


ORIGINAL RESEARCH

Dehorning impacts white rhinoceros behaviour less than social events: evidence from Botswana

V. Pfannerstill¹ , R. Härdtner², O. S. Maboga³, N. Balkenhol¹, E. Bennett^{4,*} & M. Scheumann^{5,*}¹Wildlife Sciences, University of Goettingen, Göttingen, Germany²Conservation Biology, University of Goettingen, Göttingen, Germany³Rhinos Without Borders, Maun, Botswana⁴Okavango Research Institute, University of Botswana, Maun, Botswana⁵Institute of Zoology, University of Veterinary Medicine Hannover, Hannover, Germany

Keywords

aggressive interactions; calving; *Ceratotherium simum simum*; social behaviours; dehorning; movement rate; poaching; vocalization.

Correspondence

Vera Pfannerstill, Wildlife Sciences, University of Goettingen, Büsgenweg 3, 37077 Göttingen, Germany.

Email: vpfanne@gwdg.de

*Joint senior authorship.

Editor: Matthew Hayward

Received 18 November 2022; revised 30 July 2023; accepted 10 August 2023

doi:10.1111/jzo.13115

Abstract

Dehorning is a conservation measure used to protect rhinoceroses ('rhinos') from being poached by removing most of the visible horn and thus reducing the monetary reward for the risk that a poacher takes. Rhinos use their horns in comfort and aggressive social behaviours. The loss of the horn might result in a decrease in aggressive and affiliative behaviours and an increase in avoidance behaviours after dehorning due to a reduced effectiveness and potential discomfort when using the nasal body part. The dehorning procedure, which includes chasing and immobilization, can lead to the separation of groups and might therefore result in fewer social interactions. To estimate whether the stress of the dehorning procedure and the loss of the horn affect the activity budget of the rhino, we compared general activities and horn-related behaviours before and after dehorning. We observed nine (six females and three males) wild white rhinos (*Ceratotherium simum simum*) in Botswana for 1 month before and 1 month after dehorning. The proportions of feeding, resting, comfort, aggressive, avoidance and affiliative behaviours did not change significantly within 1 month after dehorning. We observed sex-specific changes in proportions of locomotion and in vocalization rates, which we linked to the chasing during the procedure and to the social events of two births in the study population. Effects of the dehorning itself seemed to be weak and short-lived. Our results suggest that dehorning has no major impact on rhino behaviour. However, there is a key need to investigate the effectiveness of dehorning in reducing poaching events.

Introduction

One of the drivers of the ongoing biodiversity crisis is the illegal harvesting of animals, that is poaching (IPBES, 2019; Morton et al., 2021). Rhinoceroses (hereafter called 'rhinos') are some of the most targeted species in wildlife poaching, and the numbers of all five species combined have decreased from 29 085 in 2012 to 26 261 individuals at the end of 2021 (Emslie et al., 2016; Ferreira et al., 2022; Save The Rhino International, 2022). This decrease is due to poaching and illegal trafficking that supplies a market for rhino horn in south-east Asia, where increasing wealth forms a growing group of customers who can afford rhino horn medicine (Cheung et al., 2021; Dang Vu, 2021; Dang Vu & Nielsen, 2018), ceremonial drinks to improve business relations or carvings and jewellery made out of rhino horn (Dang Vu et al., 2022; Milliken & Shaw, 2012; Rademeyer, 2016; Truong et al., 2016).

The populations of Asian rhinos have decreased to a few tens (Javan *Rhinoceros sondaicus* and Sumatran rhino *Dicerorhinus sumatrensis*) or a few thousand individuals (greater one-horned rhino *Rhinoceros unicornis*; Ferreira et al., 2022). African rhinos had been extensively overharvested between 1970 and 1990 but recovered through conservation efforts (Ferreira et al., 2022). The demand for rhino horn increased in 2008 and poaching developed into a war-like conflict between conservationists and organized international criminals (Rademeyer, 2016). African black rhinos are listed as critically endangered because of the poaching-related population decline (Emslie, 2020b). White rhinos are only listed as near threatened (Emslie, 2020a) but have the largest total losses in individuals to poaching (Ferreira et al., 2022; International Rhino Foundation, 2022). Campaigns aiming to reduce the illegal demand for rhino horn have so far been unsuccessful (Dang Vu et al., 2020; Dang Vu & Nielsen, 2018), and corruption

supports a transnational organized crime network (Milliken & Shaw, 2012; Rademeyer, 2016). There are several approaches to reduce poaching by reducing demand, providing supply or protecting the animals more intensively (Haas & Ferreira, 2018a). For the latter one, managers invest in anti-poaching patrols and technological equipment to catch poachers in reserves (Kammaing et al., 2018; Moore et al., 2018; Reuter & Bisschop, 2016) or armed rangers guard every individual around the clock (Patton et al., 2018). However, for large populations in inaccessible areas, individual guarding is very expensive and requires unsustainable logistical efforts (Haas & Ferreira, 2018b).

The incentive for poaching can be reduced through dehorning rhinos, whereby most of the horn is removed in a veterinary procedure (Badenhorst et al., 2016; du Toit & Anderson, 2013; Kock & Atkinson, 1993). To prevent injury to the animal, the horn growth plate together with 9–11 cm horn is left intact (Badenhorst et al., 2016; Ververs, 2018). Rhino horn regrows at an approximate rate of 10% annually (Patton, 2021); therefore, dehorning should be repeated every 12–24 months (Lindsey & Taylor, 2011; Rachlow & Berger, 1997). The first dehorning operations in 1989 in Namibia and 1991 in Zimbabwe were undertaken as emergency measures to respond to sudden increases in poaching when ranger patrols and prosecution of poachers did not suffice to halt the poaching (Kock & Atkinson, 1993; Lindeque, 1990). Extensive research about the possible effects of dehorning on rhinos was thus not possible beforehand. Dehorning is now applied widely with 2217 reported dehorning incidences in African range states from 2018 to 2021 (Ferreira et al., 2022) and not only used as a poaching deterrent but also to prevent injury between rhinos in high-density populations or to harvest and stockpile horn for financial gain (Taylor et al., 2014; Trendler, 2014). Previous studies found no effects of dehorning on rhino survival and reproduction rates (Chimes et al., 2022; du Toit & Anderson, 2013; Kock & Atkinson, 1993; Lindeque & Erb, 1995; Penny, White, MacTavish, MacTavish, et al., 2020) and hormonal stress responses to dehorning are only short-term (Badenhorst et al., 2016; Penny, White, MacTavish, Scott, & Pernetta, 2020). Behaviour studies mostly focussed on specific behaviours such as fighting (Patton et al., 2018) and horn rubbing (Penny et al., 2021). With this study, we aim to add an immediate before-after comparison analysing all occurring rhino daytime behaviours, thereby responding to calls for such research, especially for white rhinos (Badenhorst et al., 2016; du Toit & Anderson, 2013; Lindsey & Taylor, 2011; Patton et al., 2018).

White rhinos are megaherbivores that spend most of the day feeding and resting (Owen-Smith, 1973; Rees, 2018). Dominant white rhino males defend territories, whereas females and subordinate males occupy overlapping home ranges (Owen-Smith, 1975). Females are usually accompanied by their youngest calf and sometimes by other females and subadults, but, when giving birth, the female isolates herself for several weeks (Owen-Smith, 1974). Through this dynamic spatial organization, white rhinos often move in groups (Owen-Smith, 1975) and display a large repertoire of social interactions (Jenikejew et al., 2020).

Vocalizations play an important role in intra-sexual communication (Cinková & Policht, 2016; Cinková & Shrader, 2020, 2022) and can be linked to rhino social networks (Jenikejew et al., 2020). Group size affects the number of social interactions and the vocalization rate, because white rhinos are prone to communicate more when they have more neighbours standing by at short distances (Jenikejew et al., 2020). Since the dehorning operation is a stressful procedure which includes chasing and immobilization (Badenhorst et al., 2016) it can lead to the separation of groups (Pfannerstill & Maboga, 2021), resulting in less affiliative behaviour and reduced vocalization rates.

Additionally, the loss of the horn is expected to affect rhino behaviour. The horn of an adult rhino weighs around 7 kg (Pienaar et al., 1991). Removing such a heavy part of the head will change the centre of gravity and the rhino's perception of weight on the head. There is no evidence that white rhinos use their horns during general activities such as feeding and resting, in contrast to black rhinos that use their horns to break branches to access browse (Joubert & Eloff, 1971). However, it can be assumed that dehorning affects comfort behaviour and social interactions. Regarding the comfort behaviour, white rhinos rub their horns against objects (Pienaar et al., 1991; Rachlow, 2001) and use them during wallowing to test the consistency of the mud (Owen-Smith, 1973).

During social interactions, rhinos use their horns in fights or in playful horn wrestling but also as weapons in fights (Owen-Smith, 1974, 1975). Fights between two males can take place at territory boundaries or with subordinate males that challenge the territory owner (Owen-Smith, 1975). Females use their horns in socio-negative interactions to deter approaching males or other females and calves from their feeding places. Horn growth is faster in males than in females (Rachlow & Berger, 1997), and although horn size is not the deciding factor for female mate choice (Kretzschmar et al., 2020), it can affect the rhino's dominance status (Penny et al., 2022). Thus, we expect that costly horn-related aggressive behaviours will be reduced after dehorning because of the reduced effectiveness and risk of injuries with a shortened horn. Instead, rhinos should switch to more effective behavioural displays or avoid social interactions.

However, Penny et al. (2021) found no effects of dehorning on rubbing and wallowing and Penny (2019) noted no differences in affiliative and aggressive behaviours between horned and dehorned populations. On the other hand, in a study where rhinos were dehorned because of high aggression and observed before and after dehorning, the number of fights between males was reduced by 68% after dehorning (Patton et al., 2018). Furthermore, fights were not a cause of death in populations of dehorned rhinos, compared to 17% of deaths caused by fights in a population of horned rhinos (Chimes et al., 2022). Since rhinos lack their weapons for fights after dehorning, a decrease in aggressive and an increase in avoidance behaviour would be expected to avoid costly injuries. This might be more prevalent in males than in females, because only males defend territories, and because in black rhinos, horn size influences social dominance among males but not females (Berger & Cunningham, 1998).

The aim of this study was to investigate effects of dehorning (procedure and horn loss) on rhino behaviour, including general activities, comfort behaviour and social interactions in a before-after comparison within 2 months around the dehorning event. We hypothesized that there would be (i) no effects of dehorning on general rhino activities such as resting, feeding and locomoting; (ii) no effects of dehorning on comfort behaviour; (iii) less aggressive behaviour after dehorning than before, especially in male rhinos; (iv) more avoidance behaviour after dehorning than before; (v) less affiliative behaviour after dehorning; (vi) lower vocalization rates after dehorning.

Materials and methods

Ethics statement

This paper contains observations of natural behaviour from wild white rhinoceros (*Ceratotherium simum simum*). A research permit (ENT 8/36/4 XXXXII 58) was issued by the Ministry of Environment, Natural Resources Conservation and Tourism of Botswana. The dehorning was carried out by experienced and qualified veterinarians from the Department of Wildlife and National Parks as part of the country-wide rhino dehorning operation (Mguni, 2020; Senyatso, 2021). No animal was injured, and no adverse effects were observed immediately following the dehorning.

Study area and subjects

The study was conducted from March to May 2020 with free-roaming white rhinos in a private reserve of approximately 33 000 ha in Botswana. The name and exact location of the reserve are not stated for security reasons (Clements *et al.*, 2020). The vegetation consisted of grasslands and mixed savannah bushland. Lions (*Panthera leo*) were present at the study site, which may prey on rhino calves (Le Roex & Ferreira, 2020). The study population consisted of one subadult female and eight adult rhinos (five females, three males) that were identified through their individual ear notches (Rhino ID in Table 1). The rhinos were habituated to vehicles as monitoring personnel visited them daily. All females except one subadult had dependent calves during the observation period. The rhinos formed temporary associations of two to eight individuals (Owen-Smith, 1975; Shrader & Owen-Smith, 2002). All rhinos of the population were dehorned on the 11th or 12th of April 2020. The observations after dehorning began 4 days after the event because regular monitoring patrols were given higher priority than the research observation, and the researcher therefore did not have access to the study area earlier.

Video and audio recording

We performed focal animal observations (Altmann, 1974) between 6:30 am and 11:30 am and between 4:30 pm and 6:45 pm. These times were selected as the most active hours for rhinos to increase the chance to observe a wide range of social behaviours (Owen-Smith, 1973). As the rhinos moved

freely in the reserve, we had to search for them every day. Each rhino was observed a maximum of once per day and for logistical reasons, we were able to observe 1–3 individuals per day. To account for effects of time of day and temperature on rhino activity (Owen-Smith, 1973), we semi-randomized recording times to balance morning and afternoon observations for each individual. After sighting a rhino or a group of rhinos, we approached them in a vehicle up to a distance of 10–30 m, depending on visibility, loudness of background noises such as wind, and the behavioural state of the rhino. Recordings were started when the engine of the vehicle was switched off and when the rhino had returned to its previous behaviour before possible disturbance by the approaching vehicle. Rhinos were videotaped for approximately 30 min using a Sony α 65 camera (Sony Corporation, Thailand) and a Medion video camera (Medion AG, Essen, Germany). Audio recordings were made using a Sennheiser omni-directional microphone (MKH 8020; Sennheiser, Wedemark, Germany; flat frequency response from 10 to 20 000 Hz \pm 5 db) covered with a wind shield and fitted on a boom pole. The microphone was connected to a Zoom F4 Field recorder (set at 44.1 kHz sampling rate, uncompressed.wav format). When the focal animal moved out of recording range during the observation, as indicated by listening to the live recording with headphones, or out of sight behind vegetation, we stopped the recording, changed the position of the vehicle and continued recording from the new position. After 30 min, we either started a new searching process or switched focal observations to another individual in the same group. When recording the same group, we waited for approximately 5 min before starting a new observation to avoid autocorrelation of the data to the previous observation. Although we aimed to observe each animal six times before and six times after dehorning with three morning and three afternoon observations each, we could not choose the dehorning date and observations sometimes had to be stopped early, for example due to rain that would mask rhino vocalizations. Therefore, total observation durations differed among individuals (Table 1).

Video analysis

All behaviour videos were synchronized with respective audio recordings and analysed using the software Observer XT (version 12, Noldus Information Technology, Netherlands, Noldus, 1991). After a pre-survey of 25 videos, we re-examined, extended and adapted the ethogram by Jenikejew *et al.* (2020) to our observations of free-roaming rhinos and used the modified ethogram (Table S1). According to our hypotheses, we focussed on the following categories: general activity, comfort, aggressive, avoidance and affiliative behaviours. Although vocalizations were classified according to the literature (Jenikejew *et al.*, 2020; Linn *et al.*, 2018, 2021; Policht *et al.*, 2008; Table S1) we grouped for them for analyses because none of them occurred at sufficiently high frequencies for separate analyses. We calculated the frequency of the point events by dividing the number of point events by the observation duration in minutes. We noted the nearest neighbour to the focal

Table 1 Details about nine white rhino study subjects observed between March and May 2020 in Botswana before and after a dehorning event

Rhino ID	Year of birth	Age at time of observation (approximately, in years)	Sex	Observation duration before dehorning (hh:mm:ss)	Observation duration after dehorning (hh:mm:ss)	Observation duration after dehorning (hh:mm:ss)	ID and age of calf at beginning of observation
WF344	2017	3 (subadult)	F	02:24:48	03:34:52	–	–
WF306	2014	6	F	02:46:29	03:07:36	–	WF11 – 9 months
WF304	2013	7	F	02:52:45	03:00:23	–	WM19 – 9 months
WF305	2013	7	F	03:02:27	03:09:47	–	WF14 – 6 months
WF349	2013	7	F	02:10:59	03:00:27	–	WF6 – New-born end of March 2020
WF335	2000	20	F	02:53:37	02:59:12	–	WF21 – 4 months
WM311	2012	8	M	02:45:14	03:01:21	–	–
WM331	2012	8	M	02:30:32	03:00:11	–	–
WM312	2010	20	M	03:00:21	02:58:52	–	–

Rhino ID refers to the identifying ear notches.
F, female; M, male.

animal, its proximity in adult rhino body lengths (2.5–3 m, Owen-Smith, 1973) and for all social behaviours the interaction partner using the same method as Jenikejew *et al.* (2020).

To ensure reliability of the behaviour coding, 25% of the observations were compared with the coding of a second observer. Inter-observer reliability was high with 85% agreement for durations and 78% agreement for point events. Lower agreement in point events was caused by the rarity of the events and by different reaction times of the observers.

Statistical analysis

We had a total of 110 observations from all nine focal individuals (six females, three males) before and after dehorning (female before: 36, female after: 39, male before: 17, male after: 18). For each behaviour, we created a model in which we added the proportion of time of the respective behaviour as the dependent variable using the `cbind` function in R, which defined the time when the behaviour was observed (success) versus the time when the behaviour was not observed (failure) (Zach, 2021). Fixed effects were dehorning status and sex and their interaction, and we included Rhino ID as random intercept in each model to account for repeated measurements of the same individual. We ran generalized linear mixed models with the beta-binomial family (logit-link-function) and zero-inflation structure to account for the high number of zeros (`glmmTMB` package, Brooks *et al.*, 2017). We performed model diagnostics with the `DHARMA` package (Hartig, 2022). We used the corrected Akaike's Information Criterion (AICc) to identify the most parsimonious models using the `aictab` function from the package `AICcmodavg` (Mazerolle, 2020). The model with the fewest predictors that was within two AICc of the model with the lowest total AICc was chosen. If a model other than the null model (intercept+random effect only) was the most parsimonious, we performed post hoc tests with the `emmeans` function (Lenth, 2021), whereby estimates were compared pairwise between explanatory factor levels on

a log-odds ratio scale due to the link function applied in the model. For graphical presentation, we divided the duration of the behaviour by the observation time to obtain behaviour proportions.

To analyse vocalization rates, we divided the sum of vocalizations of the focal animal by the respective observation duration to get a standardized vocalization rate per minute. The vocalization rate was left-skewed, and we therefore transformed the data to square root values. Since the two observations with the fight between males before dehorning were outliers in the vocalization rate, we excluded them from the following analysis. We ran generalized linear mixed models (`lmer` function from the `lme4` package, Bates *et al.*, 2015) on the transformed data, with the fixed factors dehorning status, number of neighbours, sex, and the three-way interaction among them, and focal animal as the random factor. We used the `dredge` function from the package `MuMIn` (Barton, 2022) to identify the most parsimonious model. Any competitive models with $\Delta AIC < 2$ were averaged using the `model.avg` function to estimate model-averaged parameter values.

All statistical analyses were performed in R (v4.0.3 (2020-10-10), The R Foundation for Statistical Computing), using the packages `tidyverse` (Wickham *et al.*, 2019) for workflow and `ggplot2` (Wickham, 2016) for visualization. We considered *P*-values below 0.05 as statistically significant.

Results

The most prominent rhino behaviours throughout the observations were resting and feeding (Fig. 1). A high proportion of aggressive behaviour was observed in two observations on the same day through a fight between two males (WM312 and WM331). The female WF349 calved during the observation period and showed a higher proportion of feeding and comfort behaviour before calving (up to observation four) and more resting and affiliative behaviour after calving. The female WF306 showed a higher proportion of affiliative behaviour

than other rhinos, which was in this case playing with calves in observation six and nine and playing with calves and other adults in observation 11. In comfort behaviours, we did not observe wallowing and rubbing was only observed after dehorning.

For resting and feeding, the null model was the most parsimonious (resting: $AICc = 1377.03$, $AICc\omega = 0.42$; feeding: $AICc = 1409.39$, $AICc\omega = 0.22$, Fig. 2a,b), so dehorning status, sex or their interaction did not have any significant effect on these behaviours.

For locomotion, the model with the interaction between dehorning status and sex was the most parsimonious; no other models were competitive ($\Delta AICc = 2.56$, $AICc\omega = 0.64$). Before dehorning, males showed significantly more locomotion than females (log-odds ratio = 0.51 ± 0.13 , d.f. = 103, $t = -2.56$, $P = 0.04$), whereas after dehorning, female locomotion was similar to males. Females showed more locomotion after dehorning than before (log-odds ratio = 1.87 ± 0.38 , d.f. = 103, $t = 3.06$, $P = 0.02$) whereas males appeared to locomote less after dehorning than before, but this result was not significant (Fig. 2c).

For comfort, aggressive and affiliative behaviour, the null model was the most parsimonious (comfort: $AICc = 522.18$, $AICc\omega = 0.21$; aggressive: $AICc = 171.14$, $AICc\omega = 0.46$; affiliative: $AICc = 477.23$, $AICc\omega = 0.25$; Table S2, Figure S1). Dehorning status, sex or their interaction did not have a significant effect on these behaviours.

For avoidance behaviour, there were not enough data points to include the interaction in the model, and we only ran the additive models. The null model was the most parsimonious ($AICc = 179.35$, $AICc\omega = 0.24$, Table S2, Figure S1), thus,

dehorning status and sex did not have a significant effect on avoidance behaviour.

For the vocalization rate, the model with the interaction between dehorning status and sex plus the interaction between number of neighbours and sex was the most parsimonious ($AICc = -610.13$, $AICc\omega = 0.51$), but the model with the interactions between dehorning status and sex plus number of neighbours and sex plus the interaction between dehorning status and neighbours was competitive ($\Delta AICc = 0.97$, $AICc\omega = 0.32$), and we averaged both models (Table 2).

The vocalization rate was higher for males than for females and increased with the number of neighbours, but this effect was smaller for males than for females (Table 2, Fig. 3a). Males showed a lower vocalization rate after dehorning than before (Fig. 3b).

Discussion

Studying the effects of dehorning on rhino behaviour, our results did not show evidence for changes in proportions of resting, feeding, comfort, aggressive, avoidance and affiliative behaviours during the more active morning or afternoon hours caused by dehorning. This supports our hypothesis that dehorning did not affect feeding, resting and comfort behaviour, but rejects our hypothesis that aggressive, avoidance and affiliative behaviours are affected by dehorning. Furthermore, we detected sex-specific changes in the proportions of locomotion and of vocalization rates before and after dehorning, in contrast to our expectations.

Our first hypothesis that general activities would not change after dehorning was partly supported, as we did not find effects of dehorning on resting and feeding behaviour. This is in line

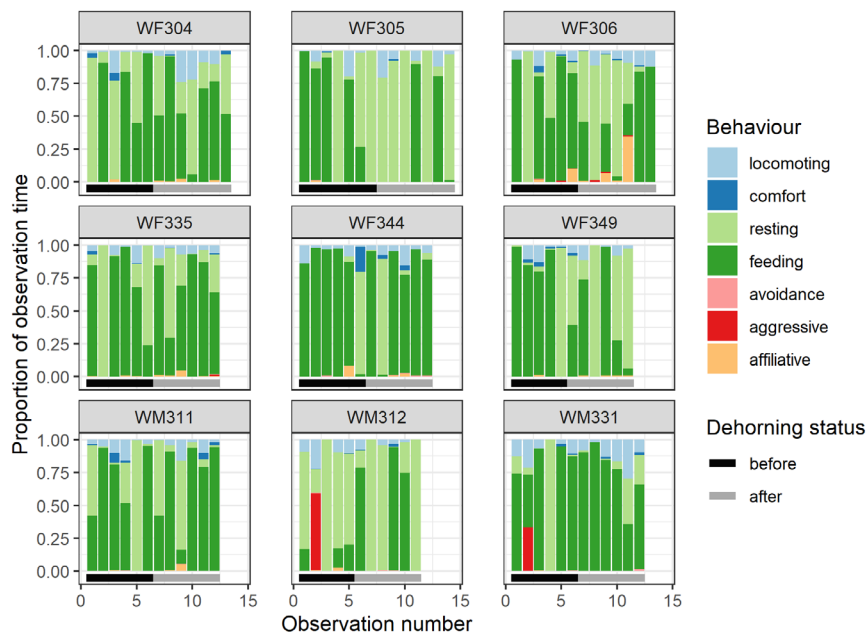


Figure 1 Proportion of observation time of behaviours per observation before and after a dehorning event for nine focal rhinos (six females, three males) observed between March and May 2020 in Botswana.

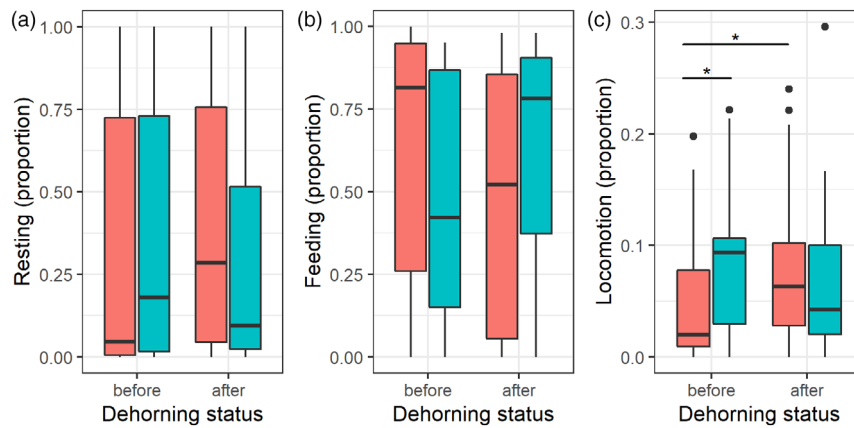


Figure 2 Boxplots of behaviour proportions for the general activities (a) resting, (b) feeding and (c) locomotion in dependence of dehorning status and sex based on data collected in 110 focal animal observations (female before: 36, female after: 39, male before: 17, male after: 19) from nine white rhinos (six females, three males) between March and May 2020 in Botswana. Note different scales for y-axes, red = females, blue = males, stars indicate significant differences.

Table 2 Model-averaged parameter values explaining variation in white rhino vocalization rates according to dehorning status, sex and number of neighbours based on data collected in 110 focal animal observations (female before: 36, female after: 39, male before: 17, male after: 19) from nine white rhinos (six females, three males) between March and May 2020 in Botswana

Parameter	Estimate	Adjusted Std. Error	z value	P value
(Intercept)	0.021	0.005	4.463	<0.001
Dehorning.status_before	0.004	0.006	0.776	0.438
Sex_male	0.020	0.008	2.496	0.013
Neighbours	0.010	0.002	5.504	<0.001
Dehorning.status_before * Sex_male	0.018	0.007	2.413	0.016
Neighbours * Sex_male	-0.014	0.003	4.709	<0.001
Dehorning.status_before * Neighbours	-0.001	0.002	0.530	0.596
Neighbours * Sex_male	-0.014	0.003	4.709	<0.001

Significant effects are highlighted in bold.

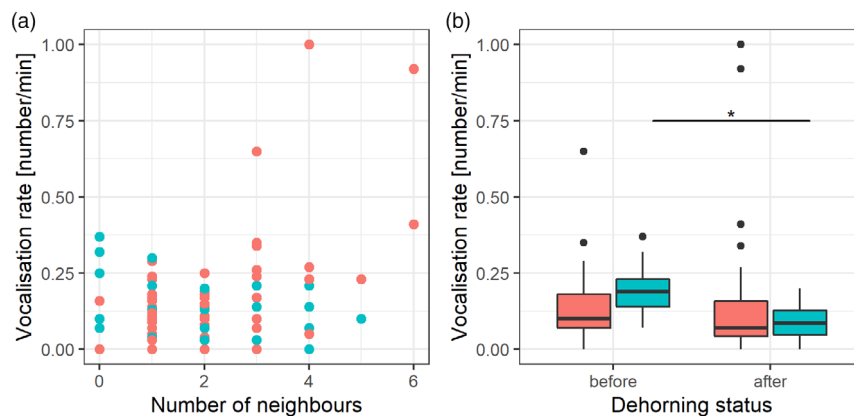


Figure 3 Vocalization rate (number of vocalizations per minute) in dependence of (a) number of neighbours and sex and (b) dehorning status and sex based on data collected in 110 focal animal observations (female before: 36, female after: 39, male before: 17, male after: 19) from nine white rhinos (six females, three males) between March and May 2020 in Botswana. Red = females, blue = males. The star indicates a significant difference.

with previous studies on short-term stress responses (Badenhorst *et al.*, 2016; Penny, White, MacTavish, Scott, & Perretta, 2020) and suggests that dehorning also did not cause stress within the 1-month-observation period. In some observations, we did not record feeding behaviour, coincidentally several times in the same focal animal, but this is related to our limited focal observation time, as we encountered the rhino on these days when it was resting.

Interestingly, we found effects of dehorning on locomotion. Males showed more locomotion than females before dehorning, which aligns with a study by Seidel *et al.* (2019) that observed larger distances moved by male than female black rhinos. This might be caused by the territorial behaviour of males, who may patrol their territory daily to place scent marks (Owen-Smith, 1971), whereas females usually only move from one feeding patch to the next. The increase of locomotion in females after dehorning might be related to the avoidance of the vehicle from which the rhinos were chased and darted for the dehorning operation, despite their previous habituation (Pfannerstill & Maboga, 2021). Surprisingly, in males we observed the reverse pattern. This might be explained by two reasons: First, a decrease of locomotion by males after dehorning can be explained by avoiding costly conflicts at the territory border due to the loss of the horn as a weapon (Duthé *et al.*, 2023). Second, we observed males searching for females that had isolated themselves to give birth shortly before dehorning. This observation is interesting because previous reports only describe males following females that are in oestrus (Owen-Smith, 1973). However, in the greater one-horned rhino it was observed that 12 h before birth females increase their urination rate and displayed urine spraying, a behaviour females typically display during oestrus (Roth *et al.*, 2004). Thus, it could be assumed that a similar behaviour in white rhinos may increase male attraction even if the female is not oestric. In one focal observation, the male WM312 followed and even tried to mount WF342, who gave birth in the first week of April. This observation contributed to more recorded male locomotion before dehorning than after. Weather could have affected behaviour because rhinos usually tend to move more on cooler, cloudy days (Owen-Smith, 1973), but the weather changed from cool and rainy in March to hotter and sunnier in May and it is therefore an unlikely explanation for the observed increase in locomotion. Therefore, we conclude that changes in locomotion behaviour after dehorning could be caused by avoiding vehicles due to the negative experience during the dehorning operation, which has been observed in other studies (e.g. Jachowski *et al.*, 2012), but might also be explained by social events.

Our hypothesis that comfort behaviour would not change after dehorning was supported, but we observed that rubbing, a behaviour which involved the horn, occurred only after dehorning and not before. This could be explained by physical irritation and rhinos exploring the new feeling of their face after dehorning. Similar observations were made by Penny *et al.* (2021) who recorded only two horn rubbing events by horned rhinos in contrast to 31 horn rubbing events by dehorned rhinos. Thus, the effects of dehorning might not be detectable through the rare occurrence of the specific

behaviours that involve the horn. Furthermore, it is not clear what amount of horn is needed to show horn-related behaviours. However, rhinos are able to adapt to the strong change in their facial structure as horns occasionally break off and wear down naturally; such adaptation has been shown in previous dehorning studies (Kock & Atkinson, 1993; Patton, 2021; Penny *et al.*, 2022). Studies analysing the behaviour after natural horn loss would be helpful to disentangle the effects of the dehorning procedure and the horn loss itself.

We found no effects of dehorning on aggressive, avoidance and affiliative social behaviours, but several of these occurred rarely and for short durations. Our observations of rare events were limited due to time constraints. We observed only one fight, which occurred before dehorning. Thus, our results neither confirm a decrease (Patton *et al.*, 2018) nor an increase (Penny *et al.*, 2022) of agonistic social interactions after dehorning, but the low number of aggressive interactions observed supports the classification of white rhinos as the most social rhino species (Shrader & Owen-Smith, 2002). Since the dehorning in the study by Patton *et al.* (2018) was undertaken to reduce the number of fights, effects of dehorning on aggressive behaviour might have only been observable due to an atypically high rate of aggressive interactions before dehorning.

We had expected an increase in avoidance behaviour after dehorning as rhinos would have lost their weapon for aggressive encounters and therefore should avoid social confrontations, resulting in more escaping behaviour. However, in a previous study on the same population we observed that rhinos were solitary for about 1 week after dehorning (Pfannerstill & Maboga, 2021), which already decreased social interactions. Thus, during this time, rhinos showed less direct avoidance behaviour because they were not displaced by other rhinos. The solitary movement lasted only a week, and our observations began 4 days post-dehorning and continued for 1 month, so the effect of the solitary movement was very short-lived. Our results therefore indicate that dehorning had no strong effect on avoidance behaviour within the 1-month observation period. On the other hand, rhinos communicate substantially via olfactory signals (Marneweck *et al.*, 2017, 2018, 2019) and avoidance behaviour can have taken place via reading scent marks, long before it was possible to observe physical encounters.

We expected less affiliative behaviour after dehorning caused by stress related to the dehorning operation. However, most affiliative behaviours occurred between females and their calves that stayed together throughout the observation time and the proportions of affiliative behaviour therefore did not change. In the case of the female that gave birth shortly before dehorning, the proportions of affiliative behaviour presumably increased as a response to the presence of the new-born calf and not to the dehorning. Overall, finding no changes in affiliative behaviour aligns with the study by Penny (2019), who found similar frequencies of cohesive behaviour in a dehorned and a horned population.

Vocalization rates generally increased with the number of neighbours. This confirms that rhinos use vocal communication mainly at short distances and more neighbours mean more potential communication partners, resulting in more frequent

vocalizations (Jenikejew *et al.*, 2020). Males showed lower vocalization rates after dehorning than before, but this was most likely related to the births before dehorning and less social contacts after dehorning. When a male searched for females shortly before they gave birth, he called them with contact calls, contributing to higher vocalization rates before dehorning. Including the two outliers of the fight, where the two males were vocalizing continuously, would increase the difference in the vocalization rate before and after dehorning. This points towards a possible indirect effect of reduced aggressive interactions after dehorning, thereby supporting the findings by Patton *et al.* (2018) and Chimes *et al.* (2022). Future research could examine affiliative and aggressive call types separately to identify changes in vocalization rates depending on the social context.

There are limited opportunities to observe wild rhinos around dehorning events; therefore, our results are based on a small number of individuals. However, with nine individuals, our sample size is comparable to other studies (Patton *et al.*, 2018: $n = 6$, Penny *et al.*, 2022: $n = 6$). For logistical reasons, our observation times were relatively short and rare events such as a fight after dehorning might therefore not have been observed due to a sampling effect. Nevertheless, our method of focal animal sampling that includes following an individual provides the opportunity to observe it at different locations and in different social groupings, which might not be possible using stationary camera traps at water holes (Penny *et al.*, 2021). Furthermore, rare behaviours such as rubbing remained rare events with occurrence sampling on a larger number of individuals over longer observation periods (Penny *et al.*, 2021) and our results are therefore likely an adequate representation of rhino behaviour. All but one observed female had a calf, and one gave birth during data collection, so this could have affected our results concerning affiliative behaviour, and our findings may not be applicable to other populations; further investigations with larger sample sizes should therefore be undertaken. Still, our study adds valuable observations to the existing literature from adults of both sexes in a population where all individuals were dehorned at the same time.

To conclude, we found very limited evidence for effects of dehorning on rhino behaviour within 1 month. When compared to social events – two births and a fight – that occurred in the same timeframe and induced visible behavioural changes, our results suggest that dehorning has no strong effect on the rhino behaviours that we measured. In the light of our findings, dehorning can thus be seen as a reasonable method from an animal ethics point of view. However, the benefits of dehorning as a management measure should be weighed against possible disadvantages. There are risks to animal welfare associated to the immobilization that is necessary prior to dehorning (du Toit & Anderson, 2013; Lindsey & Taylor, 2011; Trendler, 2011) and dehorned rhinos might be less able to defend themselves against predators, leading to higher calf mortality (Le Roex & Ferreira, 2020). If dehorning is efficient in reducing poaching, then immobilization and the possible loss of a calf would be the smaller risk compared with the possible loss of an adult female through poaching, which also has compound effects of losing future calves (Nhleko

et al., 2022). Our research permit did not include the analysis of poaching data, but previous studies showed that the proportion of poached rhinos was not different between horned and dehorned populations (Chimes *et al.*, 2022) and suggested that also dehorned rhinos need continuous protection (Dang Vu *et al.*, 2022; Kock & Atkinson, 1993; Lindsey & Taylor, 2011). Further research is therefore necessary to evaluate the effectiveness of dehorning in reducing poaching events in comparison with other conservation measures, including the development of income-generating activities for local communities around rhino reserves or value creation of living rhinos (Ferreira *et al.*, 2022), so that resources for rhino conservation can be allocated most efficiently.

Acknowledgments

We thank the Department of Wildlife and National Parks and Government of Botswana for the research permit and our collaboration partners in Botswana, Rhino Conservation Botswana Trust, for logistical support. We thank Johannes Signer for assistance in R scripting and Suzanne van Beeck Calkoen for help with data analysis. VP was granted PhD scholarships by the German Academic Exchange Service (DAAD) and the German Business Foundation (SDW). Field work equipment was funded by the Oklahoma City Zoo Conservation Action Now! Fund, Pittsburgh Zoo & PPG Aquarium Conservation and Sustainability Fund, Riverbanks Zoo and Garden Satch Krantz Conservation Fund. Open Access funding enabled and organized by Projekt DEAL.

Author contributions

VP, EB and MS designed the study. VP and OM collected the data. RH and VP analysed the videos and the data. VP drafted the paper and EB, MS, RH and NB revised the paper for intellectual content. All authors approved the final version for submission.

Conflict of interest

The authors declare no known conflict of interest.

Data availability

Video and audio data are stored at the Institute of Zoology of the University of Veterinary Medicine in Hanover and can be provided by the authors upon reasonable request. Behaviour data tables can be accessed at DOI [10.5281/zenodo.7286117](https://doi.org/10.5281/zenodo.7286117).

REFERENCES

- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, **49**, 227–267.
- Badenhorst, M., Otto, M., van der Goot, A. C., & Ganswind, A. (2016). Stress steroid levels and the short-term impact of routine dehorning in female southern white rhinoceroses (*Ceratotherium simum simum*). *African Zoology*, **51**, 211–215.

- Barton, K. (2022). *MuMIn: Multi-model inference. R package.*
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.
- Berger, J., & Cunningham, C. (1998). Natural variation in horn size and social dominance and their importance to the conservation of black rhinoceros. *Conservation Biology*, **12**, 708–711.
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, **9**, 378–400.
- Cheung, H., Mazerolle, L., Possingham, H. P., & Biggs, D. (2021). Rhino horn use by consumers of traditional Chinese medicine in China. *Conservation Science and Practice*, **3**, e365.
- Chimes, L. C., Beytelli, P., Muntiferi, J. R., Kötting, B., & Neville, V. (2022). Effects of dehorning on population productivity in four Namibia sub-populations of black rhinoceros (*Diceros bicornis bicornis*). *European Journal of Wildlife Research*, **68**, 58.
- Cinková, I., & Policht, R. (2016). Sex and species recognition by wild male southern white rhinoceros using contact pant calls. *Animal Cognition*, **19**(2), 375–386. <https://doi.org/10.1007/s10071-015-0940-7>
- Cinková, I., & Shrader, A. M. (2020). Rival assessment by territorial southern white rhinoceros males via eavesdropping on the contact and courtship calls. *Animal Behaviour*, **166**, 19–31. <https://doi.org/10.1016/j.anbehav.2020.05.013>
- Cinková, I., & Shrader, A. M. (2022). Individuality, species-specific features, and female discrimination of male southern white rhinoceros courtship calls. *Animal Cognition*, **25**, 769–782. <https://doi.org/10.1007/s10071-021-01591-4>
- Clements, H. S., Knight, M., Jones, P., & Balfour, D. (2020). Private rhino conservation: Diverse strategies adopted in response to the poaching crisis. *Conservation Letters*, **13**, e12741.
- Dang Vu, H. N. (2021). When cheap talk is not that cheap – interviewing the super-rich about illegal wildlife consumption. *International Journal of Social Research Methodology*, **25**, 697–702.
- Dang Vu, H. N., & Nielsen, M. R. (2018). Understanding utilitarian and hedonic values determining the demand for rhino horn in Vietnam. *Human Dimensions of Wildlife*, **23**, 417–432.
- Dang Vu, H. N., Nielsen, M. R., & Jacobsen, J. B. (2020). Reference group influences and campaign exposure effects on rhino horn demand: Qualitative insights from Vietnam. *People and Nature*, **2**, 923–939.
- Dang Vu, H. N., Nielsen, M. R., & Jacobsen, J. B. (2022). Conserving rhinos by legal trade: Insights from a choice experiment with rhino horn consumers. *Ecological Economics*, **193**, 107287.
- du Toit, R., & Anderson, N. (2013). Dehorning rhinos. *Wildlife Ranching*, **6**, 82–85.
- Duthé, V., Odendaal, K., van der Westhuizen, R., Church, B., Naylor, S., Boshoff, S., Venter, M., Prinsloo, M., Ngwenya, P., Hanekom, C., Kelly, C. P., Walker, T. W. N., Rasmann, S., & Defossez, E. (2023). Reductions in home-range size and social interactions among dehorned black rhinoceroses (*Diceros bicornis*). *Proceedings of the National Academy of Sciences of the United States of America*, **120**, e2301727120.
- Emslie, R. (2020a). *Ceratotherium simum*. The IUCN red list of threatened species 2020. *IUCN Red List of Threatened Species*, e.T4185A45813880.
- Emslie, R. (2020b). *Diceros bicornis*. The IUCN red list of threatened species 2020. *IUCN Red List of Threatened Species*, e.T6557A152728945.
- Emslie, R., Milliken, T., Talukdar, B., Ellis, S., Adcock, K., & Knight, M. H. (2016). African and Asian rhinoceroses – status, conservation and trade. In *A report from the IUCN species survival commission (IUCN SSC) African and Asian rhino specialist groups and TRAFFIC to the CITES secretariat pursuant to resolution conf. 9.14, CoP17 (Rev. CoP15)* (pp. 1–21). CITES CoP15.
- Ferreira, S. M., Ellis, S., Burgess, G., Baruch-Mordo, S., Talukdar, B., & Knight, M. H. (2022). African and Asian rhinoceroses – status, conservation and trade. *Report of the African Rhino Specialist Group to the CITES CoP19*, **75**, 1–18.
- Haas, T. C., & Ferreira, S. M. (2018a). Finding politically feasible conservation policies: The case of, finding politically feasible conservation policies: The case of wildlife trafficking wildlife trafficking. *Ecological Applications*, **28**(2), 473–494.
- Haas, T. C., & Ferreira, S. M. (2018b). Optimal patrol routes: Interdicting and pursuing rhino poachers. *Police Practice and Research*, **19**, 61–82.
- Hartig, F. (2022). Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models [R package DHARMa version 0.4.6]: Comprehensive R Archive Network (CRAN).
- International Rhino Foundation. (2022). Updated poaching numbers from Kruger National Park. <https://rhinos.org/blog/updated-poaching-numbers-from-kruger-national-park/>
- IPBES. (2019). *The global assessment report on biodiversity and ecosystem services: Summary for policy makers*. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.
- Jachowski, D. S., Slotow, R., & Millsbaugh, J. J. (2012). Physiological stress and refuge behavior by African elephants. *PLoS One*, **7**, e31818.
- Jenikejew, J., Chaignon, B., Linn, S., & Scheumann, M. (2020). Proximity-based vocal networks reveal social relationships in the southern white rhinoceros. *Scientific Reports*, **10**, 15104.
- Joubert, E., & Eloff, F. C. (1971). Notes on the ecology and behaviour of the black rhinoceros *Diceros bicornis* Linn. 1758 in South West Africa. *Madoqua*, **3**, 5–53.
- Kammaing, J., Ayele, E., Meratnia, N., & Havinga, P. (2018). Poaching detection technologies-a survey. *Sensors*, **18**, 1474.
- Kock, M. D., & Atkinson, M. W. (1993). *Report on dehorning of black (Diceros bicornis) and White (Ceratotherium simum)*

- rhinoceroses in Zimbabwe*. Department of National Parks and Wild Life Management.
- Kretzschmar, P., Auld, H., Boag, P., Ganslößer, U., Scott, C., van Coeverden de Groot, P. J., & Courtiol, A. (2020). Mate choice, reproductive success and inbreeding in white rhinoceros: New insights for conservation management. *Evolutionary Applications*, **13**, 699–714.
- Le Roex, N., & Ferreira, S. M. (2020). Age structure changes indicate direct and indirect population impacts in illegally harvested black rhino. *PLoS One*, **15**, e0236790.
- Lenth, R. V. (2021). *Emmeans: Estimated marginal means, aka least-squares means*. R package.
- Lindeque, M. (1990). The case for dehorning the black rhinoceros in Namibia. *South African Journal of Science*, **86**, 226–227.
- Lindeque, M., & Erb, K. P. (1995). Research on the effects of temporary horn removal on black rhinos in Namibia. *Pachyderm*, **20**, 27–30.
- Lindsey, P. A., & Taylor, A. (2011). *A study on the dehorning of African rhinoceroses as a tool to reduce the risk of poaching*. South African Department of Environmental Affairs.
- Linn, S. N., Boer, M., & Scheumann, M. (2018). First insights into the vocal repertoire of infant and juvenile southern white rhinoceros. *PLoS One*, **13**, e0192166.
- Linn, S. N., Schmidt, S., & Scheumann, M. (2021). Individual distinctiveness across call types of the southern white rhinoceros (*Ceratotherium simum simum*). *Journal of Mammalogy*, **102**, 440–456.
- Marneweck, C., Jürgens, A., & Shrader, A. M. (2017). Dung odours signal sex, age, territorial and oestrous state in white rhinos. *Proceedings of the Royal Society B: Biological Sciences*, **284**, 20162376.
- Marneweck, C., Jürgens, A., & Shrader, A. M. (2018). The role of middens in white rhino olfactory communication. *Animal Behaviour*, **140**, 7–18.
- Marneweck, C., Jürgens, A., & Shrader, A. M. (2019). The first report of urine overmarking of pro-oestrus female dung by a male white rhino. *African Zoology*, **54**, 175–179.
- Mazerolle, M. J. (2020). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. R package.
- Mguni, M. (2020). *Gov't dehorn rhinos as poaching crisis deepens*. Mmegi.
- Milliken, T., & Shaw, J. (2012). *The South Africa–Viet Nam Rhino Horn Trade Nexus: A deadly combination of institutional lapses, corrupt wildlife industry professionals and Asian crime syndicates*. TRAFFIC.
- Moore, J. F., Mulindahabi, F., Masozera, M. K., Nichols, J. D., Hines, J. E., Turikunkiko, E., & Oli, M. K. (2018). Are ranger patrols effective in reducing poaching-related threats within protected areas? *Journal of Applied Ecology*, **55**, 99–107.
- Morton, O., Scheffers, B. R., Haugaasen, T., & Edwards, D. P. (2021). Impacts of wildlife trade on terrestrial biodiversity. *Nature Ecology & Evolution*, **5**, 540–548.
- Nhleko, Z. N., Ahrens, R., Ferreira, S. M., & McCleery, R. A. (2022). Poaching is directly and indirectly driving the decline of South Africa's large population of white rhinos. *Animal Conservation*, **25**, 151–163.
- Noldus, L. P. J. J. (1991). The observer: A software system for collection and analysis of observational data. *Behavior Research Methods, Instruments, & Computers*, **23**, 415–429.
- Owen-Smith, R. N. (1971). Territoriality in the white rhinoceros (*Ceratotherium simum*) Burchell. *Nature*, **231**, 294–296.
- Owen-Smith, R. N. (1973). *The behavioural ecology of the white rhinoceros*. PhD thesis, The University of Wisconsin.
- Owen-Smith, R. N. (1974). The social system of the white rhinoceros. In V. Geist & F. Walther (Eds.), *The behaviour of ungulates and its relation to management* (pp. 341–351). International Union for Conservation of Nature and Natural Resources.
- Owen-Smith, R. N. (1975). The social ethology of the white rhinoceros *Ceratotherium simum* (Burchell 1817*). *Zeitschrift für Tierpsychologie*, **38**, 337–384.
- Patton, F. (2021). A rudimentary assessment of rhinoceros horn regrowth in Africa based on photographs. *Pachyderm*, **62**, 135–142.
- Patton, F., Campbell, P., & Genade, A. (2018). The effect of dehorning adult male rhinos on the frequency of fighting at Ziwa rhino sanctuary. *Pachyderm*, **59**, 114–115.
- Penny, S. G. (2019). *The impact of dehorning on the white rhinoceros (Ceratotherium simum) and the evaluation of novel anti-poaching tactics*. PhD thesis, University of Brighton.
- Penny, S. G., White, R. L., MacTavish, D., MacTavish, L., Scott, D. M., & Pernetta, A. P. (2020). Does dehorning lead to a change in inter-calf intervals in free-ranging white rhinoceros? *Pachyderm*, **61**, 191–193.
- Penny, S. G., White, R. L., MacTavish, L., Scott, D. M., & Pernetta, A. P. (2020). Negligible hormonal response following dehorning in free-ranging white rhinoceros (*Ceratotherium simum*). *Conservation Physiology*, **8**, coaa117.
- Penny, S. G., White, R. L., Scott, D. M., MacTavish, L., & Pernetta, A. P. (2021). No evidence that horn trimming affects white rhinoceros horn use during comfort behaviour and resource access. *Animal Biology*, **71**, 243–259.
- Penny, S. G., Withey, M., White, R. L., Scott, D. M., MacTavish, L., & Pernetta, A. P. (2022). Changes in social dominance in a group of subadult white rhinoceroses (*Ceratotherium simum*) after dehorning. *African Zoology*, **57**, 32–42.
- Pfannerstill, V., & Maboga, O. S. (2021). Not so solitary? White rhinos seek company when relaxed. *Pachyderm*, **62**, 130–134.
- Pienaar, D. J., Hall-Martin, A. J., & Hitchins, P. M. (1991). Horn growth rates of free-ranging white and black rhinoceros. *Koedoe*, **34**, 97–105.
- Policht, R., Tomášová, K., Holečková, D., & Frynta, D. (2008). The vocal repertoire in northern white rhinoceros *Ceratotherium simum cottoni* as recorded in the last surviving herd. *Bioacoustics*, **18**, 69–96.
- Rachlow, J. L. (2001). Tree rubbing by white rhinos: Potential functions of an undescribed behavior. *Alces*, **37**, 447–456.

- Rachlow, J. L., & Berger, J. (1997). Conservation implications of patterns of horn regeneration in dehorned white rhinos. *Conservation Biology*, **11**, 84–91.
- Rademeyer, J. (2016). *Tipping point: Transnational organised crime and the 'war' on poaching*. Global Initiative against Transnational Organized Crime.
- Rees, C. (2018). *The translocation of white rhino (Ceratotherium simum) to the Okavango Delta, Botswana*. Dissertation, University of Bristol.
- Reuter, E., & Bisschop, L. (2016). Keeping the horn on the rhino: A study of Balule nature reserve. In G. Potter & A. Nurse (Eds.), *The Geography of Environmental Crime* (pp. 149–186). Palgrave Macmillan.
- Roth, T. L., Bateman, H. L., Kröll, J. L., Steinetz, B. G., & Reinhart, P. R. (2004). Endocrine and ultrasonographic characterization of a successful pregnancy in a Sumatran rhinoceros (*Dicerorhinus sumatrensis*) supplemented with a synthetic progestin. *Zoo Biology*, **23**, 219–238.
- Save The Rhino International. (2022). Poaching numbers. <https://www.savetherhino.org/rhino-info/poaching-stats/>. Accessed July 4, 2022.
- Seidel, D. P., Linklater, W. L., Kilian, W., Du Preez, P., & Getz, W. M. (2019). Mesoscale movement and recursion behaviors of Namibian black rhinos. *Movement Ecology*, **7**, 34.
- Senyatso, K. (2021). *Press release 22 Oct. 2021: The history of rhino and elephant poaching in Botswana*. Ministry of Environment, Natural Resources and Tourism Botswana.
- Shrader, A., & Owen-Smith, R. N. (2002). The role of companionship in the dispersal of white rhinoceroses (*Ceratotherium simum*). *Behavioral Ecology and Sociobiology*, **52**, 255–261.
- Taylor, A., Brebner, K., Coetzee, R., Davies-Mostert, H., Lindsey, P., Shaw, J., & 't Sas-Rolfes, M. (2014). *The viability of legalising trade in rhino horn in South Africa*. Department of Environmental Affairs.
- Trendler, K. (2011). Dehorning rhino: Welfare, ethics and behavioural issues. In B. G. Daly, A. Greyling, Y. Friedmann, S. Downie, R. du Toit, R. Emslie, M. Eustace, J. Malan, K. Nghidinwa, C. O'Criodain, & K. Trendler (Eds.), *Perspectives on dehorning and legalised trade in rhino horn as tools to combat rhino poaching* (p. 7). Endangered Wildlife Trust.
- Trendler, K. (2014). Rhino horn: "There is never the right way to do the wrong thing". Assessing the risks of rhino horn trade. *A Journal of Argument Presented at the April 2014 Conference in South Africa*, 7.
- Truong, V. D., Dang, N. V., & Hall, C. M. (2016). The marketplace management of illegal elixirs: Illicit consumption of rhino horn. *Consumption Markets & Culture*, **19**, 353–369.
- Ververs, C. (2018). *Breeding on the brink of extinction: What can we learn from game-ranched white rhinoceroses (Ceratotherium simum simum)?* Dissertation, Ghent University.
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemond, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., ... Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, **4**, 1686.
- Zach. (2021). How to use cbind in R (with examples). Statology. <https://www.statology.org/cbind-in-r/>

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Boxplots of behaviour proportions for comfort, aggressive, avoidance and affiliative behaviour in dependence of dehorning status and sex based on data collected in 110 observations (female before: 36, female after: 39, male before: 17, male after: 19) from nine white rhinos (six females, three males) between March and May 2020 in Botswana. Note different scales for y-axes.

Table S1. Ethogram for focal animal observations of free-roaming rhinos in Botswana.

Table S2. Overview of corrected Akaike's Information Criterion (AICc) values of models testing effects of dehorning status and sex on rhino behaviours based on data collected in 110 observations (female before: 36, female after: 39, male before: 17, male after: 19) from nine white rhinos (six females, three males) between March and May 2020 in Botswana. 0 = null model; + = additive model dehorning status+sex; * = model including dehorning status, sex, and the interaction between dehorning status and sex; DeltaAICc = difference in AIC value to the best model; AICcWt = Akaike weights or model probabilities; Cum.Wt = Cumulative Akaike weights; LL = Log-likelihood of the model. All models included the rhino ID as a random factor to account for repeated observations of the same individual.