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

7

8 **Samuel G. Penny^{1*}, Rachel L. White¹, Dawn M. Scott², Lynne MacTavish^{1,3}**
9 **& Angelo P. Pernetta¹**

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11 ¹ Ecology, Conservation and Zoonosis Research and Enterprise Group, School of Pharmacy
12 and Biomolecular Sciences, University of Brighton, Brighton, BN2 4GJ, United Kingdom

13 ² School of Life Sciences, Keele University, Keele, Staffordshire ST5 5BG, United Kingdom

14 ³ Rustenburg, Northwest Province, South Africa

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19 *) Corresponding author; e-mail: S.Penny2@brighton.ac.uk

20

21 **Abstract**

22 Rhino species use their horns in social interactions but also when accessing resources, rubbing and in interspecific
23 defence. The current poaching crisis has seen southern white rhinos (*Ceratotherium simum simum*) increasingly
24 dehorned as a conservation management practise, but few studies have evaluated whether the procedure has any

25 behavioural effects. This study sought to document and describe horn-contingent behaviours during resource
26 access, wallowing and rubbing in freeranging white rhinos and establish whether dehorning, also known as horn
27 trimming, impacts on their frequency or function. Data were collected through camera trapping and field
28 observations at two sites in South Africa. The results provide no evidence that dehorning disrupts digging
29 behaviours during mineral consumption or wallowing and suggests that dehorning is unlikely to have a strong
30 biological impact on resource access. Furthermore, the frequency of horn-rubbing behaviours did not appear to
31 be influenced by levels of horn growth. This suggests the procedure has a limited impact on these aspects of the
32 species' ecology and provides support that dehorning can be employed as a management tool to reduce poaching
33 in freeranging populations of white rhino.

34

35 **Keywords**

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

37 **Introduction**

38

39 High poaching rates of African rhinoceros species are beginning to reduce the gains in
40 population growth made over the last few decades (Ferreira et al., 2018), with 4.6% of Africa's
41 rhino population lost to poaching in 2017 (Knight, 2019). This has been driven by high demand
42 for African rhino horn in Asian markets where it supplants the horn available from the rarer
43 Asian rhino species (Vigne & Martin, 2018). In response to this crisis, private and state reserves
44 in southern Africa are increasingly trimming the horns of their rhinos (a procedure referred to
45 as dehorning from here on) in an attempt to reduce the chance of poaching (Rubino and Pienaar,
46 2018; Knight, 2019). The dehorning procedure removes most of a rhino's horn mass and is
47 usually repeated after an interval of 12–24 months of regrowth, depending on poaching risk
48 (Lindsey and Taylor, 2011).

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

58 In black rhinos, horn size asymmetries were reported as a predictor of dominance
59 during some agonistic confrontations between horned individuals (Berger and Cunningham,
60 1998). In contrast, du Toit and Anderson, (2013) reported that the dehorning of black rhinos
61 did not affect the spatial locations of monitored individuals, finding no evidence of increased

62 displacement. Recent research into the effects of dehorning in white rhinos found no evidence
63 that the procedure influenced the duration of intercalf intervals or caused a long-term
64 physiological stress response (Penny et al., 2020a, 2020b). However, findings by Kretzschmar
65 et al. (2020) on the indicators of reproductive success in horned white rhinos was contradictory,
66 identifying a strong positive correlation between horn size and the number of calves sired in
67 one group of males but a negative correlation within another.

68 Berger et al. (1993) investigated the effects of dehorning on calf survivorship in black
69 rhinos and suggested that the higher mortality rates observed were due to increased hyena
70 predation. However, Lindique and Erb (1996) proposed other factors such as drought as an
71 alternative explanation, and du Toit and Anderson (2013) reported no differences in black rhino
72 calf mortality rates before and after dehorning. No studies have investigated the effects of
73 dehorning on white-rhino predation, but given the rarity of such predation events (Owen-Smith,
74 2013), it is unlikely to have a major impact on their survival.

75 The Sumatran (*Dicerohinus sumatrensis*) and black (*Diceros bicornis*) rhino utilise
76 their horns to pull down branches and break stems to facilitate browsing (Van Strien, 1985;
77 Owen-Smith & Danckwerts, 1997). In contrast, there are no reports of white rhinos using their
78 horns as a foraging tool, which is likely a result of them being short-grass grazers (Shrader et
79 al., 2006). There are no accounts of any rhino species using their horns to dig for water,
80 although black rhinos have been observed using their forelimbs to dig holes during dry
81 environmental conditions (Ritchie, 1963). Both Sumatran and black rhinos exhibit geophagous
82 behaviour, using their horns to break up earth and soft rocks at salt licks (Ritchie, 1963; Borner,
83 1979). Furthermore, a black rhino was observed digging with its horn prior to placing its mouth
84 in mud in an apparent attempt to relieve buccal irritation following consumption of a toxic
85 plant (Naudé et al., 1997).

86 Rhinos also dig with their horns during wallowing behaviours (Wilson et al., 2020)
87 which act to protect the skin from parasites and aid in thermoregulation on hot days (Metrione
88 & Eyres, 2014). However, unlike the horns of several tropical bovid species (Picard et al.,
89 1999), rhino horns have no thermoregulatory function as they are made of keratin and lack a
90 vascularised bony core (Boy et al., 2015). Prior to wallowing, Sumatran rhinos dig soil from
91 the banks of pits with their horns and feet, a practise that likely acts to thicken the consistency
92 of the mud (Van Strien, 1985). White rhinos have been observed both pushing their horns into
93 mud before wallowing and deliberately ingesting soil (Owen-Smith, 1973). Thus if dehorning
94 disrupts the ability of white rhinos to dig it could affect their access to some minerals or affect
95 wallowing behaviours.

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

107 The frequencies of horn-rubbing behaviours can vary between individuals but are
108 assumed to remain near constant throughout an adult rhino's life (Pienaar et al., 1991). For
109 adult white rhinos, the rate of horn growth decreases with age (Rachlow & Berger, 1997), and
110 thus the horns of some of the oldest individuals may decrease in size if the rate of rubbing

111 exceeds the horn's intrinsic growth rate (Pienaar et al., 1991). Reports suggest that adult male
112 white rhinos rub their horns more frequently than females (Pienaar et al. 1991). Observations
113 of immobilised rhinos in Kruger National Park indicated that the horn bases of adult males
114 were often smoother than the horn bases of females, which were more frayed and fibrous
115 (Pienaar et al., 1991). In subadults (<8 years old) the difference in smoothness was not so
116 defined, indicating higher rates of rubbing in adult male rhinos over females. Additionally,
117 Pienaar and Hall-Martin (1991) observed differential rates of wear in horns implanted with
118 transmitters, further suggesting that males rub their horns more frequently than females.

119 For dehorned rhinos, Pienaar et al. (1991) noted that the horns of both African rhino
120 species appear to grow back faster in the first year after horn loss. Faster rates of growth were
121 also observed in dehorned populations than horned populations with lower rates of wear
122 reported on the dorsal surfaces of regrown horn stubs than in horned rhinos (Rachlow & Berger,
123 1997). Recent work by Ververs (2018) failed to conclude whether the number of dehorning
124 events or age of a rhino at first dehorning influenced horn regrowth rates because older animals,
125 which experience lower growth rates than younger individuals, had experienced more
126 dehorning events. Thus, the faster increase in horn size observed in some populations of
127 dehorned rhinos could be explained if dehorned animals show lower rates of horn rubbing than
128 animals with intact horns.

129 Given the paucity of research on nonsocial horn use in rhinos, this study sought to
130 document and describe horn-contingent behaviours during resource access, wallowing and
131 rubbing behaviour in freeranging white rhinos and establish whether dehorning impacts on
132 their frequency or function. This included investigating whether horn-digging behaviours
133 occurred during geophagy or wallowing and if the frequency of horn-rubbing behaviours
134 changed relative to levels of horn growth. Rhinos that had recently been dehorned were
135 predicted to show fewer horn-digging behaviours than horned rhinos. Horn rubbing was

136 predicted to be lower after dehorning when horn mass was at its lowest and males were
137 predicted to rub their horns more than in females.

138

139 **Methods**

140

141 *Study area*

142

143 Behavioural observations of white rhinos took place between October 24, 2015 and November
144 15, 2017 at two field sites in Northwest Province, South Africa. Given the current rhino
145 poaching situation in South Africa (Knight, 2019), the names of field site locations have been
146 anonymised for security reasons, following African Rhino Specialist Group protocol. Both
147 sites are fenced and managed for conservation and ecotourism; Site A covers an area of 4,932
148 ha and Site B covers an area of 48,029 ha. The sites fall within the Central Bushveld Bioregion
149 and consist of broad-leaved deciduous bushveld, with a mosaic of pediment grassland, thicket
150 and woodland (Mucina et al., 2006). Rhinos were not supplementary fed but had access to
151 artificial mineral licks and water sources. Site A had a population of 17 white rhinos and
152 practises dehorning as an anti-poaching technique while Site B had a population of around 300
153 white rhinos and did not dehorn at the time of the study. The population at Site A was dehorned
154 every 12 to 24 months. Ethical approval for this study was granted by the Animal Welfare and
155 Ethics Review Board of the University of Brighton (REF: 2018-1127).

156

157 *Behavioural data collection*

158

159 Collection of data pertaining to behaviours of interest (table 1) used a combination of field
160 observations and camera trapping. These were recorded using all occurrence sampling. No

161 camera trapping occurred at Site B as logistical constraints precluded searching for and
162 revisiting locations. Convenience sampling was utilised to locate animals for field
163 observations, whereby haphazard routes were driven or walked until a rhino or group of rhinos
164 was encountered. This approach relies on the assumption that the spontaneously followed
165 search technique selected individuals from a homogeneous target population and did not give
166 subjects an unequal chance of selection (Etikan et al., 2016). Rhinos were identified via their
167 unique ear notch pattern or, in the case of calves, by that of their mother. Rhinos were classed
168 as subadults from maternal independence until they reached socio-sexual maturity. This is
169 when males become solitary and/or territorial at 10 to 12 years old and at around 7 years old in
170 females after the birth of their first calf (Owen-Smith, 1973). Field observations ended when
171 rhinos lay down to rest (for more than 60 minutes), were lost from sight or obscured from view
172 (for more than 15 minutes), or it was too dark to identify them. Field observations totalled
173 288:40 h at Site A (mean 1:26 \pm 1:12 SD, n = 201 sessions) and 73:38 h at Site B (mean 45:05
174 \pm 42:31 SD, n = 98 sessions). Behavioural observations focused on all rhinos in a group on
175 arrival, which numbered between one and nine rhinos per observation session. In total, 16
176 individual rhinos were observed at Site A (within 15–63 observation sessions each) and 178
177 individual rhinos at Site B (within 1–5 observation sessions each). Information on age–sex
178 classes and mean duration of observations per rhino can be found in table S1.

179 Camera traps [either Bushnell Trophy Cam (Essential and Aggressor) or Ltl Acorn
180 (5610WA) models] were placed at salt licks, mud wallows and rubbing posts that showed
181 recent signs of rhino activity (table 2). Cameras were attached to trees around 1.5 metres high
182 and 5–10 metres away from the focal point. Camera traps were set to operate over a 24-h period
183 with video recordings triggered by passive infrared sensors. Behaviours could be observed
184 throughout the day and night as the cameras emitted ‘low glow’ (850 nm) or ‘no glow’ (940
185 nm) infrared light in low-light conditions. Videos were recorded for 30 s and were separated

186 by intervals of 10 s between triggers to enable near-continuous observations of behaviour. The
187 operating period of each camera was calculated by subtracting the time and date of the last
188 recorded video from the time and date of camera setup.

189 All acts of geophagy and wallowing were monitored for limb- and horn-digging
190 behaviours. In geophagy, soil intake is usually selective (Abrahams, 2013) but no examples of
191 natural salt licks could be located. Therefore, cameras were placed at two artificial salt blocks
192 on six occasions to establish their usage by rhinos. Cameras were also placed at 10 mud-filled
193 depressions on 30 occasions. Cameras at the salt blocks operated for 567:33 h (table 2) and had
194 an average operational period of 81:04 ($SD \pm 42.32$ h; $n = 6$). Cameras at the mud wallows
195 operated for 3306:35 h (table 2) and had an average operational period of 110:13 ($SD \pm 49.55$
196 h; $n = 30$). Rubbing posts were identified as tree stumps, trunks and branches with evidence of
197 wear between 0.5 m and 1 m high along trails frequented by rhinos. Cameras were placed at
198 nine rubbing posts on 36 occasions. Cameras operated for 4687:43 h (table 2) and had an
199 average operational period of 130:13 ($SD \pm 4.01$ h; $n = 36$).

200

201 *Data analysis*

202

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

211 the variance explained by the fixed variables, and the conditional R^2 value, which represents
212 the variance explained by the entire model, were calculated using the delta method in the
213 *MuMIn* package (Johnson, 2014).

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

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

235 with the amount of horn growth at the time of rubbing included as a fixed effect and rhino
236 identity included as a random effect. Amount of horn growth was centred and scaled.

237

238 **Results**

239

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

258 One instance of horn digging during wallowing behaviour was recorded from a horned
259 rhino at Site B and seven instances from dehorned rhinos at Site A (six during field observations

260 and one during camera trapping). In the field observations of horned rhinos (73:38 h), an adult
261 male dug the frontal base of its anterior horn into the ground (for 61 s; fig. 1B) and a forelimb
262 (for 8 s) before wallowing in the freshly churned mud (for 533 s). After wallowing, the rhino
263 rubbed its anterior horn on a nearby branch until all large clods of mud had been dislodged. In
264 the field observations of dehorned rhinos (288:40 h), a group of five subadult rhinos dug their
265 anterior horns into a mud-filled depression (for up to 10 s each) with one rhino also digging
266 with a forelimb (fig. 1C). The rhinos had 541 to 548 days of horn growth at the time of the
267 observation. Immediately after digging, two of the rhinos wallowed (for 70 s) but all five rhinos
268 then left to follow a sixth rhino that had not stopped at the depression. In the second
269 observation, a dehorned adult male dug its anterior horn into mud (for 5 s) during 15 min of
270 wallowing. The rhino had been dehorned recently and had just 10 days of horn growth. During
271 the 3,306 h of camera trapping (approx. 138 days) at mud wallows, rhinos were observed
272 wallowing on 20 occasions, however only one of these included horn-digging behaviour. In
273 this case, a 12-month-old calf stood during wallowing to dig its anterior horn into the mud (for
274 10 s) then lay down again. The individual had been dehorned 42 days prior to the observation.

275 Two instances of horn rubbing were detected from horned rhinos during field
276 observations at Site B (73:38) and 31 instances from dehorned rhinos at Site A (four during
277 288:40 h of field observations and 27 during 4,687 h of camera trapping at rubbing posts). In
278 all cases, rhinos rubbed their horns against wooden branches, trunks and stumps (fig. 2A, B).
279 During the camera trapping at Site A, rhinos visited all nine of the monitored rubbing posts.
280 Rhinos visited the posts on 87 occasions (where either body or horn rubbing occurred;
281 calculated from 307 records of rhinos in 267 camera trap videos). The most common time for
282 using rubbing posts was between 14:00 and 16:00 h (34.9% of 307 records) and the least
283 common time was between 04:00 and 6:00 h (0.3% of 307 records; fig. 3a). Rhinos were
284 observed horn rubbing during 27 of the 87 post visits but individual identities could only be

285 established in 80 of these (from 15 different individuals). Of these identified individuals, five
286 were female and ten were male, with between 1 and 11 visits observed per animal. The first
287 horn rubbing was observed two days after dehorning and the last instance 702 days after the
288 procedure.

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

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

303

304 **Discussion**

305

306 The apparent absence of horn-contingent geophagy, coupled with observations of horned
307 rhinos digging earth with their feet and the use of artificial mineral licks without digging,
308 suggests that dehorning is unlikely to have a strong biological impact on white-rhino resource
309 access. However, the absence of a detection does not exclude the existence of horn-contingent

310 geophagy occurring in other contexts or confirm whether dehorning has the potential to disrupt
311 it as a behaviour. The usage of artificial mineral licks suggests the animals were ingesting salts
312 to satisfy a mineral deficiency, rather than consuming grit to aid digestion (Wings & Sander,
313 2007) or to neutralise toxins from clays (Brightsmith et al., 2008). There are few instances of
314 freeranging white rhinos engaging in geophagy described in the literature, but the records
315 reported here differ from those described by Owen-Smith (1973), where calves in Hluhluwe–
316 Imfolozi Park were occasionally seen nibbling at and ingesting soil around termite mounds,
317 but adult rhinos were not observed engaging in geophagy at all. Differences between
318 populations may relate to how underlying soil geomorphologies contribute towards plant
319 mineral concentrations (McNaughton, 1988), with rhinos in some habitats apparently able to
320 satisfy their dietary requirements from food or water without the need to ingest soil (Owen-
321 Smith, 1973). This can be seen in areas of the Serengeti, where high densities of grazers survive
322 without the need of salts licks because the mineral-rich grasses are nutritionally sufficient
323 (McNaughton, 1988).

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

335 suggested by Van Strien (1985) rather than simply as a test of whether or not the mud is suitable
336 for wallowing as suggested by Owen-Smith (1973).

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

352 Recent analysis by Derkley et al. (2019) suggests that the fitness costs of physiological
353 and psychological distress experienced during dehorning by the immobilisation process, such
354 as hypertension, hyperthermia and acidosis, will always be substantially lower than that
355 experienced by a poached animal (which usually ends in death). This study provides further
356 support that the procedure can be pursued as a conservation technique to manage poaching.
357 This research should aid conservation managers in understanding the biological implications
358 of dehorning and ensure future decisions consider behavioural impacts when evaluating
359 conservation outcomes. However, further research is still needed into the implications of

360 dehorning on predator defence, social behaviour and long-term fitness. Investigations into
361 whether dehorning influences horn utilisation in black rhinos would also be of conservation
362 interest given their Critically Endangered status and the usage of their horns during browsing
363 (Owen-Smith & Danckwerts, 1997; Knight, 2019).

364

365 **Conclusion**

366

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

375

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382

383

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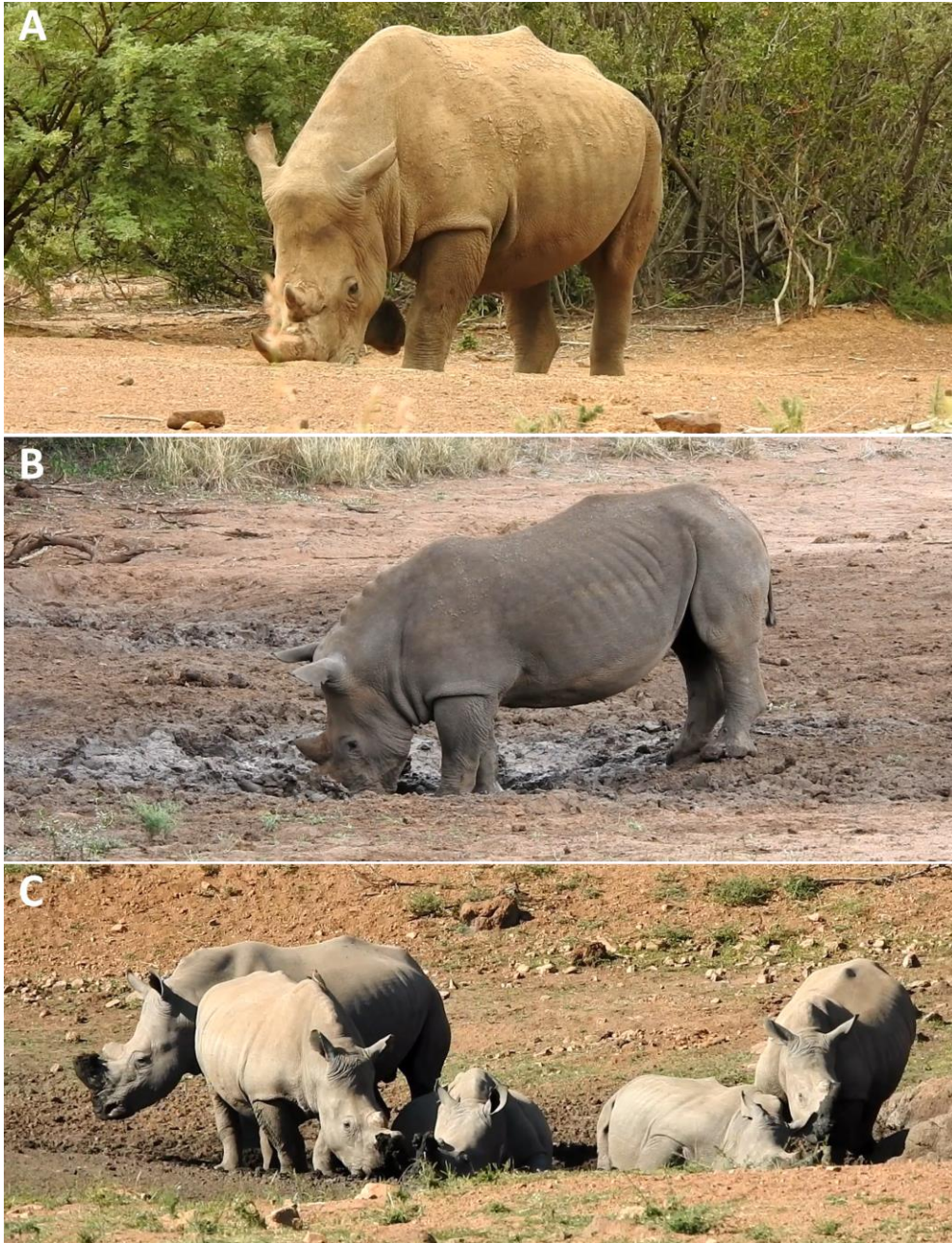
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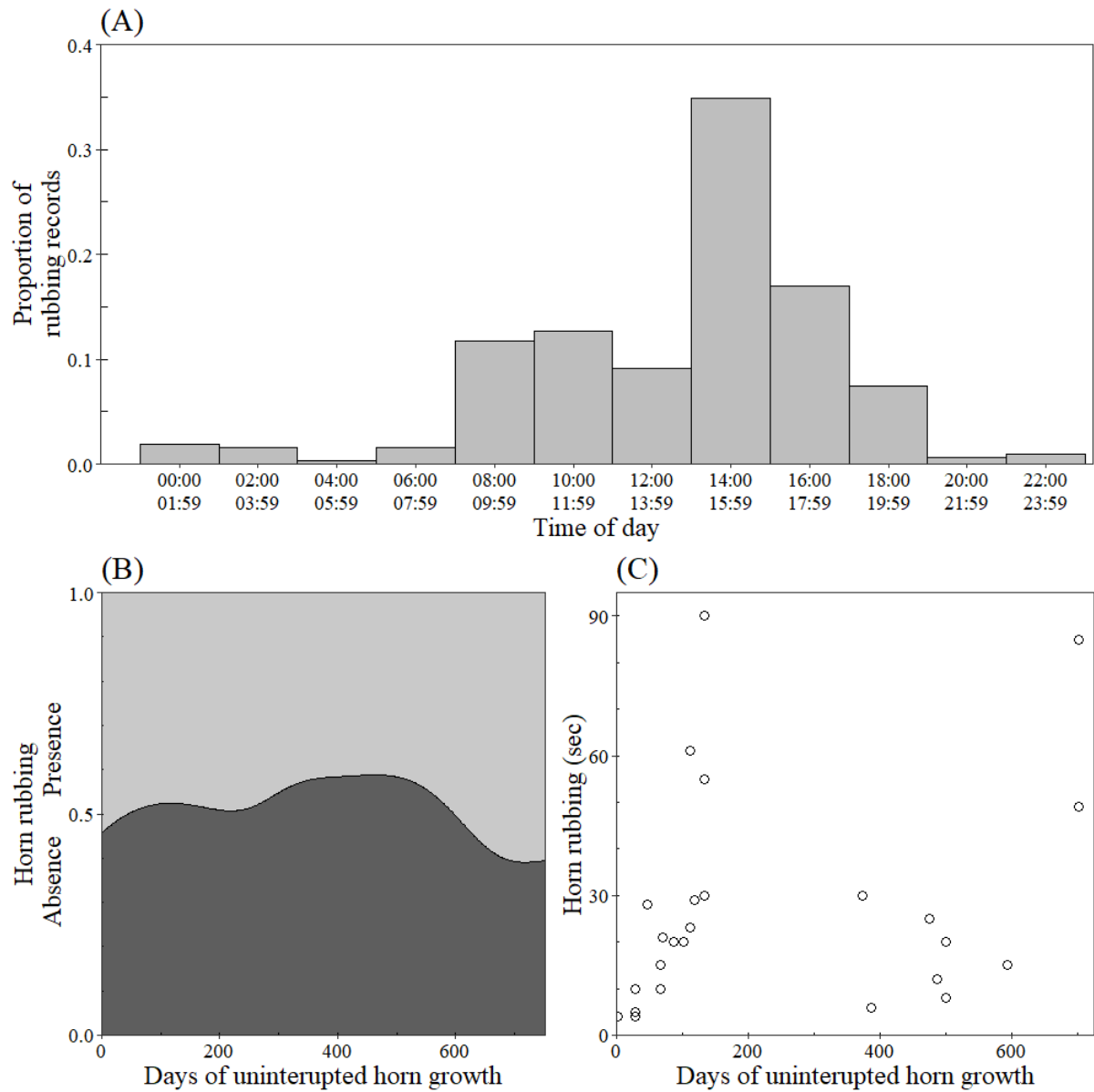
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482 Figure 1. Examples of digging behaviour in white rhinos recorded during the study: (A) A
483 horned white rhino digs with a forelimb while pressing its horn to the ground to loosen earth
484 before ingestion; (B) a horned rhino digs with its horn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



486

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



491

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

497

498 **Table 1.**

499 Behaviours of interest that were recorded by all occurrence sampling during field observations and from
500 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

501

502

503

504 **Table 2.**

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

Feature	Location ID	No of sessions	Total period (H:M)	Average period (H:M)
Rubbing post	1	4	520:38	130:09
	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
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
	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

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

509

510

511