

Comparison of mark-recapture and block-count-based estimation of black rhinoceros populations

Sam M. Ferreira^{1*} (ID)[§], Nikki le Roex^{1,2,†} (ID), Cathy Greaver¹ (ID) & Cathy Dreyer³ (ID)

¹Savanna Node, Scientific Services, SANParks, Skukuza, 1350 South Africa

²Institute for Communities and Wildlife in Africa, University of Cape Town, Cape Town, South Africa

³Addo Elephant National Park, SANParks, Addo, South Africa

Received 13 May 2020. To authors for revision 19 June 2020. Accepted 18 August 2020

The impact of global wildlife trafficking on biological diversity imposes pressures on authorities to respond. Reliable estimates of population sizes of keystone species such as rhinoceroses (rhinos) are often a key requirement to evaluate the effectiveness of interventions. Black rhinoceroses (*Diceros bicornis*) are cryptic and targeted by poachers for their horns. Several interventions aim to curb the effects of poaching and achieve black rhino conservation targets in the short to medium term. We used black rhinos to evaluate the survey requirements that will allow the detection of 1% annual change in population size over a five-year period, a key short-term target for black rhinos in Kruger National Park, South Africa. We found that a mark-recapture technique provided the most precise estimates, but authorities need to mark 94% of all black rhinos. This is logistically challenging and costly. Development of inclusive conservation plans need to consider realistic measures to report outcomes and achieve effective conservation evaluation.

Keywords: black rhinos, Kruger National Park, population growth rates, conservation targets, power to detect trends, mark-recapture estimates, rhino ear notching.

INTRODUCTION

Biodiversity degrades due to global drivers of environmental change (Sala *et al.*, 2000). Trafficking fuels the wildlife trade, a key international commodity market (Rosen & Smith, 2010). Illegal overharvesting has many causes (Conrad, 2012) that can lead to declines of charismatic species like rhinoceroses (rhinos) (Emslie *et al.*, 2019). Although societal influencers pressure authorities to respond (Decker *et al.*, 2016), militarized interventions receive criticism (Dunlap & Jakobsen, 2020) often embedded in viewpoints of competing ideologies of exclusionary animal rights *versus* inclusive human rights and democracy (Madzwamuse, Rihoy & Louis, 2020). Even so, a key question is how many rhinos are left and how well are they doing?

Defining population size and change in charismatic wildlife species depends on different requirements at different scales and environmental

conditions. For instance, for various rhino species, authorities need a range of techniques (Ferreira *et al.*, 2017). Cryptic wild animals intensify the challenge (Willson, Winne & Todd, 2011), especially if few animals live in large areas. An example is the south-central black rhino (*Diceros bicornis minor*) population in Kruger National Park, hereafter Kruger, the world's rhino stronghold (Emslie & Brooks, 1999).

Continental rhino action (*e.g.* Emslie & Brooks, 1999) and South African management plans (Knight, Balfour & Emslie, 2013) have targets – typically these require at least 5% annual growth in the number of rhinos. Authorities are able to meet few of these because poaching impacts key populations (Ferreira, Greaver, Nhleko & Simms, 2018; Ferreira, le Roex & Greaver, 2019). Authorities responded to the decline of rhinos (Ferreira *et al.*, 2018; Ferreira *et al.*, 2019) with new conservation targets – 1% annual change over a five-year period (SANParks, 2020). New targets, however, may not be realistically measurable. For instance, the detection of a growth trend is a trade-off between the size of change, precision of estimates, intervals between surveys, number of

[†]Present address: Panthera, New York, NY, U.S.A.

*To whom correspondence should be addressed.
E-mail: sam.ferreira@sanparks.org



surveys and total change by the time authorities detect a change (Gerrodette, 1987). The smaller the change, the more precise estimates must be.

We use the cryptic black rhino as a case study. Surveys from 2009 to 2019 in Kruger made use of block-based sample surveys (Ferreira, Greaver & Knight, 2011; Ferreira *et al.*, 2015; Ferreira *et al.*, 2017; Ferreira *et al.*, 2018; Ferreira *et al.*, 2019; le Roex & Ferreira, 2020). Sample survey methods should provide unbiased estimates. Variance of estimates, however, increases with small populations or unevenly dispersed individuals (Ferreira & Pienaar, 2020). Threatened species, like black rhino, thus pose particular challenges for reporting authorities.

In this study, we evaluate the use of mark-recapture methods to obtain population size estimates. A mark-recapture method uses the ratio of ear-notched rhinos to 'clean' animals observed in a survey, along with the known total number of notched animals, to determine a population estimate (Seber, 1982). Such estimators also provide confidence intervals (Seber, 1982), much like block-based sample surveys do (Ferreira *et al.*, 2011; Ferreira *et al.*, 2015; Ferreira *et al.*, 2017; Ferreira *et al.*, 2018; Ferreira *et al.*, 2019; le Roex & Ferreira, 2020). The accuracy (*i.e.* the combined effect of precision and bias, Thompson 1992) of a mark-recapture estimate, however, depends on the total proportion of the population that has ear notches, as well as the recapture probability. The recapture probability depends on whether observers see live, marked individuals during the recapturing occasion (Seber, 1982).

Mark-recapture methods are preferable if they have narrower confidence intervals than the block-based sampling approach. We compare our precision of estimates with that obtained through block-based sample surveys (Ferreira *et al.*, 2011; Ferreira *et al.*, 2015; Ferreira *et al.*, 2017; Ferreira *et al.*, 2018; Ferreira *et al.*, 2019; le Roex & Ferreira, 2020). To help evaluate new performance targets (SANParks, 2020) we focus on the method with the best precision and evaluate ways to improve that. We ask what the required precision is and, if it hinges on marked rhinos, what proportion of a population should authorities mark?

MATERIALS AND METHODS

Study area

Administratively Kruger, 19 485 km² in size, has 22 Sections each with a Section Ranger responsi-

ble for socio-ecological integrity. Most of the black rhinos live in the southern part of Kruger (Ferreira *et al.*, 2011). Our study thus focused on the seven southernmost sections that cover a total area of 5366 km². These sections consist of low-lying savannas. Annual rainfall exceeds 450 mm (Gertenbach, 1980). Granite and gneiss deposits separated by Karoo sediment combine with wooded savanna comprising *Sclerocarya caffra* and *Acacia nigrescens* on basalts and mixed *Combretum* spp. and *Acacia* spp. on granites (Gertenbach, 1983).

Data collection

SANParks engaged in individual ear-notching 102 black rhinos in the seven sections that comprised our focal study area from 2016 to 2019 (Table 1). Ear notches provide a visual identification method for rhinos even if observation is from a helicopter. Observers can recognize an individual based on a specific pattern of ear notches that veterinarians cut out of a rhino's ear. Using high-quality digital cameras to take images of rhinos while conducting helicopter-based aerial surveys eases recognition. The locations of notches on the ears of a rhino link to a numbering system that provides an individual rhino's identification number (Ngene *et al.*, 2011). Veterinarians and pilots assisted with the capture of individuals using helicopter-based platforms for darting following the South African standards (SABS, 2000).

Monitoring of marked rhinos is intensive. Game guides, researchers and field rangers contribute sightings to an ongoing and updating database. Given the records of observations and knowledge of deaths, we presumed that 62 adults, 27 young adults and subadults and 2 juveniles were still alive and available for observation at the time of the survey. These rhinos thus served as marked rhinos available for 'recapturing' during the ensuing aerial survey.

SANParks conducts aerial surveys of rhino

Table 1. Summary of black rhinos notched in Kruger National Park between January 2016 and shortly before the start of our survey in 2019. We used individual ear notches and assigned ages (see Brooks & Adcock, 1997) to individuals at the time of capture.

Age category	Age class	Male	Female
Adult	F (>7 years)	26	38
Young adult	E (>3.5–7 years)	10	9
Subadult	D (>2–3.5 years)	4	3
Juvenile	C (>1–2 years)	5	7

populations in Kruger during the early dry season in August and September each year. Surveys use a helicopter as observation platform and target the 11 ranger sections in southern Kruger. SANParks marks 3 km × 3 km blocks across the Kruger and randomly chooses 878 of these blocks as annual survey blocks (Ferreira *et al.*, 2015). Of these, 487 are within the 9138 km² of Kruger south of the Olifants River where most black rhinos live. Each year since 2013, observers have counted black and white rhinos (*Ceratotherium simum*) in most of these blocks depending on logistical challenges in a specific year (Ferreira *et al.*, 2015; Ferreira *et al.*, 2017; Ferreira *et al.*, 2018; Ferreira *et al.*, 2019; le Roex & Ferreira, 2020).

During 2019, SANParks adapted the standard sample-based annual survey to help evaluate the use of mark-recapture approaches. SANParks surveyed all the blocks south of the Olifants River including ones that were not part of the usual sample survey each year. To reduce costs of surveying and ease strain on observers, SANParks combined four 3 km × 3 km blocks to survey blocks 6 km × 6 km in size. Observers, however, recorded in which 3 km × 3 km block they made an observation.

The survey used a helicopter from 17 August 2019 to 16 September 2019. Surveyors systematically completed transects comprising a 200 m observation strip on each side of the helicopter within each block, with flights 45 m above ground at a speed of 65 knots. The survey team comprised a pilot, a data recorder and two observers. For each black rhino encountered, surveyors also checked for ear notches and recorded the individual ear notch code when an individual had an ear-notch. Observers also noted the age, sex and geographical position of each rhino encountered. Assigning ages followed Brooks & Adcock (1997).

Mark-recapture analyses

The known number of rhinos present at the start of the census allowed us to use the Lincoln-Petersen estimator with Chapman correction (Chapman, 1951) to obtain mark-recapture population estimates during the single census. The method assumes a closed study population with no deaths, births or movements between the field visits to mark and recapture individuals. The estimator also assumes that marks remain the same and are present between the marking and recapturing occasions which observers record correctly (Seber, 1982). By using ranger observa-

tion records of notched rhinos, we defined the number of marked rhinos available at the time of the survey. This reduced the time interval between marking (*i.e.* number of rhinos available with notches at the time of the start of a survey) and recapturing (*i.e.* the time elapsed when observers completed a survey). In our case, that time interval was 31 days. This minimized the chance of non-compliance with the key assumptions of the estimator.

We applied four analytical approaches. The first used a batch-marking method. In this case, the analysis did not recognize individual notches and recorded a rhino as marked or not, irrespective of previous sightings of that individual. This approach could be useful if population recovery results in high numbers of rhinos and consequently the depletion of unique ear-notch markings – ear notches have a limited number of patterns that authorities can use (see Ngene *et al.*, 2011). We acknowledge that the batch-marking method without individual recognition inadvertently violates assumptions of no double counting, but we include the approach for illustrative purposes. It is thus unlikely that the batch-mark method without individual recognition may produce estimates with the best precision values.

In the second instance, we recognized individual notches allowing removal of repeat observations. Aerial coverage of the focal study area is not possible in one day. While black rhinos have high levels of site fidelity within their home ranges during the dry season (le Roex, Dreyer, Viljoen, Hofmeyr & Ferreira, 2019), individuals can still move from one block to abutting blocks between the times that surveyors were sampling blocks. Applying the batch-marking method to the reduced dataset allowed us to test whether the use of unique notches improved precision of estimates.

Observers see dependent black rhino calves only when they see their mothers. The detection probability of a calf is not equal to the other age classes, but links to that of the mother. Our third approach thus calculated estimates by age groups and added age group estimates together using the *FSA* package (Ogle, Wheeler & Dinno, 2019) in R v3.6.1 (R Core Team).

The final approach corrected for the absence of marked A- and B-class calves (A-class calves: <3 months old; B-class calves: 3 months to 1 year old; Brooks & Adcock 1997). First, we calculated the observed ratio of A- and B-class calves to the rest

of the population irrespective of whether individuals had marks. Next, we estimated the population excluding A- and B-class calves. Then, we used the ratio to estimate the number of calves relative to the estimated population size without A- and B-class calves. Combining estimates of calves and individuals other than calves provided a population estimate. To obtain confidence intervals we made use of Monte Carlo simulation methods (Hammersley & Handscomb, 1964). We randomly extracted a value from an assumed normal distribution of estimates without A- and B-class calves and multiplied that with a randomly extracted value from the assumed normal distribution of the observed ratio. We added this value to the randomly extracted population estimate excluding A- and B-class calves to get a total population estimate. One-hundred thousand iterations allowed us to extract the median as a point estimate and the 2.5% and 97.5% percentiles as estimates of lower and upper confidence limits respectively (Ferreira & Greaver, 2016).

Mark-recapture population estimates came from the *FSA* package (Ogle *et al.*, 2019) in R v3.6.1 (R Core Team). We calculated confidence intervals as a percentage of the point estimate (percentage confidence intervals) that serves as a measure of precision. Comparing extracted variances for each estimate using an $F_{\max}$ -test helped us to identify the approach with the best precision, *i.e.* significant narrowest confidence interval.

Block-based sample estimates

We extracted data for the randomly placed blocks in 2013 that surveyors target each year within the focal seven sections (Ferreira *et al.*, 2015; Ferreira *et al.*, 2017; Ferreira *et al.*, 2018; Ferreira *et al.*, 2019; le Roex & Ferreira, 2020). This totalled to 305 blocks used to derive a block-based population estimate for our focal study area. We used the same estimation approach as before (Ferreira *et al.*, 2015; Ferreira *et al.*, 2017; Ferreira *et al.*, 2018; Ferreira *et al.*, 2019; le Roex & Ferreira, 2020). The approach uses Jolly's estimator to calculate uncorrected estimates from sample surveys (Jolly, 1969). The methodology then correct estimates for availability bias (*i.e.* rhinos are present, but concealed from observation by vegetation cover; Caughley, 1974) and observer bias (*i.e.* even though rhinos are not hidden, some observers do not see them, due to varying observation skills; Seber, 1982). Detection bias is a third correction we account for (*i.e.* rhinos

are not hidden, but an observer finds it hard to see a rhino, for instance when it is further away from the helicopter; Buckland, Anderson, Burnham & Laake, 1993).

Availability bias arises from restricted visibility of rhinos on a block and associates with the vegetation cover of that block at the time of a survey. To estimate availability bias, we used published relationships to estimate vegetation cover and then used that to estimate proportion of rhinos missed. As few as 73.6% of black rhino

$$y = 1 + \left[0.001 - \frac{0.264 - 0.001}{1 + \left(\frac{x}{34.41} \right)^{19.63}} \right], r^2 = 0.841, \text{ where } y \text{ is}$$

the percentage of rhinos seen and x is the vegetation cover) could be visible and available for sampling in areas with high vegetation cover (Ferreira *et al.*, 2015). Observers do not measure woody cover easily or on an annual basis. We thus used the relationship between vegetation cover (Bucini *et al.*, 2011) and the Normalized Difference Vegetation Index (NDVI) (vegetation cover = $(0.019 \times \text{NDVI}) - 22.67$, $r^2 = 0.32$; Ferreira *et al.*, 2018) to estimate vegetation cover, then rhino visibility that provides availability bias for each block. We corrected estimates by dividing the estimated values by the percentage of rhinos visible.

Calculations from a previous survey provided values for observer bias when observers noted 96.2% of the visible rhinos (Ferreira *et al.*, 2011). We multiplied the estimates already corrected for availability bias by the percentage of visible rhinos noted by observers. Detection bias is negligibly low because observation strips were the same width as the first distance class previously used in establishing a detection function for distance sampling (Kruger, Riley & Whyte, 2008).

We used the same methodology as before that randomly drew a value from each of the distributions of estimates and biases that then produce an estimate corrected for bias using the approach described above. By repeating this 100 000 times, we could extract the median as an estimate with the 2.5% and 97.5% percentiles as the 95% confidence limit (Ferreira *et al.*, 2015; Ferreira *et al.*, 2017; Ferreira *et al.*, 2018; Ferreira *et al.*, 2019). We calculated as before the percentage confidence interval and use an $F_{\max}$ -test to check how precision of block-based sampling estimates compared with that derived through mark-recapture approaches.

Optimal marking requirements

After identifying the approach with the highest

precision, we used that approach to estimate precision required to detect 1%, 2%, 5% and 10% annual changes over a five-year period (Gerrodette, 1987). Detecting trends at a given annual change trades off intervals between surveys, number of surveys and total change by the time analysts detect a trend. The trade-off is sensitive to confidence intervals of estimates. We thus fixed the interval between surveys at one year and the total surveys at six to cover a five-year period. A five-year period typically reflects the time over which authorities set rhino conservation targets. We then used Gerrodette's (1987) inequality considering that capture-recapture estimates have coefficients of variance (cv) of an estimate (N) with dependence on abundance scaling to $1/\sqrt{N}$ (de la Mare, 1984) as

$$[\ln(1+r)]^2 n(n-1)(n+1) \geq$$

$$12 \left(z_{\alpha/2} + z_{\beta} \right)^2 \left\{ \frac{1}{n} \sum_{i=1}^n \ln \left[\frac{cv_i^2}{(1+r)^{i-1}} + 1 \right] \right\}$$

where r is the finite fractional rate of change per time, n is the number of surveys, z is the value of a standardized random normal variable such that the area under one tail of the probability density function beyond z_{α} is α with α set at 0.05 reflecting the probability of concluding that a trend in abundance is occurring, when in fact it is not, and β set at 0.2 reflecting the probability of concluding that no trend is occurring, when in fact it is. The power to detect a trend is $1-\beta$ (Gerrodette, 1987). To identify the required precision for this specific survey design that will allow detection of 1% to 10% annual changes, we estimated cv 's required at 1%, 2%, 5% and 10% annual change (r) to satisfy the inequality. We then converted that to a percentage confidence interval (confidence interval expressed as the percentage of an estimate) and plotted resultant values against percentage annual change. We fitted a power relationship to derive a generalized equation allowing prediction of percentage confidence intervals required at any percentage change from 1% to 10% per year.

To model the proportion of marked individuals required to obtain a confidence interval that allows a 1% to 10% change through annual surveys over a five-year period, we used the Lincoln-Petersen population and variance estimator (Chapman, 1951). We arbitrarily chose a population size of N of which we assigned a proportion (P_m) of individuals hypothetically marked to give the number with marks (M) in the modelling. The empirically calculated fraction of known marked individuals

observed during our survey (p_o) allowed us to define the number of marked animals our model survey would observe (m). Estimating $p_o(N-M)$ provides the number of unmarked animals (n) our model survey would observe. Using M , m and n as inputs into the Lincoln-Petersen estimator would give N , but importantly we could use the inputs to estimate variance (Chapman, 1951) from which we estimated percentage confidence intervals.

Our generalized equation allowed us to predict percentage confidence intervals required to detect changes from 1% to 10% per annum at 1% increasing intervals. At each percentage, we varied P_m until the percentage confidence interval estimated through the Lincoln-Petersen estimator equalled that required. We plotted the resultant P_m against annual percentage change and fitted a polynomial to obtain a generalized equation that predicts marked proportions required for detection of a specific annual rate of change.

RESULTS

We presumed 91 black rhinos with notches were alive at the start of the survey. Observers recorded 214 black rhinos of which 64 had notches. After confirming individual notches, nine records were repeat observations (14%) resulting in 55 unique observations. Observers thus saw 60.4% of assumed known animals.

Population size estimates for (a) the batch-mark method, (b) batch-mark without repeats, (c) by age class groups, and (d) age class groups with A+B calf adjustment were similar. Point estimates ranged from 303 to 334 (Table 2). Estimates by age class groups had significantly narrower confidence intervals than any of the other approaches (groups vs batch-mark: $F_{303,311} = 2.29$, $P < 0.01$; groups vs no repeats batch-mark: $F_{337,311} = 3.44$, $P < 0.01$; groups vs calf adjustment: $F_{332,311} = 1.82$, $P < 0.01$). All four approaches, however, had higher estimates than that estimated using the block-based sampling approach. In addition, all mark-recapture estimates had narrower confidence intervals than that estimated through block sample technique for the same seven sections (Table 2, batch-mark vs block-based sampling: $F_{245,303} = 1.87$, $P < 0.01$; no repeats batch-mark vs block-based sampling: $F_{245,337} = 1.25$, $P < 0.03$; groups vs block-based sampling: $F_{245,311} = 5.64$, $P < 0.01$; calf adjustment vs block-based sampling: $F_{245,332} = 2.33$, $P < 0.01$).

Detecting annual change of 1% over a five-year period required high precision. Percentage confi-

Table 2. Population estimates for the four mark-recapture methods. CI, Confidence interval; PCI, percentage confidence interval calculated as the confidence interval expressed as a percentage of the estimate.

Method	Estimate	95% CI	95% PCI
Batch-mark	303	250–375	41.3
Repeat observations removed	337	273–426	45.4
By group	311	275–347	23.2
By group + calves	332	278–390	33.7
Block-based sampling	245	165–336	69.8

dence interval required being 5.2% or less of the estimate (Fig. 1). The most precise estimate of 311 black rhino needed a confidence interval of 303 to 319. Authorities needed to mark 94%, or 292, of all black rhinos to achieve that (Fig. 1). To detect 5% annual change over a five-year period required 11.7% confidence intervals and the individual marking of at least 70% of black rhinos. To detect 10% annual change over a five-year period, percentage confidence intervals needed to be

16.6% and 54% of black rhinos needed marks (Fig. 1).

DISCUSSION

Our study addressed the challenge of estimating the size of a small population dispersed over a large area as is the case for black rhino in Kruger. Our evaluation of mark-recapture methods (Seber, 1982), an alternative approach to the block-based sample surveys used in Kruger

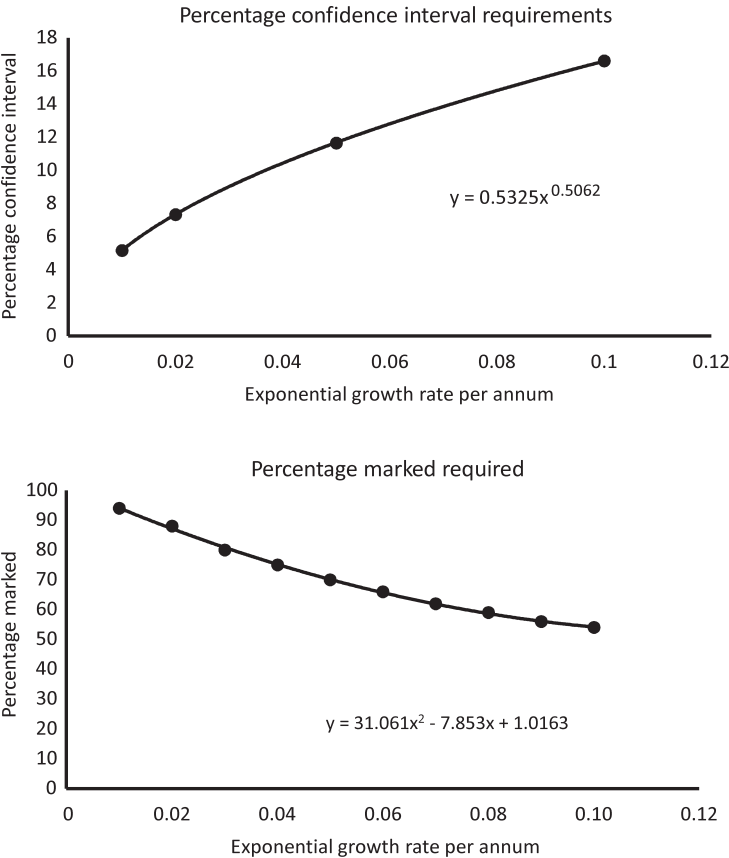


Fig. 1. Precision (percentage confidence interval) and marking (percentage marked) requirements to detect annual black rhino population changes ranging from 0.01 (1%) to 0.1 (10%) per annum over a five-year period.

(Ferreira *et al.*, 2011; Ferreira *et al.*, 2015; Ferreira *et al.*, 2017; Ferreira *et al.*, 2018; Ferreira *et al.*, 2019; le Roex & Ferreira, 2020) highlighted that all analytical mark-recapture approaches produced similar estimates to each other. Although individual identifications allowed the removal of repeat observations, it did not significantly change the results of the batch-mark population estimate. Notching with unique markings did not alter estimates derived from aerial mark-recapture for black rhino. Calculating population estimates by group and adjusting for lower calf detection also did not change the estimates significantly. All the mark-recapture approaches, however, produced point estimates higher than that estimated through the block-sample approach.

Differences in block-sample and mark-recapture point estimates may originate from how these methods account for biases. Observers seldom see all individual animals because availability, detectability, observer and sample biases occur (see Ferreira *et al.*, 2015). For instance, availability bias occurs when rhinos are present but are concealed from observation by vegetation cover. Observer bias happens when all rhinos are visible, but some observers do not see them due to varying observation skills. Detection bias relates to observers finding it hard to see a rhino, for instance when it is further away from the helicopter. Block-based sample surveys account for these biases (Ferreira *et al.*, 2018). Depending on woody cover, observers can miss up to 26.4% of black rhinos (Ferreira *et al.*, 2015). Block-based sample surveys assume detectability bias as negligible because the observation strip is narrow at 200 m from the helicopter (Ferreira *et al.*, 2015), while observers miss 3.8% of individuals available to be seen (Ferreira *et al.*, 2011).

Mark-recapture approaches account for biases by estimating the proportion of marked animals observers missed. In our study, observers did not see 39.6% of marked animals, a similar proportion to the 42.9% of marked rhinos missed in a previous study (Ferreira & Pienaar, 2020). Unrecorded deaths of notched individuals prior to the survey may result in a bias overestimate. Even so, block-based sample surveys most likely under-correct for biases reducing estimates for black rhinos.

Our results have implications on a continental scale. South Africa plays a key role in African rhino conservation. For instance, the African Rhino Specialist Group reported 1792 south-central and 208 southwestern black rhinos in 2012 (Emslie,

Milliken & Talukdar, 2012), 1560 south-central and 254 southwestern black rhinos in 2015 (Emslie *et al.*, 2015), and 1632 south-central and 331 southwestern black rhinos in 2017 (Emslie *et al.*, 2019) for South Africa. Southwestern black rhino numbers grew at 9.1% (95% CI: 5.6–12.6%) and will reach 435 (95% CI: 391–483) by 2020. South-central black rhinos grew at –2.1% (95% CI: –5.8–1.6%) only reaching 1533 (95% CI: 1372 to 1712) by the end of 2020.

South Africa had two short-term conservation goals (2010 to 2020) embedded within national rhino conservation policies. The first was to achieve 5% per annum population growth for two indigenous subspecies of black rhino. The second was to have at least 2800 south-central black rhinos and 260 southwestern black rhinos (*D. b. bicornis*) by 2020 (Knight *et al.*, 2013). South Africa achieved black rhino conservation goals for the southwestern subspecies, but failed to do so for south-central black rhinos.

For south-central black rhino, Kruger holds a key population (Emslie & Brooks, 1999), which declined from 627 (95% CI: 588–666) in 2008 (Ferreira *et al.*, 2011) to 268 (95% CI: 191–342) in 2019 (le Roex & Ferreira, 2020) because of poaching impacts (Ferreira *et al.*, 2018). Over the same period, black rhinos were resistant to drought impacts (le Roex & Ferreira, 2020). South Africa adopted an integrated approach to curb poaching in 2014 (DEA, 2014). Kruger is a focal population where SANParks set new targets, one of which is 1% annual growth (SANParks, 2020).

These various targets of population growth introduce challenges to detect changes in population size. The precision of population estimates plays a key role (Gerrodette, 1987). The better the precision (*i.e.* narrower percentage confidence interval), the easier the detection of a trend. Mark-recapture analyses by age group outperformed all other mark-recapture analytical approaches as well as the block-based sampling method. This approach requires percentage confidence intervals to be 5% of the population estimate. Authorities need to mark nearly all black rhinos. Even detecting the short-term target of 5% annual growth of South African black rhinos (Knight *et al.*, 2013) requires the marking of 70% of black rhinos. Slightly more realistic is when authorities seek to measure peak performance (Ferreira *et al.*, 2011; Ferreira & Greaver, 2016). Black rhino cows can have their first calves at 5 years of age and then calves every two years thereafter until

they are approximately 35 years old (Owen-Smith, 1988). Top performing populations grow at 7% per annum (e.g. Ferreira *et al.*, 2011; Ferreira & Greaver, 2016). To detect 7% annual change over a five-year period requires a 13.9% confidence interval and the individual marking of 62% of all rhinos.

Our analyses suggest that conservation policies should consider realistic metrics. For existing policies, authorities should extract complimentary metrics. Our analyses, however, focused on a single marking and recapturing approach. Using multiple recapture approaches through continuous notching and marking of rhinos over time will allow additional value. For instance, multiple marking and recapture approaches allow estimation of population sizes as well as survival rates of marked individuals using both discrete (Barker *et al.*, 2004) and continuous time capture-recapture models (Hwang & Chao, 2002). Most black rhinos live in small isolated populations with well-kept management records (e.g. Linklater, Law, Gedir & du Preez, 2017). Observing individually marked rhinos establishes a history that also allows extraction of age at first calving and calving intervals (e.g. Eberhardt, 1988). This allows developing survival and fecundity schedules to help evaluate short-term conservation goals. Such approaches can complement existing methods of estimating black rhino population sizes and provide robust information to evaluate conservation effectiveness.

ACKNOWLEDGEMENTS

We are grateful for the support as well as participation in aerial surveys by SANParks staff Don English, Steven Whitfield, Greg Bond, Marius Renke, Marius Snyders, Rob Thomson, Craig Williams, Neels van Wyk, Julie Bryden, Marc McGill, Izak Smit, Judith Botha and Corli Wigley-Coetsee. Additional assistance came from Ben Wigley, Mark Bourn, JJ Smith and Dawid van Zyl. Pauli Viljoen assisted with record keeping during aerial surveys and notching. We thank Johan Malan, Markus Hofmeyr, Peter Buss and Guy Hausler from the SANParks Veterinary Wildlife Services for assistance with rhino captures and notching. We are also thankful to state veterinarians Lin-Marie Lorient and Louis van Schalkwyk for additional veterinary support. We are appreciative of the World Wildlife Foundation, the Peace Parks Foundation and the SANParks Park Development Fund who provided funding for the project.

*ORCID iDs

S.M. Ferreira:  orcid.org/0000-0000-0000-0000

N. le Roex:  orcid.org/0000-0000-0000-0000

C. Greaver:  orcid.org/0000-0000-0000-0000

C. Dreyer:  orcid.org/0000-0000-0000-0000

REFERENCES

- Barker, R.J., Burnham, K.P. & White, G.C. (2004). Encounter history modelling of joint mark-recapture, tag re-sighting and tag-recovery data under temporary emigration. *Statistica Sinica*, 14, 1037–1055.
- Brooks, P.M. & Adcock, K. (1997). *Conservation plan for the black rhinoceros (Diceros bicornis) in South Africa*. Pietermaritzburg, South Africa: Rhino Management Group.
- Bucini, G., Hanan, N.P., Boone, R.B., Smit, I.P.J., Saatchi, S., Lefsky, M.A. & Asner, G.P. (2011). Woody fractional cover in Kruger National Park, South Africa: remote-sensing-based maps and ecological insights. In M.J. Hill & N.P. Hanan (Eds), *Ecosystem function in savannas: measurement and modelling at landscape to global scales* (pp 219–237). London, U.K.: CRC/Taylor and Francis.
- Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. (1993). *Introduction to distance sampling: estimating abundance of biological populations*. Oxford, U.K.: Oxford University Press.
- Caughley, G. (1974). Bias in aerial survey. *Journal of Wildlife Management*, 38, 921–933.
- Chapman, D.G. (1951). Some properties of the hypergeometric distribution with applications to zoological sample censuses. *University of California Publications in Statistics*, 1, 131–160.
- Conrad, K. (2012). Trade bans: a perfect storm for poaching? *Tropical Conservation Science*, 5, 245–254.
- Decker, D., Smith, C., Forstchen, A., Hare, D., Pomeranz, E., Doyle-Capitman, C., Schuler, K. & Organ, J. (2016). Governance principles for wildlife conservation in the 21st century. *Conservation Letters*, 9, 290–295.
- DEA. 2014. *Minister Edna Molewa leads implementation of integrated strategic management of rhinoceros in South Africa*. Pretoria, South Africa: Department of Environmental Affairs. Retrieved from: https://www.environment.gov.za/mediarelease/molewa_integratedstrategicmanagement_rhinoceros on 30 April 2019.
- de la Mare, W.K. (1984). On the power of catch per unit effort series to detect declines in whale stocks. *Report of the International Whaling Commission*, 34, 655–661.
- Dunlap A. & Jakobsen J. (2020) Claws & teeth: the militarization of nature. In *The violent technologies of extraction* (pp. 73–90). Palgrave Pivot, Cham. https://doi.org/10.1007/978-3-030-26852-7_4
- Eberhardt, L.L. (1988). Using age structure data from changing populations. *Journal of Applied Ecology*, 25, 373–378.
- Emslie, R. & Brooks, M. (1999). *African rhino: status survey and conservation action plan*. Gland, Switzerland: IUCN.
- Emslie, R.H., Milliken, T. & Talukdar, B. (2012). *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 (RevCoP15)*. CoP16 Doc. 54.2 Annex 2. Geneva, Switzerland: CITES Secretariat.
- Emslie, R.H., Milliken, T., Talukdar, B., Ellis, S., Adcock, A. & Knight, M.H. (2015). *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 (RevCoP15)*. CoP17 Doc. 68 Annex 5. Geneva, Switzerland: CITES Secretariat.
- 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)*. CoP18 Doc. 83.1 Annex 2. Geneva, Switzerland: CITES Secretariat.
- Ferreira, S.M., Bissett, C., Cowell, C.R., Gaylard, A., Greaver, C., Hayes, J., Hofmeyr, M., Moolman-van der Vyver, L. & Zimmermann, D. (2017). The status of rhinoceroses in South African national parks. *Koedoe*, 59, 1–11.
- Ferreira, S.M. & Greaver, C. (2016). Re-introduction success of black rhinoceros in Marakele National Park. *African Journal of Wildlife Research*, 46, 135–138.
- 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, 192–205.
- Ferreira, S.M., Greaver, 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. *PLOS ONE*, 10, p.e0127783.
- Ferreira, S.M., Greaver, C., Nhleko, Z. & Simms, C. (2018). Realization of poaching effects on rhinoceroses in Kruger National Park, South Africa. *African Journal of Wildlife Research*, 48, doi.org/10.3957/056.048.013001
- Ferreira, S.M., le Roex, N. & Greaver, C. (2019). Species-specific drought impacts on black and white rhinoceroses. *PLOS ONE*, 14, p.e0209678.
- Ferreira, S.M. & Pienaar, D.J. (2020). Evaluating uncertainty in estimates of large rhinoceros populations. *Pachyderm*, provisionally accepted.
- Gerrodette, T. (1987). A power analysis for detecting trends. *Ecology*, 68, 1364–1372.
- Gertenbach, W.D. (1980). Rainfall patterns in the Kruger National Park. *Koedoe*, 23, 35–43.
- Gertenbach, W.D. (1983). Landscapes of the Kruger National Park. *Koedoe*, 26, 9–121.
- Hammersley, J.M. & Handscomb, D.C. (1964). *Monte Carlo methods*. London, U.K.: Methuen.
- Hwang, W. & Chao, A. (2002). Continuous-time capture-recapture models with co-variates. *Statistica Sinica*, 12, 1115–1131.
- Jolly, G.M. (1969). Sampling methods for aerial censuses of wildlife populations. *East African Agricultural and Forestry Journal*, 34, 46–49.
- 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.
- Kruger, J.M., Reilly, B.K. & Whyte, I.J. (2008). Application of distance sampling to estimate population densities of large herbivores in Kruger National Park. *Wildlife Research*, 35, 371–376.
- Le Roex, N. & Ferreira, S.M. (2020). Rhino birth synchrony and resilience to climate impact. *African Journal of Ecology*, submitted.
- le Roex, N., Dreyer, C., Viljoen, P., Hofmeyr, M. & Ferreira, S.M. (2019). Seasonal space-use and resource limitation in free-ranging black rhino. *Mammalian Biology*, 99, 81–87.
- Linklater, W.L., Law, P.R., Gedir, J.V. & du Preez, P. (2017). Experimental evidence for homeostatic sex allocation after sex-biased reintroductions. *Nature Ecology & Evolution*, 1, 1–3.
- Madzwamuse, M., Rihoy, E. & Louis, M. (2020). Contested conservation: implications for rights, democratization, and citizenship in southern Africa. *Development*, 63, 67–73.
- Ngene, S., Bitok, E., Mukeka, J., Okita-Ouma, B., Gakuya, F., Omondi, P., Kimitei, K., Watol, Y. & Kimani, J. (2011). Census and ear-notching of black rhinoceros (*Diceros bicornis michaeli*) in Tsavo East National Park, Kenya. *Pachyderm*, 49, 61–69.
- Ogle, D.H., Wheeler, P. & Dinno, A. (2019). *FSA: Fisheries Stock Analysis*. R package version 0.8.25. <https://github.com/droglenc/FSA>
- Owen-Smith, R.N. (1988). *Megaherbivores: the influence of large body size on ecology*. Cambridge, U.K.: Cambridge University Press.
- R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rosen, G.E. & Smith, K.F. (2010). Summarizing the evidence on the international trade in illegal wildlife. *EcoHealth*, 7, 24–32.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A. & Leemans, R. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287, 1770–1774.
- SABS. (2000). *Translocation of certain species of wild herbivore: Code of Practice*. Pretoria, South Africa: South African Bureau of Standards. SABS 0331, ISBN 0-626-12377-1
- SANParks. (2020). *Strategic Plan: 2020/21-2023/24*. Pretoria, South Africa: SANParks.
- Seber, G.A.F. (1982). *The estimation of animal abundance and related parameters*. New Jersey, U.S.A.: Blackburn Press.
- Thompson, S.K. (1992). *Sampling*. New York, U.S.A.: John Wiley & Sons.
- Willson, J.D., Winne, C.T. & Todd, B.D. (2011). Ecological and methodological factors affecting detectability and population estimation in elusive species. *Journal of Wildlife Management*, 75, 36–45.