Evaluating uncertainty in estimates of large rhinoceros populations

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Abstract

Estimates of the numbers of living rhinoceroses inform management interventions. Several techniques assist authorities in obtaining estimates. For large populations, authorities use sample-based methods. Estimates for the number of rhinos living in Kruger National Park (Kruger) make use of sample-based block surveys. Critics of this approach allege that the authorities place sample blocks mostly in areas with high rhino numbers and that this, together with correction for various biases, inflates estimates. The critics also claim that the percentage confidence intervals (PCIs) associated with estimates are too large and propose total area counts as an alternative. We assess these criticisms by comparing the results of a sample-based survey with those of a near concurrent total count. We found that sample surveys appeared to focus on areas with higher rhino densities, but rhino movements in and out of the survey area confounded results. Moreover, total counts do not produce reliable estimates when surveyors fail to account for biases inherent to all sampling procedures. Bias corrections used by sample surveys most likely underestimate the number of rhinos that surveyors miss, contrary to the allegations of critics that sample-based techniques inflate population estimates. Even so, estimates that transparently report uncertainties detected a significant decline in white rhinos from 8,968 (95% CI: 8,394–9,564) in 2013 to 4,116 (95% CI: 2,994–5,726) in 2018. The trends in the black rhino population also indicate a decline from 627 (95% CI: 588–666) in 2009 to 291 (95% CI: 151–441) in 2018. Conducting block-based sample surveys for large populations that correct for biases provides useful information for decision makers. Given that South Africa, specifically Kruger makes substantial contributions to continental rhino numbers, reporting to international bodies such as CITES should transparently include the uncertainties associated with population estimates.

Résumé

Les estimations du nombre de rhinocéros vivants orientent les interventions de gestion. Plusieurs techniques permettent aux autorités d'obtenir des estimations. Pour les populations importantes, les autorités utilisent des méthodes basées sur des échantillons. Les estimations du nombre de rhinocéros vivant dans le parc national du Kruger (Kruger) s'appuient sur des enquêtes par sondage par blocs. Les détracteurs de cette approche allèguent que les autorités placent les blocs d'échantillonnage principalement dans des zones où le nombre de rhinocéros est élevé et que cela, combiné à une correction pour divers biais, gonfle les estimations. Les critiques affirment également que les intervalles de confiance en pourcentage (ICP) associés aux estimations sont trop importants et proposent comme alternative des comptages totaux des aires. Nous évaluons ces critiques en comparant les résultats d'une enquête par sondage aux résultats d'un comptage total qui a eu lieu presque simultanément. Nous avons constaté que les enquêtes par sondage semblaient se concentrer sur les zones à haute densité de rhinocéros, mais les résultats ont été faussés par le mouvement des rhinocéros dans et hors de la zone d'enquête. De plus, les comptages totaux produisent des estimations non fiables lorsque les enquêteurs ne tiennent pas compte des biais inhérents à toutes les procédures d'échantillonnage. Les corrections de biais utilisées par les enquêtes par sondage sous-estiment probablement le nombre de rhinocéros que les enquêteurs manquent, contrairement aux allégations des critiques selon lesquelles les techniques par sondage gonflent les estimations de population. Des estimations qui rapportent les incertitudes de manière transparente ont détecté une baisse significative des rhinocéros blancs de 8 968 (IC à 95%: 8 394–9 564) en 2013 à 4 116 (IC à 95%: 2 994–5 726) en 2018. Les tendances démographiques des rhinocéros noirs indiquent également un déclin de 627 (IC à 95%: 588–666) en 2009 à 291 (IC à 95%: 151–441) en 2018. Les enquêtes par sondage par blocs qui corrigent les biais et qui sont utilisées pour d'importantes populations, fournissent des informations utiles aux décideurs. Étant donné que l'Afrique du Sud et Kruger contribuent de manière substantielle au nombre de rhinocéros continentaux, les rapports aux organismes internationaux tels que la CITES devraient inclure les incertitudes associées aux estimations des populations de manière transparente.

Introduction

Populations of the two extant species of African rhinoceros displayed contrasting trends in the period 2012–2017. In 2017 there were 18,067 white rhinos (*Ceratotherium simum*) representing a decline from 21,316 in 2012. However numbers of black rhinos (*Diceros bicornis*) increased during the same period to 5,561 in 2017 compared to 4,845 in 2012 (Emslie et al. 2019). Trends in South Africa, which holds the largest numbers of both species, define continental trends. Authorities detected a decline in white rhinos in the world's premier rhino stronghold, Kruger National Park (Kruger), during 2016, which continued during 2017, with the (Ferreira et al. 2019). The trends in black rhino are uncertain (Ferreira et al. 2019).

The decline in the white rhino population in Kruger has taken place despite several management interventions intended to safeguard the species. SANParks, the Kruger management authority, adopted South Africa's multi-pronged integrated rhino management strategy in 2013[1]. This comprises a mix of intensive anti-poaching operations, innovative biological management (including translocations), and a range of measures that aim to ensure the long-term sustainability of rhino populations, including disruption of organized crime syndicates and providing alternative economic opportunities for local people.

Public criticism of SANParks, fuelled by arrests of rangers in Kruger accused of collaborating with poachers[2], focuses on internal corruption, including allegations of underreporting of dead rhinos[3]. Carcass detection is indeed unlikely to be perfect (Huso 2011) with authorities estimating that rangers miss 20% of carcasses (Ferreira et al. 2018b). In addition, critics allege that survey techniques inflate rhino population sizes[4].

Estimating animal abundances is challenging (Caughley 1974). Availability (Caughley 1974), observer (Seber 1982) and detection (Buckland et al. 1993) biases all affect observer estimates. Moreover, in the case of sample-based surveys, sample error is a source of imprecision in estimates (Walsh et al. 2001). Estimates of populations are considered accurate, and therefore reliable, when bias is low and precision is high (accuracy = bias^2 + precision; Thompson 1992). Precise estimates, however, allow robust detection of changes, providing biases remain constant (Gerrodette 1987). For small rhino populations—like most present-day populations in Africa—registration studies or total counts (Ferreira et al. 2017) provide exact numbers of animals encountered during the survey, even though observers most likely do not see each individual. Authorities, however, cannot know or see every individual for large populations and therefore use sample surveys (e.g. Ferreira et al. 2011). In so doing, they have to make a trade-off between precision and costs when determining sampling effort (e.g. Ferreira and van Aarde 2009).

Authorities reporting on rhino estimates rarely report bias and sample errors (e.g. Emslie et al. 2019). This is not the case in Kruger. Estimates of rhino populations make use of sample-based block surveys and surveyors report bias as well as sample errors (e.g. Ferreira et al. 2019). However, the block-based

[1] https://www.environment.gov.za/mediarelease/molewa_integratedstrategicmanagement_rhinoceros

[2] https://lowvelder.co.za/470282/two-field-ranger-arrested-kruger-national-park

[3] https://www.pressreader.com

[4] https://oxpeckers.org/2015/06/kruger-rhino-numbers-in-crisis-says-expert

sample survey used in Kruger, described below, has been widely criticised[4].

We focus on three critiques of sample surveys in this study. The first critique is that sampling focuses on areas with high rhino densities, which inflates estimates. Sample-based extrapolations to a total area are then likely to exceed total counts of that same area. The second critique is that sample-based estimates come with large confidence intervals and hence low precision. The precision of estimates should then be higher when authorities do a total count. We use results from a sample-based survey, a partial total survey carried out as part of the sample-based survey, and an independent total survey to evaluate these two predictions.

The third critique is that the procedure for estimating bias (Ferreira et al. 2011; 2015) overestimates the numbers of animals missed by the survey. As a result, corrections of observations for biases unrealistically inflate population estimates. If this is so, then bias estimations for sample surveys should exceed actual biases, which can be calculated when true population numbers are known. In this study, the existence of a sub-population of black rhinos with ear notches, whose numbers are known, allowed us to calculate the fraction of marked rhinos that observers missed to evaluate this prediction.

Finally, we evaluate the continued impact of poaching in Kruger and conclude that rhino declines in Kruger persisted throughout 2018.

Materials and Methods

Study area

The study took place in Kruger, and focused on southern Kruger because this is the main stronghold of rhinos in the National Park (NP). In the 2017 survey (Ferreira et al. 2019), rangers recorded fewer than 100 black and white rhinos in northern Kruger, compared to more than 3,000 in southern Kruger. The Olifants River separates northern from southern Kruger. Southern Kruger covers 9,138 km^2 and is divided for management purposes into two regions, Marula North and Marula South, which in turn comprise ranger sections 1–5 and 6–11 respectively. Southern Kruger consists mainly of low-lying savannahs where annual rainfall exceeds 450 mm. Granite and gneiss deposits separated by Karoo sediment combine with wooded savannah comprising marula (*Sclerocarya caffra*) and knob thorn (*Senegalia nigrescens*) trees on basalts and mixed bushwillows (*Combretum spp.*) and thorn trees (*Acacia spp.*) on granites to create a range of different landscape types across southern Kruger (Ferreira et al. 2015).

Data collection

Sample surveys

We collated data from a sample survey undertaken between 16 August and 12 September 2018. The survey targeted the 11 ranger sections in southern Kruger using a helicopter. Observers counted black and white rhino in 488 blocks, each 3 × 3 km in size, randomly distributed across southern Kruger following the method described by Ferreira et al. (2015). Surveyors observed 400 m wide transects (200 m on each side of the helicopter) flying at 45 m height and 65 knots (120 km/h) speed within each block. A pilot, data recorder and two observers comprised the survey team. Surveyors recorded the position, species and number of individuals when they encountered rhinos.

The 2018 survey covered 44.2% of Kruger's Marula North Region (246 blocks) and 51.9% of the Marula South Region (242 blocks). Surveyors also targeted additional blocks in sections 9 and 10 to achieve a total survey covering the entire area in these two sections (comprising 79 and 72 blocks in sections 9 and 10 respectively). Surveyors also checked for ear notches on black rhinos and recorded individual identifications in section 10.

Total surveys

For comparison, we collated data from total surveys conducted by park rangers of Marula South (27 September to 5 October 2018) and Marula North (13 to 21 November 2018). Surveyors defined 8 × 8 km blocks for ease of counting, with 77 and 85 blocks in Marula South and Marula North respectively. The helicopter flight procedure during the counts was identical to the sample counts, but pilots reduced the speed to 45 knots (83 km/h) in areas with thick vegetation.

Data analyses

Population estimates

Jolly's estimator allowed us to calculate uncorrected section-specific estimates from sample surveys (Jolly 1969). We corrected 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). A third bias relates to detection (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 et al. 1993). In this study, we give bias values as the percentage of animals seen compared to, if the bias was zero. For example, if availability bias results in 10% of animals being hidden from view, the value of availability bias is then 90%.

Availability bias arising from restricted visibility of rhinos on a block and is associated with the vegetation cover of that block at the time of a survey. Visibility was calculated as:

$$y = 1 + \left(a - \frac{b - a}{1 + \left(\frac{x}{c}\right)^{-d}} \right)$$

where y is the percentage of time where a rhino is visible, x is woody vegetation cover, a, and b, c and d are constants that describe and inverse sigmoid function (Ferreira et al. 2015). In this case, b represents the asymptote of the fraction of rhinos missed as vegetation cover increases. In the surveyed area in Kruger in 2018, as few as 73.6% of black rhino

$$y = 1 + \left(0.001 - \frac{0.264 - 0.001}{1 + \left(\frac{x}{34.41}\right)^{-13.63}} \right),$$

$r^2 = 0.841$) and 82.9% of white rhinos

$$y = 1 + \left(0.003 - \frac{0.171 - 0.003}{1 + \left(\frac{x}{41.47}\right)^{-12.78}} \right),$$

$r^2 = 0.987$) were visible and available for sampling in areas that were within the range of woody vegetation cover values. The lower value for black rhinos reflects the fact that they are browsers and spend more time in woody vegetation, where they are harder to see. Because observers cannot measure woody cover easily and do not do so on an annual basis, we used the relationship between vegetation cover and the Normalized Difference Vegetation Index (NDVI) (vegetation cover = (0.019 × NDVI) – 22.67, $r^2 = 0.32$; Ferreira et al. 2018) to estimate vegetation cover and then rhino visibility and hence availability bias for each block. We corrected estimates by dividing the estimated values by the percentage of rhinos visible as predicted using the procedure described above.

Values for observer bias were based on calculations from a previous survey. In this case, observers noted 96.2% of the rhinos visible at the time of survey (Ferreira et al. 2011). We further multiplied the estimates already corrected for availability bias by the percentage of visible rhinos noted by observers. We assumed that detection bias is low because observation strips were the same width as the first distance class previously used in establishing a detection function for distance sampling (Kruger et al. 2008).

Both uncorrected Jolly's estimates and bias estimates are calculated as values with associated confidence intervals. Each uncorrected estimate and estimate of bias is thus a point estimate with an associated statistical distribution. We randomly drew a value from each of the distributions of estimates and biases. We used these values to calculate a corrected estimate. We repeated this process 100,000 times and extracted the median as a point estimate for the corrected estimate, with the 2.5% and 97.5% percentiles as the lower and upper confidence limits, respectively, of the 95% confidence interval.

Critique 1: Sample survey blocks are located where there are many rhinos

To evaluate whether sample blocks are inadvertently placed only in areas with high rhino numbers, we used observations made during total surveys. We extracted the number of white and black rhinos seen in each section. We then extracted the number of white and black rhinos seen within the blocks during the sample survey for each section. Note that sections had different percentage of coverage by the random blocks. Using the percentage covered, we extrapolated expected total for that section from the number seen in the sample blocks.

Survey blocks during a total survey are unlikely to contain the same number of rhinos, as rhinos can also move between them. In both surveys, surveyors can miss or recount individuals thereby creating sampling error (Walsh et al. 2001). We used the observations of rhinos seen within blocks during the sample survey to estimate the number of rhinos (as well as the upper and lower confidence limits) that surveyors could be expected to see during a total count in a section. We then calculated the percentile value in the distribution of predicted counts that corresponded to the value that surveyors recorded during total counts. If the critique holds, then the values recorded by surveyors noted should mostly correspond to low percentile values in distribution, i.e. rhino numbers predicted by the sample counts should be on average higher than total counts.

A further challenge is that movements of rhinos could substantially influence the section-specific comparisons given the time elapsed between sample and total surveys. We thus compared the locations of individuals that surveyors noted in the randomly located blocks during sample surveys and in the total surveys of the same area. We inspected the spatial distributions of observations in sample and total surveys and visually identified localities where the distributions did not appear to overlap. We then used optimized hot spot analyses, an ArcGIS tool that aggregates incident data and identifies clusters of high values (hot spots) and low values (cold spots) using the Getis-Ord G^* statistic (Getis and Ord 1992). We standardized from coldest (0) to hottest (1) for illustrative purposes.

There were two types of non-overlap in hotspots. Type 1 was an area where we recorded rhinos in at least 90% of the survey blocks during the sample survey, which we defined as a 'hotspot', but observers saw no rhinos during the total survey. Type 2 was an area where observers did not record rhinos in at least 90% of the survey blocks in the sample survey, but where rhinos were recorded during the total survey. Non-overlaps of spatial distribution hotspots (i.e. high concentration of rhinos) between sample and total surveys served as indication that rhino movement may influence section-specific comparisons.

Critique 2: The 95% confidence interval of the population estimate is large

Previous rhino estimates in Kruger have a PCI of approximately 25% (e.g. Ferreira et al. 2018). PCI is the difference between the upper and lower 95% confidence limits expressed as a percentage of the estimated value (Ferreira and van Aarde 2009). A larger PCI means there is more uncertainty in the estimate. Critics of the sample techniques used for rhinos suggest that 100% aerial coverage of an area or total counts could reduce the uncertainty[5].

Reducing uncertainty is important if authorities seek to detect changes. Conservation targets for South Africa seeks 5% annual growth in the short term, typically 5 years (Knight et al. 2013). We used Gerrodette's (1987) inequality model to define the PCI needed to detect a 5% annual growth with annual surveys over a 5-year period (i.e. 6 surveys). We then checked how PCIs of sample estimates change as the aerial survey percentage coverage of an area increases, and compared these PCIs with the PCI required detecting 5% change over a 5-year period.

We focused on white rhinos in sections 9 and 10, where observers surveyed 3 × 3 km blocks covering the entire section during the sample survey. This allowed us to apply the sample-based estimation approach for different sample sizes. As the sample size increases, the percentage area covered by the aerial survey in a specific section increases. We randomly resampled blocks over a range of sample sizes, calculated the aerial survey percentage area covered and, for each randomly generated survey, estimated population size and confidence intervals in 1,000 iterations.

For each of the 1,000 iterations, we calculated a PCI. We fitted a power relationship to describe the relationship between PCI and aerial survey percentage coverage of an area. To establish the relationship, we calculated the average in bins of 10% and used these point estimates as inputs for fitting the relationship. Using this derived relationship, we could estimate the aerial survey percentage coverage required for the PCI needed to detect a 5% change over a 5-year period.

We also considered a second standard commonly used to assess confidence intervals, namely that a PCI of 40% corresponds to an estimated value with a standard error of 10%. We thus also calculated the aerial survey percentage coverage required to achieve a 40% PCI.

[5]See for example the discussion on the online forum 'Africa Wild': https://africawild-forum.com/viewtopic.php?t=4696&start=40 [Accessed 30 April 2019].

Critique 3: Sample surveys use overestimated bias corrections

For this part of the analysis, we focused on section 10 where observers in the sample survey recorded individual identifications of those black rhinos with ear notches. This enabled calculation of the percentage of individually marked black rhinos that surveyors observed.

Following the procedures outlined above, we used the NDVI extracted for blocks in section 10 to estimate vegetation cover and then calculated the percentage of black rhinos that will be visible if they were within a block for a given vegetation cover. This provided an estimate and 95% confidence intervals of the total percentage of black rhinos in blocks in section 10 likely to be recorded by observers. If sample surveys use overestimated bias corrections then the estimated percentage of black rhinos seen during sample surveys should be lower than the percentage of marked black rhinos seen.

Results

Observations

During the 2018 sample survey, surveyors counted 1,988 white and 140 black rhinos in southern Kruger

Table 1. Results of sample and total surveys of black and white rhinos in southern Kruger in 2018. For each section (1–11) and region (Marula North and Marula South) we report the number of sample blocks, the percentage of the area covered during the sample survey, numbers counted in the sample survey, extrapolated total numbers (with 95% confidence intervals in brackets), and actual numbers seen during the total survey.

			White Rhino			Black Rhino		
Section	**Blocks**	**Area (%)**	**Seen during sample survey**	**Extrapolated number**	**Seen during total survey**	**Seen during sample survey**	**Extrapolated number**	**Seen during total survey**
1	59	46	19	41 (19–92)	18	0	0	2
2	32	38	73	195 (73–337)	78	4	11 (4–23)	1
3	46	44	65	148 (65–242)	119	3	7 (3–17)	8
4	42	42	67	162 (67–239)	138	1	2 (1–7)	6
5	65	50	290	581 (396–767)	500	9	18 (9–34)	26
Marula North	244	45	514	1127 (620–1677)	853	17	38 (17–81)	43
6	20	34	55	160 (55–268)	93	4	12 (4–27)	2
7	49	52	276	528 (356–669)	442	32	61 (32–93)	58
8	50	57	68	120 (68—185)	126	6	11 (6–20)	2
9	40	53	378	710 (515—905)	594	13	23 (13–48)	21
10	33	56	559	999 (789–1210)	817	59	105 (67–144)	59
11	50	55	138	253 (164–342)	267	9	17 (9–31)	16
Marula South	242	52	1474	2770 (1947–3579)	2339	123	229 (131–363)	158
Southern Kruger	**485**	**48**	**1988**	**3897 (2567–5256)**	**3192**	**140**	**269 (148–444)**	**201**

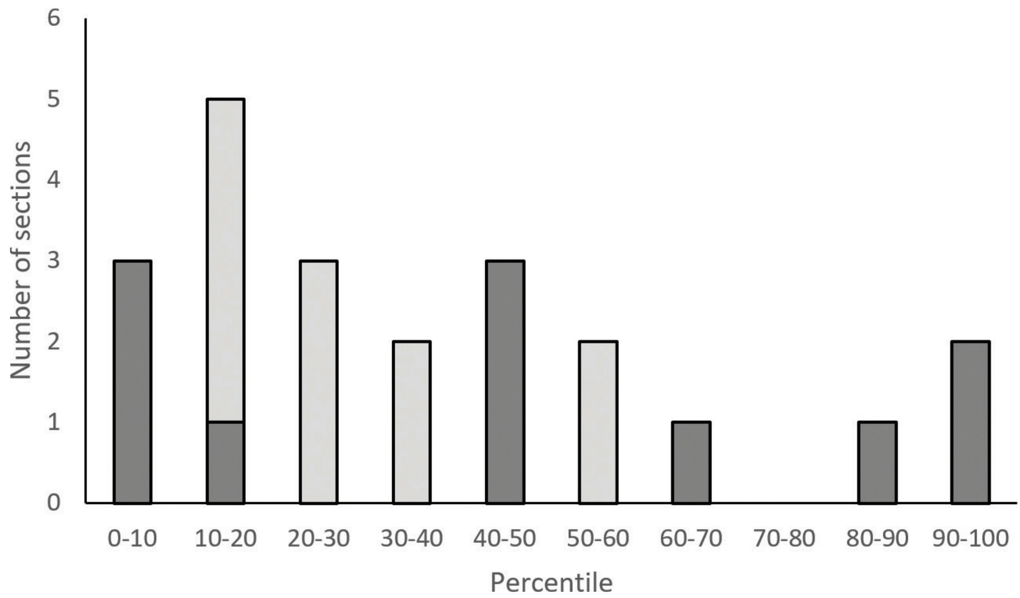

Figure 1. Comparison of results of total and sample survey of white (light bars) and black rhinos (dark bars) in southern Kruger in 2018. The graph shows distribution of total survey counts for the 11 sections of southern Kruger against percentiles (in 10% bins) of the distribution of totals predicted by the sample surveys.

(Table 1). During the total survey in southern Kruger, surveyors recorded 2,339 white and 158 black rhinos in Marula South, while they noted 853 white and 43 black rhinos in Marula North. Rangers reported only 46 to 47 white and 12 black rhinos in northern Kruger during 2018, confirming southern Kruger as the stronghold of rhinos in the NP.

Population estimates

Based on observations during the sample survey it was estimated that 4,116 (95% CI: 2,994–5,726) white rhinos lived in Kruger in 2018, compared to the 5,150 (95% CI: 4,767–5,540) in 2017 (Ferreira et al. 2019). For black rhinos, the 2018 sample survey estimated 291 (95% CI: 151–441) black rhinos living in Kruger, compared to 507 (95% CI: 427–586) in 2017. Thus for white rhinos there is a fairly substantial overlap between the 95% confidence intervals (CI) of the two surveys, whereas for black rhinos there was only a marginal overlap (Ferreira et al. 2019).

Sample and total survey comparison

During the total survey, observers mostly recorded values for white rhino that were in the lower percentile of values predicted by the sample surveys (fig. 1). Total survey values for nine sections fell between the 0–10% and 30–40% percentiles of corresponding values predicted by the sample surveys. For black rhinos, total survey values for seven sections were lower than the 50% percentile value (i.e. the median value) predicted by the sample surveys (fig. 1). Note that, for black rhino, total count values for two sections fell between the 80–90% and 90–100% percentiles in the sample surveys. Disregarding species, 72.3% of the section-specific total count values were lower than the 50% percentile value of the distribution predicted by the sample surveys for the corresponding section.

We noted several locations of both Type 1 and Type 2 non-overlap when we compared the spatial distribution of observations made for sample and total surveys (fig. 2). The sample survey recorded high concentrations of white rhinos in five localities where the total survey recorded few white rhinos. For instance, a di stribution hotspot in the south-western parts of Marula North recorded by the sample survey was not found by the total survey. There were two localities where rhinos were found by the total survey, but where the sample survey recorded very few rhinos.

Similarly, three localities were recorded as black rhino distribution hotspots during the sample survey but not during the total survey, while the total survey

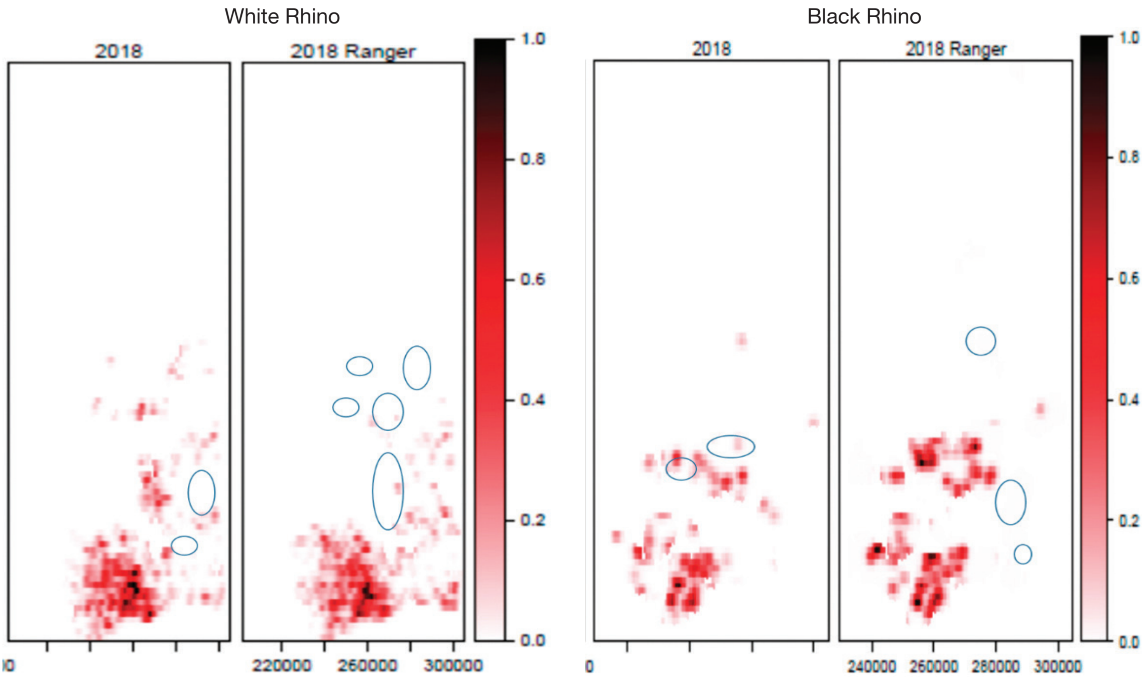

Figure 2. Distributions of white and black rhinos in southern Kruger during the normal sample survey carried out in September 2018 (2018) and the total survey initiated by rangers and carried out in October and November 2018 (2018 Ranger). The ovals show areas where rhinos were absent but identified as 'hotspots' in the other survey, indicating mismatches in distribution of rhinos between the various surveys. The colour intensity corresponds to an increasing index of number of rhinos noted on blocks, as shown in the colour scale bars. Note that the axes have no meaning and contain minimized information for rhino security purposes.

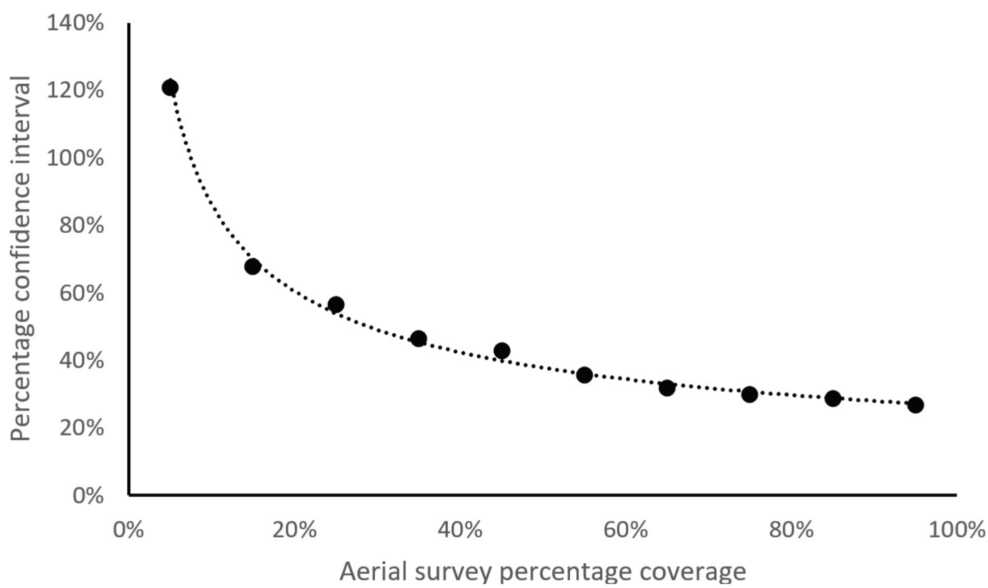

Figure 3. Percentage confidence intervals (PCIs) for prediction of rhino populations as a function of the aerial survey percentage coverage, based on analysis of aerial surveys in southern Kruger (sections 9 and 10) in 2018.

recorded black rhino as being present in two localities where they were absent during the sample survey.

Confidence intervals

Using Gerrodette's (1987) inequality model, we estimated that maximum PCIs required detecting a 5% annual change over a five-year period range from 7.74% if authorities survey rhinos annually to 6.53% if authorities survey rhinos every five years. Using the white rhino data for sections 9 and 10, PCI values (y) initially decrease fast as the percentage aerial survey coverage of an area (x) increases, but then that rate of decrease slows down at higher percentage aerial survey coverage (y=0.267$x^{-0.512}$, r^2 = 0.99, fig. 3). Note that even at 100% percentage aerial survey coverage, bias corrections could result in PCI values of approximately 25%.

Disregarding bias corrections, for white rhinos, surveyors need 76.8% coverage to achieve PCIs that allow detection of 5% annual growth with annual surveys over a five-year period. Authorities need to cover 100% of the area if they want to do only two surveys five years apart. A population estimate with a standard error of equal to 10% of the population estimate will require an aerial survey percentage coverage of 46.7%. During the 2018 sample survey, the coverage of sections by sample surveys ranged from 34% to 57%, giving a coverage of 48% of southern Kruger as a whole (Table 1).

Bias comparisons

Woody cover estimates for section 10 ranged from 30.6% to 45.1% cover. This translated to predicted black rhino visibility ranging from 74.4% to 95.7% at the time of the survey. Combining black rhino visibility with the observer bias of 96.2% of visible rhino seen by observers resulted in an overall estimate of bias that equates to surveyors recording 75.8% (95% CI: 71.6%–86.9%) of the black rhinos present.

There were 21 black rhinos with individual ear notches at the time of the survey of section 10. Surveyors saw 57.1% (12) of them, substantially fewer than what modelled bias corrections predicted (the value of 57.1% is outside the statistical distribution of predicted biases). This suggests that bias corrections in standard surveys substantially underestimate biases associated with aerial observations of black rhinos.

Discussion

Some critics have voiced concerns that sample-based estimates for rhinos in Kruger are unreliable. Specifically these critics maintain 1), that sampling focuses on areas with high rhino densities, introducing sampling errors that inflate estimates; 2), that estimates have wide confidence intervals and hence low precision; and 3), that the procedure for estimating bias results in overestimates of biases that further inflate population estimates. As noted above, forums and debates raise concerns and generally, the proposed solution is to do a total count at regular intervals to obtain more precise and accurate estimates.

With respect to the first concern, we obtained variable results. Although total counts in several sections corresponded to percentiles below 50% in the range of predictions of sample surveys, total counts in several sections corresponded to high sample survey percentiles. Generally, for white rhinos, more total counts corresponded to low percentiles than high percentiles. We recorded similar patterns, but of less magnitude and with some notable exceptions, for black rhinos. Taken together, these results suggest that sample counts inadvertently focused on areas with high rhino densities.

However, these differences and the disproportionate number of total counts corresponding to lower sample survey percentiles may also result from movements of animals. This could particularly affect white rhinos, which are grazers, for which Kruger's seasonal rainfall, affect food availability. The sample survey took place earlier in the dry season than the total surveys. Grass biomass and distribution decline as the dry season progress (Vetter 2009). A redistribution of white rhino is thus likely. Several areas recorded as hotspots in the sample survey, were found to contain few rhinos during the total surveys. The low numbers recorded by the total surveys may well have been the result of movement responses to food and water availability, which displaced the rhinos to areas outside of the survey area in southern Kruger.

One particular non-overlap area was a section of Marula North, where observers saw white rhino in large numbers during the sample survey. White rhinos were completely absent when the total surveyors counted the same area approximately one month later.

This area in the Marula North region abuts a number of private reserves. No fence separates Marula North from these reserves, which provide a high density of water holes (Smit et al. 2020). This starkly contrasts with the restricted number of localities where NP managers provide water in the Marula North region. In addition, managers of the private reserves also mow open areas to stimulate grass growth, specifically at the onset of the growing season (Fisher et al. 2014). In the time that elapsed between the sample and total surveys, it is likely that a substantial number of rhinos moved into adjacent private reserves in response to food and water availability.

Black rhinos, as browsers, are unlikely to make such movements. Browse conditions do not change markedly during typical dry seasons (Sankaran et al. 2004), although droughts can have substantial impacts. Black rhinos are territorial, occupying well-set home ranges, but congregate in preferred locations close to water (le Roex et al. 2019).

Sample surveyors saw few black rhinos in two areas where total surveyors saw several black rhinos a month later. At the same time, the sample surveyors saw black rhinos in three areas where the total surveyors did not record any individuals. All five these non-overlap incidences involved few rhinos. These differences most likely reflect rhinos missed because of availability and observer biases.

Biases combined with precision determines the accuracy (Thompson 1992) and thus reliability of estimates. Authorities that use aerial-based sample surveys for large populations (rhinos: Ferreira et al. 2017; African elephants Chase et al. 2016) trade off precision of information for lower survey costs (Ferreira and van Aarde 2009). We used PCI (Ferreira and van Aarde 2009) as a measure of precision.

Our analyses demonstrate how PCIs decreased as the aerial survey percentage coverage of an area increased, as found elsewhere (Ferreira and van Aarde 2009). Importantly, we noted that PCI did not fall below ca. 25% even if authorities surveyed the total area. This result highlights that authorities may not obtain sufficiently reliable estimates by conducting total counts and that biases should always be taken into consideration when reporting survey results.

The purpose for which an estimate is obtained is important. For instance, population estimates with standard errors equal to 10% of the population estimate may suffice for several policy needs such as for reports to CITES (e.g. Emslie et al. 2019). Our analyses of white rhinos in two sections suggest that in such instances a percentage coverage of 46.7% will suffice. The surveys conducted in Kruger, typically cover >47% of the total area. Note, however, that percentage aerial survey coverage requirements also depend on local population density (Ferreira and van Aarde 2009).

If managers need to detect trends in a population this imposes additional requirements. Previous evaluations for black rhinos suggested that surveys every two years at 20% coverage with random blocks optimize authorities' ability to detect the direction, but not the magnitude of change (Ferreira et al. 2011). However, the magnitude of change is often precisely what interests the authorities. For instance, our analysis suggests that approximately 77% coverage by aerial surveys would be required in order to assess fulfilment of the target of 5% annual growth over a five-year period (Knight et al. 2013) at the white rhino densities in the two focal sections at the time of our study (disregarding bias errors). PCIs of aerial surveys are indeed large. The inability to reduce PCIs to below ca. 25% even if aerial survey coverage is total, highlights the impossibility of eliminating biases.

The third critique is that block-based sample surveys overestimate biases and thus population numbers. However, our results suggest there is a substantial underestimation of these biases. Observations of marked black rhinos in one section suggested that observers missed about 40% of the rhinos present. The bias corrections extracted for block-based sample surveys suggested that observers missed only about 25% of the rhinos present.

Our results highlights some challenges. Although the block-based sample survey approach explicitly considers biases when calculating population estimates (Ferreira et al. 2011, 2015), values are underestimates. Population estimates are then also likely to be underestimates, contrary to some of the concerns raised. Authorities could consider a completely independent technique such as mark-recapture approaches (Seber 1973). Authorities, in fact, should consider different techniques depending on total abundance or rhino density on a case-by-case basis (Ferreira et al. 2017).

The decline of white and perhaps black rhinos since 2013 (Ferreira et al. 2019) imposes some further challenges to the achievement of reliable estimates.

When population densities are low, the distribution of individuals tends to cluster and this further reduces the precision of population estimates by sample surveys (Ferreira and van Aarde 2009). Thus as populations get smaller, the confidence intervals of population estimates will get larger. This occurred in the case of population estimates of both black and white rhinos, whose PCIs in 2018 (black rhino: 290, PCI: 99.7%; white rhino: 2,732, PCI: 66.3%) were larger than those noted in 2017 (black rhino: 159, PCI: 31.4%; white rhino: 773, PCI: 15.0%; Ferreira et al. 2019). In such instances, complimentary information is a key requirement. For instance, deriving recruitment and death rates allowed evaluation of the effects of droughts and poaching on black and white rhino vital rates in Kruger (Ferreira et al. 2019).

Although the 2018 confidence intervals overlap with those of 2017 (Ferreira et al. 2019), the trend in white rhino population estimates since 2013 (8,968, 95% CI: 8,394–9,564, Ferreira et al. 2015) reflects a significant decline. For black rhinos, 627 (95% CI: 588-666, Ferreira et al. 2011) were recorded in Kruger in 2009, significantly higher than numbers estimated during 2018.

These declines are primarily associated with disruptive poaching (Ferreira et al. 2018). Poaching may be even greater than is reported due to imperfect detection of carcasses (Huso 2011). Furthermore, unknown numbers of deaths of dependent calves when poachers kill cows, together with the loss of future calves, represent additional impacts of poaching.

Conclusion

Reporting uncertainties of estimates carry broader implications. For instance, at the CITES meeting in Johannesburg, South Africa in 2016, the AfRSG reported 20,378 white rhinos and 5,250 black rhinos for Africa in 2015 (Emslie et al. 2015). South Africa contributed significantly to these numbers: 90.4% of white rhinos and 36.1% of black rhinos. Nine South African provinces reported very small numbers based on total counts or registration studies of three sub-species of black rhino occurring on state, partnership and private land. Hluhluwe-iMfolozi Park and Kruger reported separately. Here, authorities used sample counts and reported the 95% confidence intervals. Including these uncertainties, South Africa had 1,431–1,605 south-central, 261 south-western and 78 eastern black rhinos in 2015. With regard to white rhino, taking account of the confidence intervals of estimates for the two key populations, South Africa had between 18,395 and 20,895 white rhinos in 2015. The implications of these uncertainties on decision-making, for example by CITES, are unknown, but one can expect greater urgency to be shown if authorities report low numbers, compared to when they report high numbers.

Total counts provide an exact number of individuals known to be alive at the time of a survey. Over- or underestimation of numbers may inflate yearly differences. Applying various approaches including total counts may not substantially improve reliability, largely because all approaches are vulnerable to inherent biases involved in observing rhinos. Applying relevant approaches that consider case-specific constraints (Ferreira et al. 2017) would require use of complimentary data on fecundity and survival. Even so, authorities should report uncertainties when reflecting on the detection of trends so that that these can inform conservation interventions.

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