found that the strongest social ties were maintained between calf-less adults and subadults in these dyads. Considering these findings, we recommend that management plans attempt to house immature females with calf-less adult females, as they may be necessary to the social landscape of immature females and, ultimately, improve their welfare.

KEYWORDS

ceratotherium, social behavior, welfare, zoo animal

1 | INTRODUCTION

The southern white rhinoceros (*Ceratotherium simum simum*; hereon SWR) is the most common and social species of rhinoceros (Hutchins & Kregar, 2006; L. Metrione & Eyres, 2014; Owen-Smith, 1975). Currently, the SWR relies on the help of human management to conserve genetic diversity and sustain population size (Emslie, 2020). Unfortunately, reproductive success has been inconsistent among ex

situ SWR, which threatens the growth of the zoo-housed population and the future of the species (L. Metrione & Eyres, 2014; Swaisgood et al., 2006).

For social animals, like the SWR (Swaisgood et al., 2006), providing social interaction is essential to promoting good welfare (Rose & Croft, 2015). As social bonds are common among wild conspecifics, similar social opportunities must be presented to animals under human care. Conversely, preventing access to

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preferred social partners has been found to negatively affect group cohesion and is associated with stress responses (Rault, 2012). Assessing which individuals an animal chooses to associate with can improve well-being by informing management decisions like group housing and transfers. Developing our understanding of SWR sociality and behavior is therefore necessary for advancing these animals' population management and welfare.

To date, there is evidence that social interactions play a significant role in the well-being of zoo-managed SWR (Hutchins & Kreger, 2006; Martínez et al., 2022; L. C. Metrione & Harder, 2011). Fecal glucocorticoid metabolites (fGCM), often used as a metric to assess stress (Sheriff et al., 2011), have been linked to social opportunities and herd composition. Adult females housed with a female companion known since adolescence, for example, were found to maintain lower levels of fGCM than those housed with novel or male companions (L. C. Metrione & Harder, 2011). In addition, SWR housed in smaller groups with lower rates of interspecific interactions have been found to maintain higher levels of fGCM compared to those in larger groups with more rates of interaction (Scott, 2020). Such metabolites are associated with stress and can cause a shift in resource allocation among biological functions (Moberg & Mench, 2000), including imposing a cost on reproductive success (Boonstra et al., 1998).

Little is known about the specific social needs of SWR. Males are generally solitary, whereas groups of females are often composed of 2–6 individuals (Estes, 1991; Owen-Smith, 1975). Nursing mothers, however, will separate themselves from other rhinos until their calf is weaned and may even show aggression toward previous offspring during this time (Hutchins & Kreger, 2006; Patton et al., 2016). Subadult and adult females often form temporary bonds or semi-stable grazing herds (Hutchins & Kreger, 2006; L. C. Metrione et al., 2007). Unfortunately, how these social partners are chosen remains unknown. The fluid social structure of wild SWR is difficult to replicate in zoo settings due to habitat size constraints and individual availability of animals. Few studies have been able to examine how varying zoo management practices affect rhino sociality, especially in large family groups (Cinkova & Bıcık, 2013; Martínez et al., 2022).

The North Carolina Zoo (NC Zoo) presents an ideal opportunity to explore the nature of social bonds between female SWR. NC Zoo hosts a herd that maintains three unique and important qualities: (1) it is multigenerational, (2) it is composed of diverse types of kin, and (3) it is one of the largest SWR herds among facilities accredited by the Associations of Zoos and Aquariums. This study maintained three core research objectives.

First, we examined seasonal and temporal behavior changes to understand the herd's general well-being. Comparing activity budgets between wild and zoo-housed animals has often been used as a noninvasive means to assess well-being via the degree to which animals engage in natural behaviors (Auer et al., 2021; Huettner et al., 2021; Veasey et al., 1996) over abnormal or stereotypic behaviors (indicators of poor well-being) (Mason, 1991). For zoo-housed SWR, Carlstead and Brown (2005) found that stereotypic pacing behaviors were more frequent in females with greater

variability in fecal corticoid excretions, an indicator of stress, and that high variability correlated with acyclicity in mature females (Carlstead & Brown, 2005). We intend to build on this work by exploring how this herd's behaviors and activities change daily and seasonally and comparing them to wild SWR activity budgets.

Second, we explored social preferences across different kin and age categories. Our multigenerational herd included grandmother–granddaughter, mother–nursing offspring, mother–weaned offspring, aunt–niece, and unrelated dyads. Though kin selection theory (Hamilton, 1964; Silk, 2002) predicts social bonds to be strongest among more closely related individuals, it is unclear how social bonds conform among SWR. We also explored the effect of age differences on observed patterns of sociality. In free-ranging SWR populations, upon leaving the natal group, adult females without nursing calves have been observed associating with sexually immature “subadult” females, creating what has been referred to as a “buddy system” (Hutchins & Kreger, 2006; Shrader & Owen-Smith, 2002). Shrader and Owen-Smith (2002) suggest these associations benefit both the subadult and the adult with predator avoidance, protection from territorial males, and enhanced familiarization with unknown environments. We aimed to quantify such associations under a human-managed group.

Finally, using social network analysis (SNA), we explored the overarching social structure of the females, including the directionality of social interactions. SNA is a powerful tool used to quantify association patterns within groups and populations of known individuals (Croft et al., 2008; Krause et al., 2009; Wey et al., 2008). This method has improved our understanding of social networks and social preferences across a wide range of social animals (ungulates: De Freslon et al., 2020; lions: Dunston et al., 2017; birds: Snijders et al., 2014; primates: Pasquaretta et al., 2014) and social systems (matrilocal: Wittemyer et al., 2009; patrilocal: Morrison et al., 2020; fluid/fission-fusion: Kelley et al., 2011). Here, we use SNA and related analyses to gain a deeper understanding of social preferences among SWR.

This exploration into the behavior and sociality among zoo-housed SWR is essential to improving the management of these animals for their health and well-being. The information gained from activity budgets and network analyses can reveal the needs of individuals and deepen our understanding of how to promote positive welfare as part of wider management practices.

2 | METHODS

2.1 | Focal animals

NC Zoo houses eight rhinos of varying relatedness (Figure 1). All adult focal individuals have spent no less than 15 years at the NC Zoo, and all four immatures were born at the zoo. They were managed as a fluid social herd, where mothers and their nursing calves were sometimes separated from subadults and calf-less adult females, most often due to temperature constraints. The calf-less rhinos were not given habitat access if the temperature fell below a

32°F, but nursing mothers and their calves were kept off habitat for temperatures below 40°F. Weather and maintenance permitting, they were often left on habitat overnight. Otherwise, they would only have access from 8 a.m. to 4 p.m. Even so, this managed social structure mimics that of wild SWR, where nursing mothers are known to isolate themselves, while calf-less females maintain semipermanent bonds with one another (Hutchins & Kreger, 2006; L. C. Metrione et al., 2007; Scott, 2020).

Individuals were identified by horn profile and body size, using a spotting scope and binoculars. Each rhino was given a coded ID with "M" for "Mother," "A" for "Adult," "S" for "Subadult," and "C" for "Calf" followed by a 1 or 2. Any changes in horn shape due to wear or damage were noted for future identification. The North Carolina Zoo Research committee approved this study.

2.2 | Study site

Watani Grasslands at NC Zoo is a 162 m² mixed-species habitat with tall fescue grass and mud wallows (Figure 2). The enclosure size remained consistent throughout the study.

2.3 | Data collection

All data were recorded on an electronic tablet using the ZooMonitor app (Ross et al., 2016), a software platform designed for behavioral data collection (Wark et al., 2019). Behavioral observations were conducted 2 days per week, consisting of 30 min sessions per focal individual between 7 a.m. and 12 p.m. or 12 p.m. and 5 p.m. An online random number generator (Calculator.net, 2021) was used to create a list of focal subjects for each day of observation to minimize collection bias. Collection for each session began when a focal animal was in view and identified. Data were collected from November 2020 to June 2021 for 70 observation days and 242 observation hours, 145 total hours for the calf-less females, and 97 total hours for the mother/calf pairs. The calf-less females were observed more often with 36 h total each for Adult 1, Subadult 1, and Subadult 2, and 37 h for Adult 2. This was due to more consistent access to the habitat when temperatures were below 40°F. In contrast, Mother 1 and Mother 2 were observed for 24 h each, Calf 1 for 26 h, and Calf 2 for 23 h. Mother/calf pairs spent 95% of their total observed time with the calf-less females, while calf-less females spent 71% of their total observed time with the mother/calf pairs.

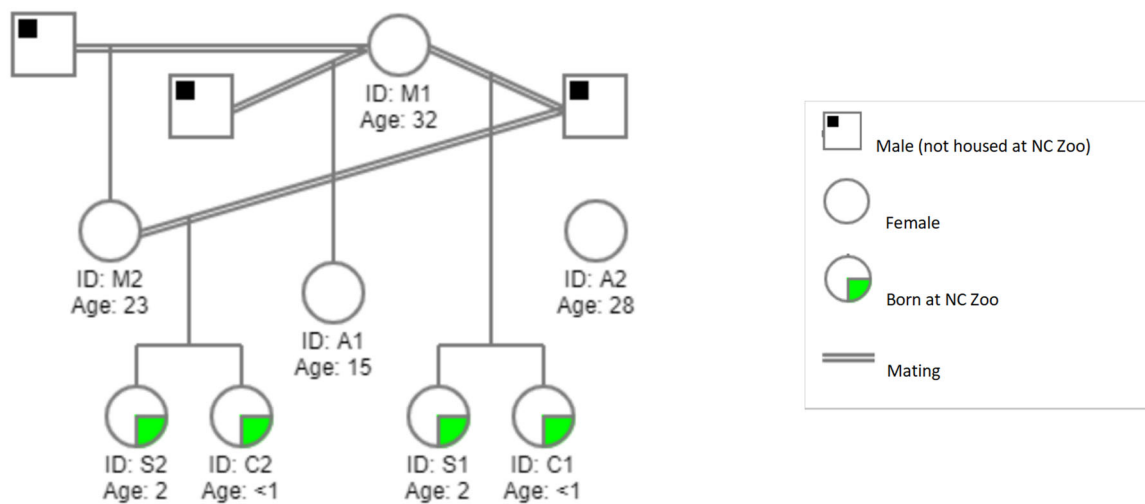


FIGURE 1 Rhino pedigree at the NC Zoo. The age of each individual in years has been listed below their given ID number. Mating is represented by a double line. NC Zoo, North Carolina Zoo.



FIGURE 2 An aerial view of Watani Grasslands Exhibit at the zoo.

TABLE 1 Ethogram for interval behaviors.

Category	Behavior	Description
Eating		
	Eating	Oat, browse, hay, and so forth
	Drinking	Drinking water
Grazing		Pulling grass from the ground
Self-maintenance		
	Itching	Rubbing body on object
	Wallow	Bathing in mud/water
	Horn rubbing	Rubbing horn on an inanimate object
	Defecating/urinating	Defecating or urinating
Investigation		
	Enrichment interaction	Interacting with or manipulating enrichment
	Digging	Upturning soil with feet or horn
	Dung/urine smelling	Smelling dung/urine
	Flehmen	Flehming without conspecific nearby
Active		
	Walking	Moving from one locale to another
	Running	Moving from one locale to another faster than a walk
	Standing	Upright on all four feet and no other behaviors
Active rest		
	Resting while standing	Upright with four feet on the ground, head down, eyes closed
	Lying down, head up	Lying down on the ground with head up
Inactive rest		
	Lying down, head down	Lying down on the ground with head down
Other		
	Unlisted behaviors	Notes taken
Keeper interaction		
	Interacting with keepers	Interacting with keepers during feeding/training
Social		
	Social	Interacting with a conspecific (no qualifiers)
Out of view		The animal cannot be seen from the vantage point

Note: Categories are highlighted in light gray.

The ethograms for this study were adapted from NC Zoo's rhino staff and three similar white rhino behavior studies: (1) an unpublished ethogram from the Rhino Rescue Center, (2) one used across zoological parks in Europe (Jenikejew et al., 2020), and (3) one conducted on Northern White Rhino at a zoological park in Dvůr Králové (Cinková, 2006; Cinková & Bičík, 2013). We divided the ethogram of interval behaviors (Table 1) into eight broad categories: eating, grazing, self-maintenance, investigation, active, active rest, inactive rest, keeper interaction, and other. "Eating" was defined as having supplementary food provided by keepers, and "grazing" was defined as pulling and eating grass growing on the habitat. "Resting" behaviors combined data from inactive and active rest categories. If social behaviors were observed during interval sampling, they were recorded as "social" with no specific qualifiers. However, if an animal was observed walking or running while following another individual,

the behavior was recorded as "walking" or "running" for that interval sample. All-occurrence social behaviors (Table 2) were categorized as affiliative, aggressive, or defensive, and the initiator and recipient of the behavior were recorded. If an animal was observed calmly walking or trotting while following another individual, the behavior was recorded as "following" and categorized as an affiliative behavior.

The distance between individuals and the focal subject was recorded during each interval as well as their nearest neighbor (Nunez et al., 2015). Proximity over time is often used as a measure of sociality in SWR (Jenikejew et al., 2020; Owen-Smith, 1975; J. Silk et al., 2013). Prior research indicates that wild SWR with strong pair bonds maintain a distance within 25 m (Hutchins & Kreger, 2006; L. Mettrone & Eyres, 2014), however, a 2016 study of wild rhinos defined animals within 10 m of one another over 24 h as "associated" (Patton et al., 2016). Furthermore, one study in zoo-housed SWR

TABLE 2 Ethogram for all occurrence behaviors.

Category	Behavior	Description
Affiliative/cohesive		Positive/associated with bonding
	Following	Focal animal locomotes after a conspecific that is changing location intentionally to stay in close proximity
	Sniffing/ snout contact	Focal animal gently explores the body of another conspecific (except the snout) with its snout
	Social flehming	Focal animal flehms while scenting a urinating/defecating conspecific close by
	Naso-nasal sniffing	Focal animal contacts the nasal region of another conspecific with its own snout in a slow and gentle manner
	Ano-genital sniffing	Focal animal sniffs the anogenital region of another conspecific
	Head placing	Focal animal lays its head on the back of another conspecific
	Body contact	Focal animal touches or brushes another conspecific with any part of its body (except snout) or leans or rubs itself against a conspecific
	Lick	Focal animal touches another conspecific with its tongue
	Pant	Chesty inhalation/exhalation that may indicate a contact seeking call
	Lifting	Focal animal lifts another conspecific's head or leg with its head/horns
	Social play	Mock charging, chasing, or wrestling
	Nurse	Focal animal suckles from mother
	Whine	High pitched call from calf to mother
Agonistic/aggressive		Negative/associated with aggression
	Displace	Focal animal incites a conspecific to change its position/location after approaching or agonistic interaction
	Advancing	Focal animal approaches another conspecific with head lowered, usually accompanied by vocalizations
	Nodding	Focal animal swings its head back and forth toward another conspecific
	Horn stare	Focal animal stands horn to horn in front of another conspecific with an uplifted head
	Horn prod	Focal animal pokes conspecific with its horn
	Pushing	Focal animal presses any part of its body against another conspecific making it change the position/location
	Chasing	Focal animal follows another conspecific, which tries to keep the animal at a distance by trotting
	Charge	Focal animal moves with a lowered head toward another conspecific and stops suddenly without causing body contact
	Attacking	Focal animal hits its horns against another conspecific
	Horn clashing	Escalated confrontation following attacking involving both animals hitting their horns against each other
	Ears pinned	Focal animal lays ears back during social interaction, usually accompanied by a head thrust
	Roar	Rumbling vocalization with mouth open with head and ears back
	Snort	Quick nasal exhalation toward conspecific
Agonistic/defensive		Negative/associated with submission
	Avoiding	Focal animal changes its position/location after being approached by a conspecific displaying agonism
	Escaping	Focal animal moves away from a conspecific in a trotting/running manner after an agonistic interaction

Note: Categories are highlighted in light gray.

TABLE 3 Interval proximity denotations.

Category	Subcategory	Description
Contact	Touching	0 m between individuals
Close proximity	Within one body length	<3 m between individuals
	Within two body lengths	<6 m between individuals
Association	Over two body lengths	6–15 m between individuals
Not associated	Out of eye-line	>15 m between individuals

vocalizations placed animals in proximity if they were within one body length (3 m) of one another (Jenikejew et al., 2020). For practicality, body length estimations were adapted from multiple methodologies, and so animals within two body lengths (<6 m) were considered in “close proximity” (Bonaparte-Saller & Mench, 2018), within 6–15 m were “associated” (Patton et al., 2016), and anything greater than 15 m was recorded as “not associated” (Nunez et al., 2015) (Table 3). Ultimately, close proximity (<6 m) data were used in association analyses as 82% of all nearest neighbors were within two body lengths.

2.4 | Data analysis

2.4.1 | Activity budgets

Activity budget analyses relied only on data derived from the subadult and calf-less adult females due to more consistent access to the habitat than mothers with nursing calves. Microsoft Excel was used for data management and analysis.

Average observed behaviors were first quantified by calculating the percent of the total recorded intervals spent performing each behavior each observation day, then calculating the average across seasons. Intervals in which focal animals were not visible from the vantage point (or “out of view”) were removed from the total interval count before calculations. Seasons were qualified as Fall (September to November), Winter (December to February), Spring (March to May), and Summer (June to August). These seasons were based on delineations in pasture quality of fescue, which grows best in spring and fall in the northern hemisphere (Roberts et al., 2009). It should be noted that no data were collected for the months of July, August, September, or October, which limited the sample sizes of the Fall and Summer seasons.

Similar calculation methods were then used to determine activity by time of day, where averages were calculated via sessions within hour intervals. Intervals where the focal animal was not visible, were removed before analysis.

2.4.2 | Social bond strength

A composite sociality index score (CSI from hereon) was calculated to quantify social bond strength between dyads, as it is an established

tool for assessing social bond strength within a dyad (Lynch et al., 2017; J. B. Silk et al., 2006; J. Silk et al., 2013).

The equation is as follows:

CSI equation:

$$\frac{\frac{G_{ij}}{G_{xy}} + \frac{P_{ij}}{P_{xy}}}{2}}$$

The CSI was calculated for “n” number of 30 min sessions, where G_{ij} represents the total number of affiliative interactions within the dyad of interest and P_{ij} represents the number of recorded intervals of close proximity (<6 m) within the dyad of interest. G_{xy} represents the average number of affiliative interactions across all possible dyads, and P_{xy} represents the average number of recorded instances of close proximity across all possible dyads. Given these terms, the higher the CSI score, the stronger the social bond. CSI scores were aggregated across all observation months and were rounded to the nearest two decimal places

CSI scores were analyzed for significant correlations between both relatedness and age difference. First, we explored variation in the social bond strength across dyads (N) by the coefficient of relatedness (r): Mother–daughter ($r = .5$, $N = 6$), full sisters ($r = .5$, $N = 2$), grandmother–granddaughter ($r = .25$, $N = 2$), half-sisters ($r = .25$, $N = 9$), aunt–niece ($r = .25$, $N = 2$), and unrelated ($r = 0$, $N = 7$) (Boyce, 1983; Wyttenbach, 2012). Simple linear regression calculations in Microsoft Excel were used to determine a correlation between the coefficient of relatedness and CSI scores. Following kin selection theory, we predicted that the closest bonds would be between mothers and daughters ($r = .5$). Then, to examine variations in bond strength due to age difference, each animal was labeled either “immature” (i.e., prereproductive age or <7 years of age) or “adult” (reproductive age or ≥ 7 years of age) (Jenikejew et al., 2020; Marneweck et al., 2017). CSI score and age difference were evaluated for significance using standard error bars across these three categories of dyads: immature–immature, adult–immature, and adult–adult. Significance in correlation would be viewed as preferential social bond trends.

2.4.3 | SNA

Association indices using proximity data (within two body lengths) were calculated through SOCPROG software, a software designed

specifically to analyze social network data (Whitehead, 2009, 2019). Association data were run through temporal analysis and permutations tests to find preferred and avoided associations (Whitehead, 2009, 2019). The commonly-used half-weight index was employed in these calculations as this limits bias by considering the probability of the observer missing these animals when they are together or apart due to poor visibility (when animals were out of view) (Lusseau et al., 2003; Whitehead, 2009, 2019). The temporal analysis option in SOCPROG was used to find lagged association rate (LAR) or the probability that two individuals will continue to associate over time and the null association rate (NAR) which would support the null hypothesis that no association preferences are shown over time (Whitehead, 2009, 2019). A best-fit model for preferred associations was chosen based on the model with the lowest quasi Akaike information criterion (QAIC) (Whitehead, 2009, 2019). These models included "preferred companions," or long-term associations, "casual acquaintances," or associations that diminish over time, and "rapid disassociations," or associations that start and end suddenly (Lusseau et al., 2003; Whitehead, 2009, 2019). Further statistical analyses in SOCPROG revealed the complexity of the herd's dynamics using strength (indicating strong associations with others), eigenvector centrality value (indicating strong associations with strongly associated individuals), reach (indirect connectedness with others), clustering coefficients (indicating strong associations among an individual's associates), and affinity (indicating strong associations with individuals with high strength) to determine the presence of central or influential individuals to the cohesion of the herd (Whitehead, 2009, 2019).

Interaction rates were also calculated via SOCPROG (Whitehead, 2009, 2019), and the produced matrix was run through UCINET (Borgatti, Everett et al., 2002) followed by NETDRAW

(Borgatti, 2002) to create a social network graphic of affiliation between dyads. Within the graphic, individuals are represented by "nodes," and associations among individuals are connected by lines. The line's thickness, or "weight," suggests a higher interaction rate, and the direction of the arrow points from the initiator to the recipient (Croft et al., 2008). Asymmetry tests in SOCPROG were conducted to show a significant difference in the interaction rates within dyads, and the direction of that asymmetry was determined via the NETDRAW graphic matrix (Sueur & Petit, 2008; Whitehead, 2009, 2019). Reciprocity was evaluated using the Mantel Z-test option in SOCPROG to see if individuals preferred to interact with individuals that reciprocated affiliative behaviors (Whitehead, 2009, 2019). These measures were crucial to revealing which individuals showed a preference within a given social bond and can therefore inform caretakers of the social needs of specific animals (Sueur & Petit, 2008).

3 | RESULTS

3.1 | Activity budgets

3.1.1 | Season

A seasonal comparison suggests clear trends in behaviors (Figure 3). Grazing behaviors decreased from 36% in Fall to 19% in Winter and Spring, then increased to 32% in Summer. Resting behaviors increased from ~25% in Fall and Winter to over 30% in Spring and Summer. Observed social behaviors decreased from ~4% in Fall to ~1% in Spring and Summer. Eating behaviors decreased from ~23% in Fall to ~9% in Winter and Spring, then increased to 32% in Summer. Active behaviors were lowest at ~9% in the Summer and highest at 23% in the winter. Active behaviors were

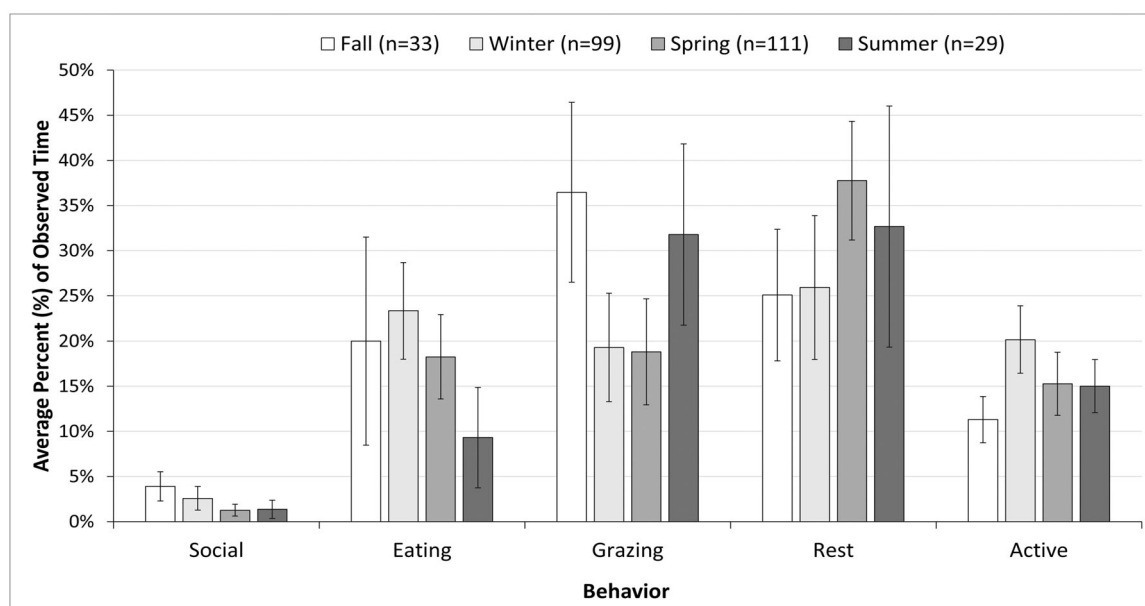


FIGURE 3 Aggregated average seasonal activity budget. Bars represent standard error, and "n" represents the number of 30 min observation sessions.

lowest in the Fall at ~11% and highest in the winter at ~20%. Social behaviors were highest in fall at ~4% and fell consistently to ~1.5%. The standard error suggests no significant difference in social behavior across seasons.

Overall, individuals spent an average of 44.32% of their time eating or grazing, 30.37% of their time resting, and 17.73% of their time engaged in social or active behaviors across all seasons between 8 a.m. and 5 p.m. No stereotypic behaviors were observed. No significant differences were found between the activity budgets of the calf-less females when the mother/calf dyads were on or off habitat.

3.1.2 | Time of day

We then examined how daily activities change over a day, from 7 a.m. to 4 p.m. (Figure 4). Resting and eating behaviors fluctuated the most, whereas social and active behaviors remained consistent throughout the day. These SWR were found to spend approximately 50% of their observed time resting between 12 p.m. and 1 p.m. About 40% of the time between 9 a.m. and 10 a.m., and again from 3 p.m. to 4 p.m. was spent eating.

3.2 | Social bond strength

The overall mean CSI score was 1.0 (min = 0.08, max = 5.28), and trends remained consistent throughout the study. We, therefore, characterized “weaker” bonds as those with a CSI score under 1.0, “moderate” social bonds as a score of 1.0–2.0, and “strong” bonds

greater than 2.0. Each female had no more than two strong bonds. Both mother–calf pairs exhibited the strongest social bonds (4.87 and 5.28), but mothers shared weak bonds (CSI < 1) with all other members of the group, including their older offspring. Due to mother–calf pairs having outlying scores, they were removed from CSI correlation analyses.

Mean CSI scores varied across coefficients of relatedness (“*r*” values). For *r* values of .5, the mean CSI score was 0.27, *r* values of .25 were found to have a mean CSI of 0.68, and *r* values of 0 were found to have a mean CSI of 1.05. However, regression analysis of all CSI scores to *r* values for $R^2 > 0.5$ reveal no statistically significant correlation between bond strength and relatedness ($R^2 = 0.135$).

Mean CSI scores also varied across the three age category dyads: adult–adult (mean CSI = 0.54), adult–immature (mean CSI = 0.77), and immature–immature (mean CSI = 0.55). Though adult–immature dyads have an overall higher average CSI score than other dyads, standard error bars suggest no statistical difference between the three categories (Figure 5).

3.3 | SNA

Association analysis of proximity in SOCPROG showed significantly preferred and avoided associations (Figure 6 and Table 4). Temporal analysis (Figure 6) reveals that the LAR between any two individuals is consistently higher than the NAR. Thus, we reject the null hypothesis that there were no preferred associations over these time lags (Whitehead, 2009, 2019). Association rates were shown to gradually decrease over time. A potential explanation was determined via the best-fit model with the lowest QAIC. Here, the best fit

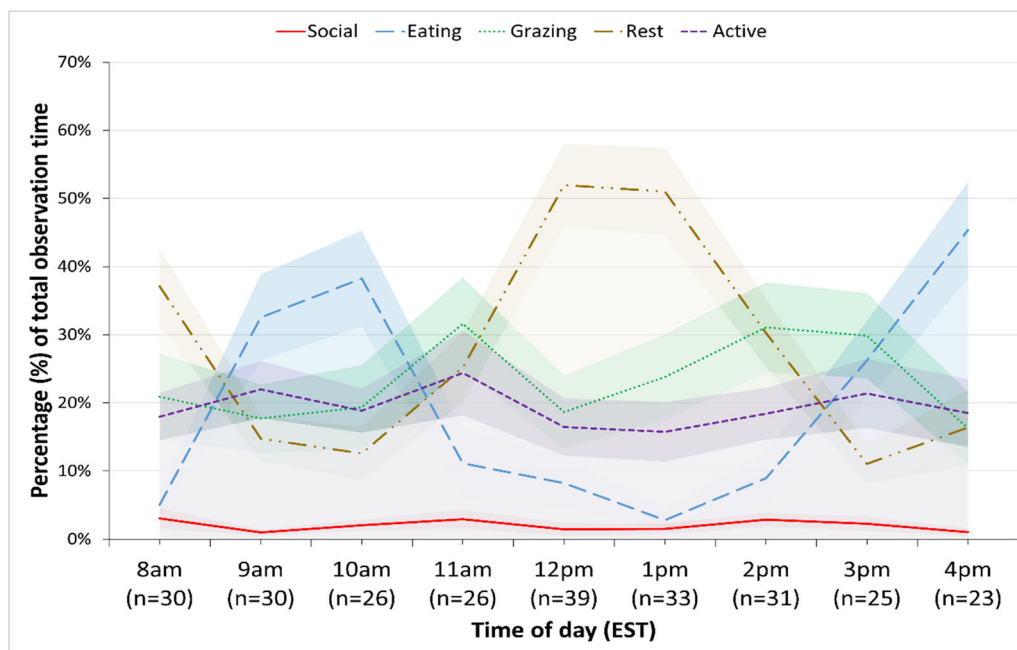


FIGURE 4 Average activity budget over time of day. Shading represents standard error and “*n*” represents the number of 30 min observation sessions.

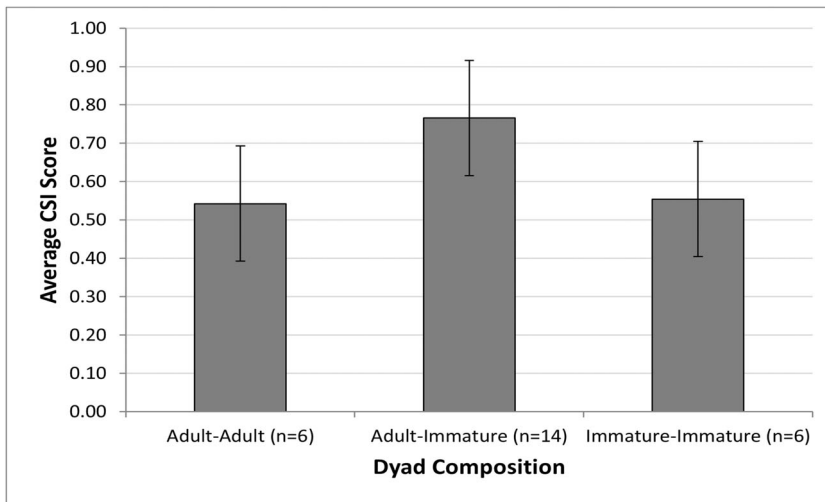


FIGURE 5 Average composite sociality index (CSI) scores for each type of dyad composition. Error bars represent standard error and “n” represents the number of dyads.

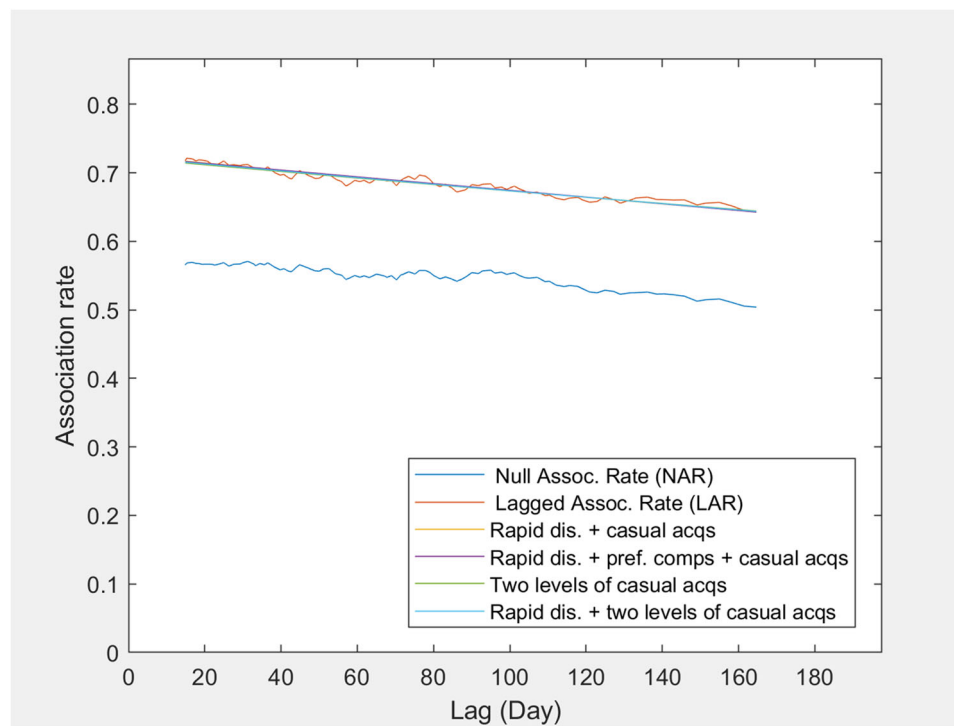


FIGURE 6 Temporal association analysis calculated in SOCPROG. The null association rate (NAR) is drawn in the dark blue, the lagged association rate (LAR) is drawn in red, and the best-fit models are transposed over the LAR in yellow, purple, green, and light blue.

model suggested that the herd contained two levels of casual acquaintances, however, this value differed negligibly ($\Delta\text{QAIC} \leq 2$) from three other models suggesting rapid disassociations combined with casual acquaintances or casual acquaintances and preferred companions (Figure 6) (Whitehead, 2009, 2019).

Permutation tests in SOCPROG after 1000 permutations for a p -value of .05 (Table 4) calculated the significantly preferred and avoided associations between dyads. Preferred associations were found between each subadult/adult, adult/adult, subadult/subadult, and mother/calf dyad (Whitehead, 2009, 2019). Avoided associations

were found between each adult/calf, subadult/calf, mother/subadult, and mother/adult dyad. Mother/mother and calf/calf dyads did not show significant avoidance of one another despite low association indices.

The results from the network analysis in SOCPROG (Whitehead, 2009, 2019) based on proximity indicate that Subadult 1 was most frequently in close proximity, or associated, with others (greatest network strength), had high association indices with other individuals with high association indices (highest eigenvector centrality) and was most indirectly

TABLE 4 Association indices matrix calculated in SOCPROG.

Individual	Adult 1	Adult 2	Calf 1	Calf 2	Mother 1	Mother 2	Subadult 1	Subadult 2
Adult 1								
Adult 2	0.99*							
Calf 1	0.47^	0.41^						
Calf 2	0.56^	0.57^	0.55					
Mother 1	0.43^	0.41^	1.00*	0.49				
Mother 2	0.53^	0.52^	0.57	0.99*	0.51			
Subadult 1	0.98*	0.99*	0.53^	0.64^	0.53^	0.67^		
Subadult 2	1.00*	0.99*	0.43^	0.54^	0.45^	0.55^	1.00*	

Note: Significantly preferred associations are starred, while avoided associations are marked with a caret.

TABLE 5 Associative measures from the network analysis.

ID	Strength	Eigenvector	Reach	Clustering coefficient	Affinity
Subadult 1	5.34*	0.41*	24.48*	0.65	4.58
Adult 2	4.96	0.39	23.27	0.68	4.69
Subadult 2	4.96	0.39	23.3	0.68	4.7
Adult 1	4.88	0.38	23.03	0.69*	4.72*
Calf 2	4.34	0.33	19.99	0.65	4.61
Mother 2	4.34	0.33	20	0.65	4.6
Calf 1	3.96	0.3	17.97	0.63	4.54
Mother 1	3.82	0.29	17.48	0.64	4.58
Overall means (SE)	4.58 (0.54)	0.35 (0.04)	21.19 (2.67)	0.66 (0.02)	4.63 (0.07)

Note: The highest values in each column are starred.

TABLE 6 Matrix of rounded *p*-values for dyadic asymmetry calculated in SOCPROG.

Individual	Adult 1	Adult 2	Calf 1	Calf 2	Mother 1	Mother 2	Subadult 1	Subadult 2
Adult 1								
Adult 2	0.02*							
Calf 1	1.00	0.10						
Calf 2	0.32	0.00*	0.34					
Mother 1	0.41	0.08	0.00*	0.41				
Mother 2	1.00	1.00	0.07	0.00*	0.39			
Subadult 1	0.00*	0.00*	0.34	0.22	0.21	0.09		
Subadult 2	0.00*	0.00*	1.00	0.62	0.16	0.10	1.00	

Note: Starred values are significantly asymmetric.

connected to others (furthest reach). Our analysis also revealed that Adult 1 was well associated with other highly associated individuals (highest clustering coefficient and affinity) but weakly connected to the herd compared to the other calf-less females. Mother/calf dyads had the lowest network strength, eigenvector values, and reach (Table 5).

Asymmetrical affiliation among these dyads was found to vary in significance (Table 6). Mother–calf dyads were significantly asymmetrical. Calves 1 and 2 showed preference toward their mothers, Mothers 1 and 2, respectively. Affiliative interactions were also asymmetrical among the calf-less females as affiliative interactions were heavily initiated by subadults (Subadult 1 and Subadult 2)

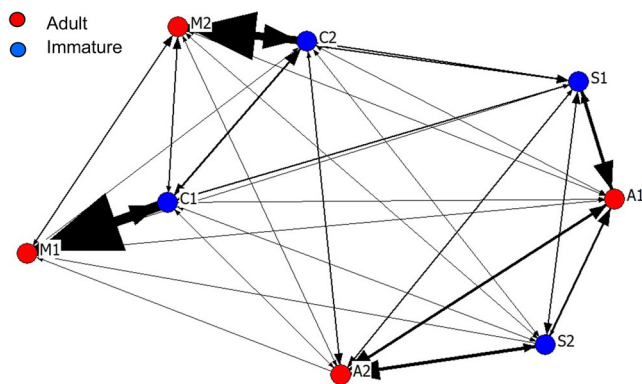


FIGURE 7 Multidimensional scaling SNA graphic from NETDRAW representing direction for all dyads using interaction rates from SOCPROG. Arrows point from the initiator to the receiver of the interaction. Heavier line weights represent a greater interaction rate (mean = 22.5, min = 2, max = 300). SNA, social network analysis.

toward adults (Adult 1 and Adult 2) (Figure 7). There was also a significant directional affiliation from Adult 1 to Adult 2, suggesting a preference between the calf-less adult females. It was also noted that there was asymmetry between Calf 2 and calf-less Adult 2, though their interaction rate overall was below the mean. No significant directional affiliation was observed between the two mother/calf pairs nor between mother/calf pairs and the calf-less subadults or adults, even between previous offspring and their mothers or vice versa. Seven out of 16 adult-immature dyads were asymmetric, and only 1 out of 6 adult-adult dyads was asymmetric. There were no asymmetric immature-immature dyads. The Mantel Z-test for reciprocity showed that individuals were more likely to affiliate with individuals that reciprocated affiliative behaviors ($p = .016$).

4 | DISCUSSION

This study evaluated the activity budgets and social dynamics within a large, multigenerational, zoo-housed SWR herd. We report that the subadult females showed preferences and maintained social bonds with calf-less adult females. Mothers with nursing calves did not maintain social relationships with others, including subadult offspring. We also provide greater insight into how activity budgets vary across seasons and times of day. Our findings illuminate the behavioral and social lives of SWR under human care. Such information retains the power to improve management practices and the health and welfare of a threatened species.

Activity budget analyses reported here indicate seasonal and daily variations in diurnal behavior. For wild SWR, diurnal behaviors are contingent on multiple factors, including the time of day and weather conditions (Goodenough et al., 2022; O'Connor, 1986; Tichagwa et al., 2020). Our herd's diurnal activities mirrored those reported in the literature (Hutchins & Kreger, 2006; O'Connor, 1986; Patton et al., 2011; Tichagwa et al., 2020), where eating and grazing

together ranged from 37% to 56% of the observed time, and diurnal resting behaviors accounted for 25%–38% of the observed time. No stereotypic behaviors were observed over the course of the study. A continuous decline in grazing and an increase in active behaviors was observed from November through February, followed by a steep increase in March. This phenomenon was most likely due to the death of the fresh grass across their habitat that commonly occurs over the winter months in the northern hemisphere (Roberts et al., 2009), where foraging decreases and exploring for foraging opportunities increases. We also reported an increase in rest behaviors when ambient temperature increased, during midday hours and in the spring and summer. These findings support previous work which illustrates that temperature, along with food availability, modulates rhino activity (O'Connor, 1986; Patton et al., 2011; Tichagwa et al., 2020). Further study during the late summer and early fall is needed to track changes over an entire year.

Our study also demonstrates social preferences among this herd of zoo-housed SWR, given different options for social partners. Surprisingly, we did not find that relatedness played a significant role in forming social bonds. Though mothers closely associated with their nursing calves, these females exhibited weak social bonds and associations with all other female rhinos. This is reflected in their low analytic values in Table 5 and their preference to avoid associations outside of their mother/calf dyads in Table 4. Immature SWR calves are heavily dependent on their mothers (Hutchins & Kreger, 2006; L. Metrione & Eyres, 2014; Shrader & Owen-Smith, 2002), therefore it is not surprising that these dyads showed strong bonds (CSI > 4) and directional preferences from the calves to their mothers (Figure 7). As in previous research (Hutchins & Kreger, 2006; Shrader & Owen-Smith, 2002), these mothers did not maintain social bonds with other females despite opportunities to interact with close relatives, including older offspring, sisters, and nieces. Temporal analysis shows that associations tend to decline over time, either due to a mixture of long- and short-term associations and/or rapid disassociations (Figure 6). This supports previous observations of “semi-stable” female herds seen in wild SWR (Hutchins & Kreger, 2006; L. C. Metrione et al., 2007). Furthermore, although anecdotal, before birthing the current nursing calves, these mothers were noted to maintain strong social bonds with other adult females in the group, suggesting the presence of a dependent calf dramatically changes the social dynamics of the herd, removing mothers as potential social partners until their calves are weaned.

While we confirm previous reports of wild SWRs, where females maintain 1–2 strong social bonds (Hutchins & Kreger, 2006; Owen-Smith, 1975; Shrader & Owen-Smith, 2002) referred to as the “buddy system” (Shrader & Owen-Smith, 2002), we also reveal directionality among these preferences. Here we show that subadult females maintain strong social bonds with calf-less adult females and that immature individuals often initiate affiliative interactions. If a nursing mother is occupied with a dependent calf, juvenile SWR may seek bonds with other adults to satisfy non-mutually exclusive needs. First, maintaining proximity to a larger conspecific may deter predation or approaches from territorial adult males or, in zoo

settings, shield nondominant individuals from dominant ones (L. C. Mettrione et al., 2007). Second, these associations may help guide immature rhinos within novel environments through the experience of an older female. Studies have shown that environmental knowledge can be gained through social learning (Bolzan et al., 2020; Ellis et al., 2019; Nunez et al., 2015). Maintaining social ties with adult SWR may be critical to the foraging and overall success of youngsters. Due to the limited sample size of this study, further studies will be needed to support this claim.

5 | MANAGEMENT IMPLICATIONS

Findings from this study have practical implications for managing SWR while under human care. For example, in winter, supplemental foraging opportunities must be available to offset seasonal deficiencies in grazing. In addition, we have shown that these subadults exhibited a preference toward calf-less adult females, suggesting that such associations may be imperative to the well-being of developing females. Cohabitation with mothers may not be as crucial to weaned, developing, immature females as access to calf-less adult females. This insight can help facilities housing rhinos encourage natural social behaviors by including unrelated adult females in their herds to increase their success under human care.

6 | CONCLUSION

This study analyzed the behavioral and social trends of a herd of eight zoo-housed, female SWR from November 2020 through June 2021. Activity budgets closely mirrored previous studies of diurnal SWR behavior and sociality data revealed strong ties between mothers and nursing calves, as well as calf-less adult and subadult females. Social network analyses produced two important findings: (1) mother–calf dyads maintained social isolation from the other females; (2) immatures pursued affiliative interactions with calf-less adults. Our study, therefore, reveals the preferences of zoo-housed SWR that can be used when creating social groupings to improve well-being. Future research would benefit from exploring sociality among different group compositions of SWR, across various ages and those including males and could be bolstered by including welfare metrics beyond observational data, including hormonal data (e.g., glucocorticoids), physiological information (e.g., growth rates, weight changes), or reproduction rates and survivorship.

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CONFLICTS OF INTEREST STATEMENT

All authors are either employed by or maintain involvement with the North Carolina Zoo.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.63xsj3v6j>, reference number 59 (Williams, 2023).

REFERENCES

- Auer, U., Kelemen, Z., Engl, V., & Jenner, F. (2021). Activity time budgets—A potential tool to monitor equine welfare. *Animals: An Open Access Journal from MDPI*, 11(3), 850. <https://doi.org/10.3390/ani11030850>
- Bolzan, A. M. S., Bonnet, O. J. F., Wallau, M. O., Basso, C., Neves, A. P., & de Faccio Carvalho, P. C. (2020). Foraging behavior development of foals in natural grassland. *Rangeland Ecology & Management*, 73(2), 243–251. <https://doi.org/10.1016/j.rama.2019.10.011>
- Bonaparte-Saller, M., & Mench, J. A. (2018). Assessing the dyadic social relationships of female African (*Loxodonta africana*) and Asian (*Elephas maximus*) zoo elephants using proximity, tactile contact, and keeper surveys. *Applied Animal Behaviour Science*, 199, 45–51. <https://doi.org/10.1016/j.applanim.2017.10.011>
- Boonstra, R., Hik, D., Singleton, G. R., & Tinnikov, A. (1998). The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs*, 68, 371–394. [https://doi.org/10.1890/0012-9615\(1998\)068\[0371:TIOPI\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1998)068[0371:TIOPI]2.0.CO;2)
- Borgatti, S. P. (2002). *NetDraw: Graph visualization software*. Analytic Technologies.
- Borgatti, S. P., Everett, M. G., & Freeman, L. C. (2002). *UCINET 6 for windows: Software for social network analysis*. Analytic Technologies.
- Boyce, A. J. (1983). Computation of inbreeding and kinship coefficients on extended pedigrees. *Journal of Heredity*, 74(6), 400–404. <https://doi.org/10.1093/oxfordjournals.jhered.a109825>
- Calculator.net. (2021). Random number generator. Maple Tech International LLC. <https://www.calculator.net/>
- Carlstead, K., & Brown, J. L. (2005). Relationships between patterns of fecal corticoid excretion and behavior, reproduction, and environmental factors in captive black (*Diceros bicornis*) and white (*Ceratotherium simum simum*) rhinoceros. *Zoo Biology*, 24(3), 215–232. <https://doi.org/10.1002/zoo.20050>
- Cinková, I. (2006). Sexual, social, and playful behavior of white rhinoceros (*Ceratotherium simum*) in zoological garden. Bachelor thesis, Palacký University Olomouc. http://www.rhinosourcecenter.com/pdf_files/122/1224748423.pdf
- Cinková, I., & Bičík, V. (2013). Social and reproductive behaviour of critically endangered northern white rhinoceros in a zoological garden. *Mammalian Biology*, 78(1), 50–54. http://www.rhinosourcecenter.com/pdf_files/142/1421570641.pdf
- Croft, D., James, R., & Krause, J. (2008). *Exploring animal social networks*. Princeton University Press. <https://doi.org/10.1515/9781400837762>
- De Freslon, I., Peralta, J. M., Strappini, A. C., & Monti, G. (2020). Understanding allogrooming through a dynamic social network approach: An example in a group of dairy cows. *Frontiers in Veterinary Science*, 7, 535. <https://doi.org/10.3389/fvets.2020.00535>
- Dunston, E. J., Abell, J., Doyle, R. E., Kirk, J., Hilley, V. B., Forsyth, A., Jenkins, E., & Freire, R. (2017). An assessment of African lion *Panthera leo* sociality via social network analysis: Prerelease monitoring for an ex-situ reintroduction program. *Current Zoology*, 63(3), 301–311. <https://doi.org/10.1093/cz/zow012>
- Ellis, S., Snyder-Mackler, N., Ruiz-Lambides, A., Platt, M. L., & Brent, L. (2019). Deconstructing sociality: The types of social connections that predict longevity in a group-living primate. *Proceedings. Biological sciences*, 286(1917), 20191991. <https://doi.org/10.1098/rspb.2019.1991>

- Emslie, R. (2020). *Ceratotherium simum*. The IUCN Red List of Threatened Species, 2020. <https://doi.org/10.2305/IUCN.UK.2020-1.RLTS.T4185A45813880.en>
- Estes, R. D. (1991). *The behavior guide to African mammals*. University of California Press.
- Goodenough, A. E., Price, T. W., Brazier, D. L., & McDonald, K. (2023). Factors affecting the behavior of captive white rhinoceros (*Ceratotherium simum simum*) and the accuracy of ad-hoc keeper data. *Zoo Biology*, 42, 45–54. <https://doi.org/10.1002/zoo.21723>
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, 7(1), 17–52. [https://doi.org/10.1016/0022-5193\(64\)90039-6](https://doi.org/10.1016/0022-5193(64)90039-6)
- Huettnner, T., Dollhaeupl, S., Simon, R., Baumgartner, K., & von Fersen, L. (2021). Activity budget comparisons using long-term observations of a group of bottlenose dolphins (*Tursiops truncatus*) under human care: Implications for animal welfare. *Animals: An Open Access Journal from MDPI*, 11(7), 2107. <https://doi.org/10.3390/ani11072107>
- Hutchins, M., & Kreger, M. D. (2006). Rhinoceros behaviour: Implications for captive management and conservation. *International Zoo Yearbook*, 40(1), 150–173. <https://doi.org/10.1111/j.1748-1090.2006.00150.x>
- Jenikejew, J., Chaignon, B., Linn, S., & Scheumann, M. (2020). Proximity-based vocal networks reveal social relationships in the southern white rhinoceros. *Scientific Reports*, 10(1), 15104. <https://doi.org/10.1038/s41598-020-72052-0>
- Kelley, J. L., Morrell, L. J., Inskip, C., Krause, J., & Croft, D. P. (2011). Predation risk shapes social networks in fission-fusion populations. *PLoS One*, 6(8), e24280. <https://doi.org/10.1371/journal.pone.0024280>
- Krause, J., Lusseau, D., & James, R. (2009). Animal social networks: An introduction. *Behavioral Ecology and Sociobiology*, 63(7), 967–973. <https://doi.org/10.1007/s00265-009-0747-0>
- Lusseau, D., Schneider, K., Boisseau, O. J., Haase, P., Slooten, E., & Dawson, S. M. (2003). The bottlenose dolphin community of doubtful sound features a large proportion of long-lasting associations. *Behavioral Ecology and Sociobiology*, 54(4), 396–405. <https://doi.org/10.1007/s00265-003-0651-y>
- Lynch, E. C., Di Fiore, A., Lynch, R. F., & Palombit, R. A. (2017). Fathers enhance social bonds among paternal half-siblings in immature olive baboons (*Papio hamadryas anubis*). *Behavioral Ecology and Sociobiology*, 71, 120. <https://doi.org/10.1007/s00265-017-2336-y>
- Marneweck, C., Jürgens, A., & Shrader, A. M. (2017). Dung odours signal sex, age, territorial and oestrous state in white rhinos. *Proceedings Biological Sciences*, 284(1846), 20162376. <https://doi.org/10.1098/rspb.2016.2376>
- Martínez, L., Silván, G., Cáceres, S., Caperos, J. M., Fernández-Morán, J., Casares, M., Crespo, B., de Andrés, P. J., & Illera, J. C. (2022). "Preliminary findings on how different management systems and social interactions influence fecal glucocorticoid metabolites in White Rhinoceros (*Ceratotherium simum*). *Animals: An Open Access Journal from MDPI*, 12, 897. <https://doi.org/10.3390/ani12070897>
- Mason, G. J. (1991). Stereotypies: A critical review. *Animal Behaviour*, 41(6), 1015–1037. [https://doi.org/10.1016/S0003-3472\(05\)80640-2](https://doi.org/10.1016/S0003-3472(05)80640-2)
- Metrione, L., & Eyres, A. (Eds.). (2014). *Rhino husbandry manual*. International Rhino Foundation. <https://www.rhinos.org/wp-content/uploads/2015/08/rhino-husbandry-manual-compressed.pdf>
- Metrione, L. C., & Harder, J. D. (2011). Fecal corticosterone concentrations and reproductive success in captive female southern white rhinoceros. *General and Comparative Endocrinology*, 171(3), 283–292. <https://doi.org/10.1016/j.ygcen.2011.02.010>
- Metrione, L. C., Penfold, L. M., & Waring, G. H. (2007). Social and spatial relationships in captive southern white rhinoceros (*Ceratotherium simum*). *Zoo Biology*, 26(6), 487–502. <https://doi.org/10.1002/zoo.20143>
- Moberg, G. P., & Mench, J. A. (Eds.). (2000). *The biology of animal stress: Basic principles and implications for animal welfare* (pp. 1–22). CABI.
- Morrison, R. E., Eckardt, W., Stoinski, T. S., & Brent, L. (2020). Comparing measures of social complexity: Larger mountain gorilla groups do not have a greater diversity of relationships. *Proceedings Biological Sciences*, 287(1931), 20201026. <https://doi.org/10.1098/rspb.2020.1026>
- Nunez, C. M. V., Adelman, J. S., & Rubenstein, D. I. (2015). Sociality increases juvenile survival after a catastrophic event in the feral horse (*Equus caballus*). *Behavioral Ecology*, 26(1), 138–147. <https://doi.org/10.1093/beheco/aru163>
- O'Connor, S. M. (1986). Activity cycles of the Southern white rhinoceros: In captivity: Implications for management. *International Zoo Yearbook*, 24(25), 297–303. <https://doi.org/10.1111/j.1748-1090.1985.tb02558.x>
- Owen-Smith, R. N. (1975). The social ethology of the White Rhinoceros *Ceratotherium simum* (Burchell 1817*). *Zeitschrift für Tierpsychologie*, 38, 337–384. <https://doi.org/10.1111/j.1439-0310.1975.tb02010.x>
- Pasquaretta, C., Levé, M., Claidière, N., Van de Waal, E., Whiten, A., MacIntosh, A. J. J., Pelé, M., Bergstrom, M. L., Borgeaud, C., Brosnan, S. F., Crofoot, M. C., Fedigan, L. M., Fichtel, C., Hopper, L. M., Mareno, M. C., Petit, O., Schnoell, A. V., di Sorrentino, E. P., Thierry, B., ... Sueur, C. (2014). Social networks in primates: Smart and tolerant species have more efficient networks. *Scientific Reports*, 4(1), 7600. <https://doi.org/10.1038/srep07600>
- Patton, F., Campbell, P., & Genade, A. (2016). The development of white rhino social organisation at Ziwa Rhino Sanctuary, Uganda. *Pachyderm*, 57, 112–113. <https://pachydermjournal.org/index.php/pachyderm/article/view/397>
- Patton, F., Campbell, P., Genade, A., Ayiko, R., & Lutalo, G. (2011). The behaviour of white rhinos at Ziwa Rhino Sanctuary, Uganda with particular reference to night-time activity. *Pachyderm*, 50, 77–83.
- Rault, J. L. (2012). Friends with benefits: Social support and its relevance for farm animal welfare. *Applied Animal Behaviour Science*, 136(1), 1–14. <https://doi.org/10.1016/j.applanim.2011.10.002>
- Roberts, C. A., Laceyfield, G. D., Ball, D. and Bates, G. (2009). Management to optimize grazing performance in the Northern hemisphere. In *Tall Fescue for the Twenty-first Century*, 53, 85–99. <https://doi.org/10.2134/agronmonogr53.c6>
- Rose, P., & Croft, D. (2015). The potential of social network analysis as a tool for the management of zoo animals. *Animal Welfare*, 24, 123–138. <https://doi.org/10.7120/09627286.24.2.123>
- Ross, M. R., Niemann, T., Wark, J. D., Heintz, M. R., Horrigan, A., Cronin, K. A., & Gillespie, K. (2016). ZooMonitor (Version 1) [Mobile application software]. <https://zoomonitor.org>
- Scott, S. E. (2020). Conservation ecology and social behaviour of southern white rhinoceros (*Ceratotherium simum*). Manchester Metropolitan University (Doctoral Thesis), Manchester, UK. <https://e-space.mmu.ac.uk/id/eprint/627216>
- Sheriff, M. J., Dantzer, B., Delehanty, B., Palme, R., & Boonstra, R. (2011). Measuring stress in wildlife: Techniques for quantifying glucocorticoids. *Oecologia*, 166, 869–887. <https://doi.org/10.1007/s00442-011-1943-y>
- Shrader, A., & Owen-Smith, N. (2002). The role of companionship in the dispersal of white rhinoceroses (*Ceratotherium simum*). *Behavioral Ecology and Sociobiology*, 52, 255–261. <https://doi.org/10.1007/s00265-002-0506-y>
- Silk, J., Cheney, D., & Seyfarth, R. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology: Issues, News, and Reviews*, 22, 213–225.

- Silk, J. B. (2002). Kin selection in primate groups. *International Journal of Primatology*, 23, 849–875. <https://doi.org/10.1023/A:1015581016205>
- Silk, J. B., Alberts, S. C., & Altmann, J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*, 61(2), 197–204. <https://doi.org/10.1007/s00265-006-0250-9>
- Snijders, L., van Rooij, E. P., Burt, J. M., Hinde, C. A., Van Oers, K., & Naguib, M. (2014). Social networking in territorial great tits: Slow explorers have the least central social network positions. *Animal Behaviour*, 98, 95–102. <https://doi.org/10.1016/j.anbehav.2014.09.029>
- Sueur, C., & Petit, O. (2008). Organization of group members at departure is driven by social structure in Macaca. *International Journal of Primatology*, 29(4), 1085–1098. <https://doi.org/10.1007/s10764-008-9262-9>
- Swaisgood, R. R., Dickman, D. M., & White, A. M. (2006). A captive population in crisis: Testing hypotheses for reproductive failure in captive-born southern white rhinoceros females. *Biological Conservation*, 129(4), 468–476. <https://doi.org/10.1016/j.biocon.2005.11.015>
- Tichagwa, T., Pegg, N., Ndagurwa, H. G. T., & Zhuwau, C. (2020). Factors influencing the diurnal behaviour of white rhino (*Ceratotherium simum simum*) in Matobo National Park, Zimbabwe. *African Journal of Ecology*, 58(4), 766–777. <https://doi.org/10.1111/aje.12770>
- Veasey, J. S., Waran, N. K., & Young, R. J. (1996). On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator, using the giraffe (*Giraffa camelopardalis*) as a model. *Animal Welfare*, 5, 139–153.
- Wark, J. D., Cronin, K. A., Niemann, T., Shender, M. A., Horrigan, A., Kao, A., & Ross, M. R. (2019). Monitoring the behavior and habitat use of animals to enhance welfare using the ZooMonitor app. *Animal Behavior and Cognition*, 6(3), 158–167. <https://doi.org/10.26451/abc.06.03.01.2019>
- Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: A promising tool for the study of sociality. *Animal Behaviour*, 75(2), 333–344. <https://doi.org/10.1016/j.anbehav.2007.06.020>
- Whitehead, H. (2009). SOCPROG programs: Analysing animal social structures. *Behavioral Ecology and Sociobiology*, 63(5), 765–778. <https://doi.org/10.1007/s00265-008-0697-y>
- Whitehead, H. (2019). SOCPROG: Programs for analyzing social structure. Dalhousie University. <http://whitelab.biology.dal.ca/SOCPROG/Manual.pdf>
- Williams, B. (2023). Exploring the behaviors and social preferences of a large, multi-generational herd of zoo-housed southern white rhinoceros (*Ceratotherium simum simum*), 2020–2021, Dryad, Dataset. <https://doi.org/10.5061/dryad.63xsj3v6j>
- Wittemyer, G., Okello, J. B., Rasmussen, H. B., Arctander, P., Nyakaana, S., Douglas-Hamilton, I., & Siegismund, H. R. (2009). Where sociality and relatedness diverge: The genetic basis for hierarchical social organization in African elephants. *Proceedings. Biological sciences*, 276(1672), 3513–3521. <https://doi.org/10.1098/rspb.2009.0941>
- Wytenbach, R. (2012). Relatedness. Hoylab Cornell. <http://hoylab.cornell.edu/relatedness.html>

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