



No evidence that horn trimming affects white rhinoceros horn use during comfort behaviour and resource access

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Abstract

Rhino species use their horns in social interactions but also when accessing resources, rubbing and in interspecific defence. The current poaching crisis has seen southern white rhinos (*Ceratotherium simum*) increasingly dehorned as a conservation management practise, but few studies have evaluated whether the procedure has any behavioural effects. This study sought to document and describe horn-contingent behaviours during resource access, wallowing and rubbing in freeranging white rhinos and establish whether dehorning, also known as horn trimming, impacts on their frequency or function. Data were collected through camera trapping and field observations at two sites in South Africa. The results provide no evidence that dehorning is unlikely to have a strong biological impact on resource access. Furthermore, the frequency of horn-rubbing behaviours did not appear to be influenced by levels of horn growth. This suggests the procedure has a limited impact on these aspects of the species' ecology and provides support that dehorning can be employed as a management tool to reduce poaching in freeranging populations of white rhino.

Keywords

Behaviour; camera trapping; dehorning; geophagy; poaching; rhino; South Africa; wildlife management

Introduction

High poaching rates of African rhinoceros species are beginning to reduce the gains in population growth made over the last few decades (Ferreira et al., 2018), with

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4.6% of Africa's rhino population lost to poaching in 2017 (Knight, 2019). This has been driven by high demand for African rhino horn in Asian markets where it supplants the horn available from the rarer Asian rhino species (Vigne & Martin, 2018). In response to this crisis, private and state reserves in southern Africa are increasingly trimming the horns of their rhinos (a procedure referred to as dehorning from here on) in an attempt to reduce the chance of poaching (Rubino & Pienaar, 2018; Knight, 2019). The dehorning procedure removes most of a rhino's horn mass and is usually repeated after an interval of 12-24 months of regrowth, depending on poaching risk (Lindsey & Taylor, 2011).

Rhinos use their horns in intraspecific social interactions during courtship and combat, but also during play behaviour and cohesive contact (Owen-Smith, 1973). Rhinos also regularly rub their horns against objects such as rocks and trees (Pienaar et al., 1991) which may help to maintain its tapered shape (Hieronymus & Witmer, 2004). Horns are also used to access resources (Owen-Smith & Danckwerts, 1997) and in interspecific defence (Sillero-Zubiri & Gottelli, 1991). Although no research has been published on whether horn size asymmetries affect comfort behaviours or resource access, several studies have investigated its effects in social, reproductive, and predation contexts (e.g., Berger et al., 1993; Berger & Cunningham, 1998; Kretzschmar et al., 2020).

In black rhinos, horn size asymmetries were reported as a predictor of dominance during some agonistic confrontations between horned individuals (Berger & Cunningham, 1998). In contrast, du Toit & Anderson (2013) reported that the dehorning of black rhinos did not affect the spatial locations of monitored individuals, finding no evidence of increased displacement. Recent research into the effects of dehorning in white rhinos found no evidence that the procedure influenced the duration of intercalf intervals or caused a long-term physiological stress response (Penny et al., 2020a, b). However, findings by Kretzschmar et al. (2020) on the indicators of reproductive success in horned white rhinos were contradictory, identifying a strong positive correlation between horn size and the number of calves sired in one group of males but a negative correlation within another.

Berger et al. (1993) investigated the effects of dehorning on calf survivorship in black rhinos and suggested that the higher mortality rates observed were due to increased hyena predation. However, Lindique & Erb (1996) proposed other factors such as drought as an alternative explanation, and du Toit & Anderson (2013) reported no differences in black rhino calf mortality rates before and after dehorning. No studies have investigated the effects of dehorning on white-rhino predation, but given the rarity of such predation events (Owen-Smith, 2013), it is unlikely to have a major impact on their survival.

The Sumatran (*Dicerohinus sumatrensis*) and black (*Diceros bicornis*) rhino utilise their horns to pull down branches and break stems to facilitate browsing (Van Strien, 1985; Owen-Smith & Danckwerts, 1997). In contrast, there are no reports of white rhinos using their horns as a foraging tool, which is likely a result of them being short-grass grazers (Shrader et al., 2006). There are no accounts of any rhino

species using their horns to dig for water, although black rhinos have been observed using their forelimbs to dig holes during dry environmental conditions (Ritchie, 1963). Both Sumatran and black rhinos exhibit geophagous behaviour, using their horns to break up earth and soft rocks at salt licks (Ritchie, 1963; Borner, 1979). Furthermore, a black rhino was observed digging with its horn prior to placing its mouth in mud in an apparent attempt to relieve buccal irritation following consumption of a toxic plant (Naudé et al., 1997).

Rhinos also dig with their horns during wallowing behaviours (Wilson et al., 2020) which act to protect the skin from parasites and aid in thermoregulation on hot days (Metrione & Eyres, 2014). However, unlike the horns of several tropical bovid species (Picard et al., 1999), rhino horns have no thermoregulatory function as they are made of keratin and lack a vascularised bony core (Boy et al., 2015). Prior to wallowing, Sumatran rhinos dig soil from the banks of pits with their horns and feet, a practise that likely acts to thicken the consistency of the mud (Van Strien, 1985). White rhinos have been observed both pushing their horns into mud before wallowing and deliberately ingesting soil (Owen-Smith, 1973). Thus if dehorning disrupts the ability of white rhinos to dig it could affect their access to some minerals or affect wallowing behaviours.

Rhinos often rub their bodies against objects such as dead wood, rocks and trees to aid in the removal of parasites and dead skin, particularly after wallowing (Owen-Smith, 1973). All rhino species also regularly rub their horns against objects (Laurie, 1978; Van Strien, 1985; Pienaar et al., 1991; Hariyadi et al., 2010) with the resultant lateral and anterior wear potentially contributing towards its tapered shape (Hieronymus & Witmer, 2004). The functional significance of horn rubbing may extend beyond the maintenance of horn shape if rhinos select trees to ingest resin to satisfy a nutritional or medicinal need, or to convey information through scent deposition (Rachlow, 2001). For example, white rhinos have been observed rubbing their horns for longer periods against paperbark trees (*Commiphora marlothii*) than on other tree species; with Rachlow (2001) reporting how 30% of the *Commiphora* trees within a fenced reserve showed signs of rhino-induced debarking.

The frequencies of horn-rubbing behaviours can vary between individuals but are assumed to remain near constant throughout an adult rhino's life (Pienaar et al., 1991). For adult white rhinos, the rate of horn growth decreases with age (Rachlow & Berger, 1997), and thus the horns of some of the oldest individuals may decrease in size if the rate of rubbing exceeds the horn's intrinsic growth rate (Pienaar et al., 1991). Reports suggest that adult male white rhinos rub their horns more frequently than females (Pienaar et al., 1991). Observations of immobilised rhinos in Kruger National Park indicated that the horn bases of adult males were often smoother than the horn bases of females, which were more frayed and fibrous (Pienaar et al., 1991). In subadults (<8 years old) the difference in smoothness was not so defined, indicating higher rates of rubbing in adult male rhinos over females. Additionally, Pienaar & Hall-Martin (1991) observed differential rates of wear in horns implanted with transmitters, further suggesting that males rub their horns more frequently than females.

For dehorned rhinos, Pienaar et al. (1991) noted that the horns of both African rhino species appear to grow back faster in the first year after horn loss. Faster rates of growth were also observed in dehorned populations than horned populations with lower rates of wear reported on the dorsal surfaces of regrown horn stubs than in horned rhinos (Rachlow & Berger, 1997). Recent work by Ververs (2018) failed to conclude whether the number of dehorning events or age of a rhino at first dehorning influenced horn regrowth rates because older animals, which experience lower growth rates than younger individuals, had experienced more dehorning events. Thus, the faster increase in horn size observed in some populations of dehorned rhinos could be explained if dehorned animals show lower rates of horn rubbing than animals with intact horns.

Given the paucity of research on nonsocial horn use in rhinos, this study sought to document and describe horn-contingent behaviours during resource access, wallowing and rubbing behaviour in freeranging white rhinos and establish whether dehorning impacts on their frequency or function. This included investigating whether horn-digging behaviours occurred during geophagy or wallowing and if the frequency of horn-rubbing behaviours changed relative to levels of horn growth. Rhinos that had recently been dehorned were predicted to show fewer horn-digging behaviours than horned rhinos. Horn rubbing was predicted to be lower after dehorning when horn mass was at its lowest and males were predicted to rub their horns more than in females.

Methods

Study area

Behavioural observations of white rhinos took place between October 24, 2015 and November 15, 2017 at two field sites in Northwest Province, South Africa. Given the current rhino poaching situation in South Africa (Knight, 2019), the names of field site locations have been anonymised for security reasons, following African Rhino Specialist Group protocol. Both sites are fenced and managed for conservation and ecotourism; Site A covers an area of 4932 ha and Site B covers an area of 48 029 ha. The sites fall within the Central Bushveld Bioregion and consist of broad-leaved deciduous bushveld, with a mosaic of pediment grassland, thicket and woodland (Mucina et al., 2006). Rhinos were not supplementary fed but had access to artificial mineral licks and water sources. Site A had a population of 17 white rhinos and practises dehorning as an anti-poaching technique while Site B had a population of around 300 white rhinos and did not dehorn at the time of the study. The population at Site A was dehorned every 12 to 24 months. Ethical approval for this study was granted by the Animal Welfare and Ethics Review Board of the University of Brighton (REF: 2018-1127).

Table 1.

Behaviours of interest that were recorded by all occurrence sampling during field observations and from camera trap footage.

Behaviour	Definition
Geophagy	Active ingestion of earth or rock
Wallowing	Rolling or lying in mud
Limb digging	Repetitive movement of earth by the feet or limbs
Horn digging	Repetitive movement of earth by the horn
Body rubbing	Repetitive movement of the body against an object
Horn rubbing	Repetitive movement of the horn against an object

Behavioural data collection

Collection of data pertaining to behaviours of interest (table 1) used a combination of field observations and camera trapping. These were recorded using all occurrence sampling. No camera trapping occurred at Site B as logistical constraints precluded searching for and revisiting locations. Convenience sampling was utilised to locate animals for field observations, whereby haphazard routes were driven or walked until a rhino or group of rhinos was encountered. This approach relies on the assumption that the spontaneously followed search technique selected individuals from a homogeneous target population and did not give subjects an unequal chance of selection (Etikan et al., 2016). Rhinos were identified via their unique ear notch pattern or, in the case of calves, by that of their mother. Rhinos were 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 (Owen-Smith, 1973). Field observations ended when rhinos lay down to rest (for more than 60 minutes), were lost from sight or obscured from view (for more than 15 minutes), or it was too dark to identify them. Field observations totalled 288:40 h at Site A (mean $1:26 \pm 1:12$ SD, n = 201 sessions) and 73:38 h at Site B (mean 45:05 \pm 42:31 SD, n = 98 sessions). Behavioural observations focused on all rhinos in a group on arrival, which numbered between one and nine rhinos per observation session. In total, 16 individual rhinos were observed at Site A (within 15–63 observation sessions each) and 178 individual rhinos at Site B (within 1–5 observation sessions each). Information on age-sex classes and mean duration of observations per rhino can be found in supplementary table S1.

Camera traps [either Bushnell Trophy Cam (Essential and Aggressor) or Ltl Acorn (5610WA) models] were placed at salt licks, mud wallows and rubbing posts that showed recent signs of rhino activity (table 2). Cameras were attached to trees around 1.5 metres high and 5–10 metres away from the focal point. Camera traps were set to operate over a 24-h period with video recordings triggered by passive infrared sensors. Behaviours could be observed throughout the day and night as the cameras emitted 'low glow' (850 nm) or 'no glow' (940 nm) infrared light in

Table 2.

Number of locations, sessions and lengths of operating periods for camera traps placed at rubbing posts, mud wallows and salt licks at Site A.

Feature	eature Location ID		Total period (H:M)	Average period (H:M)	
Rubbing post	1	4	520:38	130:09	
01	2	2	600:44	300:22	
	3	10	1177:05	117:42	
	4	5	926:26	185:17	
	5	1	70:28	70:28	
	6	1	118:36	118:36	
	7	3	311:09	103:43	
	8	5	476:48	95:22	
	9	5	485:49	97:10	
	Total	36	4687:43	130:13	
Salt lick	10	4	346:56	86:44	
	11	2	178:05	89:02	
	Total	6	567:33	81:04	
Mud wallow	12	1	128:38	128:38	
Mud wanow	13	2	469:06	234:33	
	14	2	213:05	106:32	
	15	7	674:07	96:18	
	16	2	260:27	130:13	
	17	4	500:50	125:12	
	18	1	62:12	62:12	
	19	2	144:04	72:02	
	20	7	602:02	86:00	
	21	2	252:04	126:02	
	Total	30	3306:35	110:13	

Traps that failed to record were excluded from the totals, as were periods for which the feature became obscured (e.g., due to animal interference).

low-light conditions. Videos were recorded for 30 s and were separated by intervals of 10 s between triggers to enable near-continuous observations of behaviour. The operating period of each camera was calculated by subtracting the time and date of the last recorded video from the time and date of camera setup.

All acts of geophagy and wallowing were monitored for limb- and horn-digging behaviours. In geophagy, soil intake is usually selective (Abrahams, 2013) but no examples of natural salt licks could be located. Therefore, cameras were placed at two artificial salt blocks on six occasions to establish their usage by rhinos. Cameras were also placed at 10 mud-filled depressions on 30 occasions. Cameras at the salt blocks operated for 567:33 h (table 2) and had an average operational period of 81:04 (SD \pm 42.32 h; n = 6). Cameras at the mud wallows operated for 3306:35 h (table 2) and had an average operational period of 110:13 (SD \pm 49.55 h; n = 30). Rubbing posts were identified as tree stumps, trunks and branches with evidence of wear between 0.5 m and 1 m high along trails frequented by rhinos. Cameras

were placed at nine rubbing posts on 36 occasions. Cameras operated for 4687:43 h (table 2) and had an average operational period of 130:13 (SD \pm 4.01 h; n = 36).

Data analysis

For horn digging, no statistical analyses were undertaken on its frequency of occurrence either within or between the populations due to its rarity of observation. Instead, these data are presented descriptively. For horn rubbing, statistical analysis was conducted on data collected during camera trapping at Site A but not on data collected during field observations, again due to the latter's rarity of observation. Data were only included in statistical analyses if the rhino could be identified (supplementary table S2). All analyses were two-tailed with alpha levels set at 0.05. Generalised linear mixed models (GLMMs) with Laplace approximation were fit using the *lme4* package in R (version 3.5.1; R Core Team, 2018). The marginal R^2 value, which represents the variance explained by the fixed variables, and the conditional R^2 value, which represents the variance explained by the entire model, were calculated using the delta method in the *MuMIn* package (Johnson, 2014).

The multitude of potential rubbing posts across Site A prevented their monitoring in totality. Thus, it was not possible to determine how true rates of horn rubbing were affected by dehorning, as monitored changes in rubbing rates over time may have represented changes in the frequencies of post visitation. Instead, the first analysis looked at changes in the likelihood of horn rubbing when a rhino visited a post. A visit was defined as engagement in either body rubbing and/or horn rubbing by a rhino at a post. Discontinuous horn and/or body rubbing behaviours separated by a pause of less than 15 minutes were considered part of the same visit. Likewise, discontinuous rubbing behaviour separated by a pause greater than 15 minutes was counted as separate visits. Thus, the dataset consisted of counts of the presence or absence of horn-rubbing behaviour at posts during visits (the dependent variable) and totalled 80 observations from 15 individuals. A GLMM was fit with a binomial distribution and logit link function with the amount of horn growth at the time of rubbing and rhino sex included as fixed effects. The amount of horn growth was measured as either the number of days since a rhino's last dehorning or the number of days since birth, whichever was most recent. Rhino identity was included as a random effect to account for the repeated-measures design. Amount of horn growth was centred and scaled.

The second analysis investigated whether the duration of horn-rubbing behaviours (the dependent variable) was influenced by the amount of horn growth a rhino had at the time of rubbing. Discontinuous horn-rubbing behaviours were summed to create a single total if there was a pause of less than 15 minutes between them. The dataset consisted of 25 observations from nine individuals. A GLMM was set up with a Gaussian distribution and log link function with the amount of horn growth at the time of rubbing included as a fixed effect and rhino identity included as a random effect. Amount of horn growth was centred and scaled.

Results

No instances of horn digging were observed during geophagy in either horned rhinos at Site B (during 73:38 h of field observations) or dehorned rhinos at Site A (during the 567 h of camera trapping at salt licks or 288:40 h of field observations). However, two rhinos exhibited limb digging during the four instances of geophagy recorded from horned rhinos. In the first field observation, two horned adult males ingested dirt from a low earthen bank (Male 1 for 470 s; Male 2 for 330 s). To loosen the earth, the males dug with their feet but neither used their horns (the first male dug for 6 to 13 s on seven occasions; the second male for 10 s on one occasion). During digging, the animals lowered their heads and touched their anterior horns to the ground but their horns did not break the soil (fig. 1A). In the second field observation of geophagy, a horned adult female and her calf ingested dirt from an area of flattish ground without demonstrating limb- or horn-based digging behaviours. During the six instances of geophagy recorded from dehorned rhinos (five during a field observation and one during camera trapping) neither horn nor limb digging was observed. In the one field observation, a group of five dehorned subadult rhinos ingested dirt for up to 20 min each. The five rhinos directed aggressive behaviours towards one another throughout consumption, but no horn- or limb-based digging occurred. During camera trapping, a dehorned adult female ingested minerals from an artificial block without digging. In addition to this, two dehorned rhinos were recorded approaching and then sniffing a mineral block but did not engage in geophagy.

One instance of horn digging during wallowing behaviour was recorded from a horned rhino at Site B and seven instances from dehorned rhinos at Site A (six during field observations and one during camera trapping). In the field observations of horned rhinos (73:38 h), an adult male dug the frontal base of its anterior horn into the ground (for 61 s; fig. 1B) and a forelimb (for 8 s) before wallowing in the freshly churned mud (for 533 s). After wallowing, the rhino rubbed its anterior horn on a nearby branch until all large clods of mud had been dislodged. In the field observations of dehorned rhinos (288:40 h), a group of five subadult rhinos dug their anterior horns into a mud-filled depression (for up to 10 s each) with one rhino also digging with a forelimb (fig. 1C). The rhinos had 541 to 548 days of horn growth at the time of the observation. Immediately after digging, two of the rhinos wallowed (for 70 s) but all five rhinos then left to follow a sixth rhino that had not stopped at the depression. In the second observation, a dehorned adult male dug its anterior horn into mud (for 5 s) during 15 min of wallowing. The rhino had been dehorned recently and had just 10 days of horn growth. During the 3306 h of camera trapping (approx. 138 days) at mud wallows, rhinos were observed wallowing on 20 occasions, however only one of these included horn-digging behaviour. In this case, a 12-month-old calf stood during wallowing to dig its anterior horn into the mud (for 10 s) then lay down again. The individual had been dehorned 42 days prior to the observation.



Figure 1. Examples of digging behaviour in white rhinos recorded during the study: (A) A horned white rhino digs with a forelimb while pressing its horn to the ground to loosen earth before ingestion; (B) a horned rhino digs with its horn before wallowing in mud; (C) five dehorned rhinos with fresh earth on their horns after digging in a muddy depression.

Two instances of horn rubbing were detected from horned rhinos during field observations at Site B (73:38) and 31 instances from dehorned rhinos at Site A (four during 288:40 h of field observations and 27 during 4687 h of camera trapping at rubbing posts). In all cases, rhinos rubbed their horns against wooden branches, trunks and stumps (fig. 2A, B). During the camera trapping at Site A, rhinos visited all nine of the monitored rubbing posts. Rhinos visited the posts on 87 occasions (where either body or horn rubbing occurred; calculated from 307 records of rhinos in 267 camera trap videos). The most common time for using rubbing posts was between 14:00 and 16:00 h (34.9% of 307 records) and the least common time was between 04:00 and 6:00 h (0.3% of 307 records; fig. 3A). Rhinos were observed horn rubbing during 27 of the 87 post visits but individual identities could only be established in 80 of these (from 15 different individuals). Of these identified individuals, five were female and ten were male, with between 1 and 11 visits observed per animal. The first horn rubbing was observed two days after dehorning and the last instance 702 days after the procedure.

The frequency of horn rubbing during post visits at Site A was not significantly affected by the number of days of uninterrupted horn growth (table 3; fig. 3B). There was also no significant difference between male and female frequency of horn rubbing during post visits (table 3). Furthermore, the interaction between sex and the level of horn growth did not have a differential impact on horn-rubbing frequency (table 3). Additionally, the number of days of horn growth did not explain the duration that rhinos rubbed their horns for (table 3; fig. 3C).

Rhinos were also observed rubbing their mouths against, licking and apparently smelling the surfaces of posts. For example, a dehorned adult male was recorded intermittently licking the sap from the tilted trunk of a Sweet thorn (*Vachellia karroo*) tree and rubbing its body against it. Additionally, a horned calf was detected licking a polished wooden stump for over a minute that had no sap residue (fig. 2C). During and after nuzzling the stump, the calf lifted its head and exhibited the flehmen response, before proceeding to rub its body and horn. Both the licked branch and polished stump showed evidence of regular wear and were observed being rubbed on by other rhinos on several other occasions.

Discussion

The apparent absence of horn-contingent geophagy, coupled with observations of horned rhinos digging earth with their feet and the use of artificial mineral licks without digging, suggests that dehorning is unlikely to have a strong biological impact on white-rhino resource access. However, the absence of a detection does not exclude the existence of horn-contingent geophagy occurring in other contexts or confirm whether dehorning has the potential to disrupt it as a behaviour. The usage of artificial mineral licks suggests the animals were ingesting salts to satisfy a mineral deficiency, rather than consuming grit to aid digestion (Wings & Sander, 2007) or to neutralise toxins from clays (Brightsmith et al., 2008). There are few



Figure 2. Horn rubbing and licking behaviours at rubbing posts. (A) A horned rhino rubs its anterior horn against a stump; (B) a dehorned rhino rubs its anterior horn against a tree trunk; (C) a horned calf nuzzles a rubbing post before horn rubbing. The individuals also rubbed their heads and bodies against the rubbing posts.



Figure 3. Rhino rubbing behaviour recorded during camera trapping. (A) Breakdown of time spent horn or body rubbing where bars represent the proportion of records that occurred within each period (n = 307 records). (B) Change in conditional probability of horn rubbing against days of uninterrupted horn growth (obs. = 80, n = 15). (C) Duration of horn-rubbing behaviours against days of uninterrupted horn growth (obs. = 25, n = 9).

instances of freeranging white rhinos engaging in geophagy described in the literature, but the records reported here differ from those described by Owen-Smith (1973), where calves in Hluhluwe–Imfolozi Park were occasionally seen nibbling at and ingesting soil around termite mounds, but adult rhinos were not observed engaging in geophagy at all. Differences between populations may relate to how underlying soil geomorphologies contribute towards plant mineral concentrations (McNaughton, 1988), with rhinos in some habitats apparently able to satisfy their dietary requirements from food or water without the need to ingest soil (Owen-Smith, 1973). This can be seen in areas of the Serengeti, where high densities of

	Dependent	Fixed effects	Coefficient	Standard error	Test statistic	Р	R^2m	R^2c
1	Frequency of	Horn growth	0.099	0.464	0.214	0.830	_	_
	horn rubbing	Sex	-0.943	0.873	-1.080	0 280	_	_
		Interaction	-0.751	0.647	-1.161	0.246	-	_
		-	-	_	-	-	5.8%	18.7%
2	Duration of	Horn growth	-0.096	0.175	0.549	0.583	-	-
	horn rubbing	_	-	_	-	-	< 0.001%	31.4%

GLMM outputs showing the relationship between horn rubbing and horn growth.

Table 3.

Abbreviations: R^2m , marginal R^2 (variation in the dependent variable explained by the fixed effects); R^2c , conditional R^2 (variation in the dependent variable explained by the fixed and random effects); 1, analysis of frequency of horn rubbing (test statistic = z; N = 15, obs. = 80); 2, analysis of duration of horn rubbing (test statistic = t; N = 9, obs. = 25).

grazers survive without the need of salts licks because the mineral-rich grasses are nutritionally sufficient (McNaughton, 1988).

Dehorning did not prevent rhinos using their horns to dig at wallows, with both horned and dehorned rhinos observed engaging in this behaviour, while also using their feet. However, the infrequent observance of horn digging throughout the study prevented investigation into whether dehorning affected the frequency of hornbased digging. Digging at wallows may have been more common than observed (at just 5% of camera-trapped wallowing events), as the large size of some wallows and the placement of rhinos relative to the camera meant that clear observations were not always possible. Additionally, cameras were not out permanently and many locations were not monitored. Records of digging behaviour may also have been missed during field observations as sightlines were frequently obscured when rhinos wallowed in low depressions or in dense thickets. Given that rhinos dug for periods after wallowing had already commenced, it seems likely that the behaviour acts to improve the consistency of the mud, as suggested by Van Strien (1985) rather than simply as a test of whether or not the mud is suitable for wallowing as suggested by Owen-Smith (1973).

The amount of horn growth had no detectable effect on horn-rubbing frequency or duration and horn rubbing was observed just two days after a dehorning procedure. The hypothesis that increased horn growth rates after dehorning could be explained by a decrease in horn-rubbing frequency was therefore not supported. Interestingly, if horn-rubbing durations from the first 200 days of uninterrupted horn growth are considered only, then a positive trend can be observed in the data. This apparent steep increase may indicate that a time-limited effect on horn-rubbing duration exists but further study is needed to confirm this. There was no evidence that male rhinos rubbed their horns more frequently than females as suggested elsewhere (Pienaar & Hall-Martin, 1991). However, sampling constraints prevented the inclusion of age as an explanatory factor so it remains possible that sex differences may only be apparent between adult individuals. Investigative sniffing and mouthing behaviours indicated rhinos were aware of previous users and that rubbing posts play some role in olfactory communication as suggested by Rachlow (2001). Additionally, apparent ingestion of tree sap shows there may be some nutritional basis for the selection of certain rubbing locations. Future research could identify whether rhinos rub on a preferred species of tree.

Recent analysis by Derkley et al. (2019) suggests that the fitness costs of physiological and psychological distress experienced during dehorning by the immobilisation process, such as hypertension, hyperthermia and acidosis, will always be substantially lower than that experienced by a poached animal (which usually ends in death). This study provides further support that the procedure can be pursued as a conservation technique to manage poaching. This research should aid conservation managers in understanding the biological implications of dehorning and ensure future decisions consider behavioural impacts when evaluating conservation outcomes. However, further research is still needed into the implications of dehorning on predator defence, social behaviour and long-term fitness. Investigations into whether dehorning influences horn utilisation in black rhinos would also be of conservation interest given their Critically Endangered status and the usage of their horns during browsing (Owen-Smith & Danckwerts, 1997; Knight, 2019).

Conclusion

Despite suggestions that dehorning may impact on non-social horn-based behaviours in rhinos (Lindsey & Taylor, 2011), no evidence was found that dehorned white rhinos were functionally constrained when engaging in digging or rubbing behaviours. The dehorned rhinos engaged in similar behaviours to those of horned rhinos reported elsewhere in the literature (Owen-Smith, 1973; Hutchins & Kreger, 2006). The infrequent observance of horn use in both horned and dehorned populations shows that the social function of horns during agonistic encounters or predator defence are likely to be a more important consideration when planning management strategies for their conservation.

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Supplementary material

Supplementary material is available online at: https://doi.org/10.6084/m9.figshare.14074256

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