





Resizing Kruger National Park: Trends in numbers of rhinoceroses within priority zones



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Species typically occupy fewer sites, and average population densities decline from the centre to the edge of a species' range when the range contracts. The poaching of rhinoceroses (rhinos) for their horn has degraded the black and white rhino populations in Kruger National Park (Kruger). Rhino populations have declined, and their distributions have contracted since 2010. We surveyed the black and white rhino populations in the Kruger during 2021 and 2022. We also identified core areas where rhino densities are greater and defined these as priority conservation zones. We then tested the prediction that population growth within priority conservation zones will exceed population growth beyond these zones for both black and white rhino. The results highlighted the continued decline of the white rhino population, while the black rhino population has stabilised since 2020. Growth rates were negative for white rhinos within priority conservation zones, but higher than those beyond these zones. For black rhinos, growth in priority conservation zones was positive and higher than those beyond zones. Priority conservation zones offer an opportunity to combat rhino poaching in a more tactical manner, concentrating resources on key areas for rhino survival.

Conservation implications: We highlight complementary approaches to the existing anti-poaching tactics that focus on exploiting easier access control, situational awareness, integrity and individual-based rhino monitoring when targeting priority conservation zones within Kruger.

Keywords: range contraction; priority conservation zones; black rhino; white rhino; Kruger National Park.

Introduction

The poaching of rhinoceroses (rhinos) for their horn has degraded the black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhino populations in Kruger National Park (Kruger) (Ferreira et al. 2021). The persistence of rhinos in Kruger is key to South Africa's rhino conservation effort (Ferreira et al. 2017). By 2017, South Africa was home to 86.5% of the African continental white rhino and 37.2% of the black rhino populations. By 2020, however, the contribution of rhinos within national parks in South Africa as well as continental populations has declined. Kruger contributed 14.2% and 24.6%, and other National Parks contributed 16.6% and 2.5% to South Africa's approximately 1900 black (*D. bicornis*) and 14400 white rhinos (*C. simum*), respectively (Ferreira & Dziba 2021).

Rhinos were locally extinct from Kruger for some time because of excessive hunting, until introductions in the 1960s (Southern white rhinos, *C. s. simum*) and 1970s (South central black rhinos, *D. b. minor*) (Mabunda, Pienaar & Verhoef 2003). The White rhino population had increased to ca. 10466 individuals (Ferreira, Botha & Emmett 2012), and the black rhino population had comprised 491 individuals by 2010 (Ferreira et al. 2017). Black rhinos were performing to biological capacity by 2008, growing at 6.75% per annum (Ferreira, Greaver & Knight 2011). Due largely to poaching, by 2020, both species populations had declined substantially (white rhino to ca. 2607 individuals, and black rhinos to 202 individuals) from a decade earlier (Ferreira et al. 2021).

Although poaching continues to be a key driver of these trends (Ferreira et al. 2015), other factors also influence the Kruger rhino populations. Droughts during the summer of 2015/2016, resulted in natural white rhino mortality doubling during the drought, and birth rates halving a year after, while black rhinos were seemingly unaffected by the droughts (Ferreira, Le Roex & Greaver 2019). Despite birth rates of black rhinos being resistant and those of white rhino

resilient to drought effects (Le Roex & Ferreira 2021), and a substantial reduction in poaching during lockdowns imposed during the coronavirus disease 2019 (COVID-19) pandemic, both species abundances continued to decline (Ferreira et al. 2021). Part of this may be attributable to indirect poaching effects, for example, the loss of an adult cow results in the loss of 0.5 dependent and 4.5 future calves (Nhleko et al. 2022). The black rhino population suffered a decrease in the proportion of calves from 2008 to 2018, probably attributable to a reduction in mate finding – individuals are unevenly distributed throughout the landscape, reducing interactions – population disturbance caused by social re-organisation from poaching and in-fighting or increased calf fatality because of injuries or mortality sustained from predation (Le Roex & Ferreira 2020). The result is that both black and white rhino populations occur in Kruger landscapes comprising ecological traps, optimal habitats and sub-optimal localities (Le Roex et al. 2020). These reflections help highlight that poaching disrupted the eruptive growth phase that the white rhino population was experiencing in Kruger prior to 2010, as well as prevented the black rhinos from entering the eruptive phase of population growth (Ferreira, Pienaar & Riley 2022).

Species typically occupy fewer sites within their range, and average population densities decline from the centre to the edge of a species' range when the range contracts (Lawton 1993). Poaching induces ecological traps when rhino poaching occurs in areas of suitable habitat for rhinos but the rhinos do not actively avoid risks of mortality resulting in absolute number of deaths exceeding the absolute number of births (Le Roex et al. 2020). This leads to spatial variation in impacts on local populations (Camaclang et al. 2017). Within a protected area like Kruger, the continued reduction in population sizes of both rhino species predicts range contraction within the park. We expect that population densities and, particularly the rates of change in the centre of rhino dispersion, would exceed those in areas on the edges of rhino dispersion within Kruger.

Here we estimated population sizes of black and white rhinos within Kruger during 2021 and 2022. We expected to see a continued decline in population growth for black and white rhino populations as poaching rates exceeded the poaching threshold of 3.6% of the population poached in a year – at values higher than this threshold, populations would decrease (Ferreira et al. 2022). We then defined priority conservation zones based on ecological trap theory (Le Roex et al. 2020), and estimated population trends in rhinos within each of these zones. We predict that population growth in priority conservation zones would exceed those noted for areas beyond these zones within Kruger. We use our results to provide reflection on requirements to enhance population growth within these priority conservation zones to help achieve positive rhino conservation outcomes.

Study area

Kruger has 35 different landscape types (Gertenbach 1983) and can be split into two main regions: northern Kruger and southern Kruger. Northern Kruger (north of the Olifants river) covers 10347 km² of savannas dominated by *Colophospermum mopane*. The geology also comprises granite and gneiss deposits in the west with nutrient-rich basalts in the east. Southern Kruger (south of the Olifants river), which is the focus of the 2021 and 2022 rhino population surveys, covers 9138 km² of low-lying savannas in South Africa. Annual rainfall exceeds 450 mm. Mixed *Combretum* and *Senegalia/Vachellia (Acacia) spp.* occur on granite and gneiss deposits, separated by Karoo sediment and while wooded *Sclerocarya caffra* and *Senegalia nigrescens* savannas dominate on basalts.

Research methods and design

Population estimates

We make use of plot-based sample techniques as well as applying mark-recapture approaches to obtain population estimates. Rhino aerial population surveys have been conducted for several years in Kruger. The protocol introduced in 2013 initially followed 3 km × 3 km blocks distributed randomly across Kruger (Ferreira & Greaver 2014). This design was adapted (but the flight specifications were retained) when the flight plan equated to more time spent moving to the next plot than time spent observing. In the 2021 and 2022 rhino population aerial surveys, 11 ranger sections were targeted from 15 August 2021 to 19 September 2021 and 15 August 2022 to 08 September 2022. A map of southern Kruger (south of the Olifants river) was overlaid with 6 km × 6 km blocks. Observers systematically completed transects comprising a 200 m observation strip, recording rhinos on each side of the helicopter within each block, with flights 45 m above ground at a speed of 120 km/h (65 knots). The survey team comprised of a pilot, a data recorder and two observers, positioned with the pilot and data recorded at the front of the aircraft with the two observers directly behind, allowing for two people on each side of the aircraft to make observations. The pilot used an aviation geographic positioning system (GPS), Garmin aera 660, to track the blocks and the 400 m transect strips. The survey team, having several years of experience conducting these surveys, assigned age and sexes to most individual rhinos encountered after recording the geographical position of the observation. Age classes (A to F) were assigned to all observed rhinos using relative body sizes, following the criteria set by the Rhino Management Group (Emslie, Adcock & Hansen 1995). In addition, the survey team checked for individual ear notches on black rhinos, recording and photographing for mark-recapture purposes and noted the status of horns (Kruger management has implemented a rhino dehorning programme since 2019 [Ferreira et al. 2022]) for each white and black rhino.

The geographical observations noted during the two aerial surveys, allowed us to associate current observations with the original 3 km × 3 km sample blocks defined in 2013

(Ferreira et al. 2015), and have been used since then to estimate black and white rhino population sizes. We extracted the sightings noted on these sample blocks to ensure consistency of estimation over time despite the adapted protocol. A revised quadrant sample estimator (Seber 2002) allowed us to estimate population sizes of both black and white rhino after analysts accounted for bias (see Ferreira et al. 2015 for the detail for correction of estimates for biases). We used the 2013 availability bias assessments (i.e. derived from relationships between vegetation cover) (Bucini et al. 2011) and rhino visibility (Ferreira et al. 2015) and the relationship between vegetation cover and the average normalized difference vegetation index (NDVI) within specific blocks at a specific time (Ferreira et al. 2018). Observer bias came from estimates made during a previous black rhino survey (Ferreira et al. 2011). Detectability bias was minimal given the size of observation strips or transects being narrower than those noted by previous studies (Kruger, Reilly & Whyte 2008) when the effect of detectability bias was negligible.

The second approach comes from us being mindful of the constraints of survey techniques when population sizes are changing and are of different sizes or densities – techniques require adaptation (Ferreira et al. 2017). For instance, black rhino mark-recapture estimates were more robust for low numbers than block counts (Ferreira et al. 2020). Minimum numbers known to be alive are even more pragmatic when numbers are extremely low, hence the consideration of ranger reports only for the northern parts of Kruger. Even so, we integrate estimates from block counts and mark-recapture techniques as part of transitioning estimation requirements when populations are declining, and sample constraints are realising.

The aerial survey and mark-recapture datasets provided an opportunity for integrating estimates. For white rhinos, we made use of information originating from a broadscale dehorning initiative that started during May 2019 (Ferreira et al. 2022). This provided a complementary mark-recapture opportunity to contribute to a consolidated population estimate for white rhinos. For this purpose, we extracted the dehorning records of individual rhinos held by Ranger Services as well as Veterinary Wildlife Services of South African National Parks (SANParks). We extracted the number of new rhinos dehorned at monthly intervals since January 2019 noting when an individual rhino was dehorned as part of following up and maintaining a dehorned status. The rate of rhino survival, month to month, was calculated as:

$$\left[1 - \frac{(d_{p,i} + d_{n,i})}{(c_p c_d)} \right]^{1/12} \quad [\text{Eqn 1}]$$

incorporating the observed annual poaching rate ($d_{p,i}$) and natural death rate ($d_{n,i}$) (Ferreira et al. 2021) throughout the year (i), with the carcass persistence rate in a year (c_p) and the detection rate of such carcasses (c_d) (Ferreira & Dziba 2023).

This allowed us to estimate the number of dehorned rhinos present during September 2021 as well as September 2022, assuming the worst-case poaching pressure being the same as that observed in a specific year i . We then subtracted the known poaching and natural deaths of dehorned rhinos that rangers recorded to get a conservative estimate of the dehorned rhinos still present within the park by September 2021 and 2022.

For black rhinos, we made use of information on individually marked black rhinos. Rangers have been marking black rhinos using ear notches since the start of 2016. We extracted the individual marking records from Ranger Services and Veterinary Wildlife Services and noted the number of black rhinos marked using ear notches monthly since January 2016. Like for white rhinos, we extracted the number of new marked black rhinos at monthly intervals. The rate of rhino survival, month to month, was calculated as:

$$\left[1 - \frac{(d_{p,i} + d_{n,i})}{(c_p c_d)} \right]^{1/12} \quad [\text{Eqn 2}]$$

incorporating the observed annual poaching rate ($d_{p,i}$) and natural death rate ($d_{n,i}$) (Ferreira et al. 2021) throughout the year (i), with the carcass persistence rate in a year (c_p) and the detection rate of such carcasses (c_d) (Ferreira & Dziba 2023). We then subtracted the known poaching and natural deaths of notched black rhinos that rangers recorded to get a conservative estimate of the black rhinos with ear notches present by September 2021 and September 2022.

The estimated number of dehorned white rhino and marked black rhinos represent the number of 'marked' (M) rhinos per species at the time of a survey in either September 2021 or September 2022. We then made use of the number of rhinos seen over the entire area south of the Olifants River (n) and the number of dehorned white and ear-notched black rhinos seen while doing the survey (m) to estimate population size (N) through the Lincoln-Petersen estimator:

$$(N = \frac{nM}{m}) \quad [\text{Eqn 3}]$$

as well as confidence intervals (CIs) (Ferreira et al. 2020). Our calculations made use of Microsoft® Excel.

The above procedure provided us with a Quadrant sample and Lincoln-Petersen estimate, each with CIs. This allowed us to obtain a model average and CIs through bootstrapping techniques (DiCiccio & Efron 1996). For this purpose, we randomly extracted a value from the statistical distribution defined by the point estimate and CI of both methods and obtained the average. We repeated these 1 million times and extracted the median as an estimate, and the 2.5th percentile as the lower confidence limit, as well as the 97.5th percentile as the upper confidence limit. This provided the estimate for the area south of the Olifants River.

Numbers of both rhino species are low in northern Kruger making sample-based surveys ineffective (Ferreira et al. 2017). We therefore asked Section Rangers to provide records of sightings and a minimum number known to be present by the middle of September 2021. We added these estimates to the estimates for southern Kruger and obtained an overall estimate for Kruger during 2021.

Conservation zones

To evaluate the predictions that rates of change in the centre of rhino dispersion should exceed those at the edge, we defined core zones that considered identified areas of ecological traps and safe havens (Le Roex et al. 2020), rhino dispersion within the park since 2017 and the distribution of young and adult cows (considered to be E- and F-class cows older than 6 years of age) for both species (Emslie et al. 1995; Hillman-Smith et al. 1986). We termed these conservation zones.

Our layered approach first focussed on filtering and retaining areas previously identified as 'safe havens' (Le Roex et al. 2020). Next, the focus was on using the annual rhino aerial survey data to identify the contraction of rhino dispersion within the park to local areas as numbers decreased. For this, we categorised, for each year, the range of observations within 3 km × 3 km blocks made by observers during surveys as relatively medium, medium-high and high incidences of observations for the last five surveys (2017 to 2021, Note ArcGIS provides an option to categorise) and combined. These allow us to get a convergence of where rhinos perceive core optimal habitat relative to other places, irrespective of the year. A third layer focussed on the relative medium, medium-high and high incidences of observations of E and F-class cows (Emslie et al. 1995; Hillman-Smith et al. 1986) as we wanted to account for compound effects, which realise in additional losses when poachers kill adult cows (Nhleko et al. 2022). These overlaying layers resulted in ratings with the highest in 'safe haven' areas that had high rhino densities and high adult cow presence.

The above analyses focussed on black and white rhino separately. Overlaying the top 75% of zone ratings for both black and white rhino helped define areas, where ratings score high for both species (Priority Zones) and areas where ratings were high for one species only (white rhino zone [WRZ] and black rhino zone [BRZ]). We then used existing management blocks with a qualifier that a zone should approximate 500 km² (Table 1). We reason that the two priority zones, a WRZ and a BRZ carry the highest level of value for rhino conservation and recovery potential within Kruger. Even so, we added two Lower Priority Zones defined as areas that had high historic rhino densities and where rhino recovery may be fast through colonisation of preferred habitats. These areas were typically ecological traps (Le Roex et al. 2020) where poaching pressure caused declines in areas with optimal habitat conditions.

Conservation managers identified an additional zone of experimentation to enhance rhino habitat (Management Zone). This did not overlap with any other identified zones. Areas outside these identified zones were classified as Beyond Zones South if these were south of the Olifants River and Beyond Zones North otherwise. Note that the Management Zone was retained as part of the Beyond Zones category.

Trends in conservation zones

Following the definition of zones, we revisited rhino data annually and estimated population sizes since 2013 for each zone. For this purpose, we assigned each of the original 3 km × 3 km sampling blocks to a specific conservation zone as defined above. We anticipated that in some years, observations will be low in a zone that imposes stochastic influences on estimates of variances. Instead, we calculated the proportion of rhino observations of a species that was noted within a zone for each year *i*. We then used the estimates and statistical distribution defined by the point estimate and the CI of the estimates that we collated or calculated for each year *i* since 2013 to extract a million estimates and apportion the number of

TABLE 1: Identified conservation zones for black and white rhino in southern Kruger National Park.

Rhinos	Area (km ²)	Safe haven	Number of white rhinos [†]	Number of black rhinos [†]	95% CI	Last 5-year exponential growth rate per annum [‡] (%)
White Rhinos						
Priority Zone 1	522	Yes	792	-	727–896	-14.6
Priority Zone 2	544	Yes	593	-	535–664	-20.4
White Rhino Zone	383	Yes	225	-	197–259	-2.6
Black Rhino Zone	490	Yes	149	-	121–178	-33.9
Lower Priority Zone South	208	No	35	-	23–48	-28.5
Lower Priority Zone North	476	No	117	-	88–149	-57.8
Black Rhinos						
Priority Zone 1	522	Yes	-	54	40–72	-31.8
Priority Zone 2	544	Yes	-	17	9–26	-4.4
White Rhino Zone	383	Yes	-	13	7–20	-42.4
Black Rhino Zone	490	Yes	-	41	31–64	-20.3
Lower Priority Zone South	208	No	-	0	0	-
Lower Priority Zone North	476	No	-	0	0	-

[†], Estimates of rhinos during September 2020; [‡], Trends by the end of 2020.

rhinos each time to a specific conservation zone in that specific year i .

To test our hypotheses, we grouped all estimates within zones separate from those beyond zones for each species. We then fitted a multi-phased exponential model:

$$N_{t+1} = \begin{cases} t \leq a, N_t e^{r_a t} \\ \text{if } a < t \leq b, N_t e^{r_b t} \\ b < t \leq c, N_t e^{r_c t} \end{cases} \quad [\text{Eqn 4}]$$

where N_t is the population size at time t , and r_a reflect different exponential growth rates in different eras defined by time a , b and c .

Ethical considerations

This article followed all ethical standards for research without direct contact with human or animal subjects.

Results

Population estimates

During 2021, observers counted 893 white rhinos on 163 of the 492 blocks of 3 km × 3 km in size that were part of the sample-based survey blocks since 2013 in southern Kruger. Observers encountered a further 575 white rhinos in areas beyond these original blocks. At the same time, observers counted 57 black rhinos present on 31 of the original sample survey blocks. There were an additional 84 black rhinos beyond the 3 km × 3 km sample blocks. Rangers north of the Olifants River, however, reported 32 white and no black rhinos from field records.

During 2022, observers encountered 715 white rhinos on 126 of the original blocks. Observers encountered a further 526 white rhinos in areas beyond the original blocks. At the same time, observers encountered 58 black rhinos present on 15 of the original sample survey blocks. There were an additional 55 black rhinos beyond the 3 km × 3 km sample blocks. Rangers north of the Olifants River, however, reported 1 black and 13 white rhinos from field records.

Since the start of 2019 to the start of September 2021, SANParks dehorned 676 individual white rhinos. Poaching pressure from January 2019 to September 2021 predicted 623 remaining. When we removed the known poached ($n = 29$) and dehorned rhinos that died naturally ($n = 14$), a total of 580 dehorned white rhinos were available for observers to see during the 2021 aerial survey. Of those, observers recorded 319 during the aerial survey. By September 2022, SANParks has dehorned 1503 individual white rhinos. Poaching pressure from January 2019 to September 2022 predicted 1397 remaining and thus available for observers to see during the 2022 aerial survey. Of those, SANParks recorded 982 during the aerial survey.

Since 2016 and by the start of September 2021, SANParks marked 157 black rhinos with individual ear notches. A total of 10 marked black rhinos were known to have died – it is not clear if these were natural deaths or poached rhinos. We estimated that by September 2021, 133 marked black rhinos were available to be counted. Of those, observers recorded 68 during the aerial survey.

These observations resulted in a detection rate of 0.70 (standard deviation [SD]: 0.012, $n = 1397$) of dehorned white rhinos during 2022 compared to 0.55 (SD: 0.021, $n = 580$) during September 2021. Average detection of white rhino individuals was thus 0.66 (SD: 0.022). For black rhinos, the detection rate of notched rhinos during the 2021 survey was 0.51 (SD: 0.043, $n = 133$) compared to 0.57 (SD: 0.108, $n = 21$) in 2018 (Ferreira & Pienaar 2020) and 0.60 (SD: 0.051, $n = 91$) in 2019 (Ferreira et al. 2020). Average black rhino detection is thus 0.56 (SD: 0.085).

Model averaging Jolly estimates from observations on the sample blocks and mark recapture estimates, together with observations submitted by rangers in northern Kruger translate to a total estimated 2250 (95% CI: 1986–2513) white rhinos living in Kruger by September 2021 and an estimated 1849 (95% CI: 1711–1988) by September 2022. This reflects decreases compared to the 2607 (95% CI: 2475–2752), which occurred in Kruger during September 2020. This represents a continued annual decline in line with the overall trends noted in recent years (Ferreira et al. 2021).

For black rhino, the 2021 survey estimated 208 (95% CI: 160–255) black rhinos occurring in Kruger with CIs overlapping the 2020 estimate of 202 (95% CI: 172–237; Ferreira et al. 2021). The 2022 aerial survey estimated 205 (95% CI: 149–261) black rhinos occurring in Kruger. This is the third survey with CIs overlapping previous surveys.

Conservation zones

Our analyses resulted in four Priority Zones. Priority Zone 1 (PZ1) comprising 522 km² (52195 ha) and Priority Zone 2 (PZ2) comprising 465 km² (46464 ha) are important for both white and black rhinos. An additional BRZ contain a core area of 490 km² (48990 ha) mostly for black rhino, while a separate WRZ focusses on 383 km² (38260 ha) mostly for white rhino. Identification of lower priority zones resulted in two additional zones (Table 1).

Trends in conservation zones

Since 2020, white rhinos declined at -16.50% per annum within the conservation zones compared to -29.2% declines in other areas (Figure 1). In two of the conservation zones (Low Priority Zone North and Low Priority Zone South), population growth was positive (Table 2). Priority Zone 2 continued to record declines, some of which may link to individual rhinos moving to the two low-priority zones. The white rhino population stabilised in the WRZ.

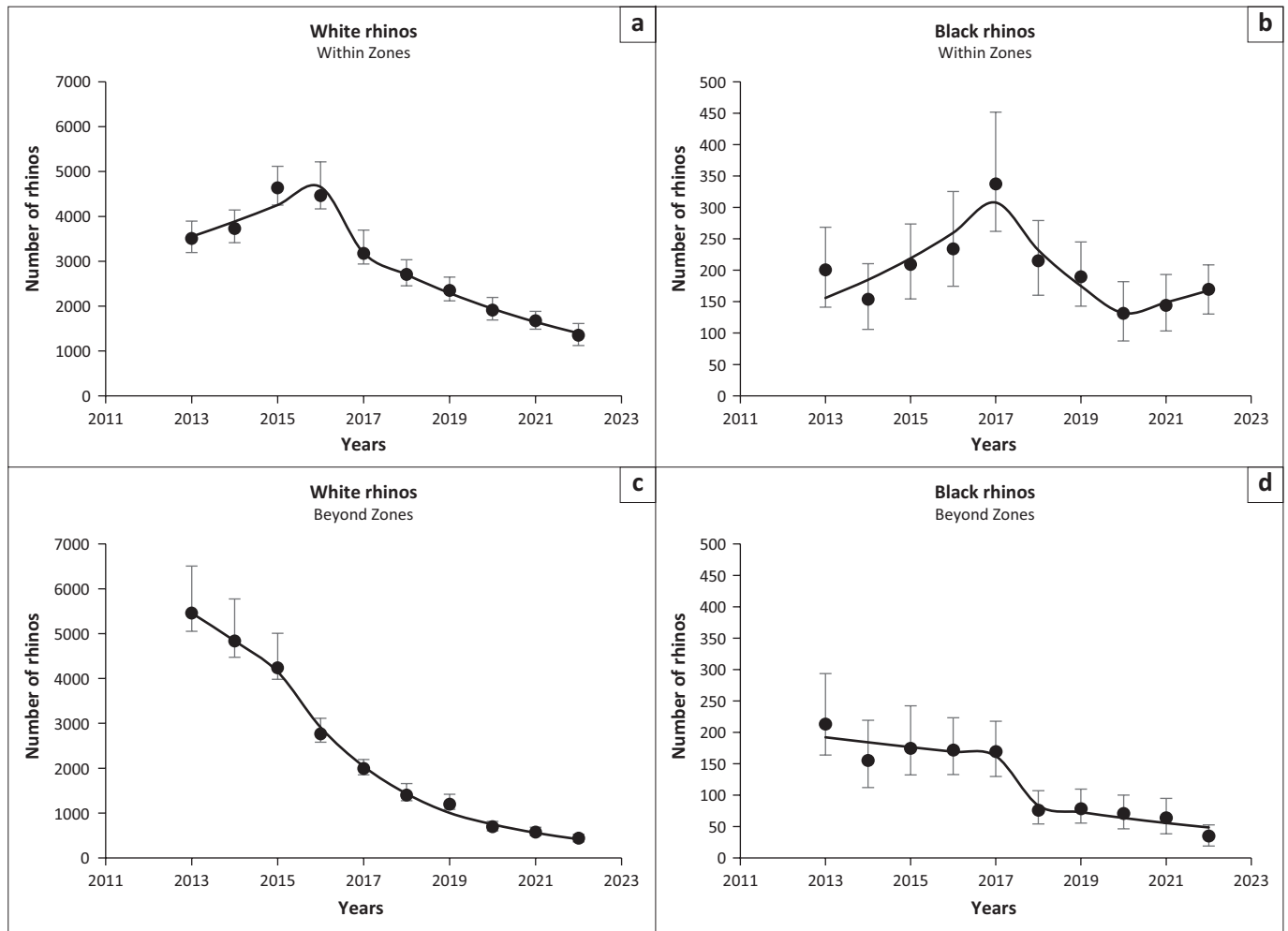


FIGURE 1: Trends of southern white rhinoceros (*C. s. simum*) and south-central black rhinoceros (*D. b. minor*) in Kruger National Park within the (a-b) focal rhino conservation zones compared to (c-d) areas beyond these zones.

TABLE 2: Changes in population trends within conservation zones for both black and white rhino.

Rhinos	Area (km ²)	Safe haven	Previous 5 year exponential growth per annum† (%)	Exponential growth per annum at 2021 (%)
White Rhinos				
Priority Zone 1	522	Yes	-14.6	-10.2
Priority Zone 2	544	Yes	-20.4	-23.2
White Rhino Zone	383	Yes	-2.6	-0.2
Black Rhino Zone	490	Yes	-33.9	-36.7
Lower Priority Zone North	208	No	-28.5	31.5
Lower Priority Zone South	476	No	-57.8	50.4
Black Rhinos				
Priority Zone 1	522	Yes	-31.8	29.7
Priority Zone 2	544	Yes	-4.4	1.4
White Rhino Zone	383	Yes	-42.4	14.6
Black Rhino Zone	490	Yes	-20.3	-36.9
Lower Priority Zone South	208	No	-	47.6
Lower Priority Zone North	476	No	-	-

†, Trends by the end of 2020.

Within the Conservation Zones, black rhino numbers increased since 2020 (12.0%) compared to other areas (-13.5%) in Kruger that exhibited declines. This associates with substantial increases in PZ1, PZ2 and the WRZ, with declines in the BRZ (Table 2).

Discussion

Global environmental change drivers, and in particular poaching, have consequences for rhinos and have thus become a serious conservation concern. Kruger has been strongly affected by one of these drivers – overharvesting and in this case, illegal killing of rhinos (Ferreira et al. 2018). Even so, the black rhino population in Kruger has fluctuated at approximately 205 individuals since 2020, a stark contrast to the declines noted in the decade up to 2020. Sadly, white rhino population sizes continued to decline, noted in the decade preceding 2020 (Ferreira et al. 2021).

A combination of various mechanisms and factors has led to the trends in the white and black rhino population numbers in Kruger. Apart from the direct poaching effects (Ferreira et al. 2018), indirect consequences through compound effects of dependent and future calf losses (Nhleko et al. 2022), social and mating disruption along with potential predation pressure (Le Roex & Ferreira 2020) following increased apex predator densities (Ferreira & Viljoen 2022), and different responses of white and black rhinos to droughts (Le Roex & Ferreira 2021) influenced trends of both species in varying ways. Mitigating risks

posed by human-induced threats thus take place in the context of several other influences.

An additional supposition is that the size of areas may play a key role. Kruger is a larger area requiring far more resources to aid in conservation and protection of rhinos. This could be accomplished through cost-efficient access control, situational awareness, enhanced staff integrity and detailed knowledge of individual rhinos in enhancing population performance (Ferreira & Dziba 2021). Most rhino populations in small areas (e.g., <1000 km² in size) containing relatively few individuals (e.g., <200 individuals) are increasing (Ferreira et al. 2022). The continental declines noted from 2017 to 2021 largely result from low performance in relative large areas (e.g., Kruger [Ferreira et al. 2021], northern Botswana [Department of Wildlife and National Parks 2022], and the Hluhluwe-Imfolozi Park [Singh & Olofinbiyi 2022]). In this context, rhino populations may benefit from 'resizing' Kruger to focus management on priority conservation zones of size <1000 km² in an attempt to gain the benefits of cost-efficient access control, situational awareness, staff integrity and detailed knowledge of rhinos (Ferreira & Dziba 2021).

The influences of various factors, such as preferred habitat, territory, mate availability and water availability, may also influence the dispersion of black and white rhino in Kruger. With the contraction of rhino dispersion in Kruger, population growth beyond core conservation zones was substantially lower than within core zones, aligning with the predictions that range contractions made (Lawton 1993). These results highlight the need for new innovative complementary tactics, such as differential responses in ecological traps versus safe areas (Le Roex et al. 2020), strategic biological management tactics that displace poaching effort from cows, strategic biological management interventions that connect isolated cows with bulls and innovative messaging (Glenn, Ferreira & Pienaar 2019).

Defining priority conservation zones makes use of various data layers, including dispersion patterns as well as previously identified safe havens based on ecological trap theory (Le Roex et al. 2020), leading to six identified zones (the location of the zones have been held back for security purposes). Within these zones, population growth varied for both species. Even so, population growth in priority conservation zones exceeded that of noted for areas beyond these zones. We noted, however, that rhinos are responding to local conditions and are rapidly re-colonising areas in the eastern part of Southern Kruger where they were previously abundant. Here especially, high poaching pressures reduced rhino densities. During 2022, however, substantive increases were taking place in the two identified lower Priority Zones. These are areas previously occupied by high numbers of rhinos and thus reflect colonisation dynamics of suitable and preferred habitat in Kruger's eastern sections. This has implications for rhino protection in core areas – SANParks should include the two low-priority zones as key core areas.

SANParks previously and continue to make use of zoning approaches when it defined the Intensive Protection Zone (IPZ) in southern Kruger, the Joint Protection Zone (JPZ) in central Kruger and the Composite Protection Zone (CPZ) for northern Kruger (Shaw & Rademeyer 2016). These were primarily directed at ways to protect rhinos through anti-poaching and security responses. For instance, the IPZ relied heavily on changing the ranger corps to effective anti-poaching units using a range of force multipliers including various technologies. The IPZ also had the most rhinos. The CPZ focussed on collaborative partnerships both to the west and east of Kruger and gave birth to the Greater Kruger Environmental Protection Forum (GKEPF). Factors such as the size of the focal operational area that potentially made access control and situational awareness challenging (Ferreira & Dziba 2021), as well as compromised ranger integrity (Rademeyer 2023) reduced conservation effectiveness. Rhinos are now nearly absent from the CPZ – rangers reported to us less than 20 individuals, mostly white rhinos, per annum for the area north for the Olifants River. In both the JPZ and IPZ, rhinos substantially declined.

At the time of defining the IPZ, JPZ and CPZ, the populations comprised 8968 (95% CI: 8394–9564) white rhinos and 414 (95% CI: 343–487) black rhinos (Ferreira et al. 2015). A key factor in influencing conservation effectiveness for rhinos is detailed knowledge of rhinos, a feature maintained through monitoring of individual rhinos in smaller populations elsewhere (Ball et al. 2019). Individual level monitoring was impractical at such large population sizes at the time of defining the IPZ, JPZ and CPZ. The range contraction of both species within Kruger and focussing conservation actions on priority conservation zones would now allow individual-based monitoring (Muntifering et al. 2017).

These reflections suggest complementary changes in the rhino protection and conservation approaches to be taken by authorities in Kruger. These focus on exploiting the likely benefits of resizing operational areas into smaller zones, embedded within the existing JPZ and IPZ in southern Kruger where most rhinos reside. Optimal sized areas most likely enhance access control, situational awareness, maintaining proud staff with high integrity and monitoring rhinos at an individual level (Ferreira & Dziba 2021).

Tactics, however, could also take guidance from alternative approaches. For instance, finite games (Sinek 2019) are approaches that encounter conditions where players are known, rules are fixed and there is an end with winners and losers. The focus is on reporting statistics and what is best for an interest group. At present the tactical refocus of rangers to anti-poaching units carry many critiques of militarisation (Lunstrum 2014) and risks linked to it (Duffy et al. 2015). Infinite games are approaches that encounter conditions where players are known and unknown, there are no rules or endpoint and no winners or losers. The focus

is on leaving a legacy and what is best for a suite of stakeholders. This suggests complementary approaches such as community policing (Brogden & Nijhar 2013) tactics inclusive of co-designing approaches with people and rangers as the capable guardians (Miró 2014) within priority conservation zones.

The recently reviewed SANParks Rhinoceros Strategy (Ferreira et al. 2022) embraced these insights and implementation at Kruger focusses on protecting and securing rhinos in priority conservation zones. Within Kruger, SANParks seek to have a similar population at which eruptive growth started (i.e., 2700) by 2030, albeit some within Kruger and some elsewhere with rhinos sourced from Kruger (Ferreira et al. 2022), acknowledging constraints imposed by disease regulations following the emergence of bovine tuberculosis within rhinos (Kamath 2022). SANParks seek to maximise the recovery potential of black rhinos in Kruger by 2030 by having 300 black rhinos within Kruger by then. Our results highlighted how focus on priority conservation zones can help to achieve rhino conservation outcomes.

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Competing interests

The authors have declared that no competing interest exists.

Authors' contributions

S.M.F. contributed to conceptual design and writing; C.G. was responsible for supervising the aerial survey; C.S. for spatial data analyses; and E.T.C. for editing and article preparation.

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Data availability

The data that support the findings of this study and the conservation zone areas are not openly available because of the sensitivity of the species and are available from the SANParks data repository <https://www.sanparks.org/scientific-services/data-information-resources/data-repository> upon reasonable request.

Disclaimer

The views and opinions expressed in this article do not necessarily reflect those of SANParks or SANBI and the publisher.

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