



Reductions in home-range size and social interactions among dehorned black rhinoceroses (*Diceros bicornis*)

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Poaching for horns and tusks is driving declines of megaherbivores worldwide, including the critically endangered African black rhinoceros (*Diceros bicornis*). By proactively dehorning entire rhinoceros populations, conservationists aim to deter poaching and prevent species loss. However, such conservation interventions may have hidden and underestimated effects on animals' behavior and ecology. Here, we combine >15 y of black rhino–monitoring data across 10 South African game reserves, comprising >24,000 sightings of 368 individuals, to determine the consequences of dehorning for black rhino space use and social interactions. While preventative dehorning at these reserves coincided with a nationwide decrease in black rhino mortality from poaching and did not infer increased natural mortality, dehorned black rhinos decreased their home range area by, on average, 11.7 km² (45.5%) and were 37% less likely to engage in social encounters. We conclude that dehorning black rhinos as an antipoaching measure alters their behavioral ecology, although the potential population-level effects of these changes remain to be determined.

dehorning | conservation | rhino | poaching | home range

The trade of mammal species that possess anatomical features of high value to humans, such as tusks and horns, fuels a multibillion-dollar illicit wildlife industry (1, 2) that poses an immediate threat to the persistence of megafauna globally (3–6). Rhino horns are sought for cultural and medicinal beliefs (7) throughout Southeast Asia, to the extent that they are estimated to be worth \$65,000 kg⁻¹—more than diamonds or gold (4). Such high demand for rhino horns has encouraged intensive poaching, leading to a >98% decline in numbers of the critically endangered black rhinoceros (*Diceros bicornis* L.) since the 1960s (Fig. 1A) (4, 6). Indeed, only ~5,000 black rhino individuals now remain on Earth (8). In an attempt to curb the poaching crisis and safeguard animals, conservation managers have responded by introducing militarized law enforcement of protected areas (4, 9, 10). However, continuing pressure of organized crime over the past two decades has caused many reserves to turn to a short-term solution of dehorning rhinos, which aims to deter poaching by removing the reward (11, 12). While the dehorning approach is heralded as a promising tool for the protection of rhino, and has been adopted widely throughout southern Africa, little is known about its implications for black rhino ecology or behavior (13).

Black rhinos are solitary animals and live within delimited home ranges (14) that vary over space and time due to changes in resource availability and population demography (15). Black rhinos are thought to be both polygynous and polyandrous (16–18), where dominant males mate with multiple females and females mate with multiple males. Home ranges in both sexes are determined by social interactions (19), which involve territorial and agonistic behaviors that collectively affect population growth (20) and are directly related to the presence and characteristics of horns (21). For instance, males with larger horns dominate 65% of encounters in male–male interactions (22). Furthermore, male reproductive success is positively correlated with home-range size, and male territories generally do not overlap because intense competition often leads to fatal fights (23). Removing horns as a poaching deterrent thus has clear potential to affect intraspecific competition for mates and space (24), reshape population spatial structure, and impact black rhino ecology and demography.

Here, we quantify the impact of dehorning on black rhino behavior by examining data on 24,760 rhino sightings from 368 individuals over 15 y of continuous monitoring (2005 to 2020) in 10 reserves in northeastern South Africa (SI Appendix, Fig. S1). We first summarize trends in both horn removal and black rhino mortality through time, evaluating whether the available data support the premise that dehorning reduces poaching-related

Significance

The global decline of megaherbivores, such as the critically endangered African black rhinoceros, is fueled by the illegal trade in tusks and horns. In an effort to curb the recent onslaught, conservationists are implementing the large-scale removal and trimming of rhinoceros horns. Although this preventative approach has coincided with a general reduction in poaching-induced mortality, we show that it also alters black rhino space use and interactions. Across 10 South African reserves, dehorned black rhinos reduced their home ranges and social encounters. The profound impacts of this antipoaching measure on black rhino behavioral ecology might have demographic consequences, yet to be determined, highlighting the importance of considering behavioral responses when weighing the net benefit of conservation interventions.

The authors declare no competing interest.

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fatalities. We then employ spatiotemporal monitoring over the entire study period to determine how dehorning affects black rhino home-range sizes. Finally, we use interaction networks to examine the impact of dehorning on black rhino social interactions.

Results

Considering all sites together, the proportion of dehorned rhinos increased rapidly from 0% in 2013 to 63% in 2020 (Fig. 1B). Concomitantly, the number of natural and poaching-related mortalities decreased over the same time period (Fig. 1C). Of the 30 recorded poached rhinos, nine were killed after the start of the intensified dehorning campaign (from 2017, where the proportion of dehorned rhinos exceeded 30%) and of those, only two animals were dehorned prior to death (Fig. 1C). The poaching offtake rate, that is, the percentage of black rhinos removed from the study populations due to poaching, declined during this period from 3.97% in 2014 to 0% in 2020 (Fig. 1D, ANCOVA year effect; $F_{1,12} = 40.97$, $P < 0.001$). Poaching at the study sites (where dehorning was particularly commissioned) declined in concert with a nationwide trend (Fig. 1D, year-by-study site interaction; $F_{1,12} = 2.03$, $P = 0.180$), but was consistently lower than the national average throughout the study period (Fig. 1D, study-site

effect; $F_{1,12} = 30.09$, $P < 0.001$). Notably, the frequency of natural mortality also decreased from 2017 to 2020 (Fig. 1C).

Our observations collectively suggest that the frequency of dehorned animals is negatively correlated with mortality due to poaching (SI Appendix, Fig. S2A; linear regression; $R^2 = 0.72$, $F_{1,6} = 19.27$, $P = 0.004$). Yet, it is important to note that these results do not establish a causal relationship between dehorning and poaching. The observed reduction in poaching events almost perfectly paralleled the broader decrease throughout South Africa and may be linked to other variables, such as increased security in game reserves, lower economic incentives for poachers (25), and, exceptionally in 2020, COVID lockdown regulations. Relatedly, a census of a black rhino population in Zimbabwe similarly found that rhino individual numbers rose in concert with an intensive dehorning campaign (13, 26, 27), but dehorning was carried out in synergy with several other interventions, such as a shoot to kill policy (27, 28). While there is therefore no conclusive evidence that dehorning contributed to the reduction in poaching, we also show that there is no evidence of dehorning leading to increased natural mortality (Chi-square test of association between cause of death and horned and dehorned mortalities; $X^2 = 1.422$; $df = 2$; P -value = 0.488). To the contrary, the natural mortality offtake rate sharply declined

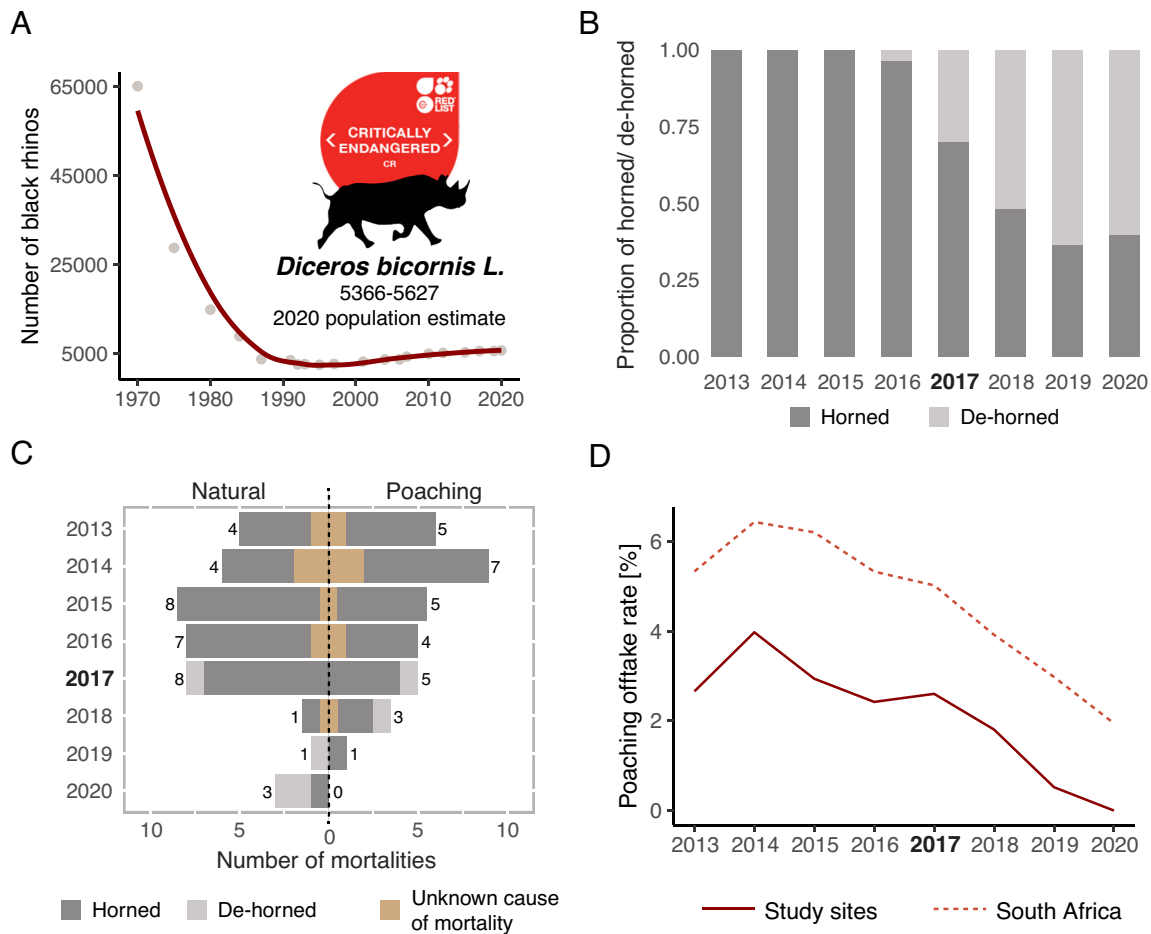


Fig. 1. Global population decline of the critically endangered black rhinoceros and recent trends of dehorning and poaching in 10 South African study sites. (A) Plot showing the global decline in the number of black rhinoceros individuals and the 2020 estimate of population size (IUCN, 2020), as highlighted by the red spline. (B) Bar graph displaying the proportion of horned (dark gray) and dehorned (light gray) black rhinos in study sites over time, with the bulk of dehorning campaigns starting in 2017 (highlighted in bold). (C) Stacked bar chart showing the number of mortalities by year in study sites of horned (dark gray) and dehorned (light gray) black rhinos by cause (left: natural mortalities; right: poaching-related mortalities). Mortalities of unknown cause (all horned) are displayed in gold and centered. (D) Plot displaying the poaching offtake rate of black rhinos in the study sites compared to that of black rhinos in South Africa over the same period. The poaching offtake rate (solid line for study sites; dotted line for South Africa at large), representing the percentage of black rhinos removed from the population by poaching, was calculated by the yearly number of poached black rhinos divided by the yearly total population of black rhinos.

alongside the poaching off-take rate from 2017 when dehorning became widespread (Fig. 1C and *SI Appendix*, Fig. S2B).

We examined whether dehorning affects black rhino home-range size by comparing the home ranges of dehorned rhinos before versus after dehorning ($N=68$; *Materials and Methods* and *SI Appendix*, Fig. S5) to those of a control (not dehorned) group ($N = 120$; *Materials and Methods* and *SI Appendix*, Fig. S6). Home ranges of male and female rhinos shrank significantly after dehorning (that is, had a negative effect size; Fig. 2), with dehorned females displaying an average decrease of 15.42 km^2 (-53.08%) and dehorned males an average decrease of 9.13 km^2 (-38.03%) compared to horned animals (Fig. 2A and *SI Appendix*, Table S1). This effect was resolutely independent from the number of sightings used to construct home ranges in both periods, and these results remained robust with varying sample sizes of individuals and sightings (*SI Appendix*, Table S2 and Fig. S7). By contrast, horned (control) rhinos actually expanded their home ranges significantly over the study period by 7.38 km^2 ($+57.02\%$) in average [females: 7.77 km^2 ($+67.55\%$); males: 7.07 km^2 ($+50.21\%$)] (Fig. 2A and C and *SI Appendix*, Table S1), accentuating the difference between the two groups. Expansion of horned rhino territories was not caused by animals occupying newly vacant dehorned rhino territory, since 95% of the time the horned control group was separated from the dehorned group in space or time (*Materials and*

Methods). Indeed, territory expansions are expected over a rhino's lifetime (29). Our results thus collectively show that dehorned rhinos reduce their home-range size, revealing horns as an important determinant of black rhino home-range area.

Black rhinos are largely solitary and sedentary but possess home ranges that overlap intersexually (19, 24, 29, 30), making home-range connectivity critical for maintaining social interactions (29, 31, 32). Particularly for a nongregarious species, communication through scent is important and thus overlap in territories is essential. For instance, adult black rhinos use dung heaps (middens) to identify other individuals, inform competitive interactions, delimit home ranges, and seek potential mates (29, 32). It follows that the observed reductions in black rhino home-range size following dehorning could have a substantial effect on black rhino social interactions. We used the three populations with sufficient consecutive data (Ithala, Manyoni, Phinda) to examine the impact of dehorning on the strength and structure of black rhino social interactions, specifically by performing within-population comparisons of interaction networks before and after dehorning ($N = 74$ individuals, *Materials and Methods*). Dehorning sharply decreased social-interaction strength in two populations (Cohen's D: Manyoni = -0.62 ; Phinda = -0.89) and induced smaller decreases in the third population (Cohen's D: Ithala = -0.19) (Fig. 3A). The impact of dehorning on black rhino

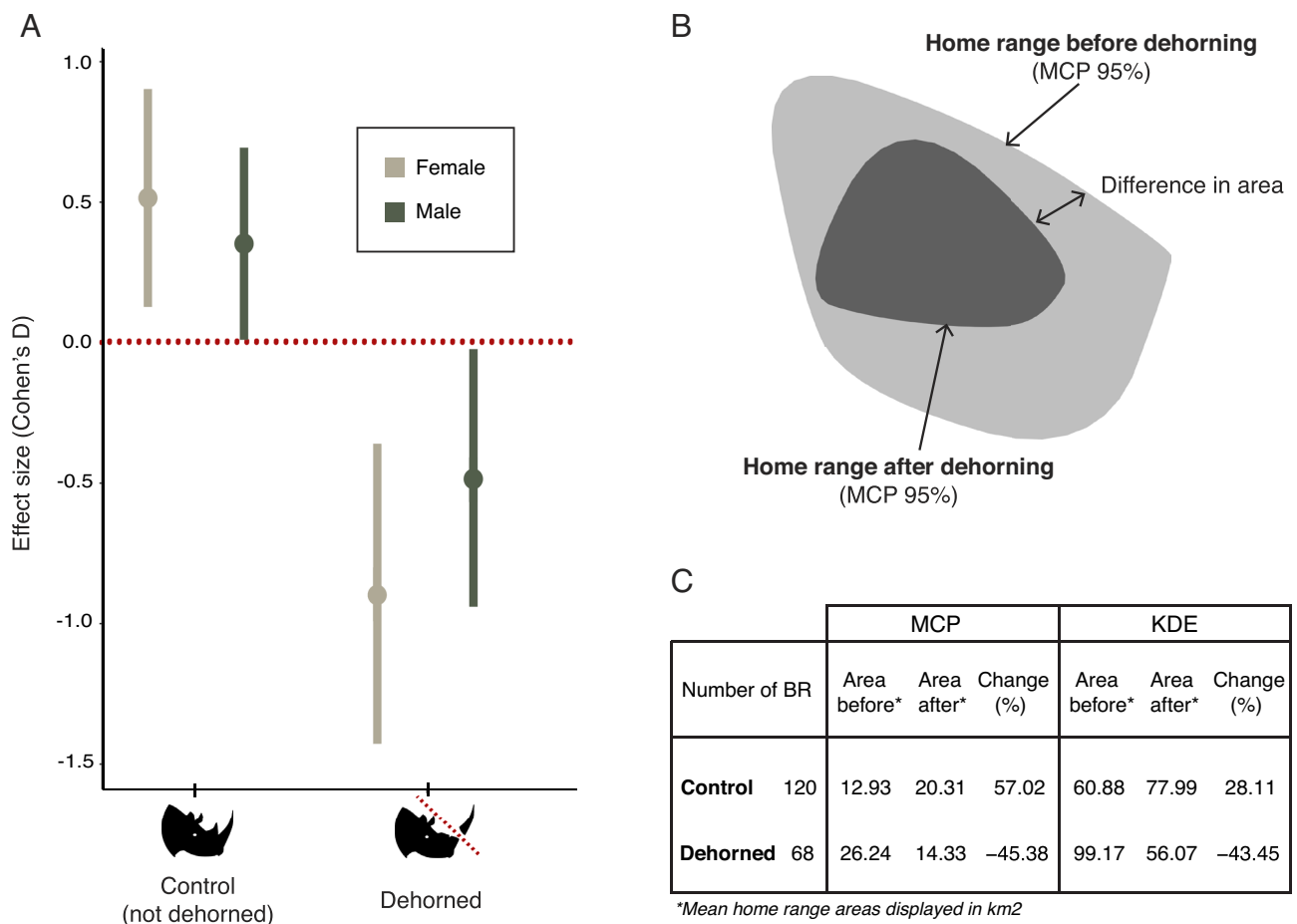


Fig. 2. Changes in black rhino home-range size after dehorning. (A) Dot plot showing average ($\pm 95\%$ CI) change in home-range area in horned control animals (Left) versus dehorned animals (Right) for both female (tan; control $N = 53$, dehorned $N = 30$) and male (green; control $N = 67$, dehorned $N = 38$) black rhinoceros, derived from minimum convex polygon (MCP 95%) calculations of effect sizes using Cohen's D with Hedge's correction [*Materials and Methods*, see *SI Appendix*, Fig. S4 for analogous results using kernel density estimates (KDE)]. (B) An example home-range size change for a randomly selected black rhino (MPGRBM-06-05), showing the home range before (light gray) and after (dark gray) dehorning. (C) Summary table showing the mean areas (km^2) of control and dehorned black rhino home ranges calculated with 95% MCP and 95% KDE and the number of black rhino in each group, across all reserves. The change (%) shows the percentage of increase or decrease in area between periods (see *SI Appendix*, Tables S1 and S2 for tables of mean area by sex and reserve).

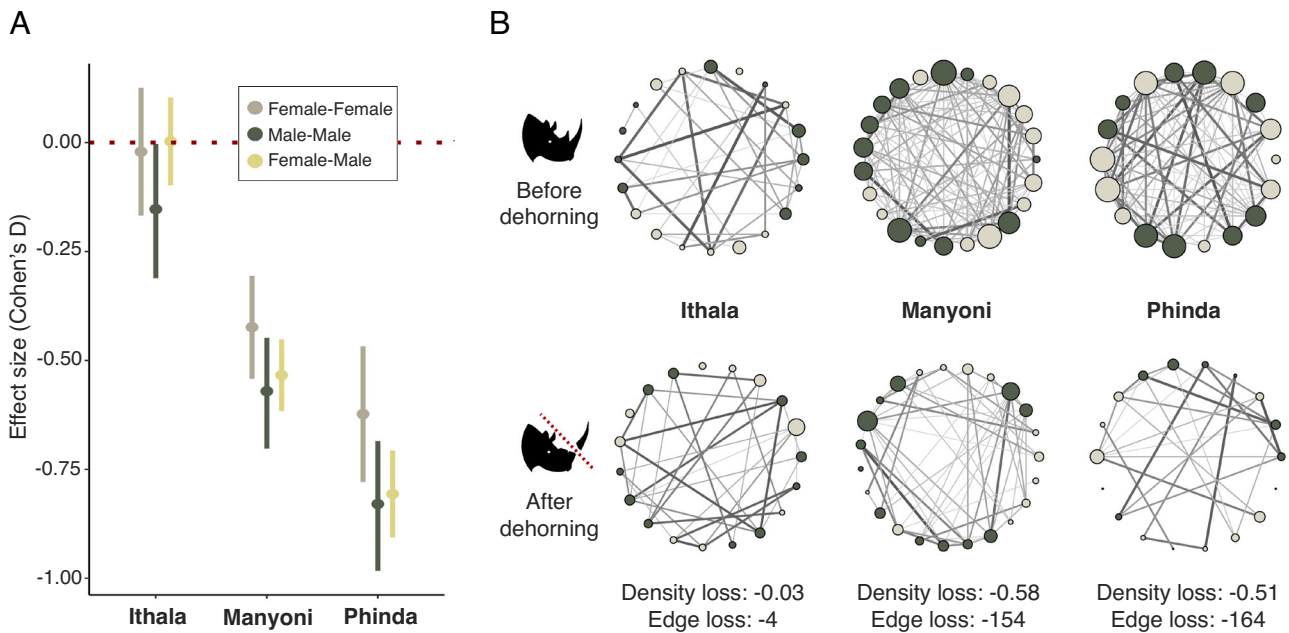


Fig. 3. Changes to black rhino social structure after dehorning. (A) Dot plot showing average ($\pm 95\%$ CI) change in social interaction strength (effect size; Cohen's D) for female–female (tan), male–male (green), and male–female (yellow) interactions in three reserves (Ithala, $N = 20$; Manyoni, $N = 23$; Phinda, $N = 18$) after dehorning, calculated based on an overlap of 95% MCPs. (B) Interaction networks showing social connectivity in the same three populations before (Top) and after (Bottom) dehorning. Each node (edge) is an individual and lines (edges) represent an interaction between two individuals, with a gradient of line thickness illustrating the strength of interaction (the amount of overlap). The size of the nodes is proportional to the number of connections each individual has. Edge and density loss correspond to the number of disappearing nodes and lines, respectively, after dehorning.

social structure was also evident from the interaction network structure (Fig. 3B), which revealed that dehorning decreased both the total number of social interactions (that is, network density) and the number of rhinos engaging in social interactions (that is, edges of the network diagram) strongly in Manyoni and Phinda and less so in Ithala.

These changes to social interactions varied by sex, with those involving males (particularly male–male interactions) being most affected by dehorning with a significant reduction at all the three sites (Fig. 3). That the Ithala population, the most recently dehorned population (Ithala in 2018, Phinda in 2017, Manyoni in 2016), underwent the smallest changes in social interactions may indicate that there is a time lag in the black rhino response to dehorning—although this is speculative and requires further validation. These results remained robust with a more restrictive analysis based on core ranges (corresponding to the most central and frequently used areas of the home ranges; *SI Appendix, Fig. S8*). More generally, these findings show that dehorning black rhinos leads to not only a decrease in their home-range size, but also a decline in the number and strength of their social interactions, especially for male rhinos.

Discussion

Dehorning is an antipoaching measure that has become popular as a rapid way to safeguard remaining black rhino populations but with hitherto unknown consequences for black rhino ecology (13). Here, we show that dehorning black rhinos is correlated with a reduction in mortality from poaching and does not induce an increase in natural mortalities. However, causation between dehorning and poaching reduction is yet to be determined and remains a pivotal question for future research. Disentangling complex socioeconomic factors is necessary to fully ascertain whether and why dehorning contributes to deterring poaching. The fact that deaths due to poaching were consistently lower through time

in the study sites than nationally could be linked to multiple characteristics such as smaller reserve size, better monitored populations, or less criminal activity in the region at the time.

Black rhinos use horns for a variety of purposes, from pulling down trees and branches (21), to scratching the ground for mineral nutrition (30), to self-defense (21), and enhancing male social status (22). Yet, while it follows that dehorning black rhinos should impact black rhino behavior, evidence for such impacts to date comes from a small number of studies on a small number of individuals and is not unanimous (22, 26, 28, 33, 34). Here, we show that dehorning has clear effects on black rhino behavior at both the individual and population levels. Such effects must be driven by even more granular cognitive and social behavioral changes, although we are unable to evaluate these in the present study. For instance, if rhinos stripped of their main armament signal vulnerability to others (22), then they may choose to retreat into smaller territories to avoid confrontations with competitors (24, 35–37) or other megaherbivore species such as elephants (35, 38). Regardless of the mechanism, by reducing both the size of home ranges and the frequency of social interactions, dehorning rhinos impacts processes important to population dynamics, raising questions about the long-term consequences for the species.

Behavioral plasticity plays an important role in the adaptation, or maladaptation, of a species to rapidly changed environmental conditions, such as due to anthropogenic disturbance (39, 40). That dehorned black rhinos display considerably reduced home-range sizes and engage in fewer social interactions might have cryptic but powerful population-level consequences for at least three reasons. First, black rhino home ranges are governed by both social interactions and resource availability (15), so dehorning could force animals into ecological traps (40) such as smaller habitats containing less or lower quality browse—with unknown consequences for individual survival and reproduction. Alternatively, smaller home ranges could also mean increased carrying capacity, with reserves able to sustain larger populations,

and decreased fighting within the species (36, 37), possibly even leading to a reduction in natural mortality. Second, changes in the number and strength of black rhino social interactions have the capacity to alter patterns of dominance and reproductive success among individuals—with potentially large implications for demographic processes. Third, by reducing the size of home ranges and limiting explorative behaviors and dispersal (41), dehorning may impair black rhino recruitment across landscapes, which is already slow (41, 42).

These considerations have direct implications for conservation management, which is typically informed by metapopulation structure and habitat carrying capacity estimations (43–45). Dehorning could alter carrying capacity calculations directly while also making the process of selecting candidates for translocation (that is, individuals that show signs of imminent dispersal) more challenging. Despite this, with the more recent (since 2021) escalation in poaching (46), the lack of evidence that dehorning increases natural mortality, and the lengthy agenda necessary to implement long-term measures (47), dehorning remains an option readily available to wildlife practitioners to buy time for this critically endangered species.

In conclusion, we suggest that while dehorning may yet prove to be an essential antipoaching measure, it must be implemented with extreme caution and be accompanied by rigorous monitoring to understand its long-term impacts on black rhino populations and evaluate its true success as a poaching deterrent. Future ecological and behavioral research regarding the ramifications of such a tool must be undertaken imperatively to assess their net effect on black rhino population persistence. In the broader picture, evaluating the effect of conservation interventions and human-induced rapid environmental change through animal behavioral indicators, such as home-range use (48, 49), is important as it can serve as an early impact indicator for cryptic consequences (39, 49, 50) and enables adaptive management.

Materials and Methods

Global Population. Global black rhinoceros population data from IUCN were used to illustrate the decline of black rhinoceros over time and construct Fig. 1A. The data were retrieved on the publicly available IUCN red list of threatened species website (<https://www.iucnredlist.org/species/65571/152728945#population>).

Study Populations. We gathered monitoring data from 10 reserves in north-eastern South Africa that hosted a total of 368 black rhinos to assess the impact of dehorning on black rhino ecology over space and time. The focal game reserves were the following: Manyoni Private Game Reserve, Ithala Game Reserve, Phinda Private Game Reserve, Pongola Game Reserve, uMkhuzo Game Reserve, Weenen Nature Reserve, Thanda Private Game Reserve, Ndumo Game Reserve, Tembe Elephant Park, and Somkhanda Community Game Reserve. These reserve range in size from 42 km² to 340 km² (SI Appendix, Fig. S1) and each was home to between 4 and 42 black rhinos. The exact number per reserve is not specified here due to security reasons.

Dehorning. Dehorning, which started for most reserves in 2017, involved immobilizing individuals prior to horn removal, usually by means of a qualified veterinarian sedating animals from a helicopter by shooting a dart into the animals' rumps. Drugs used for the sedation were a 50/50 ratio of etorphine (e.g., 2 mg for an adult bull) and thiafentanil (e.g., 2 mg for an adult bull) combined with azaperone (40 mg) and hyaluronidase (2,500 iu) with dosage varying according to body size. Once immobilized, rhinos were placed in sternal recumbency and equipped with earplugs and a blindfold to limit sensory input. Chainsaws were then used to cut posterior and anterior horns to leave a stub length of at least 10 cm. Horn stubs were then smoothed with an angle grinder and treated prophylactically for infection and dryness. Sedation was reversed with intravenous naltrexone (10 to 20× the opioid dose). Respiration was monitored during the entire procedure (<20 min). On average, dehorning occurs after every 18 mo of horn regrowth.

Monitoring Data. In all study populations, each individual black rhino was marked with a unique set of ear notches for identification and monitoring. Monitoring occurred daily across all reserves and, when an individual was sighted and successfully identified, the GPS coordinates of its location were recorded. Demographic data such as birth, death, introduction, and removal dates for each animal were also documented, as are key life events, such as dehorning date, the size of the removed horn, and cause of death. For this study, we used monitoring data encompassing the period 2005 to 2020, which included over 24,760 observations of 368 black rhinos. We assembled multiyear (2005 to 2020) location data into a matrix containing the following information: longitude, latitude, date, rhino ID, state (horned/dehorned), birth date, sex, horn size, and reserve for each observation. Animals that were not dehorned were also included in the analysis as controls. Reserve boundary shapefiles were projected in QGIS and intersected with location data to exclude incorrect GPS coordinates.

Dehorning and Poaching Rates. We calculated the number of dehorned and horned animals using all individuals present in the reserves over the same period as for mortality calculations (see below) and calculated yearly proportions.

We used mortality data (date and cause) to calculate the number of deaths that occurred naturally and due to poaching collectively in all study populations yearly from when the study reserves started intensively monitoring and investigating the cause of death, that is from 2013 to 2020. From the beginning of this period, all rhinos were accounted for monthly, and their fate is known with certainty. In some cases (all of which were horned rhinos), the cause of death could not be determined because the carcass was discovered too late. The latter were categorized as “unknown” and the stacked bar chart in Fig. 1C is centered on this category so as not to visually affect the other categories. We performed a Chi-square test with the *chisq.test* function in R-3.5.3 to assess the association between horn state (horn, dehorn) and cause of mortality for the entire study period.

We calculated the yearly poaching offtake rate, that is the percentage of rhinos taken out of the populations due to poaching as the number of deaths due to poaching divided by the number of the total population in all reserves accumulated every year. To investigate and compare poaching trends in South Africa and focal populations, we analyzed the rhino poaching data (sourced from the Department of Forestry, Fisheries and the Environment of South Africa) along with rhino population numbers (sourced from various Conference of the Parties reports for species-specific matter for rhinoceroses) for South Africa. We calculated the poaching offtake rates—that is the number of animals illegally harvested divided by the total population—and compared the study sites and South Africa over time. We compared the poaching offtake rate for black rhino only in the study sites and across the whole of South Africa. There was no complete nationwide dataset for the yearly number of poached black rhinos in South Africa (such data only exist for white rhino and black rhino combined); however, based on sporadic data for some years where the number of black and white rhinoceros poached was detailed separately, we estimated that in general black rhinos accounted for 10% of all poached rhinos. We conducted a linear regression with the *lm* function in R-3.5.3 to test the correlation between the yearly dehorning frequency (proportion in percentage of dehorned) and the poaching offtake rate in the study sites.

We calculated natural offtake rate of black rhinos in the study sites over the same time period by calculating the yearly number of natural mortalities in the study sites divided by the yearly total population of black rhinos in the study sites and compared it to the poaching offtake rate and the proportion of dehorned black rhinos. Changes in offtake rate across years and study sites were tested with ANCOVA, with year as a continuous covariate, sites as a categorical factor, and a year*site interaction term with the *lm* and *anova* functions in R-3.5.3. Offtake rates were square root-transformed to meet homoscedasticity assumptions.

Changes to Home-Range Sizes. For each dehorned animal, we estimated home ranges and calculated their sizes before versus after the date they were dehorned. We focused on animals with more than eight months of data (covering dry, wet, and transitional seasons to account for seasonal variation) and 10 sightings in both periods to ensure sufficient home-range resolution (N = 68 individuals) (SI Appendix, Fig. S5). To account for temporal home-range shifts that occur naturally during an individual's lifetime (15, 29) and avoid overestimating home-range size, we reduced the maximum time window to two years for each period (SI Appendix, Fig. S3). We then balanced the number of observations between periods for the same animal by random sampling and calculated home

ranges for each period using both 95% kernel density estimators (KDE), which is a nonparametric method that estimates the probability density function of a distribution based on observed data points (51), and with the 95% minimum convex polygon method (MCP), which calculates the minimum convex polygon around a set of points representing the minimum area that contains all the data points and assuming that the animal's home range is convex and symmetrical (52) with the package *adehabitatHR* (53) in R-3.5.3 (54). Home-range change for each animal was quantified as the difference in area covered by each individual rhino between dehorned and horned periods and expressed using effect size (Cohen's D with Hedge's correction) for males and females separately with the package *effsize* (55). To ensure that the observed home-range change was not related to natural life-cycle variation or home-range shift, we additionally estimated a control home-range change for rhinos that were never dehorned (N = 120 individuals) (*SI Appendix, Fig. S6*) in the same fashion as for dehorned animals (*SI Appendix, Fig. S3*).

To estimate the reliability of the chosen sample size (number of individuals) and minimum number of sightings to calculate home ranges, we conducted a sensitivity analysis by progressively filtering individuals based on the minimum number of sightings (>10, >15, >20, >25, >30) and calculated home ranges as described above. The results show the same trend for all groups with intensity increasing with the number of sightings (*SI Appendix, Fig. S7*). Based on this, we cautiously elected a minimum number of sightings equal to 10 to conserve a large sample size of individuals, more representative of the large number of reserves in the study. As results and conclusions based on the above criteria for MCP and KDE calculations were equivalent (Fig. 2A and *SI Appendix, Fig. S4*), we only show the visual presentation of home ranges based on MCP calculations (*SI Appendix, Figs. S5 and S6*). This is to maintain reader clarity and because MCPs are generally considered more robust for the calculation of home ranges based on a limited number of sightings than KDEs (15).

Changes to Social Interaction Networks. To estimate the impact of dehorning on social structure, we constructed within-population interaction networks and compared them prior to and after dehorning events. To build comparable representative networks, we selected populations that possessed more than 15 animals that were present over the same timeframe in horned (that is, less than 5% rhinos dehorned) and dehorned (that is, more than 50% rhinos dehorned) periods. Based on these criteria, we retained three reserves that together contained 74 rhinos for which we had sufficient temporal overlap in the dataset. We then calculated 95% MCPs (and more restrictive core-range 50% MCPs to show robustness of results,

see *SI Appendix, Fig. S8*) for animals that had a minimum of ten observations in both periods, estimated the total strength of social interactions based on area of overlap between individual rhino home ranges (32), and computed effect sizes (Cohen's D with Hedge's correction) between horned and dehorned periods at each reserve separately for male-male, female-female, and male-female interactions. Finally, we compiled area overlap data into a pairwise matrix and built an interaction network based on circular layout using the *igraph* package (56), which we used to derive changes to the number of edges (that is, the number of rhinos engaging in social interactions) and network connectivity/density (that is, density of social interactions) between horned and dehorned networks.

Data, Materials, and Software Availability. Non-sensitive original and anonymised data and R scripts created for the study are available in a persistent repository (Dryad). Sensitive data regarding animal locations and abundances are available upon reasonable request by contacting the corresponding author (VD; vanessa.duthe@unine.ch).

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1. S. K. Wasser *et al.*, Combating transnational organized crime by linking multiple large ivory seizures to the same dealer. *Sci. Adv.* **4**, eaat0625 (2018).
2. B. R. Scheffers, B. F. Oliveira, I. Lamb, D. P. Edwards, Global wildlife trade across the tree of life. *Science* **366**, 71–76 (2019).
3. M. Cardillo *et al.*, Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239–1241 (2005).
4. D. Biggs, F. Courchamp, R. Martin, H. P. Possingham, Legal trade of Africa's rhino horns. *Science* **339**, 1038–1039 (2013).
5. W. J. Ripple *et al.*, Collapse of the world's largest herbivores. *Sci. Adv.* **1**, e1400103 (2015).
6. J. A. J. Eikelboom *et al.*, Will legal international rhino horn trade save wild rhino populations? *Glob. Ecol. Conserv.* **23**, e01145 (2020).
7. H. Cheung, L. Mazerolle, H. P. Possingham, D. Biggs, Rhino horn use by consumers of traditional Chinese medicine in China. *Conserv. Sci. Pract.* **3**, e365 (2021).
8. R. Emslie, IUCN, *Diceros bicornis*. The IUCN Red List of Threatened Species 2020. e16557A152728945 (2020) <https://doi.org/10.2305/IUCN.UK.2020-1.RLTS.T6557A152728945.en>. Accessed 22 April 2021.
9. D. W. S. Challender, D. C. MacMillan, Poaching is more than an enforcement problem. *Conserv. Lett.* **7**, 484–494 (2014).
10. J. R. Muntifering *et al.*, Harnessing values to save the rhinoceros: Insights from Namibia. *Oryx* **51**, 98–105 (2017).
11. E. C. Rubino, E. F. Pienaar, Understanding South African private landowner decisions to manage rhinoceroses. *Hum. Dimens. Wildl.* **23**, 160–175 (2018).
12. T. E. Lee, D. L. Roberts, Devaluing rhino horns as a theoretical game. *Ecol. Modell.* **337**, 73–78 (2016).
13. P. Lindsey, A. Taylor, *A Study on the Dehorning of African Rhinoceroses as a Tool to Reduce the Risk of Poaching* (South African Department of Environmental Affairs, Johannesburg, 2011).
14. M. S. Mitchell, R. A. Powell, Foraging optimally for home ranges. *J. Mammal.* **93**, 917–928 (2012).
15. R. D. Plotz, W. J. Grecian, G. I. H. Kerley, W. L. Linklater, Standardising home range studies for improved management of the critically endangered black rhinoceros. *PLoS One* **11**, e0150571 (2016).
16. J. N. Garnier, M. W. Bruford, B. Goossens, Mating system and reproductive skew in the black rhinoceros. *Mol. Ecol.* **10**, 2031–2041 (2001).
17. R. N. Owen-Smith, *Megaherbivores: The Influence of Very Large Body Size on Ecology* (Cambridge University Press, ed. 1, 1988) <https://doi.org/10.1017/CBO9780511565441>. Accessed 7 May 2021.
18. J. Goddard, Home range, behaviour, and recruitment rates of two black rhinoceros populations. *African J. Ecol.* **5**, 133–150 (1967).
19. P. C. Lent, B. Fike, Home ranges, movements and spatial relationships in an expanding population of black rhinoceros in the Great Fish River Reserve, South Africa. *S. Afr. J. Wildl. Res.* **33**, 109–118 (2003).
20. K. Adcock, "The relevance of "territorial" behaviour in black rhino to their population management" in *Proceedings of a Symposium on Rhinos as Game Ranch Animals* (Onderstepoort, South Africa, 1994), pp. 82–86, Figs. 1, table 1.
21. A. Nasoori, Formation, structure, and function of extra-skeletal bones in mammals. *Biol. Rev.* **95**, 986–1019 (2020).
22. J. Berger, C. Cunningham, Natural variation in horn size and social dominance and their importance to the conservation of black rhinoceros. *Conserv. Biol.* **12**, 708–711 (1998).
23. B. Cain *et al.*, Sex-biased inbreeding effects on reproductive success and home range size of the critically endangered black rhinoceros: Rhinoceros heterozygosity-fitness correlation. *Conserv. Biol.* **28**, 594–603 (2014).
24. W. L. Linklater, I. R. Hutcheson, Black rhinoceros are slow to colonize a harvested neighbour's range. *S. Afr. J. Wildl. Res.* **40**, 58–63 (2010).
25. M. H. Holden *et al.*, Increase anti-poaching law-enforcement or reduce demand for wildlife products? A framework to guide strategic conservation investments. *Conserv. Lett.* **12**, e12618 (2019).
26. M. D. Kock, M. Atkinson, *Report on dehorning of Black (Diceros bicornis) and White (Ceratotherium simum) rhinoceroses in Zimbabwe* (Department of National Parks and Wild Life Management, 1993).
27. A. Chanyandura, V. K. Muposhi, E. Gandiwa, N. Muboko, An analysis of threats, strategies, and opportunities for African rhinoceros conservation. *Ecol. Evol.* **11**, 5892–5910 (2021).
28. S. M. Kagande, L. K. Musarunwa, Conserving the African rhinoceros. *Biodivers. Conserv.* **23**, 497–502 (2014).
29. S. C. Tatman, B. Stevens-Wood, V. B. T. Smith, Ranging behaviour and habitat usage in black rhinoceros, *Diceros bicornis*, in a Kenyan sanctuary. *African J. Ecol.* **38**, 163–172 (2000).
30. A. T. A. Ritchie, The black rhinoceros (*Diceros bicornis* L.). *Afr. J. Ecol.* **1**, 54–62 (1963).

31. W. L. Linklater, K. Mayer, R. R. Swaisgood, Chemical signals of age, sex and identity in black rhinoceros. *Animal Behav.* **85**, 671–677 (2013).
32. F. Schwabe, T. Göttert, N. Starik, S. R. Levick, U. Zeller, A study on the postrelease behaviour and habitat preferences of black rhinos (*Diceros bicornis*) reintroduced into a fenced reserve in Namibia. *Afr. J. Ecol.* **53**, 531–539 (2015).
33. J. Berger, C. Cunningham, A. A. Gawuseb, M. Lindeque, “Costs” and short-term survivorship of hornless black rhinos. *Conserv. Biol.* **7**, 920–924 (1993).
34. S. G. Penny, R. L. White, D. M. Scott, L. MacTavish, A. P. Pernetta, No evidence that horn trimming affects white rhinoceros horn use during comfort behaviour and resource access. *Animal Biol.* **13**, 1–17 (2021).
35. G. F. Grether, K. S. Peiman, J. A. Tobias, B. W. Robinson, Causes and consequences of behavioral interference between species. *Trends Ecol. Evol.* **32**, 760–772 (2017).
36. L. C. Chimes, P. Beytell, J. R. Muntifering, B. Kötting, V. Neville, Effects of dehorning on population productivity in four Namibia sub-populations of black rhinoceros (*Diceros bicornis bicornis*). *Eur. J. Wildl. Res.* **68**, 58 (2022).
37. F. Patton, P. Campbell, A. Genade, The effect of dehorning adult male rhinos on the frequency of fighting at Ziwa Rhino Sanctuary. *Pachyderm* **59**, 114–115 (2018).
38. M. Landman, D. S. Schoeman, G. I. H. Kerley, Shift in black rhinoceros diet in the presence of elephant: Evidence for competition? *PLoS One* **8**, e69771 (2013).
39. A. Sih, Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. *Animal Behav.* **85**, 1077–1088 (2013).
40. M. A. Schlaepfer, M. C. Runge, P. W. Sherman, Ecological and evolutionary traps. *Trends Ecol. Evol.* **17**, 474–480 (2002).
41. C. Reid, R. Slotow, O. Howison, D. Balfour, Habitat changes reduce the carrying capacity of Hluhluwe-Umfolozi Park, South Africa, for Critically Endangered black rhinoceros *Diceros bicornis*. *Oryx* **41**, 247 (2007).
42. W. L. Linklater, A. Shrader, “Rhino management challenges: Spatial and social ecology for habitat and population management” in *Conserving Africa’s Mega-Diversity in the Anthropocene: The Hluhluwe-iMfolozi Park Story* (Cambridge University Press, 2017), p. 265.
43. T. J. Foose, “Global management of rhinos” in *Proceedings of an International Conference: Rhinoceros Biology and Conservation*, O. A. Ryder, Ed. (Zoological Society of San Diego, San Diego, CA, Citeseeer, 1993), pp. 32–47.
44. H. Hrabar, J. T. Toit, Dynamics of a protected black rhino (*Diceros bicornis*) population: Pilanesberg National Park, South Africa. *Animal Conserv.* **8**, 259–267 (2005).
45. S. M. Ferreira *et al.*, The status of rhinoceroses in South African National Parks. *Koedoe* **59**, 1–11 (2017).
46. Z. N. Nhleko, R. Ahrens, S. M. Ferreira, R. A. McCleery, Poaching is directly and indirectly driving the decline of South Africa’s large population of white rhinos. *Animal Conserv.* **25**, 151–163 (2021), 10.1111/acv.12720.
47. S. J. Selier, E. Minin, How to reverse the rhino poaching crisis: A commentary on Nhleko *et al.* *Animal Conserv.* **25**, 164–165 (2022), 10.1111/acv.12780.
48. N. Owen-Smith, J. W. Cain, Indicators of adaptive responses in home range utilization and movement patterns by a large mammalian herbivore. *Israel J. Ecol. Evol.* **53**, 423–438 (2007).
49. O. Berger-Tal *et al.*, Integrating animal behavior and conservation biology: A conceptual framework. *Behav. Ecol.* **22**, 236–239 (2011).
50. A. L. Greggor *et al.*, Research priorities from animal behaviour for maximising conservation progress. *Trends Ecol. Evol.* **31**, 953–964 (2016).
51. B. J. Worton, Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–168 (1989).
52. D. W. Hayne, Calculation of size of home range. *J. Mammal.* **30**, 1–18 (1949).
53. C. Calenge, The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Model.* **197**, 516–519 (2006).
54. R Development Core Team, R: A Language and Environment for Statistical Computing. (Vienna, Austria: R Foundation for Statistical Computing, 2018).
55. M. Torchiano, effsize, Efficient Effect Size Computation, R Package Version 0.8.1, (2020). 10.5281/zenodo.1480624.
56. G. Csardi, T. Nepusz, The igraph software package for complex network research. *Int. J. Complex Syst.* **1695**, 1–9 (2006).