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2 Changes in social dominance in a group of subadult white rhinoceroses (*Ceratotherium*
3 *simum*) after dehorning

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14 **Abstract**

15 In many social species physical attributes correlate with dominance rankings and influence
16 the outcomes of dyadic interactions. We investigated the processes which affect white
17 rhinoceros social behaviour in response to a reduction in horn size asymmetries within a
18 group of subadult individuals. We monitored agonistic social interactions and the orderliness
19 of social rankings between six free ranging rhinoceroses before and after they underwent a
20 second dehorning procedure. We used a modified version of Landau's h to measure linearity,
21 a score of steepness to measure power asymmetry, and a measure of triangle transitivity to
22 assess relationships in the presence of null dyads. Agonistic social interactions were
23 significantly greater after the monitored dehorning procedure. Hierarchies possessed
24 significant steepness and transitivity prior to the procedure but not after. Linearity was non-
25 significant and rank order did not correspond to changes in horn size or age. Our results
26 provide the first evidence of a dominance hierarchy among free-ranging white rhinoceroses
27 outside of reproductive competition but indicate that physical attributes alone do not explain
28 social rankings. Rhinoceroses transitioned to a more egalitarian dominance structure than a
29 despotic one after the procedure, but dominance ranks were only weakly differentiated
30 within the group. Although a reduction in horn asymmetries may increase agonistic

1 behaviours through psychosocial or behavioural changes, drier climatic conditions cannot be
2 ruled out as the causative factor and as the subadult group stayed together rather than
3 dispersing, any increased fitness costs are likely to be minimal and outweighed by the benefits
4 of group membership.

5 **Key words**

6 Dehorning, horn size, hierarchy, social behaviour, South Africa; wildlife management

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1 Introduction

2 In many social species, differences in physical attributes contribute towards the outcomes of
3 agonistic interactions and influence dominance structures (Setchell and Wickings 2006). In
4 white rhinoceroses (*Ceratotherium simum*), older males are more likely to hold territories
5 than younger individuals, with neck and chest circumference but not body length shown to
6 be correlates of age (Rachlow et al. 1998). Horn size increases as rhinoceroses age (Pienaar et
7 al. 1991) so it could also act as a predictor of resource holding potential. Such an effect has
8 been observed in free-ranging horned black rhinoceroses (*Diceros bicornis*) where longer-
9 horned individuals dominated 65% of male dyadic interactions, particularly when horn
10 lengths differed by greater than 10 cm (Berger and Cunningham 1998). However, the strength
11 of these conclusions was limited by a small sample size. In our study, we sought to document
12 changes in the social behaviour of free-ranging white rhinoceroses (from here on rhino) in
13 response to a reduction in horn size asymmetries experienced after a second dehorning
14 procedure.

15 Rhino species continue to experience high rates of poaching across private and state reserves
16 in Southern Africa (Knight 2019). In an attempt to decrease the likelihood of poaching events,
17 reserves employ a range of conservation tactics often relying on a combination of approaches
18 (Rubino and Pienaar 2018). These management strategies can include regular vehicle and foot
19 patrols to intercept and deter poachers (Haas and Ferreira 2018), the translocation of rhino
20 from high risk to low risk areas (Ferreira et al. 2015), and increasingly the dehorning of animals
21 (Rubino and Pienaar 2020). Dehorning substantially reduces a rhinos' horn mass but recent
22 studies have shown this to have a minimal effect on white rhino physiology (Penny et al.
23 2020a), reproductive health (Penny et al. 2020b) and resource access (Penny et al. 2021).
24 However, there remains a paucity of research into whether dehorning affects white rhino
25 social behaviours as well into the efficacy of the procedure as an anti-poaching technique
26 (Lindsey and Taylor 2011; Patton et al. 2018a). Furthermore, no studies have addressed
27 whether rhinos experience behavioural changes between dehorning events after they have
28 been subject to an initial dehorning.

1 Dehorning acts to reduce the monetary reward available to poachers, which when practised
2 with effective security decreases poaching pressure (Du Toit and Anderson 2013). Horn sizes
3 are reduced to a stub measuring around 10 cm above the growth plate immediately after a
4 dehorning procedure (Penny et al. 2020a). However, as horn grows throughout a rhino's life,
5 repeat dehorning procedures are often necessary (Rachlow and Berger 1997). The interval
6 between procedures is dictated by an area's poaching risk, the logistics of its practise, and the
7 costs involved but it is best practise to dehorn all individuals in a population at as a similar
8 time as possible (Milner-Gulland 1999). Despite this, rhinos are sometimes dehorned
9 opportunistically with the timings between horn trimming and the variations in individual
10 horn growth rate influencing whether there are increases or decreases in horn size
11 asymmetries within a population (Lindsey and Taylor 2011).

12 White rhino horns function as an armament during social behaviours associated with conflict,
13 threat and aggression with the form, frequency and function of these behaviours dependent
14 on an individual's social position and motivational state (Owen-Smith 1975). White rhinos also
15 use their horns during socio-positive interactions and play behaviours (Owen-Smith 1973).
16 White rhinos undergo several changes in social organisation across their lifespan with changes
17 affecting their engagement with and exposure to a range of agonistic behaviours (Shrader
18 and Owen-Smith 2002). For example, around a third of adult males hold territories, which
19 provide them with spatially-exclusive reproductive access to concurrent females (White et al.
20 2007). However, recent paternity analyses indicate behaviourally-subdominant bulls may also
21 sire calves suggesting that territorial dominance is not a prerequisite for breeding success
22 (Guerier, et al. 2012). Adult females, subordinate adult males, and subadult groupings hold
23 overlapping home ranges that can encompass the territories of several territorial males.
24 Subadults rarely remain solitary, forming persistent associations with other subadults or non-
25 maternal adult female-calf pairs; most commonly these group consist of two to three
26 individuals but the formation of larger stable associations of up to six individuals can also
27 occur (Shrader and Owen-Smith 2002). Rhinos in these associations will orientate their
28 movements towards one another and stay within close proximity for continuous periods of
29 time, with these association often ending when individuals reach reproductive age, or if the
30 female they are associated with gives birth to a new calf (Shrader and Owen-Smith 2002).

1 Agonistic behaviours such as charging are often exhibited when territorially dominant males
2 confront other adult males encountered in or on the boundary of their territories (Owen-
3 Smith 1971). If an encountered male does not retreat, or is encountered far from its own
4 territory, the challenge may result in fighting which can cause territorial displacement if the
5 interloper wins (Owen-Smith 1975). In fights, rhinos repetitively thrust their horns and
6 forcefully press their bodies against one another which typically results in minor injury but in
7 extreme cases can result in serious injury or even death (Owen-Smith 1973; Patton et al.
8 2018a). On occasion, dominant males will also aggressively challenge the subadults of both
9 sexes encroaching on their territory (Owen-Smith 1975).

10 White rhinos of all age-sex classes exhibit agonistic behaviours outside of territorial contexts,
11 for example to prevent other individuals from approaching too close and during competition
12 for resources such as food, shade, and space (Metrione et al. 2007; Cinková et al. 2016).
13 Observations of subadults and calves acting submissively towards adults at feeding places also
14 suggest a dominance hierarchy may exist in contexts outside of male territory competition
15 (Cinková et al. 2016). Dominance hierarchies exist when individuals within a group show
16 asymmetries in aggressive and submissive behaviours, with some individuals giving way to
17 others (Hinde 1978). Well-defined dominance relationships are common in species for which
18 the potential for injury during altercations are high even when competition for resources is
19 low (Crowley 2001). Such a hierarchy has been documented within some captive populations
20 of white rhinos (Mikulica 1991; Cinková and Bičík 2013) but not under free-ranging conditions
21 outside of reproductive contexts.

22 A recent study into the indicators of reproductive success within a population of horned
23 rhinos in South Africa, found a strong positive correlation between horn size and the number
24 of calves sired in in one group of males but a negative correlation within another (Kretzschmar
25 et al. 2020). While anecdotal reports by Kock and Atkinson (1993) documented how four
26 dehorned large-bodied males maintained their territories despite several horned males being
27 present in the area, and that a dehorned territorial male dominated a horned intruder. It is
28 therefore ambiguous whether horn size influences behavioural outcomes and fitness in white
29 rhinos. However, if physical attributes are as important in establishing agonistic outcomes in
30 white rhinos as in other species, then individuals that are more closely matched in horn size

1 may show increases in agonistic behaviours if the results of such dyadic interactions cannot
2 be easily be predetermined. We sought to determine whether a reduction in the magnitude
3 of horn size differences affected agonistic social behaviours in free ranging subadult white
4 rhinos outside of territorial contexts. To test this, we monitored rhinos before and after they
5 were subject to a second dehorning procedure. We predicted that after the procedure, rhinos
6 would experience an increase in intraspecific agonistic behaviour and a decrease in the
7 distance between social ranks if dominance hierarchies were present.

8 **Methods**

9 ***Study site and population***

10 We observed white rhinos at a fenced reserve in South Africa between 05/04/2016 and
11 15/10/16 before and after they experienced a second dehorning procedure. The reserve was
12 managed for conservation and ecotourism and totalled 4,932 ha in area. The field site name
13 was anonymised for security reasons but fell within the Central Bushveld Bioregion.
14 Vegetation consisted of broad-leaved deciduous bushveld with a mosaic of pediment
15 grasslands and woodland (Mucina et al. 2006). The year can be roughly split into three
16 seasons: a cool dry season from May to mid-August, a hot dry season from mid-August to
17 October, and a hot wet season from November to April (Mucina et al. 2006). The majority of
18 native medium to large bodied (>10 kg) browsers and grazers were present. However, large
19 carnivore species excluding leopard (*Panthera pardus*) were absent. The reserve had a
20 population of 16 white rhinos which were not supplementary fed but had access to artificial
21 mineral licks and water sources. Rhinos also received limited husbandry, had a natural
22 breeding strategy (Emslie and Brooks 1999) and were therefore classified as a free-ranging
23 wild population under African Rhino Specialist Group criteria (Leader-Williams et al. 1997).

24 Rhinos were identified via their unique ear notch pattern and classed as subadults from
25 maternal independence until they reached socio-sexual maturity. This is when males become
26 solitary and/or territorial at 10 to 12 years old and at around 7 years old in females after the
27 birth of their first calf (Shrader and Owen-Smith 2002). Rhinos were classed as members of
28 the same social grouping if individuals had been sighted together within the preceding three
29 days. To investigate changes in intra-group social behaviour we focused our observations on

1 a stable grouping of six dehorned subadults. The group members were aged between 37.7
2 and 88 months and had a 5:1 male to female sex ratio (Table 1). Two of the six individuals
3 shared the same mother (F1 and M5), but paternal relationships were not known.

4 The six focal rhinos had been dehorned once prior to the start of our study. The rhinos were
5 then subject to a second dehorning procedure during our study (Table 1). Information on the
6 dehorning protocol is reported in Penny et al. (2020a) with horns trimmed to measure 10 cm
7 above the skin-horn interface. During the first monitored period (prior to the second
8 dehorning event) rhinos had between 17 and 20 months of horn regrowth. During the second
9 monitored period (after the second dehorning event) rhinos had between 0 to 5 months of
10 horn regrowth. Age and sex dependent differences in horn regrowth rates meant that horn
11 size asymmetries were greater before the second dehorning than after (Rachlow and Berger
12 1997) with between 0.72 kg and 2.45 kg of horn mass removed per rhino (Table 1).

13 **Insert Table 1 here**

14 ***Behavioural observations and sampling***

15 Rhinos were located through convenience sampling, whereby haphazard routes were driven
16 or walked until an individual or group was encountered. Behavioural observations typically
17 took place in the morning (sunrise to 11 am) and afternoon (3 pm to sunset) to coincide with
18 peaks in rhino behavioural activity (Patton et al. 2018b). To limit observer-triggered
19 disturbance, we followed rhinos from a distance (range: 25 to 150 metres) and observed them
20 using binoculars. Observations took place both on foot and from a stationary vehicle.

21 Behavioural observations focused on all rhinos in the group on arrival and ended when
22 animals lay down to rest (sitting or lying on the ground for greater than 60 minutes), were
23 lost from sight (for greater than 15 minutes), or it was too dark to identify them. We
24 subtracted periods where rhinos were resting (less than 60 minutes), obscured from view (for
25 less than 15 minutes), or disturbed by us from each rhino's total observation time to calculate
26 a duration of 'active' behaviour. We followed Shrader and Owen-Smith's (2002) definition of
27 disturbance where observations are considered bias if rhinos are either vigilant towards the
28 observer or in flight (running) from the observer. Repeat observation sessions were summed
29 to create a single total per rhino for both before and after their second dehorning. This

1 totalled a mean 45.2 hours per rhino (range: 43.6 - 45.9 hours, n = 6) prior to the second
2 dehorning and a mean 41.0 hours per rhino (range: 37.6 - 44.6 hours, n = 6) after the
3 procedure.

4 We recorded social behaviours by all occurrences sampling with an ethogram (Table 2)
5 adapted from other studies of white rhino social behaviour (Owen-Smith 1973; Cinková et al.
6 2016). Sequential social behaviours between the same individuals (that occurred within one
7 minute of the preceding social behaviour) were grouped together as a single independent
8 social 'event'. We coded a new social event if there was a change in participants or a gap
9 between social behaviours greater than one minute. We scored short social behavioural
10 events (less than 60 seconds in duration) in the field but made video recordings (Nikon CoolPix
11 P610) for social behavioural events longer than this to aid in their breakdown. We classified
12 each event as either agonistic (associated with conflict, threat or aggression), cohesive (socio-
13 positive), play, or other (unclear or ambiguous), similar to existing studies of white rhino
14 behaviour (Cinková and Bičík, 2013; Cinková et al. 2016) and based on previous functional
15 inference (Owen-Smith 1973). However, unlike Cinková et al. (2016) we did not score
16 independent occurrences of snort vocalisations (a threat with a nasal exhalation or inhalation)
17 as an agonistic interaction due to the difficulty in identifying a vocaliser and recipient in a
18 close proximity encounter. All methods were reviewed and approved by the Animal Welfare
19 and Ethics Review Board of the University of Brighton (REF: 2018-1127).

20 **Insert table 2 here**

21 ***Data analysis***

22 To investigate whether a reduction in horn size asymmetries influenced the frequency of
23 agonistic social behaviours, we compared rates recorded before and after a second dehorning
24 procedure. To control for differences in individual encounter rate between rhinos, only those
25 agonistic interactions that occurred between group members were considered in the analysis.
26 We used R (version 4.1.0; R Core Team 2021) to compute all statistical analyses. Following a
27 check for normality, we compared differences in the intra-group agonistic interaction rate
28 with a paired t-test through the '*t.test*' function in the base R package.

1 We defined dominance as a structural attribute of a pattern of recurring, dyadic agonistic
2 interactions between two individuals, where the resultant outcome consistently favours one
3 dyad member over another without the need for escalation (Drews 1993). Social rankings
4 were calculated for the group before and after they were subject to the second dehorning
5 procedure. For each participant, the outcome of an agonistic event was classified as a loss if
6 they displayed submissive behaviour such as a tendency to step back or retreat first from an
7 interaction, a curled tail, or a snarl vocalisation that rose to a shriek (following Owen-Smith
8 1973). If the outcome was obscured or ambiguous, neither a win nor loss was designated.

9 To assess if there was a linear dominance hierarchy (transitivity), a modified version of
10 Landau's h was calculated following de Vries (1995). For a hierarchy to be strictly linear, all
11 dyads must have a 'transitive' dominant-subordinate relationship, where if individual 'A'
12 dominates 'B', and 'B' dominates 'C', then 'A' must also dominate 'C' (Shizuka and McDonald
13 2012). To compute this, the '*getimplandau*' function in the R package 'DyaDA' (Leiva et al.
14 2010) was run on win-loss matrices collected pre- and post- the second dehorning procedure
15 (Appendix A). The index ranges from 0 or no linearity (where every individual dominates the
16 same number of other individuals) to 1 or perfect linearity (where every individual dominates
17 all animals ranked below and none of those ranked above) (Klass and Cords 2011).

18 Following this, a measure of each rhino's overall success was calculated using David's scores
19 (Gammel et al. 2003). These scores can be used to rank animals in terms of predicted
20 dominance outcomes derived from weighted sums of dyadic proportions of wins and losses.
21 Normalised David's scores were calculated from win-loss matrices on the basis of a dyadic
22 dominance index corrected for chance using the '*getNormDS*' function in the R '*steepness*'
23 package (Leiva and de Vries 2015). For David's scores, the success rate at which individuals
24 win dyadic interactions affects the size of the absolute differences between adjacently ranked
25 animals (de Vries et al. 2006). We then regressed normalised David's scores against cardinal
26 ranks to obtain a measure of the power asymmetry within the hierarchy, known as its
27 steepness (de Vries et al. 2006). This was calculated using the '*getStp*' function from the R
28 '*steepness*' package (Leiva and de Vries, 2015). To determine the significance of each
29 hierarchy's linearity and steepness, we tested the observed values against the expected
30 values of random win chances for all pairs of individuals. These were generated from 10,000

1 randomisations using the '*linear.hierarchy.test*' and '*steeptest*' functions in the R packages
2 '*steepness*' and '*DyaDA*' respectively (Leiva and de Vries 2015) which calculated the
3 proportion of times that a randomly generated value was greater than or equal to the actual
4 observed value.

5 Measures of linearity and steepness aid in comparisons of dominance between studies (de
6 Vries et al. 2006) but if pairs of individuals do not interact, the metrics rely on randomised or
7 approximated values (Shizuka and McDonald 2012). To avoid problems with null dyads, the
8 proportion of transitivity (Pt) within a subset of triads (groups of three individuals) in which
9 all interactions have been observed were also calculated for data collected pre- and post- the
10 second dehorning procedure. This measure of 'triangle transitivity' is independent of
11 measures of steepness and linearity but still indicates the level of orderliness within a
12 hierarchy (Shizuka and McDonald 2012). We computed this from binary win-loss matrices
13 using R script from Shizuka and McDonald (2012) with relationships designated a win if a rhino
14 dominated its competitor in 50% or more of its dyadic encounters. To calculate the
15 significance, the range of triangle transitivity across 1000 randomly generated networks was
16 compared against the empirical value. Here the p-value represented the proportion of times
17 that transitivity within the random network was greater than that in the empirical network.

18 **Results**

19 ***Agonistic social interaction rate***

20 Agonistic social interactions were significantly greater after the procedure than before (mean
21 difference: 0.464 agonistic social interactions per hour, 95%CI: 0.210-0.719; Figure 1) (Paired
22 t test: $t_{(5)} = 4.675$, $p = 0.006$). Two predominant forms of agonistic interaction were observed
23 among rhinos in the stable six-member social grouping, in the first, one rhino would move too
24 close to another in an indirect approach and be met with a turn or charge, often accompanied
25 by an aggressive snarl or grunt vocalisation, followed by one, both or neither rhinos moving
26 away. In the second form, an individual would directly approach another individual and
27 charge or chase them. Physical horn contact was rare with rhinos delivering or receiving a
28 horn thrust or horn to horn blow or engaging in horn fencing in 9.1% of dyads observed prior

1 to the monitored dehorning procedure (3 out of 33 dyads) and 23.3% of dyads observed after
2 (20 out of 86 dyads).

3 **Insert Figure 1 here**

4 ***Dominance rankings***

5 A winner and loser could be identified in 26 of the dyadic encounters observed prior to the
6 monitored dehorning procedure and 80 dyadic encounters after. The orderliness of
7 hierarchies varied depending on the metric used (Table 3). Measures of linearity were not
8 significantly different to those expected to occur by chance (pre: $h' = 0.657$, $p = 0.121$; post:
9 $h' = 0.657$, $p = 0.211$). Prior to the monitored dehorning procedure, social relationships
10 possessed significant steepness ($s = 0.310$; $p = 0.049$) but after the procedure steepness was
11 no different to that expected to occur by chance ($s = 0.380$; $p = 0.250$). Both pre- and post-
12 the monitored dehorning procedure, David's scores placed the female rhino in the top ranked
13 social position and eldest male in the second ranked position (Figure 2). The dominance
14 positions of the other four rhinos moved between 1 and 4 places following the procedure.
15 However, these ranks did not correspond with either age or horn mass change. Linearity and
16 steepness may have been affected by the presence of null dyads which were apparent in both
17 the pre- and post-procedure dataset (pre = 10, post = 2). Measures of triangle transitivity,
18 which consider only established relationships, were significantly different to those expected
19 by chance for data collected prior to the second dehorning procedure, where 100% of triads
20 showed transitivity ($p = 0.020$) but not for the dataset collected after the procedure, where
21 only 61.5% of triads possessed the property ($p = 0.137$).

22 **Insert Table 3 here**

23 **Insert Figure 2 here**

24 **Discussion**

25 We investigated the processes which affect white rhino agonistic social behaviour and the
26 structure of dominance hierarchies by observing animals that experienced a reduction in horn
27 size following a standardised dehorning procedure, the second such procedure the animals
28 had been exposed to. Our research is the first to demonstrate the existence of a dominance

1 hierarchy within free-ranging rhinos outside of reproductive competition. The lack of a non-
2 territorial social hierarchy reported in other studies of free-ranging rhinos is likely an artefact
3 of inadequate sampling size, due to the difficulty in observing repeat social interactions
4 between the same individuals in free-ranging populations (Clutton-Brock and Harvey 1976)
5 rather than being unique to the study population. The detection of statistically significant
6 transitivity and steepness prior to the monitored dehorning procedure but the absence of it
7 after suggests a transition to a more egalitarian dominance structure than a despotic one,
8 where the resource holding potential of some individuals was almost equal. Rhinos also
9 exhibited an increased rate of agonistic social interactions following dehorning. This suggests
10 individuals sought to reinforce their social status by engaging in more frequent agonistic
11 challenges due a more unstable hierarchy (Fairbanks 1994). This is counter to findings by
12 Patton et al. (2018a) who reported a reduction in fighting in a small population of white rhinos
13 after three adult males were dehorned. However, these rhinos were exhibiting extremely high
14 rates of fighting prior to their dehorning which may indicate that dominance hierarchies were
15 yet to be established. In our study, the response we observed may be specific to rhinos in
16 established subadult social groupings or non-territorial contexts. Furthermore, the agonistic
17 behaviours of monitored individuals were similar to those described among horned rhinos
18 (Owen-Smith, 1973; Cinková et al. 2016) suggesting that a reduction in horn size does not
19 functionally constrain this aspect of white rhino social behaviour. The existence of such
20 apparent behavioural plasticity in response to artificially shortened horns may be an
21 adaptation to the natural changes in horn size caused by growth and wear that occur
22 throughout a white rhino's lifespan (Pienaar et al. 1991).

23 ***Social dominance***

24 Prior to the monitored dehorning procedure when horn size asymmetries were greater, the
25 observed hierarchy arose through a differential success in the outcomes of dyadic encounters
26 among individuals (Hinde 1978). However, as social rankings did not correspond with either
27 horn mass or age, which are correlates of body size (Rachlow et al. 1998; Pienaar et al. 1991)
28 physical attributes are unlikely to be the sole causal factor behind the observed social
29 positions. Instead, differences in sex and behavioural history may in part explain individual
30 ranks within the hierarchy (Cinková and Bičík 2013). The top-ranked social position was held

1 by the only female within the group. This corresponds with the results of captive studies
2 which indicate that male white rhinos occupy lower social ranks than females, receiving and
3 retreating from the most challenges within a group (Mikulica 1991; Meister 1998; Cinková
4 and Bičík 2013). It also supports recent findings by Jenikejew et al. (2020) who reported higher
5 rates of agonistic calls emitted by females towards males than in other dyadic combinations.
6 Here, dynamic winner-loser feedback may provide an alternative regulatory mechanism to
7 physical attributes for establishing social position. These feedback systems are present in
8 many social species, where winning (or losing) a previous agonistic encounter can influence
9 the probability of winning (or losing) the next one (Chase et al. 2002).

10 Persistent social associations between subadult rhinos are often limited to group sizes
11 consisting of just two to three individuals (Shrader and Owen-Smith 2002), in contrast to the
12 six-individual group observed in our study. It is therefore not known if the dominance
13 asymmetries we detected exist in groups consisting of fewer individuals and further research
14 is needed to establish this. Such asymmetries have been reported between paired
15 companions in captivity (Metrione et al. 2007) but this may not transfer to free-ranging
16 conditions where rhinos have greater opportunities for dispersal.

17 Agonistic behaviours appeared to function in space-maintenance and resource competition
18 but most interactions resulted in avoidance or appeasement and thus carried little risk of
19 physical injury. White rhinos spend the majority of active periods foraging (Tichagwa et al.
20 2020) but as grass cannot be monopolised it may explain the weak differentiation in ranks
21 observed among individuals both pre- and post- the monitored dehorning. For resources that
22 are not finite, the payoff asymmetries will be relatively small (Hammerstein 1981). However,
23 some usurpable resources such as patches of shade, mud wallows and drinking pools were
24 present. Some of these habitat features may have also become smaller or scarcer during the
25 post-dehorning monitored period which corresponded with drier climatic conditions. Density-
26 dependent effects have been observed in captive white rhinos, with females housed in small
27 enclosures observed exhibiting more space maintenance vocalizations than females housed
28 in larger enclosures (Metrione et al. 2007). Therefore, increased proximity brought on by
29 drought may provide an alternative explanation for the observed increase in agonistic
30 behaviours. The group did not break-up during the monitored period despite the increase in

1 agonistic behaviours. Therefore, group membership benefits such as a decreased risk of inter-
2 and intra-specific attack along with an increased knowledge of local resources through
3 accompaniment of environmentally familiarised individuals (Shrader and Owen-Smith 2002)
4 likely outweighed any increased costs. There are likely to be few benefits for escalating
5 conflicts beyond the minor aggressive behaviours observed (Crowley 2001). However, given
6 that the benefits of occupying a higher social ranking (such as preferential access to
7 resources) are likely to exceed the costs of aggression (time and energy), and may even
8 minimise the potential for injury, the presence of a social hierarchy is likely to be adaptive.
9 Similar behaviours have been observed in African bush elephants (*Loxodonta africana*), which
10 rely on abundant and widely distributed food resources, but must still compete for access to
11 other rarer but important resources such as water, minerals, rubbing posts and some foods
12 (Archie et al. 2006).

13 Subadult associations between rhinos are temporary and may last from a few years to just a
14 few days (Shrader and Owen-Smith 2002). If, as suggested by our findings, social hierarchies
15 within subadult social groupings result from dynamic winner-loser effects rather than physical
16 traits then there may be greater costs of association in the days immediately after group
17 formation, with aggression often highest before dominance is established (Clutton-Brock and
18 Harvey, 1976). Research into whether the frequencies of agonistic behaviours and the size of
19 power asymmetries among subadult social groupings influences the duration of these
20 associations would therefore be of interest.

21 ***Future work***

22 Although our small sample size limits the strengths of our conclusions, the paucity of data on
23 the subject makes the findings reported here valuable and unique in the field of rhino
24 conservation. However, further study is needed to confirm whether the dominance
25 hierarchies we observed are present in other circumstances including under differing group
26 sizes, demographics, and environmental conditions. The observed subadult social grouping
27 will not persist into sexual maturity (Shrader and Owen-Smith 2002), so any induced changes
28 within the group will not necessarily affect reproductive success. If a reduction in horn size
29 asymmetries through dehorning affects the frequency of territorial displacement among

1 adult bulls it could lead to reproductive dominance becoming skewed towards a fewer
2 number of individuals. This was beyond the scope of the study and its evaluation is likely to
3 be hindered by the rare occurrence of territorial challenges among free-ranging adult males
4 (Owen-Smith 1973). Further work could also establish whether the magnitude of horn size
5 differences influences dyadic outcomes, as has been reported in black rhinos (Berger and
6 Cunningham 1998). Horn mass regenerates over time with regrowth faster in some
7 individuals than others (Rachlow and Berger 1997). Therefore, any behavioural changes
8 following dehorning may be time-limited if the effects only occur below a certain size or when
9 horn asymmetries are at their smallest.

10 The reserve's rhino population are representative of many smaller fenced reserves in South
11 Africa that perform dehorning, where it is best practice to dehorn as many individuals in a
12 population as possible to minimize poaching risk (Milner-Gulland 1999). However, in some
13 larger national parks, it is unfeasible to dehorn all individuals due to prohibitive costs and
14 logistical difficulties (Lindsey and Taylor 2011). Additionally, in this study it was not possible
15 to investigate changes in agonistic behaviour in relation to the first dehorning when
16 reductions in horn size would have been greatest, as the monitored social group had not yet
17 formed. Thus, further research is needed into the potential for social disruption in
18 populations with greater horn size asymmetries and the structure of hierarchies under these
19 conditions.

20 This work demonstrates that with intensive study, behavioural changes that are infrequent
21 or difficult-to-observe can be quantified in wild populations and contribute towards evidence-
22 based conservation policies. The current guidelines for dehorning as an anti-poaching tactic
23 are based on threat level and cost and recommend that the procedure is conducted every 12
24 to 36 months (Lindsey and Taylor 2011). Although a reduction in horn asymmetries may
25 increase agonistic behaviours, we do not advocate for the timings of dehorning procedures
26 to be offset within a population, as the effects may only be short-lived or manifest in
27 subadults or further alter dominance structures.

28 ***Conclusion***

1 We report the first evidence for the existence of dominance hierarchies within a free-ranging
2 white rhino population outside of male territory competition. This supports previous reports
3 by Cinková et al. (2016) and indicates that reports of such a structure within captive conditions
4 likely result from more intensive observations rather than management conditions alone
5 (Mikulica 1991; Cinková and Bičík 2013). Our findings suggest that physical attributes alone
6 do not explain a rhino's social ranking. Although we documented an increase in agonistic
7 interactions among group members following the monitored dehorning procedure, drier
8 climatic conditions cannot be ruled out as the causative factor rather than psychosocial or
9 behavioural changes resulting from the smaller size of horns or a reduction in horn size
10 asymmetries. More research is required to understand whether the impacts of dehorning
11 extend to larger dehorned populations with greater horn size asymmetries or sexually mature
12 individuals, as are studies into the success of the procedure in reducing poaching rates.

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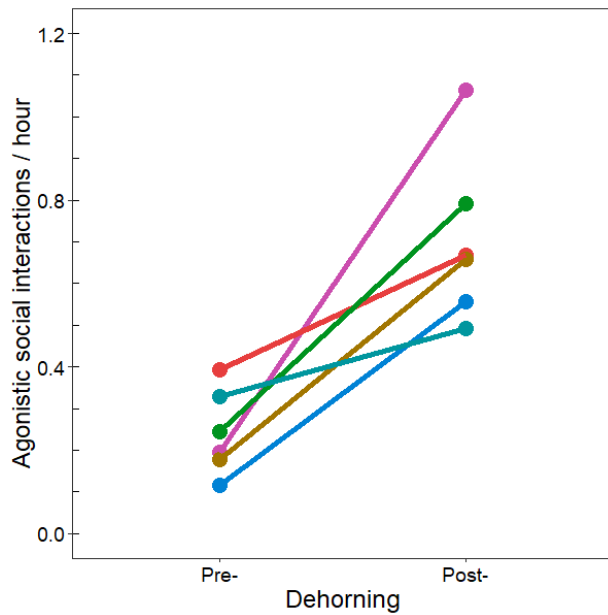
1 **Appendix A**

2 Appendix A. Win-loss matrix for six subadult rhinos involved in agonistic social interactions
 3 prior to and after a second dehorning procedure.

a_i	F1	M1	M2	M3	M4	M5
<i>Pre-procedure</i>						
F1	-	0	2	0	1	0
M1	0	-	0	3	4	6
M2	0	0	-	2	1	1
M3	0	1	0	-	0	0
M4	0	2	0	1	-	2
M5	0	0	0	0	0	-
<i>Post-procedure</i>						
F1	-	2	4	6	8	2
M1	0	-	1	6	3	4
M2	0	1	-	2	4	3
M3	0	4	4	-	5	2
M4	0	2	5	4	-	0
M5	0	2	3	3	0	-

4 Rows indicate the number of wins, columns the number of losses. a_i = animal identity, with
 5 letters sex (F: female; M: male) and numbers indicating age (from oldest to youngest within
 6 sex).

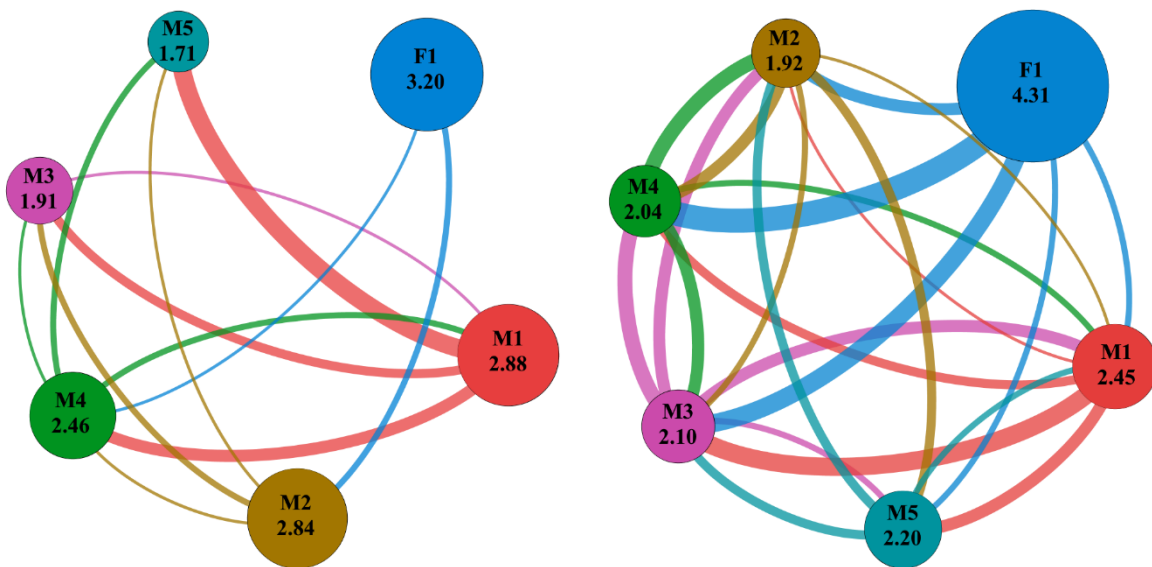
7 **Figure captions**



1

2 Figure 1. Change in the intra-group rate of agonistic social interactions before and after a
 3 second dehorning. F1 (blue), M1 (red), M2 (gold), M3 (pink), M4 (green), M5 (turquoise).

4



5

6 Figure 2. Social network of agonistic interactions between six subadult rhinos before (A) and
 7 after (B) a dehorning procedure. Node size indicates the difference in social rank by
 8 Normalized David's scores (decreasing in size clockwise). Edges (lines) that match their node

1 colour represent dyadic interactions that resulted in a win. Edge width indicates the number of
2 interactions a rhino won, varying from one (thinnest) to eight (thickest).

3

1 Table 1. Characteristics of the study population. Age is reported for rhinos at the start of the
 2 monitored period and change in total horn mass following the second dehorning.

ID	F1	M1	M2	M3	M4	M5
Sex	Female	Male	Male	Male	Male	Male
Age (months)	72.5	88.0	59.9	46.6	46.3	37.7
First dehorning	20 th Oct 2014	20 th Oct 2014	27 th Oct 2014	20 th Oct 2014	20 th Oct 2014	20 th Oct 2014
Second dehorning	2 nd Jun 2016	2 nd Jun 2016	2 nd Jun 2016	2 nd Jun 2016	2 nd Jun 2016	2 nd Jun 2016
Horn mass change (kg)	-1.18	-2.45	-0.72	-1.26	-0.83	-0.54

3

4

1 Table 2. Social behaviours recorded by all occurrences sampling.

Behavioural unit	Type	Description
Approach with threat	A	Directed movement (walk) towards a rhino leading to agonistic behaviour. Head up and ears forward, or head lowered and ears back if close.
Approach without threat (direct)	C	Directed movement (walk or run) towards a rhino leading to no agonistic behaviour. Rhinos remain in proximity to one another.
Move-away	A	Directed movement (walk) away from rhino following agonistic behaviour.
Charge	A	Rapid movement (run) towards a rhino for a distance of at least several meters, including feinted attacks.
Chase	A	Rapid movement (run) towards a fleeing rhino.
Flee	A	Rapid movement (run) away from a rhino following agonistic behaviour. Is not necessarily being chased.
Turn	A	Fast turning and raising of head and/or turning of body towards a disturbing rhino. Often includes a few quick steps.
Shoulder	A	Forcefully pressing against recipient with body/neck/head.
Nudge	O	Accidental physical contact. E.g. brushing/touching while walking/foraging.
Non-aggressive contact	C	Deliberate non-aggressive physical contact. Includes head/neck/body rubbing or mouth/lips contact against a recipient.
Naso-naso contact	C	Standing, head up, face to face, sometimes allowing noses to meet. Often the first interaction when rhinos from different groups meet.
Stare	A	Standing, horn to horn, staring at opponent. If head down and ears back, indicates submission.

Group guard	A	Two or more rhinos standing side-side or rump-rump with their heads facing outwards towards a threat. Defensive formation.
Courtship	C	Proceptive or receptive sexual behaviours including mounting and mating.
Horn thrust	A	Forceful thrusting of horn against the body of a recipient.
Horn to horn blow	A	Forceful thrusting of horn against the horn of a recipient.
Horn fencing	A	Forceful and repetitive thrusting of horn against the body/horn of a recipient. Recipient usually responds with the same. Main element of territorial fights.
Horn wrestling	P	Less-aggressive repetitive thrusting of horns against the body/horn of a recipient. Recipient usually responds with the same. Likely develops fighting skills and acts as a form of play. Instigator usually a subadult or calf.
Horn contact	C	Gentle contact of horn against the body of a recipient, includes rubbing and leaning.
Snarl	A	A loud rasping roar with head thrust forwards, ears laid back and a mouth opened
Grunt	A	A low-frequency vocalisation made with opened mouth and ears laid back
Shriek	A	A singular/series of trumpeting shrieks. An intensive shrill sound, reminiscent of the trumpeting of an elephant; made by subordinate bulls or by territorial bulls out of their home territories.
Gruff squeal	A	A throaty, rumbling squeal rising in pitch to a tensed cut-off, usually repeated in tenses; made by territorial bulls while chasing after other rhinos.
Contact calling	C	Using calls pant or hic. A series of inhalations and exhalations is emitted when a rhinoceros is isolated from its group and when approaching or staring at other animals

Snort O A nasal exhalation or inhalation

1 Behaviours were categorised as either agonistic (A): associated with conflict, threat or
 2 aggression; cohesive (C): socio-positive, (P): play behaviour, or other (O): unclear or
 3 ambiguous. Adapted from Owen-Smith (1973) and Cinková et al. (2016).

4 Table 3. Dyadic agonistic interactions between six subadult rhinos prior to and after their
 5 second dehorning.

a_i	F1	M1	M2	M4	M3	M5
Pre						
W_i	3	13	4	5	1	0
N_i	3	16	6	11	7	9
Win-loss ratio	1.00	0.81	0.67	0.45	0.14	0.00
David's score	3.20	2.88	2.84	2.46	1.91	1.71
Cardinal rank	1	2	3	4	5	6
Age rank	2	1	3	5	4	6
Horn mass rank	3	1	5	4	2	6
Post						
W_i	22	14	10	11	15	8
N_i	22	25	27	31	35	19
Win-loss ratio	1	0.56	0.41	0.35	0.41	0.42
David's score	4.31	2.45	1.92	2.04	2.1	2.2
Cardinal rank	1	2	6	5	4	3
Cardinal rank change	0	0	-3	-1	1	3

1 a_i = animal identity, with letters indicating sex (F: female; M: male); w_i = the number of
2 encounters in which animal a_i was observed to have won; N_i = the number of encounters in
3 which a_i was involved; horn mass rank is listed from largest (1) to smallest (6) change; age
4 rank is listed from oldest (1) to youngest (6).

5