

FEATURE PAPER

Poaching is directly and indirectly driving the decline of South Africa's large population of white rhinos

Zoliswa N. Nhleko^{1,2} , Robert Ahrens^{3,4}, Sam M. Ferreira² & Robert A. McCleery⁵

1 Interdisciplinary Program in Ecology, University of Florida, Gainesville, FL, USA

2 Savanna Node, Scientific Services, SANParks, Skukuza, South Africa

3 Fisheries and Aquatic Sciences Program, University of Florida, Gainesville, FL, USA

4 Fisheries Research and Monitoring Division, NOAA Pacific Islands Fisheries Science Center, Honolulu, HI, USA

5 Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, USA

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Correspondence

Zoliswa N. Nhleko, Interdisciplinary Program in Ecology, University of Florida, Gainesville, FL 32611, USA.

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Abstract

Large herbivores, particularly in water limited systems, are vulnerable to the impacts of poaching (illegal hunting) and human-induced climate changes. However, we have little understanding of how these processes can reshape their populations. With some rapidly declining populations there is a need to understand the effects of these stressors on populations of vulnerable large herbivores like the white rhino (*Ceratotherium simum simum*). We developed age-structured models for the rhino population in Kruger National Park, home to 49% of South Africa's rhinos. We wanted to determine the relative influence of poaching and climate on the current and future population size and demographics, examine the potential of a *dependency effect* (the loss of calves from poached females) and quantify the *compound effect* (loss of future young). Our results indicated that population declines were largely driven by poaching and included a *dependency effect*. Rainfall had a measurable but smaller influence on rhino populations and had an additive effect; reduced rainfall exacerbated poaching losses. Current poaching levels have resulted in a reduction to the lifetime reproductive output per cow from approximately 6 to 0.7 calves: a compound effect of 5.3 future offspring. Under current levels of poaching, we project a 35% decline in the Kruger rhino population in the next 10 years. However, if poaching intensity is cut in half, we project a doubling of the current population over the same time frame. Overall, our models showed little sensitivity to demographic and environmental parameters, except for adult survival. Our results suggest that maintaining and improving the lifetime reproductive output of rhino cows should thus be the highest management priority and that new management targets should consider both the dependency and compound effects associated with poaching on rhino cows.

Introduction

Poaching (illegal hunting) coupled with habitat changes have left many traditionally hunted species at risk of extinction (Koch and Barnosky, 2006; Rizzolo *et al.*, 2017). Poaching threatens biodiversity, deprives protected areas of revenue, and undermines their viability (Gavin, Solomon and Blank, 2010; Rizzolo *et al.*, 2017). Globally, more than 300 mammals are in danger of extinction from poaching and other forms of exploitation (Rosser and Mainka, 2002; IUCN, 2019). A disproportionate number of these endangered mammals are large terrestrial herbivores (e.g. African elephant [*Loxodonta Africana*] and hippopotamus [*Hippopotamus amphibious*]), which face threats from habitat loss and degradation as well as poaching (Milner, Nilsen and Andreassen, 2007; Ripple *et al.*, 2015).

These overexploited large herbivore populations are also increasingly stressed by human-induced climate changes (Parmesan, 2006). Large herbivore populations, particularly in water limited systems like savannas, are often shaped by rainfall (Forchhammer *et al.*, 1998; Ogutu and Owen-Smith, 2003; Owen-Smith *et al.*, 2005). Specifically, rainfall during the dry season appears to have the greatest influence on population dynamics because it maintains vegetation quality when resources are limited (Illius and O'Connor, 2000). Still, the influence of rainfall on large herbivores varies with age. For example, drought appears to reduce birth rates (Ferreira *et al.*, 2019), and juveniles may be more sensitive to harsh climatic conditions (e.g. drought, heat) because of the influence of food availability on lactation (Ogutu and Owen-Smith, 2003; Ryan *et al.*, 2006; Foley *et al.*, 2008).

While we understand how both poaching and rainfall can alter large herbivore populations, we have less understanding of how their combined effects may alter demography (Milner *et al.*, 2007). There is some evidence, at least for elephants, that competition with humans for limited resources (i.e. water, suitable habitat), which will become increasingly limited due to climate change, may lead to increased poaching losses (Ngcobo *et al.*, 2018). Our understanding of the combined effects of poaching and rainfall, however, is minimal, likely due to large herbivores' longevity, and the time lags in demographic responses (Milner *et al.*, 2007). In the face of elevated levels of poaching (Burn *et al.*, 2011; Challender and MacMillan, 2014; Duffy *et al.*, 2014) and predictions of an increasingly variable climate (Van Wilgen *et al.*, 2016) there is a need to understand the effects of these processes on vulnerable species like the white rhino (*Ceratotherium simum simum*). While white rhino (hereafter rhino) populations respond to stochastic environmental variation and increased densities of conspecifics (Rachlow and Berger, 1998; Shrader and Ogutu, 2006; Braude and Templeton, 2009), we know less about how their populations respond to poaching and climate stress. It is unclear if rhino poaching causes the indirect loss of dependent calves when an adult female is poached (the *dependency effect*; Wittemyer, Dabalén and Douglas-Hamilton, 2013). Research suggests that long-lived species with longer periods of juvenile development might be particularly vulnerable to the loss of their mother (Stanton *et al.*, 2020). For example, Asian elephant (*Elephas maximus maximus*) calves are 10 times likely to die if their mother is killed before they turn 4 years old (Lahdenpera *et al.*, 2016; Perera *et al.*, 2018). As such we have reason to believe the loss of a long-lived rhino female may reduce future population sizes, as the potential for future young is lost (the *compound effect*). Since most large mammals can only produce one offspring a year, longevity has a strong influence on overall reproductive success (Zedrosser *et al.*, 2013). However, we have little understanding of the magnitude of the *compound effect* on a poached population and the potential for climate influences to exacerbate losses. Broadly, we do not understand how variation in climate and different poaching intensities will shape the size of future rhino populations. Variation in population sizes will in turn be driven by variation and elasticity in demographic processes (e.g. recruitment, juvenile and adult survival), which respond differently to climate conditions (Gaillard *et al.*, 2000). Thus, it is important to identify the most important and sensitive demographic processes that are likely to influence future rhino population sizes. Filling these important gaps will allow us to effectively identify and propose effective management actions.

Accordingly, our goal for this study was to understand the current and the future response of the rhino population to poaching and climate variation. We predicted that modeling the loss of calves associated with the loss of a poached mother (i.e. *dependency effect*) would help explain rhino population declines. We expected that projections of constantly high poaching and dry conditions would lead to population declines, as dry conditions often lead to delayed

reproductive activity (Ferreira, Le Roex and Greaver, 2019), exacerbating any poaching related losses. Finally, we predicted adult (especially female) survival will have the most influence on population size (Eberhardt, 2002), because low adult female survival results in a reduction in reproductive output. As such, our objectives were to (i) determine the relative influence of poaching and climate on rhino population size, (ii) estimate the current rhino population size if there had been no poaching in the past, (iii) determine if a *dependency effect* explains reductions in the rhino population size, (iv) predict future rhino population sizes and quantify the *compound effect* under different climatic conditions and poaching pressures and (v) identify how variation in different demographic processes will alter future rhino population sizes.

Study Site

Our study was conducted in Kruger National Park (19 485 km², hereafter Kruger), located in the Mpumalanga and Limpopo provinces of South Africa (Fig. 1). In 2015, Kruger was home to approximately 49% of South Africa's rhino population (Ferreira *et al.*, 2018). Rhinos generally occur in the central and southern parts of the park (Fig. 1), although nothing impedes their movement to the northern parts (Pienaar, Bothma and Theron, 1993).

The central and southern parts of the park are within the lowveld bushveld climate zone and receive 500–700 mm annual rainfall between October and March (Venter, Scholes and Ehardt, 2003). The rainfall in Kruger occurs in 5-year cycles of wet (high rainfall) and dry (low rainfall), which match La Niña and El-Niño years (MacFadyen *et al.*, 2018). The El-Niño in 2015 brought hot and dry conditions to South Africa which resulted in a major drought taking place during the 2015/2016 wet season (Malherbe *et al.*, 2020).

The underlying geology consists of granite and gneiss soils in the western parts, nutrient rich basalts in the eastern parts and Karoo sediments in the parts where the granite and basalts soils join (Venter *et al.*, 2003). Vegetation in the south consists of (i) savanna woodlands on granite soils where *Combretum spp.* trees dominate and (ii) open grassy woodlands on the basalts dominated by *Sclerocarya caffra* and *Senegalia nigrescens* (Venter *et al.*, 2003).

Materials and methods

To estimate the relative influence of demographic parameters, rainfall, direct poaching, dependence-based poaching losses, and compound effects of poaching on rhino population size, we developed an age-structured model using a generalized difference equation (Hilborn and Mangel, 1997). Age-structured models are often used to analyze incomplete data in dynamic systems by combining multiple sources of observed data (Hilborn and Mangel, 1997). These models allowed us to focus on uncertainty in one parameter estimate while accounting for uncertainty in the estimate of another parameter; thus improving use of the data and improving the models. Due to the lack of data we assumed no uncertainty

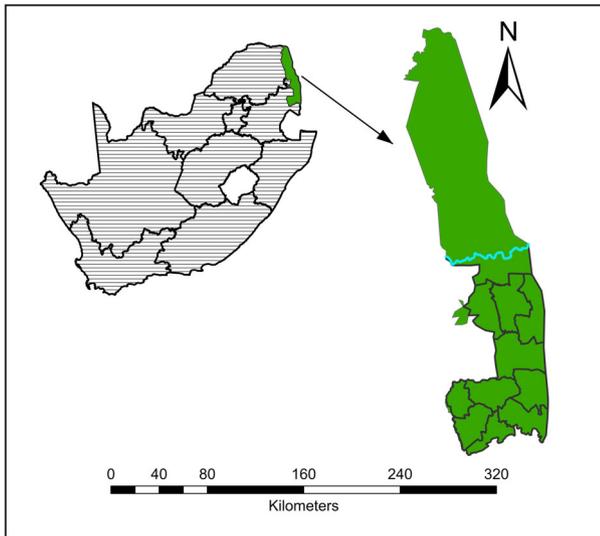


Figure 1 Map of Kruger National Park in South Africa with sections south of the Olifants River where white rhinos surveys were conducted from 1998 to 2019. The light blue line indicates the Olifants River and the polygons represent the sections where rhinos from this study were located.

in the birthing interval, proportion giving birth at each class and sex ratio. As such, we could not obtain uncertainty around reproductive rates.

Model parameters

Population size

We used population estimates from the South African National Parks (SANParks) data repository generated from two different methodologies: distance sampling and block surveys, described in detail below. Distance sampling data was available from 1998 to 2017 (except 2009, 2011, 2013 and 2015 when surveys were not done). In 2016 and 2017, estimates of population size were obtained through distance and block surveys and population estimates from both methods were used in these years. After 2017 only block survey methods were available.

Distance sampling

We used data from 1998 to 2017 collected via fixed wing aircrafts flown ≈ 76 m above ground level at speeds of 167–185 km/h (Kruger, Reilly and Whyte, 2008). Two observers on each side of the aircraft recorded the number of animals seen and the distance at which they were first seen using a frame attached to the outside of each window that had strip wires denoting four distance categories (0–50 m, 50–100 m, 100–200 m, 200–400 m). This provided a transect width of 800 m (400 m on each side of the aircraft) (Kruger *et al.*, 2008). For the 1998 to 2000 surveys we sampled 15% of the park, flying 64 transect lines placed 5.6 km apart in an

east-west orientation (Appendix S1a; Kruger *et al.*, 2008). We increased the survey effort to cover 22% of the park from 2001 to 2017 by flying 96 transect lines placed 3.7 km apart (Appendix S1b). We generated estimates using a distance sampling approach and DISTANCE ver. 4.0 software (Thomas *et al.* 2010). Following Buckland *et al.* (1993), we first examined initial histograms of count frequencies at different distances to determine truncation of observations. Next, we combined 0–50 m and 50–100 m distance categories to improve model fit. Finally, we fit different detection functions (uniform, half-normal and hazard rate and simple polynomial adjustments) with up to 3 cosine adjustment terms and selected the most parsimonious function using Akaike Information Criterion (AIC; Burnham and Anderson 2002) (Appendix S2). We evaluated each year separately and generated abundance estimates by multiplying density estimates by the total area of the central and southern region of the Kruger.

Block survey

We used block-based survey methods (Ferreira *et al.*, 2015) for the final 4 years of our models. Observers counted all rhinos within $878 \times 3 \times 3$ km blocks from a helicopter flown at 45 m above ground at speeds of 120.38 km/h (Ferreira *et al.*, 2015). The blocks were randomly distributed throughout the park and covered the 35 landscape types found in Kruger (Appendix S3; (Gertenbach, 1983) with more blocks occurring in the south region where rhinos were more prevalent (Appendix S4; (Ferreira *et al.*, 2015). We estimated rhino abundances separately for each landscape type in the sampled blocks and extrapolated to unsampled blocks focusing on the central and southern region of the Kruger. We estimated and corrected for observer bias (the probability of an observer not seeing a rhino when present), using a double observer methodology on 33 randomly selected blocks and increased our raw counts by the estimated probability of missed rhinos (Ferreira *et al.*, 2015). Additionally, we estimated and corrected for availability (obstructed by vegetation or other feature) by monitoring the visibility of 15 focal rhinos (i.e. rhino selected for extended observations) for 10 min (Ferreira, Greaver and Knight, 2011). Both the observer and availability bias estimates were obtained during the 2013 census.

Demographic estimates

We used data from the SANParks data repository and internal unpublished reports to determine the demographic makeup of the rhino population. The standing age distribution for each year was determined using helicopter-based flights (100 m above ground, ≈ 100 km/h) to assign ages and sexes to at least 100 individuals in each of the nine management zones (Appendix S5; Ferreira, Botha and Emmett, 2012). These are management zones that were designated by SANParks management from where rhinos for live sales were historically removed. We used the body size and height (Appendix S6a) as well as the size and shape of the horns

(Appendix S6b) of an individual to estimate its age (Hillman-Smith *et al.*, 1986; Emslie, Adcock and Hansen, 1995). We estimated the standing age class distribution using surveys in 2010–2017 and defined three age classes: juveniles (A, B & C age classes 0–24 months old), sub-adults (C & D classes, 2.5–7 years) and adults (F class – older than 7 years). We assumed between 20 and 50% of sub-adults and adults could reproduce (Rachlow and Berger, 1998).

Rainfall, poaching and management data

We obtained rainfall data for 20 years (1998–2019) by averaging the monthly rainfall from the 12 weather stations in our study area (Appendix S7). We used both wet (October – March) and dry season (April – September) rainfall for our models. To quantify poaching, we used records of the annual number of poached rhino carcasses found by rangers from 2007 to 2019 (Ferreira *et al.*, 2015). While vultures and scavenging activity facilitates the detection of rhino carcass, we accounted for undetected carcasses to reduce the probability of undercounting poached rhinos. Specifically, we had two observers conduct intensive aerial surveys of 10 (3 × 3 km) blocks via helicopter and record the GPS location of carcasses. Then we compared the number of carcasses seen by the two observers to those found by rangers on the same 10 blocks. Using a double observer methodology (Cochran, 1977) we estimated that rangers missed 11.5% of the carcasses (SANParks, internal report) and used this estimate to correct the annual number of carcasses counted by rangers. In addition to estimates of poaching, we used data on management removals – the numbers of rhinos removed for management purposes from 1998 to 2019. Removals were conducted to provide revenue for conservation objectives or used to establish new populations elsewhere (Ferreira *et al.*, 2012). Historically, management removals targeted sub-adult individuals, particularly females (Ferreira *et al.*, 2012), however, recent increases in poaching have reduced management removals by as much as 80% (Ferreira *et al.*, 2012).

Demographic analysis

We used age-structured models using a generalized difference equation (Hilborn and Mangel, 1997) to predict numbers of individuals in different age classes over time (1998–2019). We used the models to account for variation in juvenile production, survival potential as a function of rain dependent food availability, management removals, poaching losses, and the potential impact of poaching losses of mature females on associated juveniles (Pascual, Kareiva and Hilborn, 1997). We predicted the numbers (N) of individuals at different ages (a) over time (t) using a balance model (Equation 1) that accounted for age specific natural survival (S_a), the proportion of individuals in an age susceptible to management removals (v_a^m), the proportion of individuals in an age susceptible to poaching (v_a^p), the removal rate (U_a^m) of fully susceptible individuals, and the poaching rate (U_a^p) of individuals fully susceptible to poaching removed.

$$N_{a+1,t+1} = N_{a,t} S_a \times (1 - v_a^m U_a^m) (1 - v_a^p U_a^p) \quad (1)$$

The management removal ($U_a^m U_a^p$) and poaching ($U_a^p U_a^m$) rates (Equation 2) were conditioned on estimates of the total population size vulnerable to each removal type. This approach ensures that the actual observed removals (R) or individuals poached (P) are removed each time step but allows the removal rate to be constrained to <1 to prevent numerical instability. These rates are then used in Equation 1.

$$U_a^m = R_t / \sum_a v_a^m N_{a,t} \text{ or } U_a^p = P_t / \sum_a v_a^p N_{a,t} \quad (2)$$

We estimated age specific survival as a constant maximum rate (S_a') for each age or as a hyperbolic function of per capita available resources (F_t) where γ_a determines the per capita food level at which survival drops to half the maximum value (Equation 3). Note that when γ_a is set to 0 the maximum age survival rate is used each year. Per capita food availability was modeled as a scaled function of rainfall (RF_{*t*}).

$$S_a = S_a' \frac{F_t}{\gamma_a + F_t} \text{ where } F_t = \frac{1.25RF_t}{\sum_a N_{a,t}} \quad (3)$$

Since grass growth depends on the amount and distribution of rainfall, we calculated a food effect by using an established relationship between dry season rainfall and fresh grass growth (Mduma, Sinclair and Hilborn, 1999). Studies have shown that food supply is usually inadequate during the dry season which can lead to mortalities (Knight, 1995; Dudley *et al.*, 2001). Following (Hilborn and Mangel, 1997), we used a regression equation for grass growth on monthly dry season rainfall with the slope of 1.25 (Mduma, Sinclair and Hilborn 1999). A similar equation was used to mediate birthrate (Equation 4) where br_a is the age specific birth rate and γ_{br} is the per capita food availability where the age specific birth rate drops to half the maximum value br_a' .

$$br_a = br_a' \frac{F_t}{\gamma_{br} + F_t} \text{ where } F_t = \frac{1.25RF_t}{\sum_a N_{a,t}} \quad (4)$$

We used the best available estimates to determine rhino's demographic parameters: birth frequency in rhino, population sex ratio, and senescence age (Table 1) and assumed these were constant over time. When available, we used published and unpublished demographic estimates from the Kruger rhino population. If these estimates were not available, we used estimates from other populations (Table 1). We assumed the population size at time 0 ($N_0 = 1998$) to be known. We used the model to estimate the influence of rainfall on food availability as well as the effect of combined removals through poaching and management removals (Appendix S8) on rhino birthrates, age specific survival and population growth rate. We estimated these dynamic parameters by maximum likelihood (Pascual *et al.*, 1997) assuming Gaussian error structure and the estimated uncertainty for each population estimate (Hilborn and Mangel, 1997; Pascual *et al.*, 1997). Note that in 2016 and 2017 population estimates from distance and block surveys were used since there

was no reason to assume one method was superior to the other. To understand the relative influence of climate and poaching on rhino population growth and examine the potential for a *dependency effect*, we evaluated three scenarios.

Scenario 1

In the first scenario, we assumed changes in population were influenced by changes in rainfall and the resulting changes in survival due to food effects. We used this scenario to determine the relative influence of rainfall in the absence of poaching.

Scenario 2

In the second scenario, we assumed changes were a result of rainfall plus poaching, where poaching removals were assumed to come from the sub-adult and adult populations. This scenario allowed us to determine if patterns in rhino population demography could be explained by the poaching of sub-adult and adult individuals.

Scenario 3

Finally, for scenario 3, we made the same assumptions as scenario 2 plus an additional assumption that there were indirect mortalities of calves from the loss of their mothers. For scenario 3, the calves (i.e. up to 2 years) of all poached adults and a portion of sub-adults died. Not knowing the proportion of sub-adults in the poached population, we trialled different biologically reasonable values (5–50%). Based on model performance, 20% was a good fit for scenarios 2 and 3.

To compare our three scenarios, we assessed model fit based on a visual inspection of model fit to observed estimates and likelihood ratio tests. Likelihood ratio tests are based on Wilks's theorem (Wilks 1938) where two times the difference between loglikelihoods can be approximated with a χ^2 -distribution with degrees of freedom equal to the dimensionality difference between the models. For models with similar dimensionality, a likelihood difference of 2 would result in a p-value of slightly less than 0.05. Next, we generated likelihood profiles to produce confidence intervals for calf, sub-adult and adult survival, food effect on juveniles, adults and birthrates following the theoretical statistics described by Kendall and Stuart (1979). This allowed us to investigate how the variation in each parameter influenced demographic responses and population growth using Markov

Table 1 A priori known demographic parameters derived from published and unpublished literature on the biology of white rhinos

Description	Origin
Starting population – 2280	SANParks unpublished data
Birth frequency – 2.5 years	(Owen-Smith, 1982, 1988; Bertschinger, 1994)
Senescence age – 30	(Bertschinger, 1994)
Sex ratio – 0.54	SANParks unpublished data

chain Monte Carlo (MCMC) simulations where parameter values were drawn randomly assuming a normal distribution defined by the 95% confidence intervals (Gaillard *et al.*, 1998; Gaillard and Yoccoz, 2003). To quantify the potential for future direct and indirect impacts of poaching we assumed constant rainfall, survival and poaching and projected the models into the future, from 2020 to 2030. We also projected future population estimates using the best fitting model, modified to evaluate different poaching and climate scenarios and the sensitivity of model parameters.

Variable rainfall and poaching models

We developed two modified models to understand the sensitivity and influence of food effects and survival parameters on future populations. First, we set juvenile, sub-adult, adult survival to their upper limits and food parameters to their lower limits (based on the likelihood profiles from the best fitting model). Second, we set survival parameters to their lower limits and food effects to their upper limits. We developed two additional modifications to understand the influence and sensitivity of our model to weather. We set rainfall to (i) high and (ii) variable (high and low) rainfall conditions. Under the variable model rainfall fluctuated every 5 years, to correspond with the cyclical regional weather patterns (MacFadyen *et al.*, 2018).

To understand how variation in poaching might influence future rhino populations, we projected the baseline model and the modified models based on different poaching pressures. We examined future populations under current (i.e. 2019) poaching levels and levels that were a 50% and 80% reduction of the current level. This allowed us to understand how reductions in poaching could alter future rhino population sizes. Then we used the baseline model and modifications to understand the magnitude of a *compound effect* under different conditions. We calculated the compound effect as lifetime reproductive success by determining the number of potential calves a female would produce if there was (i) no poaching, (ii) poaching but no calf losses and (iii) poaching plus calf losses. We then linked different poaching levels to the potential calf numbers under poaching with no calf loss and poaching with calf loss to determine the number of calves that a female would produce under different poaching pressures.

Results

Climate, poaching and dependency effects scenarios

In general, the pattern observed from census data was that of a steadily declining rhino population following the increase in poaching rates around 2007/2008. Evaluating our models, we found scenario 1 (rainfall only) with a log likelihood of 229.52 ($\Delta L = 39.04$; $p < 0.0001$; ΔL is the delta loglikelihood change between model 1 and model 2) did not fit the observed data well (Fig. 2a). Scenario 2 (rainfall and direct poaching) had a log likelihood of

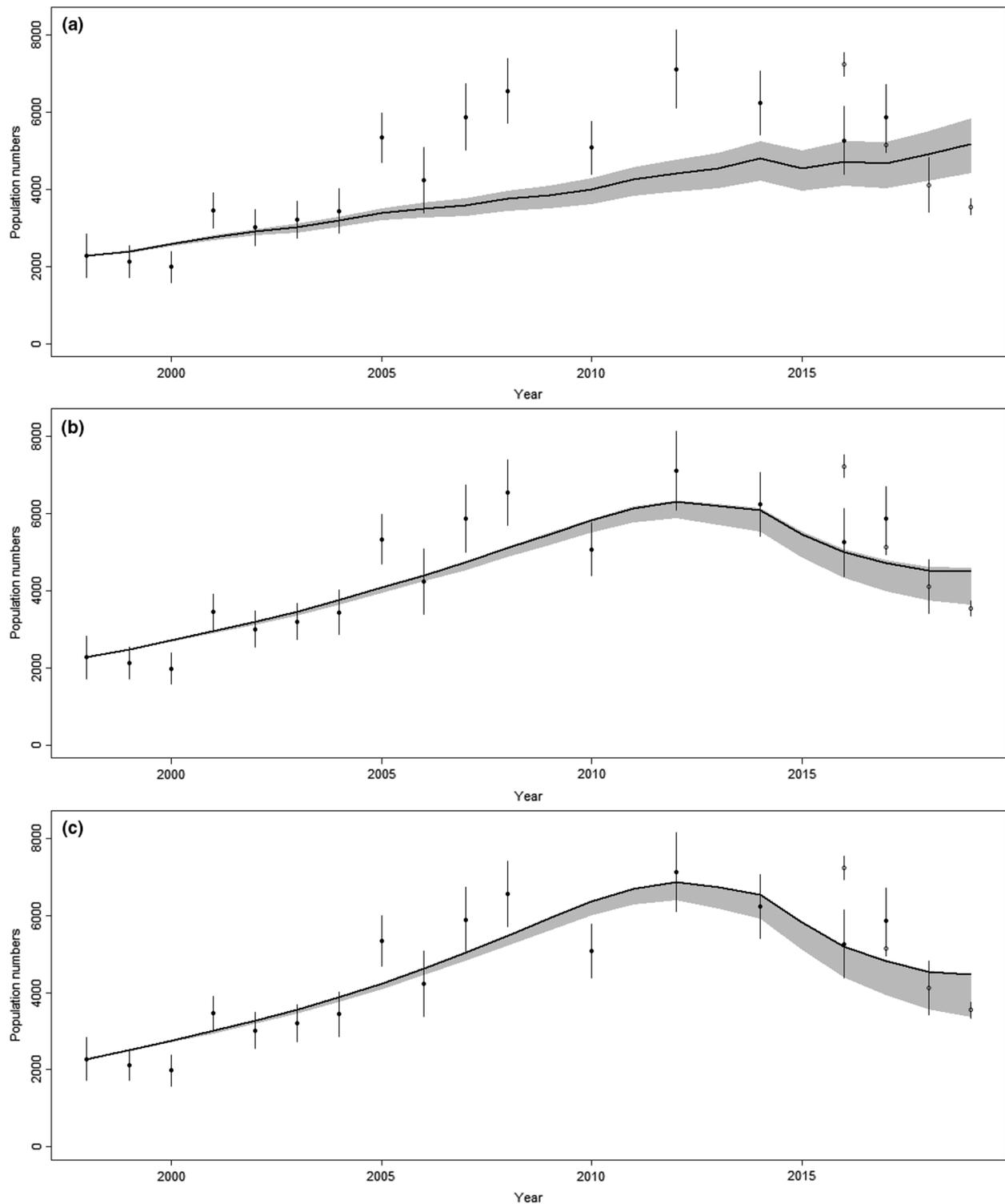


Figure 2 Fit of the age structured population model (black line) to white rhino population estimates (black dots = distance sampling surveys, open dots = block census surveys, with standard error bars) for the Kruger National Park from 1998 to 2019 under three modeling scenarios (a) no poaching model (rainfall affects food availability), (b) the direct poaching model (rainfall plus poaching of adults and sub-adults affecting demographic parameters), and (c) the combined direct and indirect poaching model (rainfall plus poaching of adults and sub-adults and the indirect mortalities of calves from the loss of their mothers). Light gray polygon depicts the 95% quantile of population trajectory from Markov chain Monte Carlo simulations.

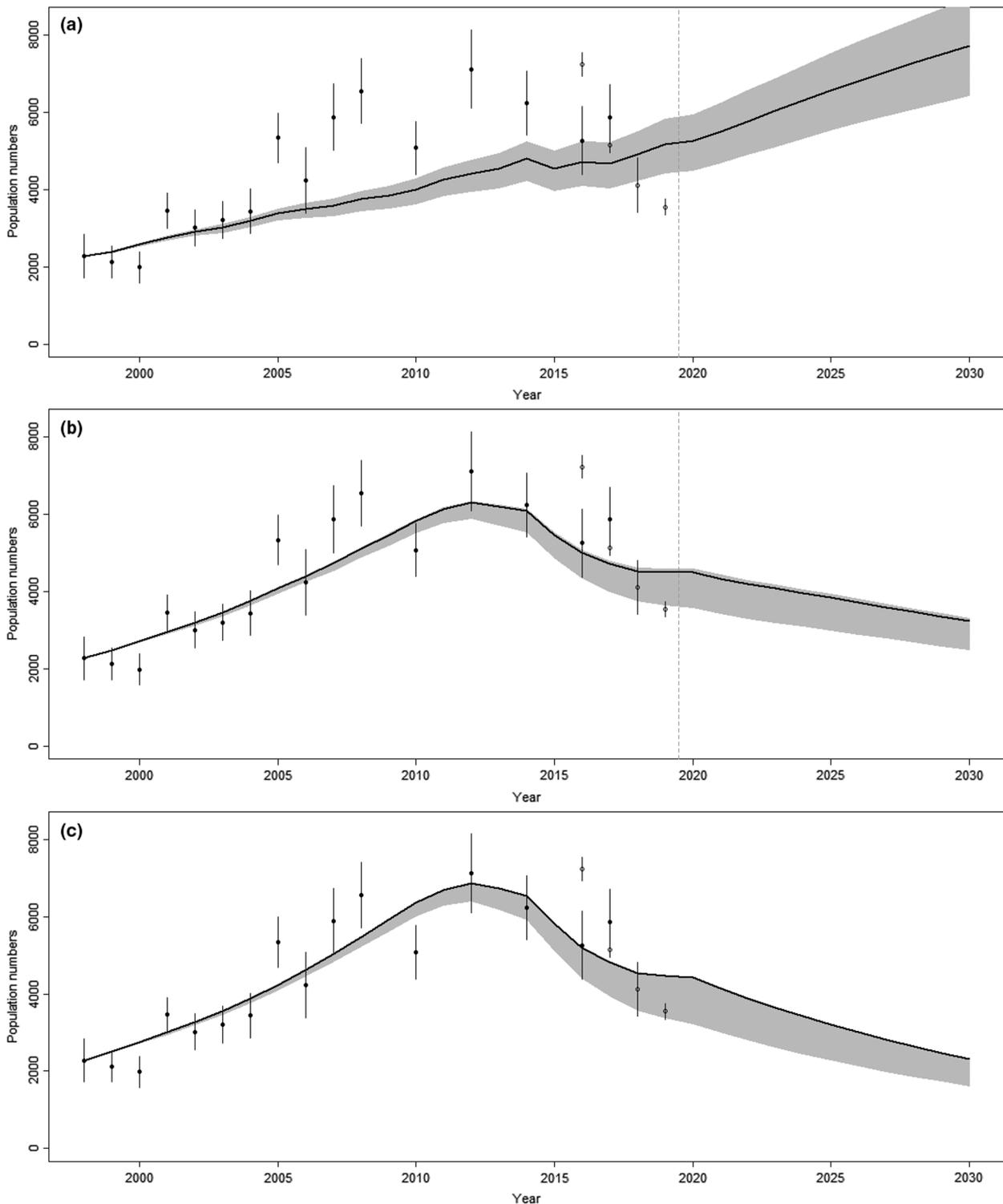


Figure 3 Predicted population trajectory (black line) to the year 2030 for the Kruger National Park white rhino population (black dots = distance sampling population estimates; open dots = block census population estimates, with standard error bars) using age-structured population models under three scenarios (a) no poaching model (rainfall affects food availability), (b) the direct poaching model (rainfall plus poaching of adults and sub-adults affecting demographic parameters), and (c) the combined direct and indirect poaching model (rainfall plus poaching of adults and sub-adults and the indirect mortalities of calves from the loss of their mothers). Light gray polygon depicts the 95% quantile of the population trajectory from Markov chain Monte Carlo simulations. The dashed vertical line indicates the year when forward projections start; projections were done under current (2019) poaching rates and average rainfall.

Table 2 Population estimates and reproductive success for the Kruger National Park white rhino population under different poaching levels and model scenarios (1) the combined direct and indirect poaching model (rainfall plus poaching of adults and sub-adults and the indirect mortalities of calves from the loss of their mothers), (2) high survival and low food effect, and (3) low survival and high food effect (4) high rainfall, (5) variable rainfall

Model	2030 estimate under current poaching	50% of current poaching	20% of current poaching	Lifetime reproductive – no poaching	Lifetime reproductive – poaching	Lifetime reproductive – poaching + calf loss
Baseline Model	2312	5383	8685	5.70	0.73	0.52
High Survival, low food effect	2107	4894	7881	5.93	0.75	0.53
Low survival, high food effect	2072	4811	7745	5.93	0.75	0.53
High rainfall	2345	5443	8825	5.86	0.74	0.53
Variable rainfall	2326	4687	7915	5.93	0.75	0.53

Where food effect refers to food availability due to the amount of dry seasoning rainfall.

190.48 ($\Delta L = 3.65$; $p = 0.0069$) and was a better fit than scenario 1 (Fig. 2b). However, scenario 3 (rainfall, direct and indirect poaching) with a log likelihood of 186.83, was the best fitting modeling, and supported the prediction that poaching can have direct and indirect effects on the population because of the loss of calves that have not been weaned (Fig. 2c).

In the absence of poaching (scenario 1) we estimated a population of 7100 (6410–8994) rhinos in the year 2030 (Fig. 3a). When we projected the model with rainfall and direct poaching (scenario 2) to the year 2030 we estimated

3078 (2528–3334) individuals, a 13.3% decrease from the 2019 estimate (Fig. 3b). Projecting the best fitting model (scenario 3), we estimated a population of 2312 (1724–2364) individuals by 2030. This would be a 35% decline from the 2019 population estimate (Fig. 3c).

Variable rainfall and poaching models

Evaluating the model with increased rainfall, we estimated 2345 (1711–2400) rhinos in the year 2030, an increase of about 2% from baseline predictions with average rainfall (Table 2). Alternatively, the model with variable rainfall resulted in a 0.6% increase from baseline predictions with 2326 (1707–2377) rhinos predicted for the year 2030. Using the best fitting model (scenario 3), we found that a 50% reduction in poaching would result in a doubling of the population by the year 2030, with a total of 5383 (4031–5491) rhinos. Furthermore, an 80% reduction in poaching would result in 8685 (6522–8843) rhinos in the year 2030.

The compound effect

If no further poaching occurred after 2019 and average rainfall conditions prevailed, we would expect a rhino female to produce 5.7 calves. However, the *compound effect* of poaching on rhino resulted in a substantial reduction of this prediction to 0.73 calves per female if direct poaching continues. Accounting for a continuation of both direct and indirect poaching we would expect a female's lifetime reproductive output to be 0.52 calves (Table 2).

Variation in demographic processes

Investigating how the variation of dynamic parameters influenced demographic responses and population growth, we found that besides survival, the initial three models (rainfall, rainfall and direct poaching, and rainfall, direct and indirect poaching) had minimal sensitivity to variation in parameters (age specific survival, food effects on juveniles, adults, and birthrates; Table 3). For scenario 1 we found limited

Table 3 Maximum likelihood estimations (MLE) for demographic parameters from the Kruger National Park white rhino population model based on 3: (A) no poaching model (rainfall affects food availability), (B) the direct poaching model (rainfall plus poaching of adults and sub-adults affecting demographic parameters), and (C) the combined direct and indirect poaching model (rainfall plus poaching of adults and sub-adults and the indirect mortalities of calves from the loss of their mothers)

Model	Parameter	MLE (95% CI)
Scenario 1	Calf survival	0.99 (0.94–0.99)
	Sub-adult survival	0.99 (0.98–0.99)
	Adult survival	0.99 (0.99–0.99)
	Food effect on juveniles	0 (0–0.034)
	Food effect on adults	0.015 (0–0.017)
Scenario 2	Calf survival	0.99 (0.91–0.99)
	Sub-adult survival	0.99 (0.96–0.99)
	Adult survival	0.99 (0.98–0.99)
	Food effect on juveniles	0 (0–0.014)
	Food effect on adults	0.002 (0–0.003)
Scenario 3	Calf survival	0.99 (0.94–0.99)
	Sub-adult survival	0.99 (0.98–0.99)
	Adult survival	0.99 (0.99–0.99)
	Food effect on juveniles	0 (0–0.006)
	Food effect on adults	0.0006 (0–0.001)
	Food effect on birthrates	0 (0–0.012)

variation in both sub-adult and adult survival (0.97–0.99) suggesting that sub-adults and adults were buffered from impacts caused by changes in rainfall. Calf survival varied between 0.91 and 0.99, which suggests that calves were vulnerable to impacts caused by changes in rainfall. We found a weak but measurable (0–0.053) food effect on birthrates suggesting changes in rainfall influence reproduction (Table 2). For scenario 2, we again found limited variation in both sub-adult and adult survival (0.97–0.99) and variable calf survival 0.91–0.99. We found a weaker food effect for juvenile survival (0–0.014), adult survival (0–0.003) and on birthrates (0–0.025) suggesting that poaching accounted for more variation in population growth than rainfall (Table 3). Finally, for scenario 3 we again found limited variation in both sub-adult and adult survival (0.97–0.99). Calf survival was unsurprisingly most variable (0.89–0.99), indicating that the combined effects of rainfall and indirect poaching had a sizeable influence on calf survival. We found a weak food effect for juvenile (0–0.006) and adult (0–0.001) survival and birthrates (0–0.012). Survival parameters had the most measurable influence on population size (Table 2). There was a 10% decrease in the population estimate from the best fitting model when we set the survival parameters to their lower limits and the food parameters to their upper limits.

Discussion

We present evidence that the dramatic decline in Kruger's rhino population size was predominantly a function of increased poaching, starting in 2008 (Thomas, 2010). Additionally, we show that the subsequent change in the rhino population size was a function of direct loss of individuals plus the indirect loss of calves from the *dependency effect*. Furthermore, we found support for rainfall having an additive effect on poaching losses, with poached populations further depressed by cyclic rainfall patterns.

Our best model for the rhino population in Kruger predicted a further 35% decline by 2030 (2019 = 3549; 2030 = 2296) if current poaching rates continue. Field observations (Maggs, K. SANParks pers. comm.) also support the idea that dependent calves and juveniles die when their mothers are poached. Calves run away from poachers and may die from overheating, dehydration, hunger and predation (Maggs, K. SANParks pers. comm.). Having found evidence for the indirect effects of poaching on calves, it is likely that calf mortalities have been underreported. This is likely due to their reduced persistence on the landscape relative to adult rhinos (Sanparks, internal report).

One of the reasons that the rhino population in Kruger is likely to continue to decline without an intervention or change in poaching rates is because of the loss of lifetime reproductive potential. Without poaching a female can produce approximately 6 calves, but with current poaching levels, the lifetime reproductive output is reduced to 0.7 calves – a *compound effect* of approximately 5.3 offspring. When we also account for the *dependency effect*, the lifetime reproductive success of a rhino cow is reduced to a dismal 0.5 offspring, not enough to sustain a population (Sodhi

et al., 2009). This impact is further compounded because, on average, half of the lost offspring would have been females whose lifetime reproductive output was also lost.

A reduction in poaching would allow the population to recover, our models predicted that a 50% reduction in poaching would result in the doubling of the population size by 2030. This result concurs with previous research showing that when rhinos are afforded better protection populations can recover (Amin *et al.*, 2006). Similarly, in another mega-herbivore, a poached elephant population in Tanzania rebounded when poaching was stopped (Foley and Faust, 2010).

Our models suggest that climate impacts were minimal compared with those of poaching; however, we did see clear linkages between rhino reproduction, population growth and rainfall. Our climate only model predicted the 2020 population size (5097) to be 44% greater than the current 2019 population (3549) if the current climate conditions persisted. This is a lower estimate than targeted by the Biodiversity Management Plan (Knight, *et al.*, 2015). However, with the climate predictions for southern Africa, and Kruger specifically, suggesting longer dry seasons and higher temperatures, these targeted population sizes may not be realistic (Van Wilgen *et al.*, 2016). While rhinos do not appear to respond to normal climatic variability (Shrader and Ogutu, 2006), substantial drought can cause reductions in recruitment and increase mortality (Ferreira *et al.*, 2019). Our models highlight the potential for climate induced declines to exacerbate poaching losses by an additional 10% decrease in rhino population over the next decade.

Like other studies (Gaillard *et al.*, 1993, 1998; Ogutu and Owen-Smith, 2003; Foley *et al.*, 2008), we found both climate and poaching accounted for the variation in juvenile survival. However, the variability of juvenile survival did not have consequences for population growth. Instead, adult survival had the greatest measurable changes to projected population size estimates. A reduction in adult survival resulted in lower reproductive rates and population growth. Research has shown that for long-lived species proportional changes in juvenile survival have less effect on population growth than proportional change in adult survival (Gaillard *et al.*, 2000; Eberhardt, 2002; Gaillard and Yoccoz, 2003).

Model considerations

We made several assumptions for our models that were likely to influence our results. We assumed all dependent calves and juveniles died when their mothers were poached because dependent calves cannot fend for themselves. We also assumed some demographic parameters to be constant when realistically they would vary over time and this variability would increase the uncertainty in the population trajectories. Additionally, based on model fit we assumed 20% of the poached population was sub-adults. We also assumed that the loss of younger females would have the same effects on the population as the loss of older females. An older female may have already contributed most of her calves per lifetime into the population, whereas a

younger female may have not. Modeling this individual level of variation requires high quality data on age-specific survival and other fitness components (Gaillard *et al.*, 2000; Richard *et al.*, 2014) not available for our study. Finally, we acknowledge that there would be greater uncertainty in our reproductive estimates if we understood the uncertainties around birthing intervals. It is also important to note that our future predictions do not include the effects of management removals. Kruger removes rhinos as part of range expansion initiatives and to generate revenue (Ferreira *et al.*, 2012; Clements *et al.*, 2020). Our predictions, however, are likely realistic because the complexities of bovine tuberculosis quarantine requirements limit the movement of rhinos (Miller *et al.*, 2018), and current poaching rates do not allow for the removal of rhinos without the potential for further population declines (Ferreira *et al.*, 2012).

Management implications

Large mammal populations are limited by the number of reproductive females (Gaillard *et al.*, 2000; Gosselin *et al.*, 2014). Ensuring and improving the lifetime reproductive output of rhino cows should thus be the highest priority for rhino management as it will result in high population growth rates. Antipoaching initiatives for apprehending poachers must be coupled with an effective legal system that distinguishes and places emphasis on population impacts associated with the poaching of cows over bulls. As deterrents, we recommend those convicted of poaching a rhino cow get harsher sentences. This would likely involve amendments to existing sentencing laws, but it could be achieved by demonstrating the negative impacts associated with poaching cows. Live rhino cows are worth more than bulls, even when you ignore the cost of future calves. In 2016, bulls sold for R270 000 at auction, while a cow plus a heifer calf sold for R500 000 (SANParks intern. Report). This is revenue that was used to fund conservation initiatives, which has been lost since the halting of live rhino auctions due to poaching. We also recommend dehorning female rhinos that reside in high poaching areas to deter poachers. Any short-term stresses detected in rhino's fecal glucocorticoid metabolites from the procedure (Badenhorst *et al.*, 2016) do not appear to impact rhinos physiologically (Penny *et al.*, 2020), nor their reproductive success (Penny *et al.*, 2019). Finally, managers should also consider translocating female rhinos or deterring them away from high poaching areas, potentially by manipulating their perception of predation risk through the introduction of predator cues (e.g. humans and lions; Cromsigt *et al.*, 2013; Clinchy *et al.*, 2016). Harnessing animal's fear has been suggested as a management strategy for deterring animals away from areas with high mortality risk (Cromsigt *et al.*, 2013; Kuijper *et al.*, 2019).

With the increasing likelihood of droughts (Cherwin and Knapp, 2012; Craine *et al.*, 2013) and little indication that wildlife poaching will abate (Burn *et al.*, 2011; Challender and MacMillan, 2014; Duffy *et al.*, 2014), large herbivores may be particularly vulnerable to population declines. South Africa has

failed to achieve its white rhino targets for 2020 (Knight, *et al.*, 2015). If authorities seek to achieve the population targets in the next two decades, poaching levels must be reduced. Additionally, we recommend a revision of population targets (Emslie and Brooks, 1999; Knight, *et al.*, 2015) to account for the effects that a changing climate will have on rhino populations, as well as both the dependency and compound effects associated with the poaching of rhino cows.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix 1: Map showing the transect lines flown during the distance sampling of the Kruger National Park white rhino annual survey in 1998–2000.

Appendix 2: Distance sampling model results for the Kruger National Park white rhino population from 1998–2017.

Appendix 3: Landscapes within Kruger National Park (Gertenbach 1983).

Appendix 4: Map showing the 3x3 km blocks flown during the annual rhino surveys in the central and southern region of Kruger National Park.

Appendix 5: Map showing the location of the nine management zones in the south region of Kruger National Park flown during the white rhino demographic surveys.

Appendix 6: The protocol for estimating the age of a white rhino based on the height.

Appendix 7: Total dry season (April - September) rainfall from 1998 to 2019 in the central and southern parts of Kruger National Park.

Appendix 8: Model variables and the rationale for their inclusion in the white rhino age structured models.