RESEARCH ARTICLE

Sample-based estimates of elephants in Kruger National Park, South Africa

Sam Ferreira[1,2], [§], Erin Crowhurst[1,3]*, Cathy Greaver[1] & Chenay Simms[1]

[1]*Savannah Node, Scientific Services, SANParks, Skukuza, 1350 South Africa*
[2]*Department of Conservation & Marine Sciences, Cape Peninsula University of Technology, Belville, 7535 South Africa*
[3]*Groen Sebenza Programme, SANBI, Pretoria, South Africa*

Received 1 July 2024. To authors for revision 18 July 2024. Accepted 28 August 2024

Increasing trends in elephant population numbers in South Africa contrast those in most other range states. Most of South Africa's elephants occur in Kruger National Park (Kruger). Elephant population estimates and trends in these are key aspects of evaluating their conservation status. Authorities in Kruger traditionally made use of elephants observed during total aerial surveys. This approach, however, has no measures of precision of the population estimates. Total aerial surveys also assume that sample errors and various biases have negligible impact on population estimates. We aimed to demonstrate and explore a sample-based methodology to obtain the most reliable population estimates and trends. Total and sample aerial surveys of elephants were simultaneously used to develop sample-based estimates with confidence intervals for the Kruger elephant time series. During 2020, sample errors resulted in an approximately 15% underestimate of the number of elephants in Kruger. The aerial survey that accounted for sample errors estimated 31 324 elephants (95% CI: 28 457–34 191) present in Kruger. Comparison with the 2013 sample-based estimate predicts annual exponential growth of 5.3% (95% CI: 3.7–7.0%). Correct estimates with precision are important to inform assessments of the conservation status of elephants and how this may change.

Keywords: Kruger National Park, elephant numbers, population trends, total aerial survey, sample aerial surveys.

INTRODUCTION

Population trends in species often form the key basis of conservation concerns (Craigie *et al.*, 2010). Most conservation management plans have expectations of increasing populations over time (Dybala *et al.*, 2017), while the Conference of the Parties at the Convention on the International Trade in Endangered Species (CITES) meetings use trends in populations of several species to decide on trade proposals (Harfoot *et al.*, 2018). Often authorities face difficult decisions when trends differ between ecological regions. African elephants (*Loxodonta africana*) epitomize this – recent information highlighted trends in southern Africa and in particular South Africa, contrasting the rest of the African continent (Chase *et al.*, 2016).

Total aerial surveys conducted during the dry season of most years provided annual elephant numbers in Kruger (Ferreira *et al.*, 2017). These surveys aimed to determine the elephant estimates by counting elephants encountered while flying the river catchment areas typically at 165–185 km/hr and 90 m above the ground following contours at variable intervals (Whyte, 2001). This technique ignored uncertainties that can originate from sampling error and bias (Caughley, 1974, 1977), limiting robust detection of trends (Gerrodette, 1987) and optimal cost-efficient aerial survey designs (Ferreira & Van Aarde, 2009).

Detecting a trend carries trade-offs (Gerrodette, 1987) between the magnitude of change that authorities wish to detect, the aerial survey interval, the number of aerial surveys and the total change by the time of trend detection. We aimed to explore a sample-based methodology to obtain the most reliable population estimates that improves trend detection. Precision of estimates is a key contributor – it is harder to detect change in populations that have estimates with low precision compared to those with high precision. Precision in this context typically refers to the reliability or

*To whom correspondence should be addressed.
E-mail: erin.crowhurst@sanparks.org

ISSN 2410-8200 [Online only] — DOI: https://doi.org/10.3957/056.054.0122

repeatability of the survey results, indicating, how closely repeated measurements or estimates would agree with each other. Authorities seldom have the resources to do repeated surveys at a particular time and rely on modern statistical and analytical methods for robust assessment of precision. Precision often originates from sampling error linked to the variability or uncertainty associated with measuring a subset of the larger statistical population (Morrison, Block, Strickland, Collier & Peterson, 2008).

Precision, along with several biases – availability bias (the availability of the animal to be recorded, *e.g.* hidden under trees), detectability bias (the visibility of the animal when it is available to be seen, *e.g.* elephants covered in mud in a freshly burnt area) and observer bias (observer seeing/recording the animal when it is both available and detectable), influence the accuracy of any aerial survey technique (Caughley, 1974). Accuracy, a measure of agreement of an estimate to real values (Everitt, 2002), includes a bias and precision component, where accuracy = bias^2 + precision (Thompson 1992). Precision of estimates, however, is critical for trend detection (Gerrodette, 1987).

In addition, it is costly to conduct aerial surveys at the scale of protected areas the size of Kruger National Park (Kruger) in South Africa. Optimal surveys seek to define the effort required that provide robust precision of estimates. While densities and distribution do influence the necessary sampling effort, it is generally advised that precision improves minimally beyond 50% coverage of an area using randomly placed sample units (Ferreira & van Aarde, 2009). Essentially, surveyors do not observe significant precision improvements that would justify the additional costs associated with increasing area coverage.

The Kruger elephant population contributed to 62.6% of South Africa's elephant population by 2015 (Thouless *et al.*, 2016) and thus dictates trends in elephants reported for the country (Chase *et al.*, 2016). Using sample approaches that allows optimal and cost-efficient ways to survey elephants and detect trends in their numbers, thus play a key role informing and evaluating various conservation efforts. We design and implement a statistical methodology to help estimate elephant population sizes and detect trends in these using sample-based approaches.

We use data on elephants encountered during annual rhino aerial surveys in Kruger during 2013, 2015, 2017 (Ferreira *et al.*, 2015; Ferreira *et al.*, 2017; Ferreira, le Roex & Greaver, 2019) and 2020 (present study) to estimate confidence intervals that account for sampling errors. The approach uses sample blocks of known size with flights at 120 km/hr and 45 m above the ground along transects 400 m apart (Ferreira *et al.*, 2015).

Methods for conducting total surveys will have different detection of elephants compared to the standards used for sample surveys because flight speeds and altitude differ (see Laake *et al.*, 2008). Even so, total elephant aerial surveys during 2015 (Ferreira, Greaver & Simms, 2017) and 2017 (present study) allowed us to develop approximations of sample-based estimates for the historical elephant estimates of Kruger. We then provide an updated historical time series with confidence intervals of estimates for Kruger from 1900 to 2020, allowing us to reflect on conservation management and monitoring implications.

STUDY AREA

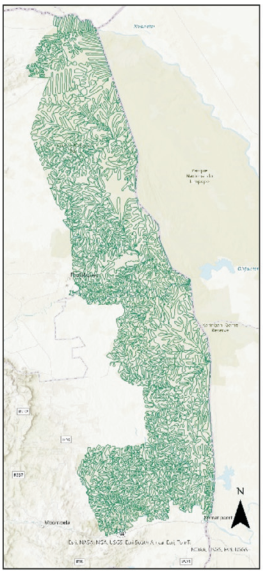
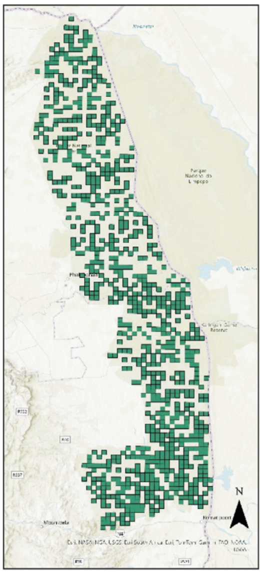
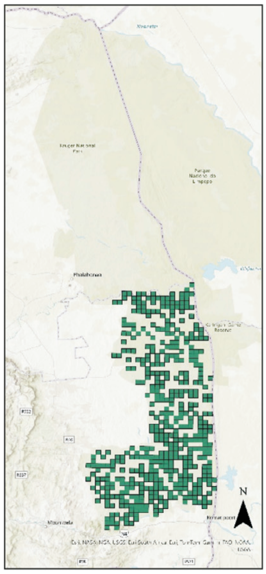
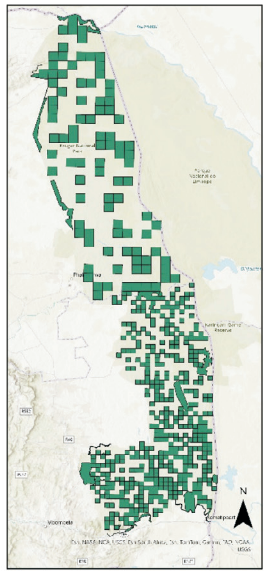
Kruger (23.9884°S, 31.5547°E) spans the low-lying savannas of northeastern South Africa. Granite and gneiss soils underlay the undulating western parts of Kruger, and nutrient-rich basalt the more level eastern plains separated by Karoo sediment (Schutte, 1986). Wooded savanna (*i.e. Sclerocarya caffra* and *Senegalia nigrescens*) and mixed *Combretum* spp., *Senegalia* spp. and *Vachelia* spp. dominate the south, while *Colophospermum mopane* are the prominent vegetation in the north (Gertenbach, 1983). Minimum and maximum temperatures range from 5.6°C to 26.8°C in winter and from 19.2°C to 34.9°C in summer (Venter & Gertenbach, 1986). The long-term mean annual rainfall for the entire park is 530 mm with most rain falling between October and March (summer).

METHODS

All aerial survey methods conducted over the years have evolved based on the availability of funding, and new understandings of requirements to detect trends (Table 1). We focused the historical total aerial counts, previous sample surveys and our own sample-survey.

We collated total aerial count data for elephants up to 2015 (see Ferreira *et al.*, 2017) and 2017 held at the SANParks Data Repository (https://www.sanparks.org/conservation/scientific-services/data-information-resources/data-repository, last accessed May 2024). These data originate from

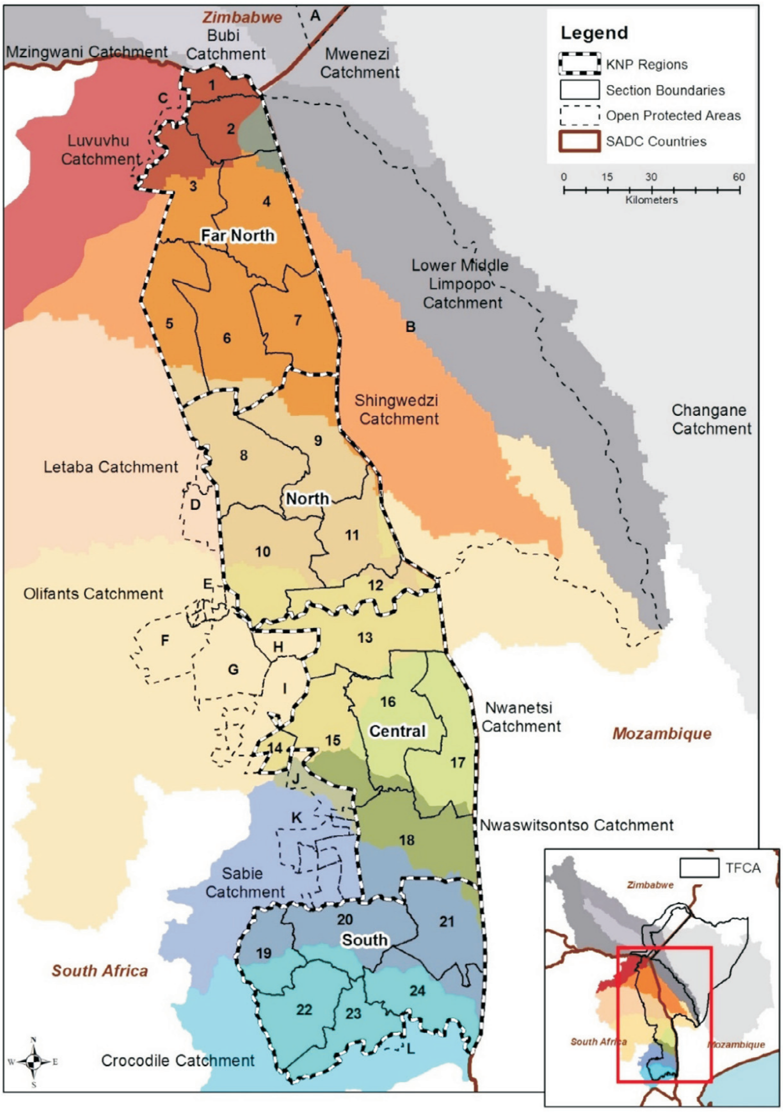
Table 1. Summary of the methodological changes when conducting the aerial survey since 1967.

1967–2017	2013	2015 & 2017	2020
			
Total count covering 100% of the area by focusing on river catchments and second-order streams.	Sample count covering 50% of the area, with 3 × 3 km blocks randomly placed across the KNP.	Sample count covering 50% of the area in southern KNP, with 3 × 3 km blocks randomly placed.	Sample count covering the park variably with 3 × 3 km blocks placed randomly in southern KNP and 6 × 6 km blocks placed randomly in the north.
Helicopter	**Helicopter**	**Helicopter**	**Helicopter**
165–185 km/hr 90 m above-ground 500–1000 m parallel to second-order streams.	120 km/hr 45 m above-ground 200 m observation strips on both sides of the aircraft along transects 400 m apart within each block.	120 km/hr 45 m above-ground 200 m observation strips on both sides of the aircraft along transects 400 m apart within each block.	120 km/hr 45 m above-ground 200 m observation strips on both sides of the aircraft along transects 400 m apart within each block.

the total aerial count method used since 1967 (Whyte, 2001). A total aerial count aims to cover 100% of the area of Kruger. Surveyors divide Kruger into 21 blocks and use a helicopter-based observation platform to search each block for elephants. Pilots fly routes at 165–185 km/hr and 90 m above ground level, focusing on second-order river catchments *c*. 500–1000 m parallel to second-order streams. Distances between flight paths vary according to vegetation cover. Surveyors will geo-reference the positions and record the number of elephants that they encounter. The helicopter-based observation platform allow pilots to circle herds for observers to check for calves as part of recording the number of elephants.

We also collated information from rhino-dedicated aerial surveys (SANParks Data Repository: https://www.sanparks.org/conservation/scientific-services/data-information-resources/data-repository, last accessed May 2024; Ferreira *et al*., 2015, 2017, 2019) and focused on aerial surveys during 2013, 2015 and 2017. Note that during 2013, SANParks randomly placed 3 × 3 km blocks across the entire Kruger to sample approximately 50% of the park. During 2015 and 2017, however, the block-based aerial survey of rhino populations focused only on 11 ranger sections in Kruger's Southern and Central regions (Fig. 1). The years 2015 and 2017 are of specific interest as these were overlapping with the standard total aerial survey of the elephant population.

During our own fieldwork in September 2020, surveyors also targeted the historical 3 × 3 km aerial survey blocks distributed randomly across



Surrounding parks / reserves

A. Gonarezhou National Park (Zimbabwe)*
B. Limpopo National Park (Mozambique)*
C. Makuya Nature Reserve
D. Letaba Ranch / Mthimkhulu Private Game Reserve
E. Phalaborwa Mining Company
F. Balule Game Reserve
G. Klaserie Private Nature Reserve
H. Umbabat Game Reserve
I. Timbavati Private Nature Reserve
J. Manyeleti Game Reserve
K. Sabi Sands / Mala Mala Game Reserves
L. Mjejane Game Reserve

Kruger Ranger Sections

1. Makuleke Contractual Park*
2. Pafuri Section*
3. Punda Maria Section
4. Vlakteplaas Section
5. Shangoni Section
6. Woodlands Section
7. Shingwedzi Section
8. Mahlangeni Section
9. Mooiplaas Section
10. Phalaborwa Section
11. Letaba Section
12. Olifants Section
13. Houtboschrandt Section
14. Kempiana Contractual Park†
15. Kingfisherspruit Section†
16. Satara Section
17. N'wanetsi Section
18. Tshokwane Section
19. Pretoriuskop Section
20. Skukuza Section
21. Lower Sabie Section
22. Stolsnek Section
23. Malelane Section
24. Crocodile Bridge Section

Fig. 1. Map of the Kruger National Park and beyond. The main panel shows the administrative boundaries of regions, ranger sections and neighbouring parks and private reserves, overlaying river catchments. The inset shows the location of Kruger within South Africa, as well as within the Great Limpopo Transfrontier Conservation Area. Map prepared by Donna Cawthorn.

**SANParks manages Makuleke Contractual Park (1) and Pafuri Ranger Section (2) as a unit, jointly referred to as Pafuri.*

†SANParks manages Kempiana Contractual Park (14) and Kingfisherspruit Ranger Section (15) as a unit, jointly referred to as Kingfisherspruit.

Kruger's Southern and Central regions. In addition, surveyors targeted 6 × 6 km aerial survey blocks distributed randomly across Kruger's Northern and Far Northern regions. SANParks previously identified areas of concern where elephant effects on various conservation values may contrast management outcomes of Kruger (Ferreira, Freitag-Ronaldson, Pienaar & Hendricks, 2012). Recent reviews identified Elephant Impact Assessment Areas (EIAs) in Kruger (Wigley-Coetsee, Greaver, Simms, MacFadyen & Ferreira, 2022). As part of the aerial survey, SANParks focused on 20 EIAs. In some instances, surveyors sampled an entire EIA, while in large EIAs, surveyors sampled 3 × 3 km or 6 × 6 km blocks that overlapped with a specific EIA (Fig. 2). Data are

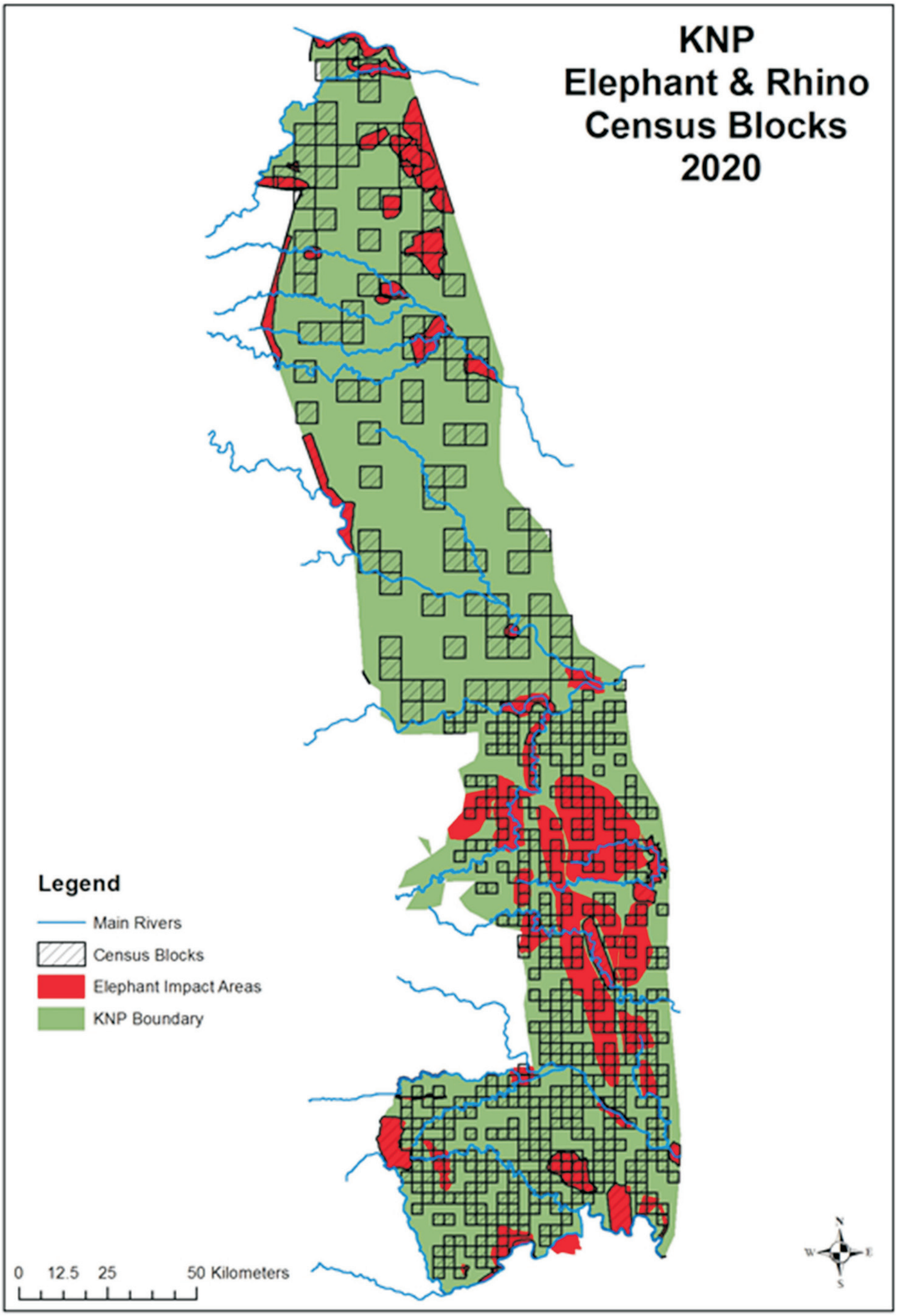


Fig. 2. Distribution of aerial survey blocks and elephant impact areas surveyed for elephants during 2020.

available from the SANParks Data Repository (https://www.sanparks.org/conservation/scientific-services/data-information-resources/data-repository, last accessed May 2024).

Observers made use of a helicopter-based observation platform and systematically completed transects comprising a 200 m observation strip on each side of the helicopter within each block or EIA, with flights 45 m above-ground at a speed of approximately 120 km/hr. The survey team comprised a pilot, a data recorder and two observers. Surveyors counted elephants during all aerial surveys, taking photographs of larger herds and counting elephants from these images after recording the geographical position of the observation.

The flight plan adjustment (lower altitude and slower speed) was implemented when the risk to rhinoceroses increased, and conservation efforts were directed at them. The lack of funds prevented both aerial surveys from taking place, so the alternative was to incorporate the elephant aerial survey into the rhino aerial survey. The slower speed and lower altitude implemented for the rhino observations would likely influence the detectability of the elephants, making it easier to observe and count them. Both methods, however, have been conducted for several years with an overlap in 2015 and 2017. This overlap provided the opportunity to consider the influence sample error has on estimates, and more particularly provide estimates of precision. Bias, although an important factor when determining the accuracy of estimates (see Thompson, 1992), is not the key attribute that can help to improve the power to detect trends (Gerrodette, 1987).

Data collected on elephants during annual rhino aerial surveys within administrative sections (Fig. 1) enabled us to use quadrant sampling (Fig. 2) approaches (Seber, 2002) to obtain sample-based estimates and confidence intervals of elephant numbers for Southern and Central Kruger during 2015 and 2017 with the assumption of nearly 100% detection. To calculate average sample count for the j section ($\bar{x}_j$), the unbiased estimate of the number of elephants within the section j ($\hat{N}_j$) and the variance ($\hat{\sigma}^2_{N_j}$), we used the equations below:

$$\bar{x}_j = \sum_{i=1}^{s_j} x_{i,j} / s_j$$

$$\hat{N}_j = \bar{x}_j S_j$$

$$\hat{\sigma}^2_{N_j} = S_j^2 \frac{\nu_j}{s_j}\left(1 - \frac{s}{S_j}\right)$$

$$\nu_j = \sum_i (x_{i,j} - \bar{x}_j)^2 / (s_j - 1),$$

where s_j blocks at random from a total of S_j blocks available in section j (Fig. 3). The number of elephants counted in a block i is x_i.

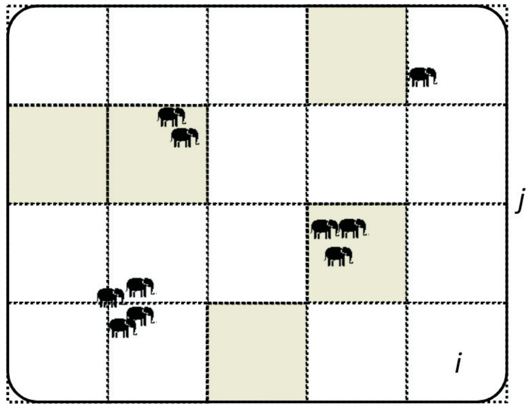


Fig. 3. Illustration depicting the statistical methodology for sample counts. The dotted-lines represent all blocks within a section (S_j) and the green shaded areas represent the sampled blocks within the section (s_j). The solid black line signifies the boundary of the section (j) with a sample block (i) represented by the dotted line. The elephant images provide an example of sightings seen.

The total aerial survey of elephants (T_t) during 2015 and 2017 of Kruger's Southern and Central regions allowed us to develop a methodology that provides confidence intervals for estimates corrected from total aerial surveys across the entire Kruger time series. Southern Kruger has six ranger sections, whereas Central Kruger has five (Fig. 1). We extracted total aerial surveys data ($T_{t,j}$) for each section (j) for 2015 and 2017 and obtained a total number of elephants per ranger section. At the same time, we used the elephant population data collated from the annual rhino aerial surveys and used a quadrant sampling approach described above to derive sample-based population estimates ($\hat{N}_{t,j}$) per section at time t (2015 or 2017). We then checked whether there was a significant linear relationship between total aerial surveys and sample estimates defined by $\hat{N}_{t,j} = aT_{t,j} + b + \varepsilon$ (with constants a and b, and error ε)

Once a linear relationship was confirmed, we developed a model for correction by considering the confidence intervals of $\hat{N}_{t,j}$. We randomly sampled with replacement 100 000 times from the statistical distribution of estimates for each section defined by $\hat{N}_{t,j}$ and its confidence interval. For each iteration, we recalculated the slope and intercept between derived sample-based estimates ($\hat{N}_{t,j}$) and the matching total aerial surveys ($T_{t,j}$). This procedure generated a sample of 100 000 slopes and intercepts. We obtained the average, as well as 2.5% and 97.5% percentile values, for the slope and intercept. The approach produced a linear model describing the relationship between sample-based estimates and total counts. Our approach equates to bootstrapping techniques of a sample of slopes generated through our iteration approach (Efron & Tibshirani, 1993).

The developed linear model allowed us to estimate approximations of sample-based estimates and confidence intervals for all historical total aerial surveys. For this purpose, we extracted all previously reported total estimates for Kruger as a whole (Ferreira *et al.*, 2017; Whyte, 2001). We again randomly sampled with replacement 100 000 times from the distributions of the slope and intercept of our model to predict a sample-based estimate for a given total count in a particular year. For each year, this procedure generated a sample of 100 000 sample-based estimates for that particular year, or time *t*. This sample allowed us to extract the median as a point estimate ($\hat{\hat{N}}_t$), as well as the 2.5% and 97.5% percentiles as lower and upper confidence limits at time *t*.

We used data collected on blocks during 2013 and 2020 that sampled all the sections of Kruger during rhino-focused aerial surveys to obtain elephant population estimates with confidence intervals for the entire Kruger for those years using a stratified random sampling approach (Seber, 2002), with an unbiased estimate of variance $\tilde{\sigma}_N^2$.

$$\tilde{N} = \sum_j \hat{N}_j = \sum_j \bar{x}_j S_j$$
$$\tilde{\sigma}_N^2 = \sum_j \hat{\sigma}_{N_j}^2 = \sum_j S_j^2 \frac{v_j}{s_j}\left(1 - \frac{s}{S_j}\right)$$

A $100(1-\alpha)$ percent confidence interval for $\tilde{N}$ is then $\tilde{N} \pm t_k[\alpha/2]\tilde{\sigma}_N$, where the degree for freedom is *k*.

$$k = \frac{\tilde{\sigma}_N^4}{\sum_j \left(\hat{\sigma}_{Nj}^4 / (s_j - 1)\right)}$$

We integrated the 2013 and 2020 sample-based estimates into the time series of approximated sample-based estimates for Kruger. This provides an updated time series of elephant population estimates since 1900.

RESULTS

The various blocks surveyed during 2020 resulted in sample coverage of 42.7% (total size: 18 984 km^2) of the area of Kruger (Southern Kruger: 55.8% of 4192 km^2; Central Kruger: 43.9% of 4946 km^2; Northern Kruger: 32.6% of 4482 km^2; Far Northern Kruger: 39.7% of 5364 km^2, Table 2). During these aerial surveys, observers noted a total of 13 216 elephants.

The relationships between sample-based estimates and minimum numbers alive on individual sections did not differ between regions ($t_{18} = 1.05$, $P = 0.30$). We therefore defined a correction relationship for Kruger by combining data for all sections. Using only point estimates, sample-estimates linearly related to total aerial surveys in a ranger section ($F_{1,20} = 29.7$, $P < 0.01$). We thus ran simulations that included uncertainty in each ranger section's sample-based estimate. This procedure defined $y = 1.15x + 242$ (slope 95% CI: 1.09–1.22; intercept 95% CI: 175–309), a generalized equation to correct Kruger's historical elephant estimates and provide population estimates with confidence intervals (Fig. 4).

The modelling approach estimated that Kruger had 8998 (95% CI: 7866–10 495) elephants during the culling period (Fig. 5). By 2017, 23 years after culling stopped, Kruger had 22 375 (95% CI: 21 064–23 707) elephants. Given the annual growth in the number of elephants encountered during total counts (*i.e.* minimum numbers alive at any time *t*) from 2012 to 2015 (1.02%), we predicted that a minimum of 16 741 elephants likely inhabited Kruger during 2013. Using the likely minimum number of elephants alive in Kruger predicted for 2013, forecasted a sample-based estimate of 19 579 (95% CI: 18 397–20 743) elephants. Our actual sample estimate in 2013 derived from the elephants recorded during the rhino block aerial survey was 21 801 (95% CI: 19 622–23 980) elephants. Although estimates and elephant densities varied between sections (Table 2), by 2020, an estimated 31 324 elephants (95% CI: 28 457–34 191) lived in Kruger. This reflects an annual exponential increase of 5.3% (95% CI: 3.7–7.0%) from 2013 to 2020.

DISCUSSION

A sample-based methodology provided estimates, as well as precision in these, of the number of elephants in Kruger. Furthermore, simultaneously using total counts and sample count surveys allowed adaptation of the historical time series of elephant estimates. Elephant numbers derived from encounters during total surveys in Kruger in 2017, reflect the largest elephant population in the park in recorded history at that time (Ferreira *et al.*,

Table 2. Estimates of elephant numbers and densities in specific Ranger Sections in Kruger National Park during 2020.

Ranger section	Area (km^2)	*n* sample units	% Area sampled	Area (km^2) sampled	Total seen	Range on units	Estimate	LCL	UCL	Density	LCL	UCL
Pafuri	743	10	53.4	397	576	0–254	1080	390	1769	1.45	0.52	2.38
Punda Maria	792	11	47.0	372	949	3–250	2018	1258	2778	2.55	1.59	3.51
Shangoni	806	6	30.5	246	232	1–84	761	149	1373	0.94	0.18	1.70
Shingwedzi	795	9	40.8	324	501	0–108	1229	659	1800	1.55	0.83	2.26
Vlakteplaas	1076	13	43.5	468	509	0–111	1170	599	1741	1.09	0.56	1.62
Woodlands	1152	9	28.1	324	721	1–216	2564	1200	3927	2.23	1.04	3.41
Far North	5364	58	39.7	2131	3488	0–254	8822	7089	10555	1.64	1.32	1.97
Letaba	558	9	58.1	324	206	0–70	355	137	573	0.64	0.25	1.03
Mahlangeni	1161	6	23.4	272	422	21–137	1803	75	3531	1.55	0.06	3.04
Mooiplaas	1032	9	31.4	324	365	0–106	1163	466	1859	1.13	0.45	1.80
Olifants	696	6	31.0	216	355	15–114	1144	439	1849	1.64	0.63	2.66
Phalaborwa	1035	9	31.3	324	777	11–173	2482	1548	3416	2.40	1.50	3.30
North	4482	39	32.6	1460	2125	0–173	6946	5138	8754	1.55	1.15	1.95
Houtboschrandt	1147	51	42.6	489	555	0–80	1303	822	1785	1.14	0.72	1.56
Kingfisherspruit	768	31	36.3	279	841	0–98	2315	1739	2891	3.01	2.26	3.76
N'wanetsi	913	39	45.1	412	346	0–143	768	414	1122	0.84	0.45	1.23
Satara	945	42	40.0	378	643	0–95	1608	1043	2172	1.70	1.10	2.30
Tshokwane	1173	61	52.4	615	1114	0–123	2126	1601	2650	1.81	1.36	2.26
Central	4946	224	43.9	2173	3499	0–143	8120	7014	9225	1.64	1.42	1.87
Crocodile Bridge	825	57	71.7	592	882	0–107	1230	941	1520	1.49	1.14	1.84
Malelane	531	33	55.2	293	844	0–163	1530	970	2090	2.88	1.83	3.94
Lower Sabie	793	45	53.3	423	511	0–78	958	634	1282	1.21	0.80	1.62
Pretoriuskop	524	20	50.8	266	484	0–160	953	676	1230	1.82	1.29	2.35
Skukuza	843	46	49.1	414	915	0–172	1863	1166	2560	2.21	1.38	3.04
Stolsnek	676	39	51.9	351	468	0–60	901	624	1178	1.33	0.92	1.74
South	4192	240	55.8	2339	4104	0–172	7436	6396	8475	1.77	1.53	2.02
Kruger National Park	18984	561	42.7	8103	13216	0–254	31324	28457	34191	1.65	1.50	1.80

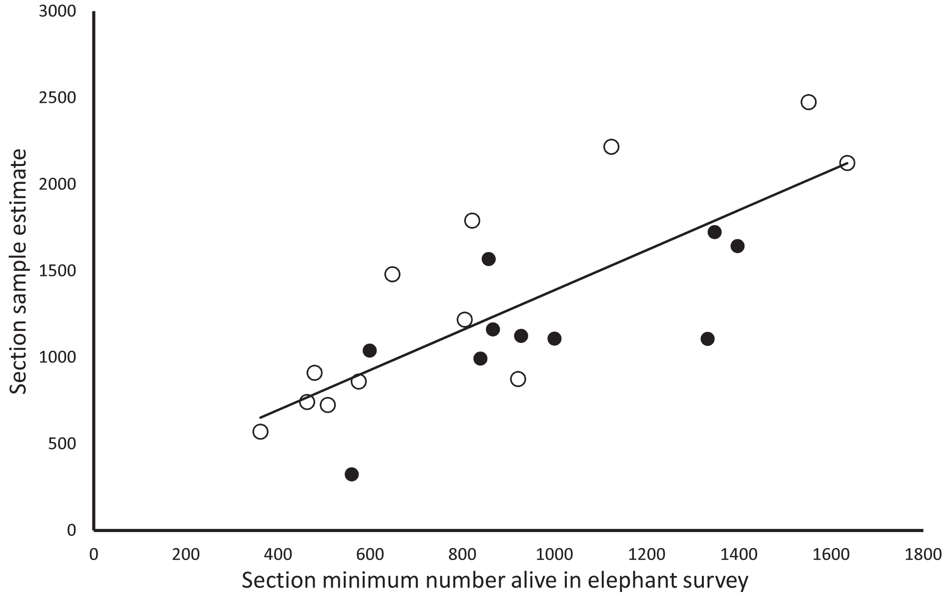


Fig. 4. The relationship between sample estimates and minimum number of elephants alive ($y = 1.15x + 242$ (slope 95% CI: 1.09–1.22; intercept 95% CI: 175–309)). Solid circles represent sections in central Kruger, open circles represent sections in Southern Kruger (see Fig. 1).

2017; Whyte, 2001). The development of sample-based elephant population estimates extracted from simultaneous rhino and elephant aerial surveys during 2015 and 2017, however, suggest that such estimates based on total counts (*i.e.* a minimum number known to be alive at the time) substantially underestimated elephant numbers. This most likely resulted from improved detection when aircraft speed and altitude were lower during sample surveys compared to that of total counts (see Laake *et al.*, 2008).

Detectability is one of the biases that influence population estimates, and precision in these (Caughley, 1974). Several factors may influence

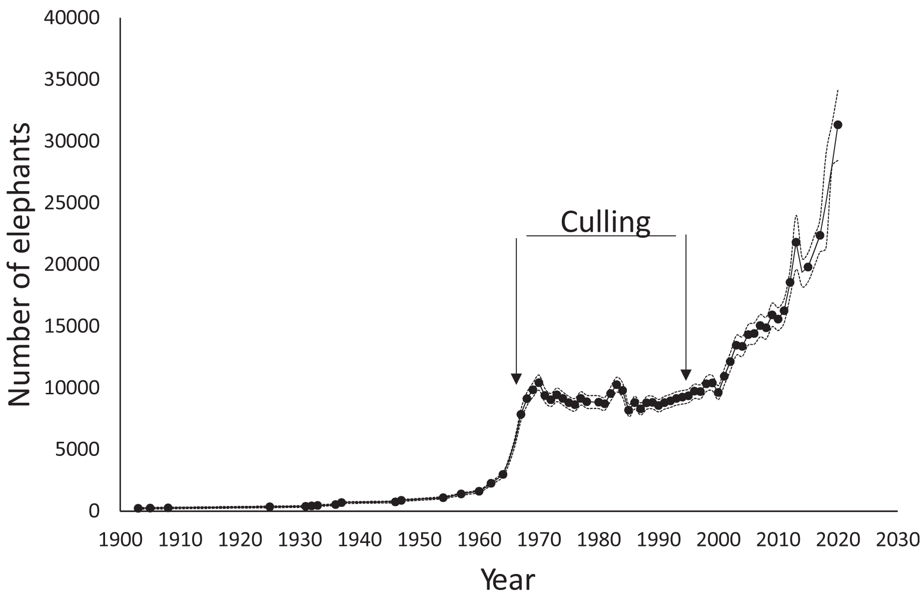


Fig. 5. Revised historical elephant population estimates for Kruger National Park. The broken lines indicate 95% confidence intervals. We also indicate the period during which elephant culling took place in Kruger National Park.

that. For one, larger-bodied animals are easier to detect than smaller ones (Bukombe *et al.*, 2016). Elephants social structure have females, and their associated dependent calves including males up to the age of as much as 10 years, aggregate into breeding herds, while subadult and adult males have loose social groupings, and often males are alone (Athira & Vidya, 2021). It is thus unlikely that body size, of for instance younger elephants, have significant effects on detection probability. Irrespective of the approach used, observers had a high probability of recording all the individuals in a group once a group is detected. Group size, however, is also a factor that could influence detection – larger groups of a species is far easier to detect than singletons (*e.g.* Ransom, 2012). We assume that such error linked to group size of elephants is likely to be relatively similarly biased irrespective of differences in speeds and altitudes that the total counts and sample surveys used. In our study, the speculated improved detection most likely link primarily to the reduced speed and lower altitude from which observers made recordings.

Our study did not explicitly account for observer and availability biases that also influence accuracy of an estimate (Caughley, 1974). Elsewhere, in Botswana, observers detected 76% of elephant herds and 87% of individual elephants present when using an aircraft travelling at 180 km/h at 91 m above-ground (Schlossberg, Chase & Griffin, 2016). In our case we made use of block surveys for rhinos to also count elephants. Estimates of observer bias when counting rhinos in Kruger, however, noted that 3.8% of rhinos that are available to be seen will not be detected (Ferreira, Greaver & Knight, 2011). This is negligibly small and likely to be even less for elephants given their body size. Availability bias for rhinos in the block surveys in Kruger depended on the rhino species – black rhinos (*Diceros bicornis*) had higher availability bias (they are smaller and more secretive) than white rhinos (*Ceratotherium simum*), while vegetation cover also played a more important role for black rhinos because of the habitats that they prefer (Ferreira *et al.*, 2015). We anticipate that for elephants, given their social structures and group sizes (Athira & Vidya, 2021), availability bias is likely to be lower than that for white rhinos which were estimated at 17.1% of individuals missed in the worst-case scenario (Ferreira *et al.*, 2015).

Disregarding the influence of biases on accuracy of elephant estimates, the estimated precisions from sample counts conducted in 2020 equated to an 18.1% percentage confidence interval (*i.e.* PCL = the 95% confidence interval expressed as a percentage of the population estimate; Barnes 2001). This is considerably lower than the median PCL of ~64% reported for elephant estimates in Africa (Junker, 2008). In addition, at 40% aerial survey coverage of an area through randomly placed sample units, 5% annual change when elephants are at densities of 1 *n*/km to 3 *n*/km will easily be detectable with three surveys every four years, *i.e.* a sample survey every two years (Ferreira & van Aarde, 2009). Making use of the rhino surveys to simultaneously also estimate elephant population sizes and confidence intervals thus provide ample statistical power to detect 5% changes (Gerrodette, 1987), and even smaller ones given that rhino surveys have taken place annually since 2013 (Ferreira, Crowhurst, Greaver & Simms, 2024).

The time series of sample-based estimates illustrate that the elephant population in Kruger is increasing. Mechanisms could associate with all the drivers of population changes – deaths, births, emigration and immigration (Sibly & Hone, 2002). Elephants move substantially from Kruger as well as into Kruger (Henley *et al.*, 2023) which could mask potential influences of density-dependence on elephant population growth at a park-wide scale. At a smaller scale, however, density-dependent changes take place close to perennial rivers (Louw, MacFadyen, Ferreira & Hui, 2021) most likely through spatial responses (MacFadyen, Hui, Verburg & van Teeffelen, 2019; Huang, van Aarde, Pimm, Chase & Leggett, 2022; Henley *et al.*, 2023) as well as consequences of elephant density on daily movement distances of cows and resultant survival of weaned calves (Young & Van Aarde, 2010). Even so, by 2020, sample-based estimates with confidence intervals are still lower than the predicted population size at which the population would fluctuate at a park-wide scale (Robson *et al.*, 2017).

We have highlighted that sample-based corrections do not explicitly account for availability-, observer- and detectability-biases (Caughley, 1974). We have also suggested that impacts of biases inherent in methods for estimating elephants (*e.g.* Walsh *et al.*, 2001) are less severe than for other mega-herbivores like rhinos (*e.g.* Ferreira *et al.*, 2015). Even so, Kruger and the region may have more elephants than the sample-based estimates reflect. Confidence intervals may be wider. Nonetheless, the 2015 elephant population sample-based estimate of 19 798 (95% CI: 18 625–20 977) had confidence intervals that did not overlap with that of 2017 (22 374; 95% CI: 21 047–23 717), whereas the confidence intervals of the 2015 sample-based population estimate did overlap with that of 2012 (18 550; 95% CI: 17 458–19 656).

The time series of elephant population estimates often have increases between aerial surveys that exceeds the theoretical maximum of closed populations with relative stable fecundity and survival schedules (Calef, 1988), as well as substantive declines, similar to variance in elephant time series noted elsewhere in southern Africa (*e.g.* Hwange National Park (Chamaillé-Jammes, Fritz, Valeix, Murindagomo & Clobert, 2008); Northern Botswana (Junker, van Aarde & Ferreira, 2008). Elephant movements most likely influence these regional patterns (Huang *et al.*, 2022). For instance, while there was limited poaching of elephants in the Kruger, periods of high poaching pressure in adjacent areas (Häefele, 2022) overlap with periods of steep elephant population increases in Kruger. This suggests elephants move into Kruger because they perceive the park as a relative safe place. Elephants make strong landscape choices, avoiding dangerous areas locally (Cook, Henley & Parrini, 2015) as well as elsewhere in Africa (Wittemyer, Keating, Vollrath & Douglas-Hamilton, 2016; Wall, Wittemyer, Klinkenberg, LeMay & Douglas-Hamilton, 2013; Wall *et al.*, 2021). In addition to perceptions that elephants have of safety in Kruger, their spatial responses to environmental gradients and perturbations within the greater region also play a key role. For instance, during a recent drought, Kruger management noted a net movement of elephants into the park from the adjacent private nature reserves (Smit, Peel, Ferreira, Greaver & Pienaar, 2020).

Using sample-based estimates can help elucidate factors that influence elephant dynamics, but precise estimates of elephant population sizes are only one of the requirements. For instance, patterns in numbers of elephants varying across space and time in the region (Chase *et al.*, 2016) provides variance in the seasonal distribution of elephants as well as how they may influence socio-ecological resilience (van de Water, di Minin & Slotow, 2022). This reflects variable intensity of habitat use due to responses of elephants to food (Marshal *et al.*, 2011; Boult *et al.*, 2019), water (Chamaillé-Jammes, Valeix & Fritz, 2007; Purdon & van Aarde, 2017), comfort (Kinahan, Pimm & van Aarde, 2007; de Knegt *et al.*, 2011;) and safety resources (Wittemyer *et al.*, 2016). This results in ecological impacts (Guldemond, Purdon & van Aarde, 2017) and conflict with people (Shaffer, Khadka, van den Hoek & Naithani, 2019) not associating with the number of elephants, but links to where elephants are, and what they are doing when they are at a specific place (Owen-Smith, Kerley, Page, Slotow & van Aarde, 2006).

In conclusion, our analyses highlighted that while elephants are abundant in Kruger, sample surveys provide estimates and precision in these that are time and resource effective. We, however, accounted only for precision through sampling error within this study, but inadvertently also noted an influence of detection bias. This may result from sample-based aerial approaches using slower flight speeds at lower altitudes than total counts. Studies should assess the further influences of the various biases on elephant population estimates. Future aerial surveys could therefore consider sample-based aerial surveys and the influences that various biases have on elephant population estimates. We emphasize, however, that quantifying the precision of elephant estimates is an important consideration for detecting trends (Ferreira & van Aarde, 2009), particularly when authorities must make trade-offs (see Gerrodette 1987) between aerial survey intervals, number of aerial surveys, and aerial survey intensity to enhance confidence in the trends (*i.e* population growth rates) derived from a time series of population estimates. Sample-based estimates with precision are important to inform assessments of the conservation status of elephants and how this may change. This information may be less important when informing how to mitigate the influence of elephants on people and other biodiversity values.

ACKNOWLEDGEMENTS

We are grateful for data made available by SANParks. USAID provided the funds for the 2020 aerial survey. The Park Development Fund of SANParks provided financial support for elephant and rhino aerial surveys during other years. We thank the SANParks pilots, section rangers and the various data recorders and observers for assisting with aerial surveys in Kruger. The Data Review Working Group, IUCN SSC African Elephant Specialist Group assisted with verification of the 2020 estimates.

§ORCID iDs

S. Ferreira: orcid.org/0000-0001-6924-1150
E. Crowhurst: orcid.org/0000-0003-1359-5894
C. Greaver: orcid.org/0000-0001-8555-9679
C. Simms: orcid.org/0000-0002-4508-0863

REFERENCES

Athira, T.K. & Vidya, T.N.C. (2021). Elephant social systems: what do we know and how have molecular tools helped? *Journal of the Indian Institute of Science*, 101(2), 257–278.

Barnes, R.F.W. 2001. How reliable are dung counts for estimating elephant numbers? *African Journal of Ecology*, 39, 1–9.

Boult, V.L., Sibly, R.M., Quaife, T., Fishlock, V., Moss, C. & Lee, P.C. (2019). Modelling large herbivore movement decisions: beyond food availability as a predictor of ranging patterns. *African Journal of Ecology*, 57(1), 10–19.
https://doi.org/10.1111/aje.12553

Bukombe, J., Senzota, R.B., Fryxell, J.M., Kittle, A., Kija, H., Hopcraft, J.G.C., Mduma, S. & Sinclair, A.R. (2016). Do animal size, seasons and vegetation type influence detection probability and density estimates of Serengeti ungulates? *African Journal of Ecology*, 54(1), 29–38.

Calef, G.W. (1988). Maximum rate of increase in the African elephant. *African Journal of Ecology*, 26(4), 323–327.

Caughley, G. (1974). Bias in aerial survey. *Journal of Wildlife Management*, 38(4), 921–933.
https://doi.org/10.2307/3800067

Chamaillé-Jammes, S., Fritz, H., Valeix, M., Murindagomo, F. & Clobert, J. (2008). Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. *Journal of Animal Ecology*, 77(1), 135–144.
https://doi.org/10.1111/j.1365-2656.2007.01307.x

Chamaillé-Jammes, S., Valeix, M. & Fritz, H. (2007). Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology*, 44(3), 625–633.
https://doi.org/10.1111/j.1365-2664.2007.01300.x

Chase, M.J., Schlossberg, S., Griffin, C.R., Bouché, P.J.C., Djene, S.W., Elkan, P.W., Ferreira, S., Grossman, F., Kohi, E.M., Landen, K., Omondi, P., Peltier, A., Selier, S.A.J. & Sutcliffe, R. (2016). Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ*, 4, e2354.
https://doi.org/10.7717/peerj.2354

Cook, R.M., Parrini, F. & Henley, M.D. (2015). Elephant movement patterns in relation to human inhabitants in and around the Great Limpopo Transfrontier Park. *Koedoe*, 57(1), 1–7.
https://doi.org/10.4102/koedoe.v57i1.1298

Craigie, I.D., Baillie, J.E.M., Balmford, A., Carbone, C., Collen, B., Green, R.E. & Hutton, J.M. (2010). Large mammal population declines in Africa's protected areas. *Biological Conservation*, 143(9), 2221–2228.
https://doi.org/10.1016/j.biocon.2010.06.007

de Knegt, H.J., van Langevelde, F., Skidmore, A.K., Delsink, A., Slotow, R., Henley, S., Bucini, G., de Boer, W.F., Coughenour, M.B., Grant, C.C., Heitkönig, I.M.A., Henley, M., Knox, N.M., Kohi, E.M., Mwakiwa, E., Page, B.R., Peel, M., Pretorius, Y., van Wieren, S.E. & Prins, H.H.T. (2011). The spatial scaling of habitat selection by African elephants. *Journal of Animal Ecology*, 80(1), 270–281.
https://doi.org/10.1111/j.1365-2656.2010.01764.x

Dybala, K., Clipperton, N., Gardali, T., Golet, G., Kelsey, R., Lorenzato, S., Melcer, Jr., R., Seavy, N., Silveira, J. & Yarris, G. (2017). A general framework for setting quantitative population objectives for wildlife conservation. *San Francisco Estuary and Watershed Science*, 15(1), 1–14.
https://doi.org/10.15447/sfews.2017v15iss1art8

Efron, B. & Tibshirani, R. (1993). *An introduction to the bootstrap.* Boca Raton, FL: Chapman & Hall/CRC. ISBN 0-412-04231-2.

Everitt, B.S. (2002). *Cambridge dictionary of statistics.* New York, U.S.A.: Cambridge University Press.

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), 1–11.

Ferreira, S.M., Crowhurst, E.T., Greaver, C. & Simms, C. (2024). Resizing Kruger National Park: trends in numbers of rhinoceroses within priority zones. *Koedoe* 66(1), a1802.
https://doi.org/10.4102/koedoe.v66i1.1802

Ferreira, S.M., Freitag-Ronaldson, S., Pienaar, D. & Hendriks, H. (2012). *Elephant Management Plan: Kruger National Park 2013–2022*. Skukuza, South Africa: South African National Parks, Scientific Services.

Ferreira, S.M., Greaver, C.C. & Knight, M.H. (2011). Assessing the population performance of the black rhinoceros in Kruger National Park. *South African Journal of Wildlife Research*, 41(2), 192–204.

Ferreira, S.M., Greaver, C., Knight, G.A., Knight, M.H., Smit, I.P.J. & Pienaar, D. (2015). Disruption of rhino demography by poachers may lead to population declines in Kruger National Park, South Africa. *PLOS ONE*, 10(6), e0127783.
https://doi.org/10.1371/journal.pone.0127783

Ferreira, S.M., Greaver, C. & Simms C. (2017). Elephant population growth in Kruger National Park, South Africa, under a landscape management approach. *Koedoe*, 59(1), 1–6.

Ferreira, S.M., le Roex, N. & Greaver, C. (2019). Species-specific drought impacts on black and white rhinoceroses. *PLOS ONE*, 14(1), e0209678.
https://doi.org/10.1371/journal.pone.0209678

Ferreira, S.M. & van Aarde, R.J. (2009). Aerial survey intensity as a determinant of estimates of African elephant population sizes and trends. *South African Journal of Wildlife Research*, 39(2), 181–191.
https://doi.org/10.3957/056.039.0205

Gerrodette, T. (1987). A power analysis for detecting trends. *Ecology*, 68(5), 364–1372.
https://doi.org/10.2307/1939220

Gertenbach, W.D. (1983). Landscapes of the Kruger National Park. *Koedoe*, 26(1), 9–121.
https://doi.org/10.4102/koedoe.v26i1.591

Guldemond, R.A.R., Purdon, A. & van Aarde, R.J. (2017).

A systematic review of elephant impact across Africa. *PLOS ONE*, 12(6), e0178935.
https://doi.org/10.1371/journal.pone.0178935

Häefele, B. (2022). The poaching of rhino and elephant as a facilitator of organised crime in the Greater Kruger National Park environment. *Acta Criminologica: African Journal of Criminology & Victimology*, 35(1), 1–24.
https://doi.org/10.10520/ejc-crim_v35_n1_a1

Harfoot, M., Glaser, S.A.M., Tittensor, D.P., Britten, G.L., McLardy, C., Malsch, K. & Burgess, N.D. (2018). Unveiling the patterns and trends in 40 years of global trade in CITES-listed wildlife. *Biological Conservation*, 223, 47–57.
https://doi.org/10.1016/j.biocon.2018.04.017

Henley, M.D., Cook, R.M., Bedetti, A., Wilmot, J., Roode, A., Pereira, C.L., Almeida, J. & Alverca, A. (2023). A phased approach to increase human tolerance in elephant corridors to link protected areas in southern Mozambique. *Diversity*, 15(1), 85.
https://doi.org/10.3390/d15010085

Huang, R.M., van Aarde, R.J., Pimm, S.L., Chase, M.J. & Leggett, K. (2022). Mapping potential connections between southern Africa's elephant populations. *PLOS ONE*, 17(10), e0275791.
https://doi.org/10.1371/journal.pone.0275791

Junker, J. 2008. *An analysis of numerical trends in African elephant populations*. (M.Sc. thesis). Pretoria, South Africa: University of Pretoria.

Junker, J., van Aarde, R. & Ferreira, S. (2008). Temporal trends in elephant *Loxodonta africana* numbers and densities in northern Botswana: is the population really increasing? *Oryx*, 42, 58–65.
https://doi.org/10.1017/S0030605308000756

Kinahan, A.A., Pimm, S.L. & van Aarde, R.J. (2007). Ambient temperature as a determinant of landscape use in the savanna elephant, *Loxodonta africana*. *Journal of Thermal Biology*, 32(1), 47–58.
https://doi.org/10.1016/j.jtherbio.2006.09.002

Laake, J., Guenzel, R.J., Bengtson, J.L., Boveng, P., Cameron, M. & Hanson, M.B. (2008). Coping with variation in aerial survey protocol for line-transect sampling. *Wildlife Research*, 35(4), 289–299.

Louw, A.S., MacFadyen, S., Ferreira, S. & Hui, C. (2021). Elephant population responses to increased density in Kruger National Park. *Koedoe*, 63(1), 1–13.
http://dx.doi.org/10.4102/koedoe.v63i1.1660

MacFadyen, S., Hui, C., Verburg, P.H. & van Teeffelen, A.J. (2019). Spatiotemporal distribution dynamics of elephants in response to density, rainfall, rivers and fire in Kruger National Park, South Africa. *Diversity and Distributions*, 25(6), 880–894.
https://doi.org/10.1111/ddi.12907

Marshal, J., Rajah, A., Parrini, F., Henley, M., Henley, S. & Erasmus, B. (2011). Scale-dependent selection of greenness by African elephants in the Kruger-private reserve transboundary region, South Africa. *European Journal of Wildlife Research*, 57, 537–548.
https://doi.org/10.1007/s10344-010-0462-1

Morrison, M.L., Block, W.M., Strickland, M.D., Collier, B.A. & Peterson, M.J. (2008). *Wildlife study design*. Berlin, Germany: Springer Science & Business Media.

Owen-Smith, N., Kerley, G.I.H., Page, B., Slotow, R. & van Aarde, R.J. (2006). A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. *South African Journal of Science*, 102(9), 389–394.

Purdon, A. & van Aarde, R.J. (2017). Water provisioning in Kruger National Park alters elephant spatial utilisation patterns. *Journal of Arid Environments*, 141, 45–51.
https://doi.org/10.1016/j.jaridenv.2017.01.014

Ransom, J.I. (2012). Detection probability in aerial surveys of feral horses. *The Journal of Wildlife Management*, 76(2), 299–307.

Robson, A.S., Trimble, M.J., Purdon, A., Young-Overton, K.D., Pimm, S.L. & van Aarde, R.J. (2017). Savanna elephant numbers are only a quarter of their expected values. *PLOS ONE*, 12(4), e0175942.
https://doi.org/10.1371/journal.pone.0175942

Schutte, I.C. (1986). The general geology of the Kruger National Park. *Koedoe*, 29(1), 13–37.
https://koedoe.co.za/index.php/koedoe/article/view/517

Seber, G.A.F. (2002). *The estimation of animal abundance and related parameters* (2nd edn). Caldwell, NJ, U.S.A.: Blackburn Press.
https://books.google.co.za/books?id=bnGaPQAACAAJ

Shaffer, L.J., Khadka, K.K., Van Den Hoek, J. & Naithani, K.J. (2019). Human–elephant conflict: a review of current management strategies and future directions. *Frontiers in Ecology and Evolution*, 6, 235.
https://doi.org/10.3389/fevo.2018.00235

Schlossberg, S., Chase, M.J. & Griffin, C.R. (2016). Testing the accuracy of aerial surveys for large mammals: an experiment with African savanna elephants (*Loxodonta africana*). *PLOS ONE*, 11(10), p.e0164904.

Sibly, R.M. & Hone, J. (2002). Population growth rate and its determinants: an overview. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357(1425), 1153–1170.
https://doi.org/10.1098/rstb.2002.1117

Smit, I.P.J., Peel, M.J.S., Ferreira, S.M., Greaver, C. & Pienaar, D.J. (2020). Megaherbivore response to droughts under different management regimes: lessons from a large African savanna. *African Journal of Range & Forage Science*, 37(1), 65–80.
https://doi.org/10.2989/10220119.2019.1700161

Thompson, S.K. 1992. *Sampling* (2nd edn). New York, U.S.A.: John Wiley & Sons.

Thouless, C., Dublin, H.T., Blanc, J., Skinner, D.P., Daniel, T.E., Taylor, R., Maisels, F., Frederick, H. & Bouché, P. (2016). *African elephant status report 2016* (Vol. 60). Occasional paper series of the IUCN Species Survival Commission.
https://doi.org/10.2305/IUCN.CH.2007.SSC-OP.33.en

van de Water, A., Di Minin, E. & Slotow, R. (2022). Human–elephant coexistence through aligning conservation with societal aspirations. *Global Ecology and Conservation*, 37, e02165.
https://doi.org/10.1016/j.gecco.2022.e02165

Venter, F.J. & Gertenbach, W.P.D. (1986). A cursory review of the climate and vegetation of the Kruger National Park. *Koedoe*, 29(1), 139–148.
https://koedoe.co.za/index.php/koedoe/article/view/526

Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., Blake, S., Strindberg, S., Henley, M., Vollrath, F., Maisels, F.,

Ferwerda, J. & Douglas-Hamilton, I. (2021). Human footprint and protected areas shape elephant range across Africa. *Current Biology*, 31(11), 2437–2445.e4.
https://doi.org/10.1016/j.cub.2021.03.042

Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V. & Douglas-Hamilton, I. (2013). Characterizing properties and drivers of long distance movements by elephants (*Loxodonta africana*) in the Gourma, Mali. *Biological Conservation*, 157, 60–68.
https://doi.org/10.1016/j.biocon.2012.07.019

Walsh, P.D., White, L.J.T., Mbina, C., Idiata, D., Mihindou, Y., Maisels, F. & Thibault, M. (2001). Estimates of forest elephant abundance: projecting the relationship between precision and effort. *Journal of Applied Ecology*, 38(1), 217–228.
https://doi.org/10.1046/j.1365-2664.2001.00578.x

Whyte, I.J. (2001). *The conservation management of the Kruger National Park elephant population*. (Ph.D. thesis). Pretoria, South Africa: University of Pretoria.

Wigley-Coetsee, C., Greaver, C., Simms, C., MacFayden, S. & Ferreira, S. (2022). *Elephant management in Kruger National Park* (Internal 15/2022). Skukuza, South Africa: Scientific Services, SANParks.

Wittemyer, G., Keating, L., Vollrath, F. & Douglas-Hamilton, I. (2016). Graph theory illustrates spatial and temporal features that structure elephant rest locations and reflect risk perception. *Ecography*, 40(5), 598–605.
https://doi.org/10.1111/ecog.02379

Young, K.D. & van Aarde, R.J. (2010). Density as an explanatory variable of movements and calf survival in savanna elephants across southern Africa. *Journal of Animal Ecology*, 79(3), 662–673.

Responsible Editor: D.M. Parker