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Title

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

Abstract

In many social species physical attributes correlate with dominance rankings and influence the outcomes of dyadic interactions. We investigated the processes which affect white rhinoceros social behaviour in response to a reduction in horn size asymmetries within a group of subadult individuals. We monitored agonistic social interactions and the orderliness of social rankings between six free ranging rhinoceroses before and after they underwent a second dehorning procedure. We used a modified version of Landau's h to measure linearity, a score of steepness to measure power asymmetry, and a measure of triangle transitivity to assess relationships in the presence of null dyads. Agonistic social interactions were significantly greater after the monitored dehorning procedure. Hierarchies possessed significant steepness and transitivity prior to the procedure but not after. Linearity was non-significant and rank order did not correspond to changes in horn size or age. Our results provide the first evidence of a dominance hierarchy among free-ranging white rhinoceroses outside of reproductive competition but indicate that physical attributes alone do not explain social rankings. Rhinoceroses transitioned to a more egalitarian dominance structure than a despotic one after the procedure, but dominance ranks were only weakly differentiated within the group. Although a reduction in horn asymmetries may increase agonistic behaviours through psychosocial or behavioural changes, drier climatic conditions cannot be ruled out as the causative factor and as the subadult group stayed together rather than dispersing, any increased fitness costs are likely to be minimal and outweighed by the benefits of group membership.

Key words

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

Introduction

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

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

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

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

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

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

A recent study into the indicators of reproductive success within a population of horned rhinos in South Africa, found a strong positive correlation between horn size and the number of calves sired in in one group of males but a negative correlation within another (Kretzschmar et al. 2020). While anecdotal reports by Kock and Atkinson (1993) documented how four dehorned large-bodied males maintained their territories despite several horned males being present in the area, and that a dehorned territorial male dominated a horned intruder. It is therefore ambiguous whether horn size influences behavioural outcomes and fitness in white rhinos. However, if physical attributes are as important in establishing agonistic outcomes in white rhinos as in other species, then individuals that are more closely matched in horn size may show increases in agonistic behaviours if the results of such dyadic interactions cannot be easily be predetermined. We sought to determine whether a reduction in the magnitude of horn size differences affected agonistic social behaviours in free ranging subadult white rhinos outside of territorial contexts. To test this, we monitored rhinos before and after they were subject to a second dehorning procedure. We predicted that after the procedure, rhinos would experience an increase in intraspecific agonistic behaviour and a decrease in the distance between social ranks if dominance hierarchies were present.

Methods

Study site and population

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

Rhinos were identified via their unique ear notch pattern and classed as subadults from maternal independence until they reached socio-sexual maturity. This is when males become solitary and/or territorial at 10 to 12 years old and at around 7 years old in females after the birth of their first calf (Shrader and Owen-Smith 2002). Rhinos were classed as members of the same social grouping if individuals had been sighted together within the preceding three days. To investigate changes in intra-group social behaviour we focused our observations on a stable grouping of six dehorned subadults. The group members were aged between 37.7 and 88 months and had a 5:1 male to female sex ratio (Table 1). Two of the six individuals shared the same mother (F1 and M5), but paternal relationships were not known.

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

Insert Table 1 here

Behavioural observations and sampling

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

Behavioural observations focused on all rhinos in the group on arrival and ended when animals lay down to rest (sitting or lying on the ground for greater than 60 minutes), were lost from sight (for greater than 15 minutes), or it was too dark to identify them. We subtracted periods where rhinos were resting (less than 60 minutes), obscured from view (for less than 15 minutes), or disturbed by us from each rhino's total observation time to calculate a duration of 'active' behaviour. We followed Shrader and Owen-Smith's (2002) definition of disturbance where observations are considered bias if rhinos are either vigilant towards the observer or in flight (running) from the observer. Repeat observation sessions were summed to create a single total per rhino for both before and after their second dehorning. This totalled a mean 45.2 hours per rhino (range: 43.6 - 45.9 hours, n = 6) prior to the second dehorning and a mean 41.0 hours per rhino (range: 37.6 - 44.6 hours, n = 6) after the procedure.

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

Insert table 2 here

Data analysis

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

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

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

Following this, a measure of each rhino's overall success was calculated using David's scores (Gammel et al. 2003). These scores can be used to rank animals in terms of predicted dominance outcomes derived from weighted sums of dyadic proportions of wins and losses. Normalised David's scores were calculated from win-loss matrices on the basis of a dyadic dominance index corrected for chance using the 'getNormDS' function in the R 'steepness' package (Leiva and de Vries 2015). For David's scores, the success rate at which individuals win dyadic interactions affects the size of the absolute differences between adjacently ranked animals (de Vries et al. 2006). We then regressed normalised David's scores against cardinal ranks to obtain a measure of the power asymmetry within the hierarchy, known as its steepness (de Vries et al. 2006). This was calculated using the '*getStp*' function from the R '*steepness*' package (Leiva and de Vries, 2015). To determine the significance of each hierarchy's linearity and steepness, we tested the observed values against the expected values of random win chances for all pairs of individuals. These were generated from 10,000 randomisations using the '*linear.hierarchy.test*' and '*steeptest*' functions in the R packages '*steepness*' and '*DyaDA*' respectively (Leiva and de Vries 2015) which calculated the proportion of times that a randomly generated value was greater than or equal to the actual observed value.

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

Results

Agonistic social interaction rate

Agonistic social interactions were significantly greater after the procedure than before (mean difference: 0.464 agonistic social interactions per hour, 95%CI: 0.210-0.719; Figure 1) (Paired t test: $t_{(5)} = 4.675$, $p = 0.006$). Two predominant forms of agonistic interaction were observed among rhinos in the stable six-member social grouping, in the first, one rhino would move too close to another in an indirect approach and be met with a turn or charge, often accompanied by an aggressive snarl or grunt vocalisation, followed by one, both or neither rhinos moving away. In the second form, an individual would directly approach another individual and charge or chase them. Physical horn contact was rare with rhinos delivering or receiving a horn thrust or horn to horn blow or engaging in horn fencing in 9.1% of dyads observed prior to the monitored dehorning procedure (3 out of 33 dyads) and 23.3% of dyads observed after (20 out of 86 dyads).

Insert Figure 1 here

Dominance rankings

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

Insert Table 3 here

Insert Figure 2 here

Discussion

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

Social dominance

Prior to the monitored dehorning procedure when horn size asymmetries were greater, the observed hierarchy arose through a differential success in the outcomes of dyadic encounters among individuals (Hinde 1978). However, as social rankings did not correspond with either horn mass or age, which are correlates of body size (Rachlow et al. 1998; Pienaar et al. 1991) physical attributes are unlikely to be the sole causal factor behind the observed social positions. Instead, differences in sex and behavioural history may in part explain individual ranks within the hierarchy (Cinková and Bičík 2013). The top-ranked social position was held by the only female within the group. This corresponds with the results of captive studies which indicate that male white rhinos occupy lower social ranks than females, receiving and retreating from the most challenges within a group (Mikulica 1991; Meister 1998; Cinková and Bičík 2013). It also supports recent findings by Jenikejew et al. (2020) who reported higher rates of agonistic calls emitted by females towards males than in other dyadic combinations. Here, dynamic winner-loser feedback may provide an alternative regulatory mechanism to physical attributes for establishing social position. These feedback systems are present in many social species, where winning (or losing) a previous agonistic encounter can influence the probability of winning (or losing) the next one (Chase et al. 2002).

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

Agonistic behaviours appeared to function in space-maintenance and resource competition but most interactions resulted in avoidance or appeasement and thus carried little risk of physical injury. White rhinos spend the majority of active periods foraging (Tichagwa et al. 2020) but as grass cannot be monopolised it may explain the weak differentiation in ranks observed among individuals both pre- and post- the monitored dehorning. For resources that are not finite, the payoff asymmetries will be relatively small (Hammerstein 1981). However, some usurpable resources such as patches of shade, mud wallows and drinking pools were present. Some of these habitat features may have also become smaller or scarcer during the post-dehorning monitored period which corresponded with drier climatic conditions. Density-dependent effects have been observed in captive white rhinos, with females housed in small enclosures observed exhibiting more space maintenance vocalizations than females housed in larger enclosures (Metrione et al. 2007). Therefore, increased proximity brought on by drought may provide an alternative explanation for the observed increase in agonistic behaviours. The group did not break-up during the monitored period despite the increase in agonistic behaviours. Therefore, group membership benefits such as a decreased risk of inter- and intra-specific attack along with an increased knowledge of local resources through accompaniment of environmentally familiarised individuals (Shrader and Owen-Smith 2002) likely outweighed any increased costs. There are likely to be few benefits for escalating conflicts beyond the minor aggressive behaviours observed (Crowley 2001). However, given that the benefits of occupying a higher social ranking (such as preferential access to resources) are likely to exceed the costs of aggression (time and energy), and may even minimise the potential for injury, the presence of a social hierarchy is likely to be adaptive. Similar behaviours have been observed in African bush elephants (*Loxodonta africana*), which rely on abundant and widely distributed food resources, but must still compete for access to other rarer but important resources such as water, minerals, rubbing posts and some foods (Archie et al. 2006).

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

Future work

Although our small sample size limits the strengths of our conclusions, the paucity of data on the subject makes the findings reported here valuable and unique in the field of rhino conservation. However, further study is needed to confirm whether the dominance hierarchies we observed are present in other circumstances including under differing group sizes, demographics, and environmental conditions. The observed subadult social grouping will not persist into sexual maturity (Shrader and Owen-Smith 2002), so any induced changes within the group will not necessarily affect reproductive success. If a reduction in horn size asymmetries through dehorning affects the frequency of territorial displacement among adult bulls it could lead to reproductive dominance becoming skewed towards a fewer number of individuals. This was beyond the scope of the study and its evaluation is likely to be hindered by the rare occurrence of territorial challenges among free-ranging adult males (Owen-Smith 1973). Further work could also establish whether the magnitude of horn size differences influences dyadic outcomes, as has been reported in black rhinos (Berger and Cunningham 1998). Horn mass regenerates over time with regrowth faster in some individuals than others (Rachlow and Berger 1997). Therefore, any behavioural changes following dehorning may be time-limited if the effects only occur below a certain size or when horn asymmetries are at their smallest.

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

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

Conclusion

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

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Appendix A

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

a_i	F1	M1	M2	M3	M4	M5
Pre-procedure						
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	-
Post-procedure						
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	-

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

Figure captions

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

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

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

Table 1. Characteristics of the study population. Age is reported for rhinos at the start of the 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	20th Oct 2014	20th Oct 2014	27th Oct 2014	20th Oct 2014	20th Oct 2014	20th Oct 2014
Second dehorning	2nd Jun 2016	2nd Jun 2016	2nd Jun 2016	2nd Jun 2016	2nd Jun 2016	2nd Jun 2016
Horn mass change (kg)	-1.18	-2.45	-0.72	-1.26	-0.83	-0.54

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

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

Table 3. Dyadic agonistic interactions between six subadult rhinos prior to and after their 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

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