Rhinoceros accounting in Kruger National Park, South Africa

Sam M. Ferreira [a,b,*], Luthando Dziba [c]

[a] Scientific Services, SANParks, Skukuza 1350, South Africa
[b] Department of Conservation & Marine Sciences, Cape Peninsula University of Technology, Bellville 7535, South Africa
[c] Conservation Services Division, SANParks, Pretoria 0002, South Africa

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ABSTRACT

Trends in rhinoceroses (rhinos) in Kruger National Park (Kruger) is of key concern. Poaching drives trends in the Park. Reconciling annual population estimates with yearly reports of poached carcasses fuels public critique. We account for trends in rhinos by extracting time series of estimates. Progressively modelling influences of management introductions and removals, effects of environmental variation and rhino density, direct impacts of poaching, consequences of imperfect carcass detection, and indirect impacts of deaths of dependent calves form the basis of accounting for rhinos. Models that considered all these influences explained 93% of white and 83% of black rhino population trends. In addition, the models predicted 2,515 white and 225 black rhinos, similar to estimates of 2,607 (95% CI: 2,475–2,752) and 202 (95% CI: 172–237) during 2020 respectively. The best model, however, predicts slow recovery with a white rhino population equivalent to pre-poaching achieved between 2030 and 2040. For black rhinos, recovery to pre-poaching population size would be between 2040 and 2050. The poaching onslaught in Kruger disrupted eruptive white rhino dynamics and prevented black rhinos from transitioning into eruptive dynamics. Authorities require innovative approaches within and beyond Kruger to help re-ignite rhino conservation.

1. Introduction

South-central black (*Diceros bicornis minor*) and southern white (*Ceratotherium simum simum*) rhinoceros (rhino) populations plummeted in Kruger National Park (Kruger) in the decade up to 2020 (le Roex and Ferreira, 2021) despite impressive anti-poaching initiatives (Rademeyer, 2018) and authorities reporting decreases in the number of poached rhino carcasses (DFFE, 2021). Accounting for these losses receives considerable public scrutiny (de Bruin, 2015), media attention (e. g. Stoddard, 2021) and queries through governance oversight mechanisms (PMG, 2021). Typically, politicians that are members of the opposition party and lobbying stakeholders cry foul play (e.g. de Bruin, 2015).

Complying with robust governance criteria does impose transparency and accountability (BIOA, 2009). Several critics argued overestimation of live rhinos (e.g. de Bruin, 2015). Critics also allege under-estimation of dead rhinos embedded within the formal annual statistics provided by authorities (BBC, 2021). So, do the numbers add up?

Obtaining population estimates for rhinos hinge on a large literature

(e.g. Seber, 2002) that guided surveying rhinos in Kruger formally quantifying biases and errors incorporated in methods (see Caughley, 1974) that provide the basis for official numbers. Availability, observer and detectability bias (Ferreira et al., 2011; Ferreira et al., 2015) as well as sample errors are explicit considerations in optimized sample surveys (Ferreira and Pienaar, 2020). These surveys provide the data for estimates and detecting trends (Ferreira et al., 2015, 2017; Ferreira, Greaver, Nhleko, & Simms, 2018; Ferreira, Greaver, Simms, & Dziba, 2021; Ferreira, le Roex, & Greaver, 2019; le Roex & Ferreira, 2021; Ferreira et al., 2011; Ferreira and Pienaar, 2020).

Accounting for the number of dead rhinos in Kruger suffers from several challenges. Authorities formally report carcasses based on the calendar year of detection of a poached rhino carcass (e.g. DFFE, 2021). This create mismatches on at least two counts. The time of detecting a carcass is not the time of death. Rangers, however, report the age of a carcass at the time of detection (Ferreira et al., 2019). In addition, rhino surveys take place during the late dry season in September each year (Ferreira and Pienaar, 2020). Poaching rates reported in the literature used the estimated date of death and record annual poaching rates based on the deaths that took place from one survey to the next (Ferreira et al.,

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2019).

Another element is that carcass detection is not perfect (Huso, 2011). Carcasses, particularly those of younger and hence smaller rhinos, can disappear before detection and are thus not available for detection later. Furthermore, rangers can make mistakes and not detect available carcasses at all during a reporting period. An associated element is the indirect effect of poaching that includes incidences of calves that depends on cows for milk and/or defence against predators or other rhinos that also die when poachers kill a cow (Nhleko et al., 2021). The realized number of rhinos that died because of poaching thus is naturally higher than what rangers realistically detect. Authorities and reporting systems (e.g. Barichievy et al., 2021; Emslie et al., 2019) that seek to account for rhinos would benefit from an understanding of these influences and allow appropriate responses.

Here, we account for the trends in black and white rhino populations in Kruger considering several accumulating influences. First, we extract rhino estimates from databases and published literature (Ferreira et al., 2011; Ferreira et al., 2015, 2017; Ferreira, Botha, & Emmett, 2012; Ferreira, Greaver, Nhleko, & Simms, 2018; Ferreira, Greaver, Simms, & Dziba, 2021; Ferreira, le Roex, & Greaver, 2019; le Roex & Ferreira, 2021; Ferreira and Pienaar, 2020), followed by extracting the history of rhino removals (Ferreira et al., 2012). From the literature (Ferreira et al., 2019; le Roex and Ferreira, 2021), we next extract estimated recruitment rates, death rates associated with natural and unknown causes, as well as poaching rates. Our next cumulative consideration for a bookkeeping model for Kruger rhinos focuses on accounting for estimated imperfect carcass detection to define fatalities associated with natural, unknown or poaching causes (Huso, 2011). Our final inclusion considers the estimated loss of dependent calves associated with the death of an adult cow (Nhleko et al., 2021). We predict that progressive inclusion of the variables improve models with population predictions for 2020 falling within the 95 % confidence interval of estimates derived from surveys during 2020 (Ferreira, Greaver, Simms, & Dziba, 2021).

Following the completion of accounting for rhinos in Kruger using a cumulative modelling approach, we use the recorded COVID-19 poaching pause noted for Kruger (Ferreira, Greaver, Simms, & Dziba, 2021) to reflect on recovery of the populations if authorities could recreate the poaching reduction benefits that accrued through South Africa's hard lockdown (DoH, 2020). We predict the outcome on a 30-year horizon for a COVID like effect. We do the same, and predict the outcome for a 30-year horizon for a scenario where poaching stopped all together.

2. Methods

2.1. Population estimates

Estimates of the population sizes of southern white and south-central black rhino made use of a variety of techniques (Ferreira et al., 2017; Ferreira, Botha, & Emmett, 2012; Ferreira, Greaver, Simms, & Dziba, 2021; Ferreira et al., 2011) since introductions started in 1961 and 1971 respectively (Ferreira, et al., 2011; Ferreira et al., 2012). We extracted estimates of both species from several sources (Ferreira et al., 2015, 2017; Ferreira, Botha, & Emmett, 2012; Ferreira, Greaver, Nhleko, & Simms, 2018; Ferreira, Greaver, Simms, & Dziba, 2021; Ferreira, le Roex, & Greaver, 2019; le Roex & Ferreira, 2021; Ferreira et al., 2011; Ferreira and Pienaar, 2020), followed by extracting the history of rhino removals (Ferreira et al., 2012). Estimates also had confidence intervals from formal estimation methods (Ferreira and Pienaar, 2020) and derivations from relationships between coefficient of variance and abundance noted before (Ferreira et al., 2012). The time series of population estimates of both species with confidence intervals thus acknowledge uncertainties as previously indicated because of four sources that all methods of counting experience (availability bias, observer bias, detectability bias and sample error; Caughley, 1974). We use the time series to construct population models that describe various influences as

well as checking how poaching effect a population from one year to the next.

2.2. Basic rhino population model

Populations change from year to year because of births, deaths, emigration and immigration (Sibly and Hone, 2002). These vital rates generate a population's growth rate from year to year. In Kruger, natural immigration and emigration do not play a major role. In the absence of any active management interventions, the population should thus change only because of the annual growth rate equivalent to the net difference between births and deaths.

Resources such as food and water, however, are exhaustible. Growth rate of a population decline as densities increase through effects that intra-specific competition have on resource use by individuals. For large mammals, density-dependence is concave (Sibly et al., 2005) when effects of reduced resource availability with increasing densities cascade into sequential effects on juvenile survival, fecundity schedules and ultimately adult survival (Eberhardt, 2002).

These theoretical dynamics form the basis of population models describing rhino dynamics given by

$$N_t = N_0 e^{\left(rt \left(1 - \frac{N_{t-1}}{K} \right) \right)}$$

and when translated to a single time step of $t = 1$ given by

$$N_{t+1} = N_t e^{\left(r \left(1 - \frac{N_t}{K} \right) \right)}$$

where N_t is the population at time t, r is the exponential growth rate and K is density at which growth will be zero.

We defined K using the estimates of 6500 kg.km^{-2} of white rhino biomass density at which annual population growth were zero in Hluhluwe-Imfolozi Game Reserve (Owen-Smith, 2007). Scaling by the adult female body mass (1600 kg; Skinner and Chimimba, 2005) as a standardized rhino unit, predicted a density of 4.07 n.km^{-2} for white rhinos in a landscape that received > 700 mm of rainfall a year (Berkeley and Linklater, 2010).

We scaled the expected density at which zero population growth may realize for Kruger down based on the relative lower average annual rainfall of 600 mm (Gertenbach, 1980) expecting a density of 3.38 n. km^{-2} for white rhinos. This aligns well with previous findings of reduced births and increase deaths of juveniles when rhino densities were higher than 3.00 n.km^{-2} in certain areas in Kruger (Ferreira et al., 2012). Converting this to a total population size across the 19,945 km^2 covered by the park suggest a K value of 69,451 white rhinos for Kruger National Park. We used this estimate as an input for the white rhino population model.

In savannas like Kruger, black rhino dietary needs scale to 3.76 browsing units per individual in a landscape that has 8.1 browsing units per 100 ha at 340 mm annual rain (Bothma et al., 2004). We used relationships of woody cover (F_c) potential explained by the mean wet season rainfall (P_w) and the severity of storms (α_w) ($F_c = 0.054P_w - 0.66\alpha_w - 0.0017P_w\alpha_w$; $r_2 = 0.65$; Good and Caylor, 2011) to obtain an estimate of the woody cover potential for Kruger with a mean annual rainfall of 600 mm (Gertenbach, 1980). We assumed severity of storms are similar – the study site of Bothma et al. (2004) and Kruger both share summer rainfall produced through thunderstorms. This predicted twice the woody cover potential in Kruger compared to the study site of Bothma et al. (2004). We could thus double the browsing units for Kruger to 16.2 units per 100 ha.

Bothma et al. (2004) provide estimates for browsing units for herbivore species. We extracted estimates for species co-occurring with black rhinos in Kruger. If all species were at equal density then the browsing units across Kruger require sharing across browsing units per

herbivore species. This result in 18.1 % of the total available browsing units allocated to black rhino. Not all species, however, live at equal density – densities (n/100 ha) and hence use of available browsing scales with body mass (m) ($\frac{n}{100ha} = \frac{10^{(-0.61log(1000m)+3.78)}}{100}$; Damuth, 1981). For black rhinos, this equates to 0.05455n/100 ha. This translates to 0.16 browsing units per 100 ha available for black rhino and converts to total *K* population of 3,199 black rhinos at which population growth will centre on zero.

2.3. Modelling progressive influences

2.3.1. Introductions and trends in the absence of interventions

The Kruger National Park had no rhinos since the early 1900s (Pienaar, 1970). Authorities introduced 351 white rhino between 1961 and 1969 (Ferreira et al., 2012) and 88 black rhinos between 1971 and 1975 (Ferreira et al., 2011). To accommodate this dynamic, effectively a management intervention that mimics immigration, we adapted the basic rhino population model as follows.

$$\text{Model 1}: \quad N_{t+1} = (N_t + N_{i,t\rightarrow t+1})e^{\left(r\left(1 - \frac{N_t + N_{i,t\rightarrow t+1}}{K}\right)\right)}$$

where $N_{i,t\rightarrow t+1}$ is the number of individuals introduced in the time step from time *t* to time *t + 1*. Authorities did very little active interventions. Since 1990, removals, however, was part of regular annual interventions for a variety of reasons (Ferreira et al., 2012). We thus used the point estimates of the time series and introduction history from 1961 to 1990 for white rhinos and 1971 to 1990 for black rhinos to fit Model 1 and estimate the growth parameter using maximum likelihood approaches (Pan and Fang, 2002). We then used the estimated growth parameter and forecast the rhino populations for 2020 using Model 1. This reflects what a point estimate of both black and white rhino would have been in the absence of management or poaching influences.

2.3.2. Accounting for management removal interventions

A key management intervention since 1990 was the removal of rhinos (Ferreira et al., 2012). Removals supported captive breeding programmes, range expansion establishing rhinos in their previous historical ranges, the sale of rhinos for revenue generation that served as the source of establishing private ownership elsewhere in South Africa (Clements et al., 2020), and the establishment of rhino strongholds as insurance investments for poaching onslaughts in Kruger (DFFE, 2016). To accommodate this dynamic, effectively a management intervention that mimics emigration, we adapted the basic rhino population model as follows.

$$\text{Model 2}: \quad N_{t+1} = (N_t + N_{i,t\rightarrow t+1} - N_{r,t\rightarrow t+1})e^{\left(r\left(1 - \frac{N_t + N_{i,t\rightarrow t+1} - N_{r,t\rightarrow t+1}}{K}\right)\right)}$$

where $N_{r,t\rightarrow t+1}$ is the number of individuals removed in the time step from time *t* to time *t + 1*. Removals of rhinos was primarily through management up to 2007 shortly before the poaching onslaught started (Rademeyer, 2018). We thus improved the model fitting and use the time series of point estimates and removal history from 1990 to 2007 for both species to fit Model 2 using a maximum likelihood approach as before (Pan and Fang, 2002). The Model 2 forecast for 2020 thus predicts what the point estimate of rhino populations would be when we accounted for introductions and removals.

2.3.3. Accounting for environmental and rhino density effects on births and natural deaths

We extracted recruitment and death rates from the literature (Ferreira et al., 2019; le Roex and Ferreira, 2021). Recruitment rate is the birth rate combined with the survival rate of calves during the first year. Recruitment rates come from information collected during annual surveys when observers note the age and sexes of observed rhinos allowing

extraction of the age and sex distributions. At the time of a survey in September of year *t*, the fraction of observations that are calves less than one year old allow an estimate of the number of calves less than one year old in the population at time *t*. Those calves are ones born and who survived during the year preceding the survey in September of year *t*. It means the population in September at time *t-1* produced the number of calves estimated in September at time *t*. Recruitment rate is then the number of calves in September of year *t* expressed as a fraction of the number of rhinos in September of year *t-1* (see Ferreira et al., 2019). The extracted recruitment rates allow us to estimate the number of calves recruited from time *t* to time *t + 1* ($N_{b',t\rightarrow t+1}$).

The extracted published death rates use a similar approach (see Ferreira et al., 2019) of the number of natural deaths recorded in the time from year *t-1* to year *t* expressed as a fraction of the population estimate in year *t-1*. This allowed us to estimate the total number of natural deaths recorded by rangers from time *t* to time *t + 1* ($N_{d',t\rightarrow t+1}$).

The finding of carcasses, however, is not perfect for three reasons (Huso, 2011). In the first instance, carcasses disappear before rangers find them due to normal carcass decomposition process (e.g. Coe, 1978). Carcass decomposition happens faster for smaller carcasses (Sutherland et al., 2013) and may depend on the density of scavengers such as spotted hyaenas, *Crocuta crocuta* (Tilson and Hamilton, 1984). Rangers typically find carcasses of sub-adult and adult rhinos. In a sample of 50 large carcasses of known age, carcasses persisted for 4.89 years (95 % CI: 4.20 – 5.60). In any particular year, the chance that a carcass will persist (c_p) is 89.8 % (95 % CI: 76.9 % – 100.0 %) (SANParks data available from an unpublished report by Scientific Services, SANParks, Skukuza - Ferreira et al., 2018. Evaluating the protection of rhinos from poaching).

In the second instance, observers will miss some of the carcasses that did not disappear and are still in the field in a period of observation. A double survey method (Fletcher and Hutto, 2006) helped us to estimate that rangers observed approximately 89.7 % (95 % CI: 88.3 % – 91.1 %) of carcasses (SANParks data available from an unpublished report by Scientific Services, SANParks, Skukuza - Ferreira et al., 2018. Evaluating the protection of rhinos from poaching) that did not disappear (c_o) because of decomposition and scavenger processes. A final aspect is the influence of the period of observation when observers search for carcasses provides. Imperfect detection is at a one-year interval (c_i) because rhino surveys takes place annually during September (see Ferreira et al., 2015).

The total probability of detecting a carcass of a rhino that died is then the product of carcass persistence (c_p), carcass observation (c_o) and the effective search interval (c_i) (Huso, 2011) (Table 1). Using these measures, we correct the total number of number deaths of adults and sub-adults recorded by rangers from time *t* to time *t + 1* to obtain an estimate of the total number of fatalities of adults and sub-adults from time *t* to time *t + 1*.

An additional consideration is the recorded effects of rhino density on survival and fecundity schedules (Ferreira et al., 2012) as well as environmental consequences for births and deaths (Ferreira et al., 2019; le Roex and Ferreira, 2021). Natural deaths of white rhinos increased in a drought, recruitment rates decreased a year later, but recovered two and three years later. Black rhinos appeared to suffer no detectable effects due to the drought (Ferreira et al., 2019; le Roex and Ferreira, 2021). Black rhino recruitment rates varied, but also declined as

Table 1

Parameter estimates used in the different sequential models. Value in parenthesis reflects 95% confidecne interval.

Parameter	Value	Reference
c_p	0.898 (0.769–1.000)	Ferreira et al., 2018. Evaluating the protection of rhinos from poaching. Unpublished Report, Scientific Services, SANParks, Skukuza
c_o	0.897 (0.883–0.911)	
c_i	1.00	
d_p	0.52	Nhleko et al. 2021.

densities decreased (le Roex and Ferreira, 2020) potentially due to increased predation when lion (*Panthera leo*) and spotted hyaena densities increased (Ferreira and Funston, 2020), or reduced mating opportunities (e.g. Courchamp et al, 1999), or social disruption of black rhinos by poaching (e.g. Tuyttens et al., 2000).

Estimated birth and death rates are available from 2009 onwards for white rhinos and for 2008, 2009 and 2013 onwards for black rhino (Ferreira et al., 2019; le Roex and Ferreira, 2021). We estimated birth and death rates for 2010 to 2012 for black rhino conservatively as the average annual rates recorded from 2013 to 2020. From 2008 to 2020 we could replace the $e^{\left(r\left(1-\frac{N_t+N_{i,t\to t+1}-N_{r,t\to t+1}}{K}\right)\right)}$ term of Model 2 by the estimated birth and death rates thereby accounting for the realized density and environmental influences on birth and natural death rates as follows.

a summary of the day of detection and/or day of death (SANParks data available from an unpublished report by Scientific Services, SANParks, Skukuza - Ferreira et al., 2018. Evaluating the protection of rhinos from poaching). We used the age of the carcass defined by rangers at the time of first detection based on various measures of the state of decomposition (e.g. Coe, 1978) to define the day of death and then calculate the number of poached rhinos in a rhino-year. A final aspect is that rhino carcass reports as part of formal statistics do not distinguish between the rhino species. We explicitly identify the species to obtain a species specific number of poached carcasses in a rhino year ($N_{p',t\to t+1}$). We incorporated all these considerations to define the number of detected carcasses in a rhino-year that we included in the model over the period 2008 to 2020 as follows.

$$\text{Model 3}: \quad N_{t+1} = \begin{cases} if\ t \leq 2007\ (N_t + N_{i,t\to t+1} - N_{r,t\to t+1})e^{\left(r\left(1-\frac{N_t+N_{i,t\to t+1}-N_{r,t\to t+1}}{K}\right)\right)} \\ else\ (N_t + N_{i,t\to t+1} - N_{r,t\to t+1}) + \left(N_{b',t\to t+1} - \frac{N_{d',t\to t+1}}{c_p c_O c_i}\right) \end{cases}$$

$$\text{Model 4}: \quad N_{t+1} = \begin{cases} if\ t \leq 2007\ (N_t + N_{i,t\to t+1} - N_{r,t\to t+1})e^{\left(r\left(1-\frac{N_t+N_{i,t\to t+1}-N_{r,t\to t+1}}{K}\right)\right)} \\ else\ (N_t + N_{i,t\to t+1} - N_{r,t\to t+1}) + \left(N_{b',t\to t+1} - \frac{N_{d',t\to t+1}}{c_p c_O c_i}\right) - N_{p',t\to t+1} \end{cases}$$

The Model 3 forecast for 2020 thus predicts what the point estimate of rhino populations would be when we also accounted for density and environmental influences on birth and natural death rates over the period from 2008 to 2020.

2.3.4. Accounting for detected poached carcasses

The detection of poached rhino carcasses have the same challenges as the detection of carcasses that died from natural causes. As indicated before, apart from these challenges, there are aspects of mismatches.

Model 4 forecasts rhino estimates that now also consider the number of detected carcasses in a rhino-year.

2.3.5. Accounting for imperfect detection of poached carcasses

The effect of imperfect carcass detection described for natural deaths is also very real for deaths caused by poaching. The next step in the model is then to include this effect on the number of deaths associated with poaching. We thus adapt Model 4 in our next progressive step as follows.

$$\text{Model 5}: \quad N_{t+1} = \begin{cases} if\ t \leq 2007\ (N_t + N_{i,t\to t+1} - N_{r,t\to t+1})e^{\left(r\left(1-\frac{N_t+N_{i,t\to t+1}-N_{r,t\to t+1}}{K}\right)\right)} \\ else\ (N_t + N_{i,t\to t+1} - N_{r,t\to t+1}) + \left(N_{b',t\to t+1} - \frac{N_{d',t\to t+1}}{c_p c_O c_i}\right) - \frac{N_{p',t\to t+1}}{c_p c_O c_i} \end{cases}$$

Governments typically reports carcasses for a calendar year (e.g. DFFE, 2021). Rhino surveys in Kruger, however, take place in September for a number of reasons (Ferreira and Pienaar, 2020). Understanding rhino population changes and accounting for poaching effects thus requires defining the observation period for detecting carcasses for the rhino-year from the middle of September (inclusive of 16 September) in year t to the middle of September in year $t + 1$ (inclusive of 15 September).

An additional mismatch aspect is that carcass reports are a mixture of

Model 5 now forecast rhino estimates that also accommodates the effects of carcass persistence (c_p), carcass observation (c_o) and the effective search interval (c_i) (Huso, 2011) (Table 1) on the detection of adult and sub-adult poached carcasses.

2.3.6. Accounting for the deaths of calves that depend on cows

Calves that are up to three years old typically depend on cows for nutrition until they are weaned just after year one and for defence

Table 2

Model selection results comparing progressive models inclusive of no interventions (No-Removal), removals added (+Remove), recent vital rates considered (+Rates), detected poaching events added (+Poached), imperfect carcass detection considered (+Detect) and calf dependency effect included (+Dependent). R_i^2 reflects the fit of a model i, $AICc_i$ provides the Akaike Information Criterion corrected for sample size effects for a model i; Δ_i is the difference between the $AICc_i$ value of model i and minimum $AICc_{i,\min}$ value of all models; g_i is the likelihood of a model, and w_i the relative weight of evidence for each model.

White rhinoceros					
Model	R_i^2	$AICc_i$	Δ_i	g_i	w_i
No-Removal	–	18.99	4.51	0.10	0.04
+Remove	–	18.58	4.11	0.13	0.04
+Rates	–	18.45	3.98	0.14	0.05
+Poached	0.95	14.47	0	1	0.34
+Detect	0.94	14.65	0.18	0.91	0.31
+Dependent	0.93	14.91	0.45	0.80	0.27
Black rhinoceros					
Model	R_i^2	$AICc_i$	Δ_i	g_i	w_i
No-Removal	0.19	11.06	1.42	0.49	0.13
+Remove	0.20	11.04	1.41	0.49	0.13
+Rates	0.26	10.99	1.35	0.51	0.13
+Poached	0.79	9.76	0.12	0.94	0.24
+Detect	0.81	9.67	0.03	0.98	0.25
+Dependent	0.82	9.64	0	1	0.25

against predators and/or other rhinos after they weaned until three years of age (Skinner and Chimimba, 2005). Effectively 52 % of calves that depend on cows will also die if poachers kill an adult cow (Nhleko et al., 2021) (Table 1). The final step in modelling progressive influences requires inclusion of additional deaths that the calf dependency effect (d_c) imposes on the population.

Identification of the gender of a poached carcass varies depending on the level of decomposition at the time of detection. In addition, rangers detect only adult and sub-adult carcasses. We assumed that poaching of sub-adult and adult rhinos is non-selective and the proportion of sub-adult and adult carcasses that are female would be equivalent to the proportion of sub-adult and adult live rhinos in the population. We extracted standing age distribution data noted for each year since 2009 for white rhinos, as well as 2008, 2009, and since 2013 for black rhinos from the SANParks data repository (https://www.sanparks.org/scientific-services/data-information-resources/data-repository). The data assigns individual rhinos into six age categories (A: ≤6 months, B: >6 months to 1 year; C: >1 year to 2 years; D: >2 years to 3.5 years; E: >3.5 to 7 years; F: >7 years; Hillman-Smith et al., 1986; Emslie et al., 1995). We use this information to estimate the proportion of E- and F-class rhinos that were female for each survey year t ($f_{p,t}$).

The extracted data also have records of E- and F-class cows that had calves. We could thus estimate the proportion of sub-adult and adult cows that had A-, B- and C-class dependent calves for each survey year ($d_{p,t}$). Using the proportion of E- and F-class cows that are female ($f_{p,t}$), a proportion of which have dependent calves ($d_{p,t}$) that would also die if poachers kill a cow (d_c) allowed us to include the calve dependency effect in our final model as follows:

Model 6 thus forecast rhino population sizes that considers all the accumulative effects.

2.4. Evaluating model fit

2.4.1. Identifying the best model

We make use of Aikaike Information Criterion (AIC) model selection (Johnson and Omland, 2004) to evaluate how well each progressive model explained rhino trends given the increased complexity. For this purpose, we calculated the residual sum of squares (*RSS*) from the difference in the model forecast for a specific year and the actual point estimate recorded for that year. We then used the small sample unbiased AIC (AIC_c) defined as follows:

$$AIC_c = -2ln\left[L\left(\widehat{\theta}_p|y\right)\right] + 2p\left(\frac{n}{n-p-1}\right), \quad with. ln\left[L\left(\widehat{\theta}_p|y\right)\right] = \left[\frac{-n}{2ln\left(\frac{RSS}{n}\right)}\right]$$

where n is the number of point estimates and p the number of variables included in a model (extracted from Johnson and Omland, 2004). We calculated the difference in the AIC_c scores of each model (i, $\Delta_i = AIC_{c,i} - AIC_{c,min}$) and that of the best model, *i.e.* the model that has the minimum AIC_c score. The likelihood of a model (g_i) given the observed point estimate data y, is then $L\left(g_i|y\right) = e^{\left(\frac{-1}{2\Delta_i}\right)}$. We used this to check the relative weight of evidence for each model (w_i) in the set of T models defined by

$$w_i = \frac{e^{\left(\frac{-1}{2\Delta_i}\right)}}{\sum_{j=i}^{T} e^{\left(\frac{-1}{2\Delta_j}\right)}}$$

2.4.2. Simplified model fit

We also calculated an index of fit irrespective of the complexity of a model, an approach that contribute to additional interpretation of a complex set of models. We made use of the adjusted R^2 measure defined as $R_{adj}^2 = 1 - \frac{\frac{RSS}{n-p-1}}{\sum_t \frac{(y_t - \bar{y})^2}{n-1}}$ where y_t is the observed point estimate at year t and $\bar{y}$ is the average observed point estimate over the entire time series of estimates (Johnson and Omland, 2004).

2.4.3. Model predictions

We checked how the best model forecasted rhino population sizes for both species for 2020 and then checked that against the population estimates obtained through aerial surveys during 2020 (Ferreira, Greaver, Simms, & Dziba, 2021). We expect that the best model should predict estimates within the 95 % confidence interval of the independently derived population estimates during 2020.

2.5. Predicting future scenarios

Evaluation of the influence of lockdowns imposed by various governments in response to the COVID-19 pandemic (see Cawthorn et al., 2021) resulted in short-term benefits of a reduction of 80 % in poaching
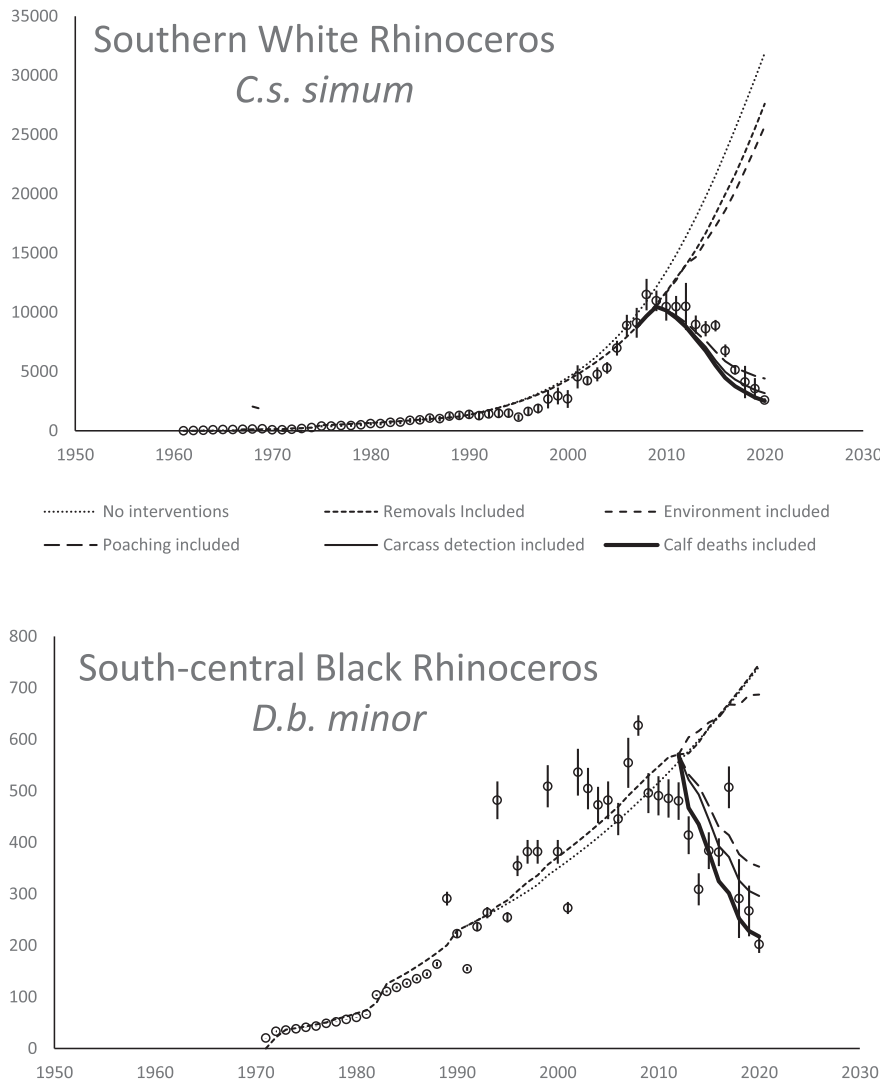
$$\text{Model 6}: \quad N_{t+1} = \left\{ \begin{array}{l} if\ t \leq 2007\ \left(N_t + N_{i,t \to t+1} - N_{r,t \to t+1}\right) e^{\left(r\left(1 - \frac{Nt + N_{i,t \to t+1} - N_{r,t \to t+1}}{K}\right)\right)} \\ \\ else\ \left(N_t + N_{i,t \to t+1} - N_{r,t \to t+1}\right) + \left(N_{b',t \to t+1} - \frac{N_{d',t \to t+1}}{c_p c_O c_i}\right) - \left(\frac{N_{P',t \to t+1}}{c_p c_O c_i} + \frac{N_{P',t \to t+1}}{c_p c_O c_i} f_{p,t} d_{p,t} d_c\right) \end{array} \right\}$$

Fig. 1. Time series of point estimates for rhinos extracted from the literature since introductions. The trend lines reflect different models. Blue reflects outcomes following introductions with no subsequent interventions. Black reflects outcomes following introductions and subsequent removals. Green reflects outcomes that include removal effects and the influence of environmental variability on recruitment and fatalities other than those caused by poaching. Brown reflects model outcomes when adding the detected poaching deaths. Red reflects model outcomes when adding the effect of imperfect carcass detection. Orange reflects model outcomes when also adding the dependent calf effect.

incidences (Ferreira, Greaver, Simms, & Dziba, 2021). We used the best model to predict the outcomes over a 30-year period if authorities manage to recreate the poaching reduction similar to a COVID-19 poaching pause, as well as if authorities manage to stop poaching altogether.

We used the population estimates reported for 2020 and the associated confidence intervals (Ferreira, Greaver, Simms, & Dziba, 2021) as input for the starting population size allowing the best model to run for 30 years. Parameter input relied on the average values and variance in these over the past 5 years estimated for recruitment, natural deaths, poaching deaths, imperfect carcass detection, proportion of sub-adult and adult rhinos that are cows and the proportion of cows with A-, B, and C-class calves to predict future numbers.

We made use of a Monte-Carlo simulation process (Hammersley and Handscomb, 1964). This required extracting a random value from the statistical distributions of the 2020 population estimates and various parameters and allowing the best model to make a time series forecast. We repeated this process 100,000 times and extracted the median population value for both scenarios for each year from 2021 to 2050. We also extracted the 2.5 % and 97.5 % percentile for each year that serve as the 95 % confidence interval for a specific year.

3. Results

Models that included poaching and associated effects had the highest weight in explaining the trends in populations of both species (Table 2). For black rhino, the model that included all the influences had the highest likelihood. The highest likelihood for white rhino was a model that included only direct poaching effects after accounting for removals and variance in vital rates.

For white rhinos, however, we focus on the model that included all the accumulative influences. Model weights for the models that included the additional accumulation of carcass detection and calf dependence was nearly equal to the model with the highest likelihood for white rhino. In addition, these more complex models had low difference in *AICc* values with the highest likelihood model for white rhinos (Table 2).

The model accounting for all the effects on white rhino trends explained 93 % of the white rhino time series since introduction and predicted a point estimate of 2,515 white rhinos during 2020 (Fig. 1), similar to the 2,607 (95 % CI: 2,475–2,752) actually estimated (Ferreira, Greaver, Simms, & Dziba, 2021). Allowing this model to play out a scenario of SANParks achieving a COVID-like level of situational awareness access control, integrity maintenance and disrupted supply chains, predicts 4,397 (3,948–4,877) white rhinos by 2030, 7,515 (6,237–8,790) white rhinos by 2040 and 12,203 (9,611–14,413) rhinos
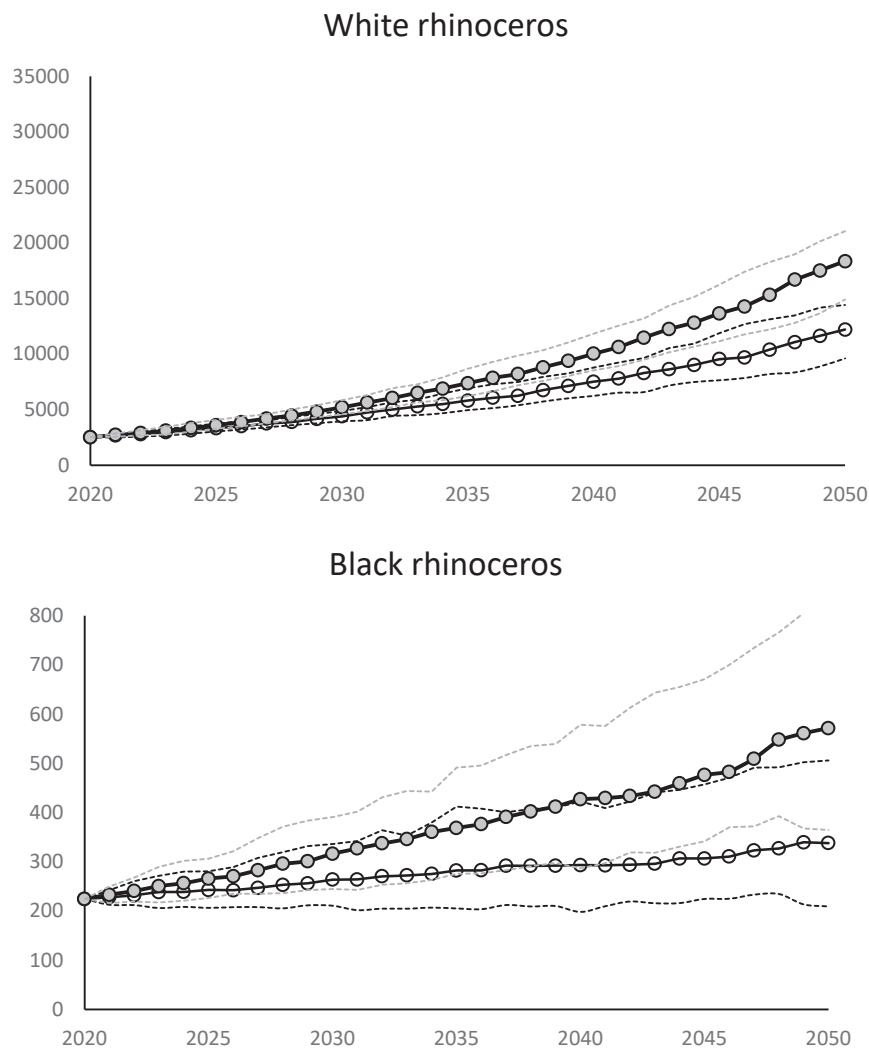
White rhinoceros

Black rhinoceros

Fig. 2. Predicted outcomes if authorities could mimic the COVID-19 poaching pause that introduced complete control over access, integrity and illegal supply chains (open symbols with dark broken lines for 95% confidence interval), or stop poaching all together (closed symbols with light broken lines for 95% confidence interval).

by 2050 given the influences on vital rates and calf dependency effects in the past ten years (Fig. 2). Achieving a zero poaching rate predicts 5,210 (4,587–5,836) white rhinos by 2030, 10,031 (8,550–11,828) white rhinos by 2040 and 18,340 (14,910–21,051) by 2050.

The black rhino model explained 83 % of the time series since introduction and predicted a point estimate of 225 black rhinos (Fig. 1), also similar to the 202 (95 % CI: 172–237) estimated during 2020 (Ferreira, Greaver, Simms, & Dziba, 2021). Achieving a COVID-like reduction in poaching pressure predicts 264 (211–336) black rhinos by 2030, 294 (198–423) black rhinos by 2040 and 338 (210–506) black rhinos by 2050 (Fig. 2). Achieving a zero poaching rate of black rhinos predicts 317 (245–391) black rhinos by 2030, 427 (287–578) black rhinos by 2040 and 572 (365–823) by 2050.

4. Discussion

Accounting for both black and white rhino that tracked the observed population estimates realized when models included all the influences. These included direct and indirect consequences of management, the environment, and illegal activities since introductions in 1961 and 1971 respectively (Ferreira et al., 2011; Ferreira et al., 2015, 2017; Ferreira,

Botha, & Emmett, 2012; Ferreira, Greaver, Nhleko, & Simms, 2018; Ferreira, Greaver, Simms, & Dziba, 2021; Ferreira, le Roex, & Greaver, 2019; le Roex & Ferreira, 2021; Ferreira and Pienaar, 2020). For both species, the chosen models predicted population sizes in Kruger that fell within the 95 % confidence intervals of estimates derived from surveys during 2020 (Ferreira, Greaver, Simms, & Dziba, 2021). Our approach thus provide an example of accounting for the trend in a population of a threatened species.

Accounting for the trends in charismatic species carries international importance. The African Rhino Specialist Group (AfRSG) and Asian Rhino Specialist Group (AsRSG) have a combined primary function of reporting on the status of rhinos on a global scale. A major contributor to African rhino estimates is Kruger where estimates have variable levels of precision generated by robust cost-efficient surveys (Ferreira and Pienaar, 2020). Carcass detection is also not perfect (Huso, 2011), while poaching records do not account for the hidden consequences such as deaths of dependent calves when poachers kill adult cows (Nhleko et al., 2021). These factors introduce uncertainty and conclusions about rhino trends at a global scale. Authorities can make Type I and II errors (I - concluding that a trend is occurring when it is not; II - concluding that a trend is not occurring when it is; Gerrodette, 1987) about trends in

rhinos. Such uncertainty introduces risks of designing inappropriate policies at various scales.

Our progressive modelling of both the black and white rhino populations in Kruger provides insight to help inform policies better. Apart from survey errors and various biases that introduce uncertainty in estimates (Ferreira and Pienaar, 2020), our best models account for influences of interventions (Ferreira et al., 2012), environmental variability (Ferreira et al., 2019; le Roex and Ferreira, 2021), direct influences of poaching (Ferreira et al., 2018), indirect influences of poaching (le Roex and Ferreira, 2020; Nhleko et al., 2021) and carcass detection errors (SANParks data available from an unpublished report by Scientific Services, SANParks, Skukuza - Ferreira et al., 2018. Evaluating the protection of rhinos from poaching). This approach represents the trends of white and black rhinos in Kruger since 1961 and 1971 respectively. Reporting the status of species inclusive of these confounding influences could improve informing policies.

Even though our model used extrapolated data for predictive purposes that carries risks (Baranyi et al., 1999), the ability of our model to track both white and black rhino populations well in Kruger provide some confidence in reflecting on the outcomes of at least two future interventions – achieving zero poaching or a COVID-19 like poaching pause (Ferreira, Greaver, Simms, & Dziba, 2021). Disregarding the intervention scenario, recovery to population sizes of both species equivalent to those in 2010 will take considerable effort and may only realize in 20 years at present dynamics even if authorities reduced poaching to zero.

Density-dependent population dynamics (Ferreira et al., 2012) impose different population growth rates as a population recover. Typically, recovering populations will grow relatively slow when populations are low relative to the expected equilibrium value around which population sizes would fluctuate. We noticed slow initial recovery, followed by higher growth rates. Since introduction of white rhino in 1961, it took nearly 30 years for the population to reach 1,381 (95 % CI: 1,075–1,687) by 1990. By 2000, 40 years after introduction, the population reached 2,683 (95 % CI: 1,933–3,433) and 10,466 (95 % CI: 9,302–11,630) by 2010 (Ferreira et al., 2012), 50 years after introduction. The realization of poaching effects (Ferreira et al., 2018) in the decade from 2010 to 2020 clearly disrupted eruptive dynamics of a recovering population.

The 30 years following the introduction of black rhinos in 1971 resulted in 382 (95 % CI: 337–427) by 2000. By 2010, 40 years after introduction, the population was 491 (95 % CI: 416–565) although estimates vary considerably more in the preceding decade (see Ferreira, Greaver, Simms, & Dziba, 2021). Poaching most likely prevented black rhinos to transition into eruptive dynamics.

Eruptive dynamics of recovering rhino populations may make key contributions to conservation targets. South Africa's Black Rhino Management Plan (Knight et al., 2013) envisaged 2,800 south-central black rhinos by 2020, of which Kruger's contribution (22 %) should have been 538 to 676 (Ferreira et al., 2017). Similarly, the White Rhino Biodiversity Management Plan for South Africa had 20,400 as a target (Knight et al., 2015) with Kruger expecting to contribute 9,854 to 10,232 (49 %) (Ferreira et al., 2017). The prevention of black rhino eruptive dynamics and the disruption of white rhino eruptive dynamics by poaching resulted in failure of Kruger's contribution.

Our model predicts relatively restrained recovery within Kruger. The 2020 white rhino estimates (Ferreira, Greaver, Simms, & Dziba, 2021) are equivalent to the estimates in 2000, a time when transition into eruptive dynamics were taking place. This suggest that authorities should consider ways to ensure that approximately 2,700 white rhinos are alive when poaching stops. Similarly, black rhinos may benefit if approximately 500 are alive by the time poaching approaches zero. It will allow the populations to transition into eruptive dynamics making up lost ground in terms of achieving rhino conservation objectives (Knight et al., 2013; Knight et al., 2015).

The declining trends noted for both rhino species in Kruger (Ferreira, Greaver, Simms, & Dziba, 2021) is not likely to reverse in the short term. For one, reducing poaching to zero or COVID-like levels carry significant logistical challenges and cost requirements primarily because of the size of Kruger (Ferreira and Dziba, 2021). This means that authorities may require establishing insurance populations for Kruger elsewhere for re-introductions when poaching stop that will then allow eruptive dynamics to boost rhino numbers. Such a complimentary approach effectively seek to exploit benefits that optimal sized areas provide for effective protection of rhinos while poaching continues (Ferreira and Dziba, 2021). Our analyses suggest having 1,350 white and 300 black rhinos in Kruger and another 1,350 and 300 respectively elsewhere may allow responses that initiate eruptive dynamics when poaching stops.

Numerous populations of rhinos beyond Kruger (Clements et al., 2020) originated through introductions from Kruger (Ferreira et al., 2012) – these are already potential insurance populations. Achieving insurance populations using Kruger stock, however, is challenging on two fronts. Removal of rhinos from Kruger will further influence the Kruger trends itself. In addition, the presence of bovine tuberculosis in some rhinos (Miller et al., 2018) limits translocation options. South Africa's animal disease regulations (RSA, 2002) impose significant and costly constraints, although not impossible, on using translocations to establish populations through founder populations elsewhere. The historic removal of rhinos from Kruger (Ferreira et al., 2012) that helped fuel range expansion of both species within South Africa (Clements et al., 2020), may thus play important roles in the recovery of rhinos in Kruger.

5. Conclusion

Accounting for rhinos require several pragmatic considerations that influence population estimates as well as detection of carcasses. In addition, key elements to consider includes further influences to poaching such as management introductions and removals, environmental variation, density feedback and indirect effect of poaching like the death of dependent calves. We illustrated that models that consider these influences adequately described dynamics of both black and white rhino addressing concerns raised by various critics (de Bruin, 2015; PMG, 2021).

Poaching disrupted rhino recovery (Ferreira et al., 2018) through disturbing the eruptive dynamics of white rhinos and preventing black rhinos to transition into eruptive dynamics. Ensuring critical population sizes by the time poaching stops are key requirements of maximize future recovery and mitigate the set-back of poaching on achieving rhino conservation objectives (Knight et al., 2013; Knight et al., 2015) and the contribution of Kruger to these (Ferreira et al., 2017).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Statement

Data is available from the SANParks Data Repository; Judith Botha, judith.botha@sanparks.org, https://www.sanparks.org/conservation/scientific_new/data_info_resources/ **Rhinoceros accounting in Kruger National Park, South Africa**

References

Baranyi, J., Pin, C., & Ross, T. (1999). Validating and comparing predictive models. *International Journal of Food Microbiology, 48*, 159–166. https://doi.org/10.1016/S0168-1605(99)00035-5

Barichievy, C., Altwegg, R., Balfour, D., Brett, R., Gordon, C., Henry, D., … Withers, O. (2021). A demographic model to support an impact financing mechanism for black rhino metapopulations. *Biological Conservation, 257*, Article p109073. https://doi.org/10.1016/j.biocon.2021.109073

BBC – British Broadcasting Corporation, 2021. Rhino poaching in South Africa falls during Covid-19 lockdown. https://www.bbc.com/news/world-africa-55889766/ (accessed 26 April 2021).

Berkeley, E.V., Linklater, W.L., 2010. Annual and seasonal rainfall may influence progeny sex ratio in the black rhinoceros. *African Journal of Wildlife Research* 40, 53-57. https://hdl.handle.net/10520/EJC117333.

BIOA – British and Irish Ombudsman Association, 2009. Guide to principles of good governance. http://www.bioa.org.uk/ (accessed 26 April 2021).

Bothma, J. D. P., van Rooyen, N., & van Rooyen, M. W. (2004). Using diet and plant resources to set wildlife stocking densities in African savannas. *Wildlife Soc. B., 32*, 840–851. https://doi.org/10.2193/0091-7648(2004)032[0840:UDAPRT]2.0.CO;2

Caughley, G. (1974). Bias in aerial survey. *J. Wildlife Manage., 38*, 921–933. https://doi.org/10.2307/3800067

Cawthorn, D. M., Kennaugh, A., & Ferreira, S. M. (2021). The future of sustainability in the context of COVID-19. *Ambio, 50*, 812–821. https://doi.org/10.1007/s13280-020-01430-9

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*, pe12741. https://doi.org/10.1111/conl.12741

Coe, M. (1978). The decomposition of elephant carcases in the Tsavo (East) National Park. *Kenya. J. Arid Environ., 1*, 71–86. https://doi.org/10.1016/S0140-1963(18)31756-7

Courchamp, F., Clutton-Brock, T., & Grenfell, B. (1999). Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution, 14*, 405–410. https://doi.org/10.1016/S0169-5347(99)01683-3

Damuth, J. (1981). Population density and body size in mammals. *Nature, 290*, 699–700. https://doi.org/10.1038/290699a0

de Bruin, L., 2015. Kruger rhino numbers in crisis, says expert. https://oxpeckers.org/2015/06/kruger-rhino-numbers-in-crisis-says-expert/ (accessed 26 April 2021).

DFFE – Department of Forestry, Fisheries and the Environment, 2016. Minister Edna Molewa highlights progress in the fight against rhino poaching. https://www.environment.gov.za/mediarelease/molewa_highlightsprogress_againstrhinopoaching/ (accessed 27 May 2021).

DFFE – Department of Forestry, Fisheries and the Environment, 2021. The department report back on rhino poaching in South Africa in 2020. https://www.environment.gov.za/mediarelease/rhinopoaching_sa/ (accessed 26 April 2021).

DoH – Department of Health. (2020). Directions issued in terms of Regulation 3(3) of the Regulations made under Section 27(2) of the Disaster Management Act, 2002 (Act No. 57 of 2002): Criteria to guide the determination of alert levels. *Government Gazette South Africa, 43599*, 3–5.

Eberhardt, L. L. (2002). A paradigm for population analysis of long-lived vertebrates. *Ecology, 83*, 2841–2854. https://doi.org/10.1890/0012-9658(2002)083[2841:APFPAO]2.0.CO;2

Emslie, R.H., Adcock, K., Hansen, H.B., 1995. Fine tuning the rhino management group age class system. Rhino Management Group, Rustenburg.

Emslie, R.H., Milliken, T., Talukdar, B., Burgess, G., Adcock, K., Balfour, D., Knight, M. H., 2019. *African and Asian Rhinoceroses – Status, Conservation and Trade. 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 (Rev. CoP17)*. http://www.rhinoresourcecenter.com/pdf_files/156/1560170144.pdf (accessed 26 April 2021).

Ferreira, S. M., Bissett, C., Cowell, C. R., Gaylard, A., Greaver, C. C., Hayes, J., … Zimmermann, D. (2017). The status of rhinoceroses in South African national parks. *Koedoe, 59*, 1–11. https://doi.org/10.4102/koedoe.v59i1.1392

Ferreira, S. M., Botha, J. M., & Emmett, M. C. (2012). Anthropogenic influences on conservation values of white rhinoceros. *Public Library of Science One, 7*, pe45989. https://doi.org/10.1371/journal.pone.0045989

Ferreira, S.M, Dziba, L., 2021. Where are rhinos safest? S. African Journa; of Science 117, 1-3. https://doi.org/10.17159/sajs.2021/11300.

Ferreira, S.M., Greaver, C.C., Knight, M.H., 2011. Assessing the population performance of the black rhinoceros in Kruger National Park. *African Journal of Wildlife Research* 41, 192-204. https://hdl.handle.net/10520/EJC117376.

Ferreira, S. M., & Funston, P. (2020). African lion and spotted hyaena changes in Kruger National Park, South Africa. *African Studies Quarterly, 19*(2), 37–50.

Ferreira, S. M., Greaver, C. C., Knight, G. A., Knight, M. H., Smit, I. P., & Pienaar, D. (2015). Disruption of rhino demography by poachers may lead to population declines in Kruger National Park. *South Africa. Public Library of Science One, 10*, pe0127783. https://doi.org/10.1371/journal.pone.0127783

Ferreira, S. M., Greaver, C. C., Nhleko, Z., & Simms, C. (2018). Realization of poaching effects on rhinoceroses in Kruger National Park, South Africa. *African Journal of Wildlife Research, 48*. https://doi.org/10.3957/056.048.013001

Ferreira, S. M., Greaver, C. C., Simms, C., & Dziba, L. (2021). The impact of a COVID-19 poaching pause on rhinoceroses. *African Journal of Wildlife Research, 51*(1), 100–110. https://hdl.handle.net/10520/ejc-wild2-v51-n1-a10.

Ferreira, S. M., le Roex, N., & Greaver, C. C. (2019). Species-specific drought impacts on black and white rhinoceroses. *Public Library of Science One, 14*, pe0209678. https://doi.org/10.1371/journal.pone.0209678

Ferreira, S.M., Pienaar, D., 2020. Evaluating uncertainty in estimates of large rhinoceros populations. Pachyderm 61, 97-108. https://pachydermjournal.org/index.php/pachyderm/article/view/8.

Fletcher, R. J., Jr., & Hutto, R. L. (2006). Estimating detection probablities of river birds using double surveys. *The Auk, 123*, 695–707. https://doi.org/10.1093/auk/123.3.695

Gerrodette, T. (1987). A power analysis for detecting trends. *Ecology, 68*, 1364–1372. https://doi.org/10.2307/1939220

Gertenbach, W. D. (1980). Rainfall patterns in the Kruger National Park. *Koedoe, 23*, 35–43. https://doi.org/10.4102/koedoe.v23i1.634

Good, S. P., & Caylor, K. K. (2011). Climatological determinants of woody cover in Africa. *Proceeding National Academy of Science USA, 108*, 4902–4907. https://doi.org/10.1073/pnas.1013100108

Hammersley, J.M., Handscomb, D.C., 1964. Monte Carlo methods, Methuen, London.

Hillman-Smith, K., Owen-Smith, R. N., Anderson, I. L., Hall-Martin, A. J., & Selaladi, J. P. (1986). Age estimation of the white rhinoceros (*Ceratotherium simum*). *Journal of Zoology, 210*, 355–379. https://doi.org/10.1111/j.1469-7998.1986.tb03639.x

Huso, M. M. P. (2011). An estimator of wildlife fatality from observed carcasses. *Environmetrics, 22*, 318–329. https://doi.org/10.1002/env.1052

Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology & Evolution, 19*, 101–108. https://doi.org/10.1016/j.tree.2003.10.013

Knight, M. H., Balfour, D., & Emslie, R. H. (2013). Biodiversity management plan for the black rhinoceros (*Diceros bicornis*) in South Africa 2011–2020. *Government Gazette South Africa, 36096*, 5–76.

Knight, M.H., Emslie, R.H., Smart, R., Balfour, D., 2015, Biodiversity Management Plan for The White Rhinoceros (*Ceratotherium simum*) in South Africa 2015-2020, Department of Environmental Affairs, Pretoria.

le Roex, N., & Ferreira, S. M. (2020). Age structure changes indicate direct and indirect population impacts in illegally harvested black rhino. *Public Library of Science One, 15*, pe0236790. https://doi.org/10.1371/journal.pone.0236790

le Roex, N., & Ferreira, S. M. (2021). Rhino birth recovery and resilience to drought impact. *African Journal of Ecology, 59*, 544–547. https://doi.org/10.1111/aje.12854

Miller, M.A., Buss, P., Parsons, S.D., Roos, E., Chileshe, J., Goosen, W.J., van Schalkwyk, L., de Klerk-Lorist, L.M., Hofmeyr, M., Hausler, G., Rossouw, L., 2018. Conservation of white rhinoceroses threatened by bovine tuberculosis, South Africa, 2016–2017. *Emerging Infectious Diseases* 24, p.2373. http://10.3201/eid2412.180293.

Nhleko, Z., McGleery, B., Ahrens, R., & Ferreira, S. M. (2021). The direct and indirect effects of poaching are driving rhino declines that can be recovered with reductions in poaching. *Animal Conservation (Early view).*. https://doi.org/10.1111/acv.12720

Owen-Smith, N., 2007. Introduction to modelling in wildlife and resource conservation. Blackwell Publishing, Malden.

Pan, J.X., Fang, K.T., 2002. Maximum likelihood estimation, in: Pan, J.X., Fang, K.T., Fang, K.T. (Eds.), Growth curve models and statistical diagnostics, Springer, New York, pp. 77-158.

Pienaar, U. D. V. (1970). The recolonisation history of the square-lipped (white) rhinoceros *Ceratotherium simum simum* (Burchell) in the Kruger National Park (October 1961-November 1969). *Koedoe, 13*, 157–170.

PMG – Parliamentary Monitoring Group, 2021. Poaching of South Africa's biodiversity; Annual Rhino Plan; Update on Elephant Master Plan; wild life economy; with Minister and Deputy Minister. https://pmg.org.za/committee-meeting/32334/ (accessed 26 April 2021).

Rademeyer, J., 2018. An unwinnable war: Rhino poaching in the Kruger, in: Reitano, T., Jesperson, S., de Lugo, L.B.R.B. (Eds.), Militarised Responses to Transnational Organised Crime, Palgrave Macmillan, Cham, pp 43-59.

RSA – Republic of South Africa, 2002. Animal Health Act, No. 7 of 2002. Government Gazette South Africa 445, 23675.

Seber, G.A.F., 2002. The estimation of animal abundance and related parameters, Second ed. Blackburn, Caldwell.

Sibly, R.M., Barker, D., Denham, M.C., Hone, J., Pagel, M., 2005. On the regulation of populations of mammals, birds, fish, and insects. Science 309, 607-610. http://10.1126/science.1110760.

Sibly, R. M., & Hone, J. (2002). Population growth rate and its determinants: An overview. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences, 357*, 1153–1170. https://doi.org/10.1098/rstb.2002.1117

Skinner, J.D., Chimimba, C.T., 2005. The mammals of the southern African sub-region, Third ed. Cambridge University Press, Cape Town.

Stoddard, E., 2021. In the war on rhino poaching, data shows private parks are doing a better job. https://www.dailymaverick.co.za/article/2021-02-09-statistics-show-rhino-poaching-in-south-africa-plunged-33-in-2020/ (accessed 26 April 2021).

Sutherland, A., Myburgh, J., Steyn, M., & Becker, P. J. (2013). The effect of body size on the rate of decomposition in a temperate region of South Africa. *Forensic Science International, 231*, 257–262. https://doi.org/10.1016/j.forsciint.2013.05.035

Tilson, R. L., & Hamilton, W. J. I. I. I. (1984). Social dominance and feeding patterns of spotted hyaenas. *Animal Behaviour, 32*, 715–724. https://doi.org/10.1016/S0003-3472(84)80147-5

Tuyttens, F. A. M., Delahay, R. J., MacDonald, D. W., Cheeseman, C. L., Long, B., & Donnelly, C. A. (2000). Spatial perturbation caused by a badger (*Meles meles*) culling operation: Implications for the function of territoriality and the control of bovine tuberculosis (*Mycobacterium bovis*). *The Journal of Animal Ecology, 69*, 815–828. https://doi.org/10.1046/j.1365-2656.2000.00437.x