KRUGER NATIONAL PARK

NXANATSENI NORTH

A POPULATION ASSESSMENT OF LIONS IN THE NXANATSENI NORTH REGION OF KRUGER NATIONAL PARK (SOUTH AFRICA): TECHNICAL REPORT ON A LION SURVEY CONDUCTED IN 2023.

Endangered Wildlife Trust



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Executive summary

Background

Following recent increases in the incidences of poaching and poisoning in the Nxanatseni North region of Kruger National Park, we conducted a survey to better understand the current status of lions.

Objective

Our primary objective was to obtain reliable estimates of lion density, abundance, sex ratio and spatial distribution.

Survey dates and area

Data were collected from 17 September to 01 December 2023. We surveyed the area known as Nxanatseni North, which consists of the following sections: Pafuri, Vlaktenplaas, Punda Maria, Shangoni, Woodlands and Shingwedzi. The combined area is ~5,162 km².

Field methods

Two field protocols were used (search encounter and camera traps) to collect data. Both protocols were designed to obtain high quality photographs that we could zoom into and be able to individually identify lions through their unique whisker spots.

Search encounter

Observation teams actively searched the survey area looking for lions. To maximise lion sightings, we did not follow a rigid protocol of pre-planned routes, but attempted to cover the survey area uniformly over the duration of the survey.

When we found lions, wherever possible, we took photographs of each lion present so that we could identify which individuals had been seen, noting when and where they were seen.

Camera traps

We deployed 100 white-flash camera traps in pairs across the area. During the first half of the survey, 50 paired stations were placed in the southern sections of Nxanatseni North, and were shifted to the northern sections (44 paired stations) in the second half of the survey.

We aimed to set stations 3 - 4 km apart, and chose sites that we deemed to be most likely to detect lions (e.g. along trails or roads, and close to water if it was in the proximity). We then inspected every lion photograph to try and identify which individuals were detected.



The Vlaktenplaas coalition consists of at least five adult males, three of which are pictured here. Photo credit: Marnus Roodbol.

Analytical methods

It is not feasible to find every lion in the landscape. Therefore we used methods that enable us to estimate the number of lions based on a sample of that population.

In other words, we use information on the individual lions that we did see to estimate those that we did not see. To do this, we used advanced spatial capture-recapture models that are widely used for large carnivores globally.

Because lions less than one year old tend to suffer high mortality, we excluded them from analysis.

Results

We drove 10,006 km in search of lions, which resulted in 91 detections of 41 individuals. Our camera traps were deployed for 2,684 trap nights. This resulted in 16 detections of 12 lions. The combined dataset consisted of 107 detections of 52 individuals (23 males, 29 females).

Using the combined dataset, we estimated there to be 105 lions in Nxanatseni North, at a density of 2.04 lions per 100 km². Lion density decreased with increased distance from water.

Table 1. Results of a lion survey conducted in the Nxanatseni North region of Kruger National Park. Results are presented with posterior standard deviations in brackets. Estimates are for lions over 1 year old.

Estimates	
Estimated Lion Density	2.04 (0.4)
Estimated Sex Ratio	1.6 F : 1 M
Lion Abundance Estimates	
Pafuri	6 (3.1)
Vlaktenplaas	19 (4.6)
Punda Maria	8 (3.7)
Shangoni	17 (5.4)
Woodlands	23 (6.2)
Shingwedzi	31 (4.3)
Nxanatseni North (all sections combined)	105 (19.6)

Discussion

Our survey represents the fifth estimate of lions in the Nxanatseni North region of Kruger: In 2005, a call-up survey estimated 283 lions; a 2008 call-up survey with reduced sampling estimated 75 lions; the 2005 survey was replicated in 2015 (119 lions) and 2023 (122 lions); our estimate of 105 lions is similar to the latter two surveys. All were conducted in the same region and are estimates of lions over the age of one year.

This represents a possible ~63% decline over the 18 years separating the surveys.

The precise reasons for this have not been investigated, but anecdotal evidence suggests that there has been an increase in targeted poaching of lions, coupled with increased levels of general bushmeat poaching.

Our results show that lion density is lowest in the Pafuri and Punda Maria sections, areas that are thought to suffer from relatively high levels of snaring, poisoning, and general poaching.

Our results provide a clear signal that distance to water is an important factor explaining the variation in lion density across the landscape. Lion density was highest close to water. In recent times, artificial waterholes have been switched off in Kruger National Park, and this will likely have had an impact on lion numbers in the Nxanatseni North region, which has a semi-arid climate.

Identifying trends in lion numbers and demographics remains crucial for their conservation, as is investigating the factors that drive those trends.

We recommend that future conservation efforts are coupled with regular population monitoring in this region to inform conservation actions and assess their effectiveness, taking an adaptive management approach.

Introduction

The Greater Limpopo Transfrontier Conservation Area (GLTFCA), which includes Kruger National Park (KNP), is thought to be one of five remaining lion conservation units in Africa that contain more than 2,000 individuals (Riggio et al. 2013).

In recent years, the northern sections of Kruger have been subjected to poaching and multiple poisoning incidents primarily targeting carnivores such as lions and leopards as well as vultures (D. English, personal communication, September 15, 2023). It is unclear what impact this may be having on large carnivores.

Since 2005, lions in Kruger have been periodically surveyed using the call-up method. In this approach, sounds of animals in distress are broadcast at high volume in the hope of attracting lions to a station in order to count them. Before the survey, a calibration exercise is sometimes conducted (e.g. Ferreira and Funston 2010) to assess response likelihood and area sampled per station. In this manner, lion surveys have been conducted in Kruger in 2005/2006, 2008, 2015 and 2023.

Estimates of population size from call-up surveys are vulnerable to sampling design and reduced and variable responses to acoustic stimuli (Young-Overton et al. 2014, Funston and Henschel 2018). In recent years, it is suspected that lions have become habituated to these sounds and do not respond as frequently as they previously did.

In this context, the current project made use of an alternative sampling approach that is robust to changes in detection probability, including those resulting from changes in lion behavior. Specifically, we used spatial capture-recapture methods, which have been used extensively elsewhere for lions, to obtain estimates of lion abundance in the Nxanatseni North region.

Objectives

Our primary objective was to obtain reliable estimates of lion density, abundance, sex ratio and spatial distribution.

To achieve this, we selected to use a spatial capture-recapture (SCR) framework. This class of model provides robust estimates of population size (Royle et al. 2013), and has been widely used to monitor lion populations in East Africa (Elliot & Gopalaswamy, 2017; Braczkowski et al., 2020; Western et al., 2022; Ngene et al., 2023), and large carnivores globally (Green et al., 2020).

It is also a flexible approach that allows practitioners to tailor field protocols according to local conditions, and to use multiple field protocols within a survey (see Elliot et al., 2021).

In an effort to obtain a rich dataset, we aimed to combine two field protocols commonly used to collect lion data for use with SCR models: search encounter (e.g. Elliot & Gopalaswamy, 2017), and camera traps (e.g. Strampelli et al., 2022).

Among our objectives, we aimed to compare the outputs from search encounter data with that of camera trap data, and to extend existing models to accommodate both field protocols, since the two approaches can be complementary.

Therefore, we designed the study such that we could estimate density from each protocol separately, and combined. We anticipated that combining the data would increase precision, and that estimates across models would be similar.

Methods

Survey Area

The study site lies in the northern reaches of Kruger National Park, nestled in the northeastern corner of South Africa. It shares borders with Zimbabwe to the north and Mozambique to the east (Figure 1).

The park boasts diverse topography, showcasing 35 distinct landscapes. Basalt soils dominate the eastern expanse, while granite soils characterise the western terrain (Ferreira & Funston 2010).

Flowing through the northern region are seasonal rivers like the Limpopo, Levubu, Mphongolo, and Shingwedzi. These seasonal rivers provide access to water at various scales throughout the year. Boreholes and dams provide additional water within a limited number of drainage lines. There are also a number of springs. The outcome is that in the Nxanatseni North region, surface water in the dry season is largely restricted to small pools in the rivers and a few localities where park management provides water (Gaylard, 2015).

This ecosystem supports a variety of herbivores. The key lion prey species are greater kudu (*Tragelaphus strepsiceros*), burchell's zebra (*Equus burchellii*), blue wildebeest (*Connochaetes taurinus*), buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*) and waterbuck (*Kobus ellipsiprymnus*) (Maruping-Mzileni et al., 2017).

Covering 5,162 km², the survey area spanned six management sections which make up the Nxanatseni North Region. These sections are: Pafuri, Vlaktenplaas, Punda Maria, Shangoni, Woodlands and Shingwedzi.

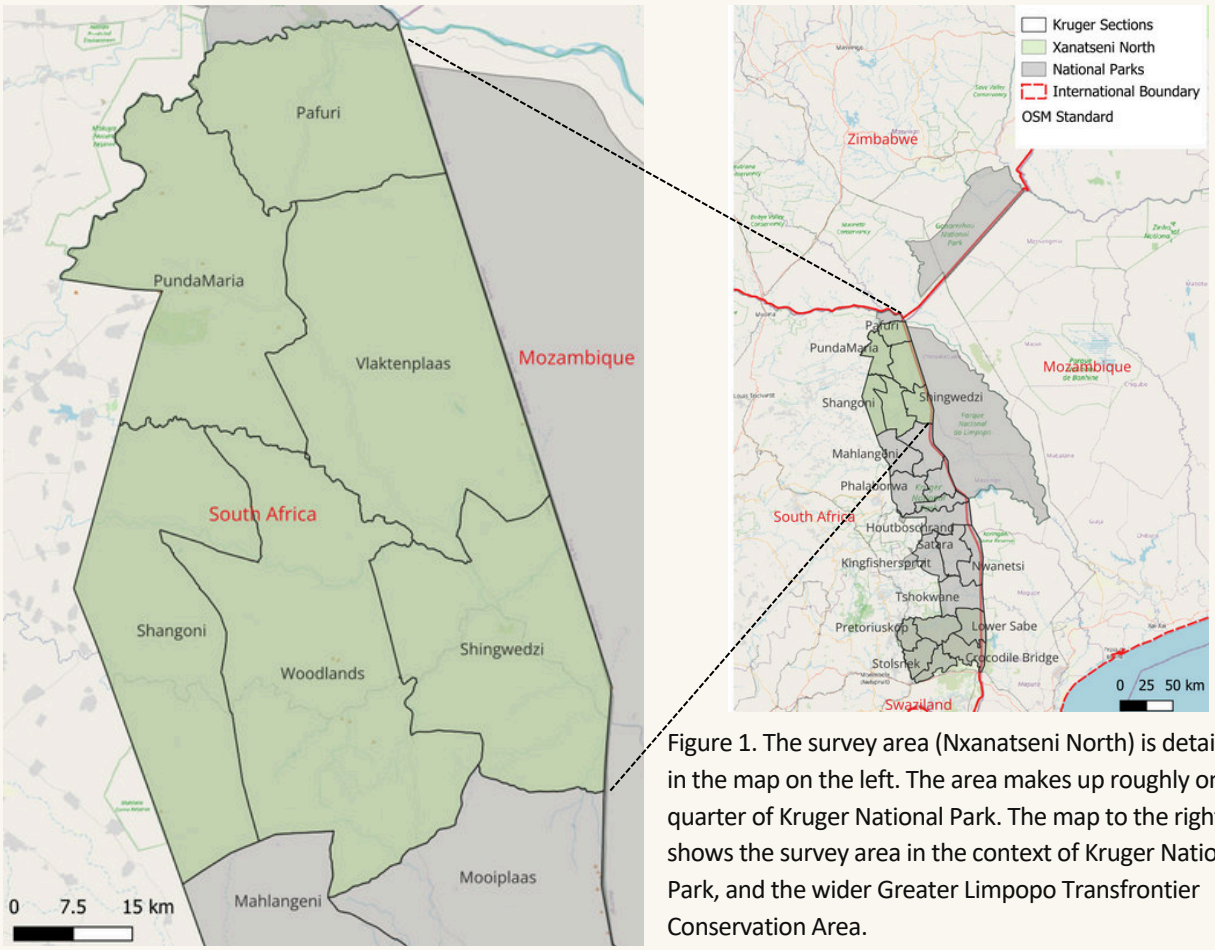


Figure 1. The survey area (Nxanatseni North) is detailed in the map on the left. The area makes up roughly one quarter of Kruger National Park. The map to the right shows the survey area in the context of Kruger National Park, and the wider Greater Limpopo Transfrontier Conservation Area.

Field Methods

Two field protocols were deployed during this survey, both of which were designed to obtain high-resolution photographs of lions that could be used to identify individuals, primarily by examining the distinctive whisker spot patterns on both sides of the face (Pennycuick & Rudnai, 1970).

Search Encounter

Observation teams in two vehicles (occassionally a third was available) actively searched the survey area during daytime hours using the unstructured, search encounter techniques described by Elliot & Gopalaswamy (2017).

Both tourism and management roads were driven, and we attempted to drive each road multiple times to avoid underrepresentation of difficult and remote roads. Occasionally, tourist sightings and communications with park personnel were used to inform searches.

Using the Cybertracker application on Android phones, the drive effort during each search endeavour was recorded (GPS point every 10 seconds), together with the location and demographic information of each lion sighting.

To individually identify the lions encountered during those search encounter efforts, whenever possible the observers took a series of close-up pictures of both sides of the face of each lion. The pictures were taken systematically such that pictures from both sides of an individual could easily be sorted in that individual's unique folder for data processing.

Camera traps

A rotational design was used, with 50 pairs of camera traps (Cuddeback X-Change Color Model 1279) being deployed in the southern sections and later, 44 pairs were deployed in the northern sections, for about 30 days each (Figure 2).

We aimed to set stations approximately 3 - 4 km apart, in line with another study on lions and other large felids using similar methods (Strampelli et al. 2022, Karanth and Nichols 2002). When using SCR models, it is not strictly necessary to eliminate 'holes' in sampling. However, incomplete coverage of an area of interest can lead to gaps when estimating the effective sample area, and this can lead to inferential challenges, particularly in communication of results. By placing camera traps 3 - 4 km apart, we aimed to avoid inferential gaps.

The exact placement of camera traps was determined by proximity to game trails, roads, waterholes, and other factors influencing the likelihood of a lion passing by, while ensuring they were always within 1 km of the original waypoint.

Extensive testing was done prior to the survey to formulate optimal camera settings and placement configuration for obtaining images of a lion's whisker spots. The complete protocol used in this study is provided in Appendix I.

These tests suggested that photos of lions that are 2 - 3 meters from the camera give the best opportunity to capture relatively clear images of the whisker spots.



Figure 2. A camera trap station placed along a trail leading to water. Photo credit: Nic Elliot

Data Processing

For both protocols, we estimated whether lions were under or over 1 year based on phenotypic features, including body size, shoulder height, nose pigmentation, and mane development. Lions estimated to be less than a year were excluded due to high mortality at this age (Packer et al., 1988).

Search Encounter

The pictures taken during each lion sighting were sorted into a folder labelled according to the date of the sighting and further subdivided into folders containing images for each individual.

Gender and a unique ID were assigned to every new individual, determined by secondary sexual characteristics and their whisker spot pattern.

The pattern of these whisker spots is unique to each individual (Pennycuick and Rudnai, 1970) and was used to create individual ID cards.

For subsequent sightings, if the whisker spots matched an existing ID catalogue, it was classed as a recapture, whereas if the whisker spots did not match, it was classed as a new individual, and a new catalogue was created.

Where we could not identify an individual at a detection (for example because the individual was too far away, or there was too much vegetation), the detection was classed as 'No ID' and was not included in the analysis.

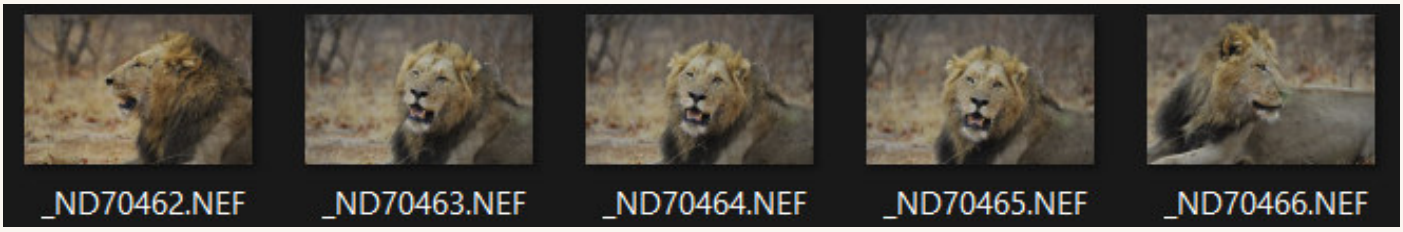
The sorting of images into the folders was done by the original observer, as was the initial identifications and catalogue creation. Thereafter, each detection was validated by four other observers who worked independently. They also studied the 'No ID' folders to ensure data were not being unnecessarily removed. Our ID protocol is detailed in Appendix II.

Camera Traps

The images were uploaded to TrapTagger (traptagger.co.uk), which tagged all images to species level. The lion images were extracted.

For each detection, observers then worked to classify each image as follows:

1. Whisker ID: We could clearly see the whisker spots of one or both sides of the face, and distinguish a pattern in the spots. The observer followed the ID protocol detailed in Appendix II, and noted whether the whisker spots were visible for the left side, the right side, or both sides.
2. Distinguishing feature: Whisker spots were not visible. The lion had a distinguishing feature that we deemed to be permanent and could be used to identify the individual. For example a scar, a missing tail tuft, ear and nose notches and other features described in Strampelli et al. (2022).
3. Unmarked: Whisker spots were not visible. The photo was clear and the camera performed to the best of its ability, but we were unable to distinguish a feature deemed to be unique and permanent.
4. Unusable: Whisker spots were not visible. For whatever reason, we were unable to clearly see the lion. For example, because of over-exposure, the lion was too far away, the image was blurred etc.



High resolution photos taken during the search encounter protocol, depicting a bilateral identification.

Analytical methods

We used Bayesian spatial capture-recapture (SCR) models to estimate key state variables. To model the spatial distribution of lions (state process) we generated a state-space by defining a 25 km buffer around the sampled area. Next we created potential activity centres, represented by equally spaced pixels (1 km²).

Unsuitable habitat (e.g. agricultural areas) was masked out (Figure 3). We assumed that lions whose activity centres were outside the state-space had a negligible chance of detection.

The value of M (the data-augmented value of abundance in the larger state-space) was set at 400 (comprising the number of individuals observed during the survey n=52, and the number of individuals augmented for the analysis nz=348), which represents the maximum number of lions possible within the state-space.

One of our objectives was to compare the estimates derived from search encounter data with those derived from camera trap data, and to extend existing models to accommodate both field protocols. To this end, we compiled the following three sets of input files to describe the manner in which individuals were detected during the survey (observation process):

(1) **Search encounter**: This consisted of a standard spatial capture-recapture array consisting of individuals, trap locations (defined by pixels of 1 km²), and sampling occasions (Figure A2). Since highly sampled traps might increase the number of detections, we included an effort covariate (logarithm of kilometers driven) per trap per day.

(2) **Camera traps**: This consisted of a standard spatial capture-recapture array consisting of individuals, trap locations, and sampling occasions (Figure A3).

(3) Combined dataset: This consisted of the separate effort files associated with each protocol, and a combined capture history file which compiled the detections from both field protocols (Figures A1 and A4).

We also included sex-specific covariates when defining the observation process. By explicitly accounting for different detection probabilities between males and females we additionally estimated the sex ratio.

We ran the models in R (R Core Team, 2023), using the same priors as Broekhuis & Gopalaswamy (2016) and adapted the code provided by Elliot & Gopalaswamy (2017) to include the camera trap data.

Each model was set to run for four chains, and initial runs were assessed for convergence using the Gelman-Rubin diagnostic (Gelman & Rubin, 1992), and by visually inspecting trace plots. We increased the number of iterations until convergence was achieved as follows:

11,000 iterations (search encounter data), 51,000 iterations (camera trap data), 11,000 iterations (combined dataset), 210,000 iterations (resource selection models, which were set to run with three chains). For each model, we set 1,000 iterations as burn in, and discarded more initial iterations if convergence was not achieved.

For each dataset, our model choice was informed by a combination of three criteria (Elliot et al., 2020): Bayesian p-value (Royle et al., 2009), the logarithm of the Marginal Likelihood using the Harmonic Mean estimator (MLHM, Dey et al., 2019), and pair-wise correlation plots between estimated parameters, where we were particularly concerned with correlations involving the density parameters.

Candidate models

We defined *a-priori* models and applied these to each of the three datasets. We used the general model formulation of Elliot and Gopalaswamy (2017). The models were formulated such that:

Model 1 assumes that basal encounter rate and the rate of decline in detection probability are sex-specific.

Model 2 assumes that basal encounter rate is independent of sex and the rate of decline in detection probability is sex-specific.

Model 3 assumes that basal encounter rate and the rate of decline in detection probability are independent of sex.

Model 4 assumes that basal encounter rate is sex specific and the rate of decline in detection probability is independent of sex.

For each dataset, the models are described as:

(1) Search encounter

Model1: N(.), λ0 (sex + effort), σ(sex)

Model2: N(.), λ0 (effort), σ(sex)

Model3: N(.), λ0 (effort), σ(.)

Model4: N(.), λ0 (sex + effort), σ(.)

(2) Camera traps

The dataset gathered from camera traps was sparse (see Results) with no female recaptures. We therefore limited the candidate models to:

Model 3, which has no sex specificity:

Model3: N(.), λ0 (traps), σ(.)

(3) Combined dataset

Model1: N(.), λ0 (sex + effort + traps), σ(sex)

Model2: N(.), λ0 (effort + traps), σ(sex)

Model3: N(.), λ0 (effort + traps), σ(.)

Model4: N(.), λ0 (sex + effort + traps), σ(.)

(4) Combined dataset with resource selection

Our field data was collected during the dry season and suggested a clustering of lions close to water sources.

While lions are not water dependent, many herbivore species are. This often results in a higher density of prey, and therefore lions, close to water, especially during the dry season in arid and semi-arid ecosystems (e.g. Valeix et al. 2010).

We therefore developed a novel SCR model that incorporates resource selection, and applied it to the combined dataset with the expectation that lion density is influenced by distance to water.

To create a covariate based on water availability, we digitised surface water from current satellite imagery by tracing the rivers and locating pools of water.

We merged this with active artificial water holes and used the resulting layer to create a raster that depicted the Euclidean distance to water from each pixel. This was added to our Habitat file and used as a density covariate (Figure 4).

Using the combined dataset we ran two additional models, using the naming convention listed above. Analysis of the other datasets suggested broad support for Model 4, and so we added resource selection to this model (Model 4.1) , and additionally ran a competing model (Model 3.1) that contained no sex-specific parameters:

Model 3.1: N(water), λ0(effort + traps), σ(.)
- identical to Model 3, but with a distance to water covariate on lion density.

Model 4.1: N(water), λ0(sex + effort + traps), σ(.)
- identical to Model 4, but with a distance to water covariate on lion density.

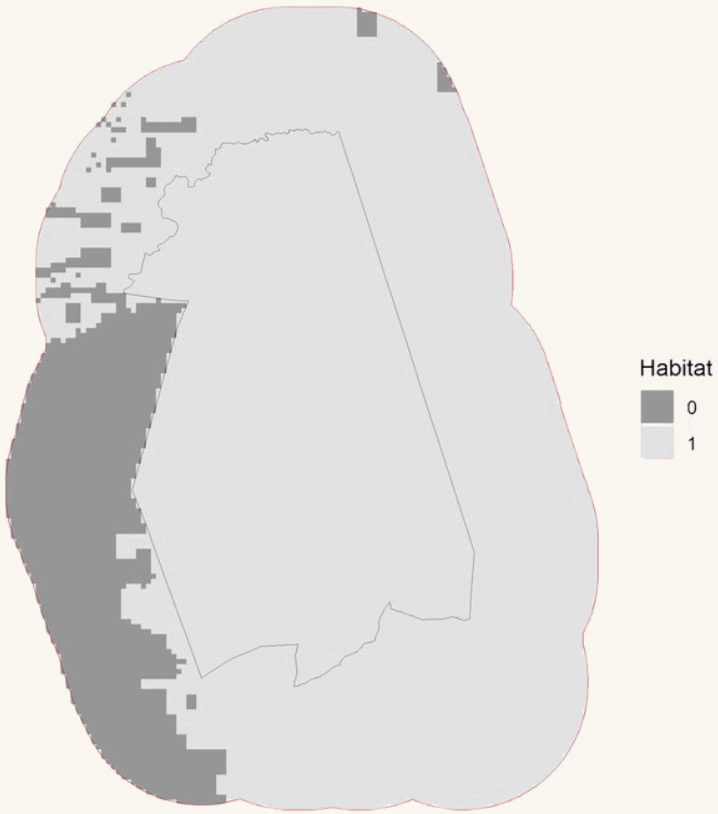


Figure 3. We created a 25 km buffer around the sampled area. We then discretised this area into 1 km² cells, each representing potential activity centres of lions. Each cell was classed as either suitable (1) or unsuitable (0) for lions.

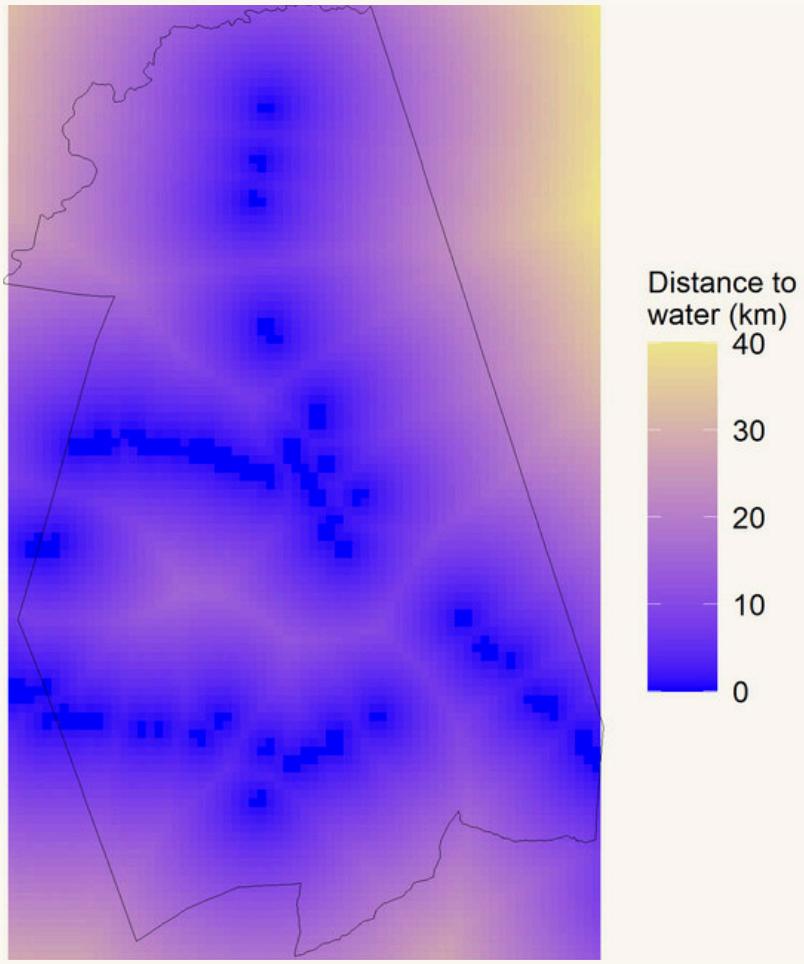


Figure 4. We created a density covariate, where each pixel represents the euclidean distance to the nearest water point.

Data Summary

Table 2. Summary table of the raw data collected using two distinct field protocols designed to obtain individual identity photographs of lions in the Nxanatseni North region of Kruger National Park, South Africa. These summaries relate only to lions over the age of one year. Note that only identified detections (where individuals were unambiguously identified using their whisker spots) were used in the analysis. Individuals were identified using their distinct whisker spot patterns using the protocol defined in Appendix II.

Parameter	Search Encounter	Camera Traps	Combined dataset
Effort	10,006 km driven	2,684 trap nights	10,006 km driven + 2,684 trap nights
* Discarded detections (Due to uncertainty of individual ID)	112	26	138
Retained detections (Unambiguous individual ID using whisker spot pattern).	91	16	107
Number of individuals identified	41 individuals with bilateral identification	12 individuals (2 with bilateral identification, 10 with single side identification)	52 individuals (1 was detected using both field protocols)
Number of males identified	18	6	23
Number of females identified	23	6	29
Number of individuals recaptured	25	4	29
Number of males recaptured	13	4	17
Number of females recaptured	12	0	12
Number of individuals detected at more than one trap	25	2	27
Average spatial recaptures	2.1	1.2	1.9
Mean of the maximum distance moved (km)	10.93	6.96	10.89

* These data were not used in the analysis, but are summarised here for reference and discussion. All other data provided in this table is what were used during analysis.

Results

Model Selection

We observed broad support for Model 4 in the analyses of both the search encounter dataset and the combined dataset. Our analysis of the sparse camera trap dataset produced estimates that were very imprecise (see Appendices).

The most precise estimates came from analysing the combined dataset (the richest dataset), which produced estimates that were very similar to those derived from the search encounter dataset.

We therefore chose to draw inference from the combined dataset and ran Model 4.1 to specifically test for resource selection. In addition, we ran the simpler Model 3.1, which contains no sex-specificity.

The marginal likelihood for Model 3.1 was highest. The pair-wise correlation plots showed minimal parameter redundancy, and the Bayesian p-values were within the extremities (0.15-0.85) indicating both models were adequate.

Given the broad support for Model 4 and the strong signal (beta.density parameter in Table 3, and Figure 5) that distance to water has a negative relationship with lion density, we select Model 4.1 for reporting the results of this survey.

In other words, the estimates derived from the combined dataset and resource selection SCR Model 4.1 were selected for reporting, and are detailed in Table 3. See Figure A1 for a plot of the raw data.

Estimates and model fit statistics from all datasets and models can be found in Appendix IV, V and VI.

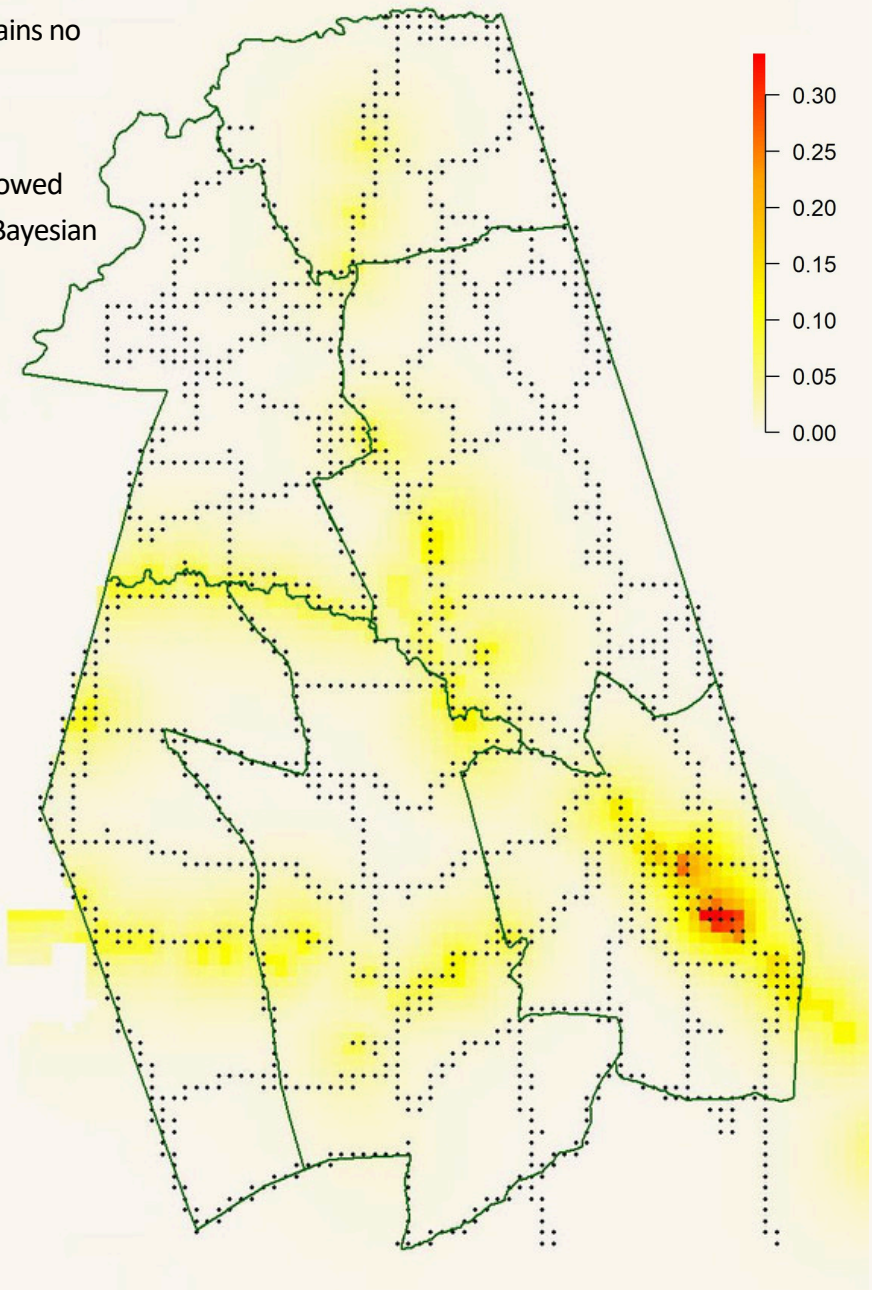


Figure 5. Pixel-specific (1 km²) lion density in Nxanatseni North region of Kruger National Park, South Africa. This output was obtained from Model 4.1 which was based on the assumption that basal encounter rate is sex specific and the rate of decline in detection probability is independent of sex. Distance to water was included as a density covariate in a resource selection-based SCR model. The outputs provide a clear signal that lion density decreases with increasing distance from water. This is most evident along the Mphongolo, and Shingwedzi rivers, where relatively higher lion density is estimated. Posterior lion density ranged from 0.0001 to 0.34 lions / km².

Model Estimates

Table 3. The results presented below are the product of an analysis of the search encounter data combined with camera trap data using Bayesian spatial capture-recapture models that incorporated resource selection. Given the broad support for Model 4 and the strong signal (beta.density parameter) that distance to water has a negative relationship with lion density, we select Model 4.1 for reporting. Estimates are posterior means and include 95% Highest Posterior Density Intervals in brackets. All estimates are for lions over the age of one year. To aid clarity, we only report the results from the selected model (Model 4.1) in this table. Data descriptions, model diagnostics, and parameter estimates for all other models are provided in the Appendices.

Parameter	Definition	Estimate
σ	Rate of decline in detection probability (DP) with increasing distance between a lion's activity centre and the centroid of a sampled grid cell	6.1 (5.0 - 7.2)
λ0	Basal encounter rate of an individual (female for sex-specific models) lion whose activity centre is located precisely at the centroid of the grid cell	0.0014 (0.0007 - 0.0022)
β1.eff	Rate of change in the complementary log-log value of DP as the (log) effort changes by one unit	0.05 (-0.01 - 0.10)
β2.eff	The change in the complementary log-log value of detection probability when camera traps are included	0.4 (-0.5 - 1.3)
βsex	Difference of complementary log-log value of detection probability between males and females	0.6 (0.0 - 1.2)
ψ	Ratio of true number of individuals in the population compared to the data augmented population M	0.3 (0.2 - 0.5)
ψsex	Proportion of lions that are male	0.4 (0.2 - 0.5)
Beta.Density	Relationship between lion density and distance to water (resource selection model)	-0.3 (-0.5 - -0.02)
Density	Estimated density of adult lion / 100 km²	2.0 (1.4 - 2.8)
Abundance		
Pafuri	Number of lions over the age of one year estimated to be resident within the specified area	6 (1 - 12)
Vlaktenplaas		19 (10 - 27)
Punda Maria		8 (1 - 15)
Shangoni		17 (7 - 27)
Woodlands		23 (11 - 34)
Shingwedzi		31 (23 - 39)
Nxanatseni North		105 (71 - 143)

Discussion

Contextualisation

Sporadic lion surveys were conducted in sections of Kruger National Park between 1974 and 2003 (Smuts 1976, 1977; Mills 1995; Funston et al. 2003). The first parkwide survey was conducted during 2005 and 2006, and estimated 1,684 (95% CI: 1617–1751) lions, using a locally calibrated call-up technique (Ferreira & Funston 2010).

A call-up survey in 2008, with reduced sampling, estimated 1,016 (95% CI: 862 – 1180) individuals (Young-Overton et al. 2014), and a 2015 call-up survey estimated 1,803 (95% CI: 1715-1891) individuals (Ferreira and Funston 2020).

Those same surveys produced estimates specific to the Nxanatseni North area, and lions over the age of one year were estimated as follows:
2005/2006: 283 lions (95% CI: 248 – 319)
2008: 75 lions (95% CI: 61 – 88)
2015: 119 lions (95% CI: 104 – 134)
In 2023, a localized call-up survey was conducted and estimated 122 lions (95% CI: 106 – 138) over one year (SANParks progress report 2023).

The results from the current survey provide an estimate of 105 individuals over one year old (HPD = 71 - 143).

Conservation Implications

Our results show that lion density is lowest in the Pafuri and Punda Maria sections where density is estimated to be 1.2 (HPD = 0.2 - 2.2) and 1.1 (HPD = 0.3 - 2.0) lions / 100 km² respectively. These areas are known to suffer from relatively high levels of snaring, poisoning and general poaching, and our results may reflect this.

Our results also indicate a clear signal that distance to water is an important factor explaining the variation in lion density across the landscape. In recent times, artificial waterholes have been switched off in the Kruger National Park, and this will likely have had a bearing on lion numbers in the Nxanatseni North region.

While lions are not dependent on water, their primary prey species typically are. Prey species congregate close to water, and lions may respond accordingly. Studies in Hwange National Park showed that lions typically select for areas within 2 km of a water hole (Valeix et al. 2010). Areas close to water may also offer reproductive advantages for lions (Mosser et al. 2009).

Across a range of studies, adult lion sex ratios averaged 2.3 females to 1 male (Périquet et al. 2014). Our observed sex ratio was 1.3 females to 1 male, but when differences in sex-specific detection probability was taken into account, we estimated the sex ratio to be 1.6 females to 1 male, perhaps suggesting a slight skew.

Conservation strategies for lions typically encompass a range of approaches aimed at safeguarding their habitats, mitigating human-lion conflicts, combating poaching and illicit wildlife trade, and fostering harmonious coexistence between lions and local communities.

Preserving lion populations in the challenging northern region of Kruger necessitates a thorough assessment of lion demographics, utilizing robust methods to reliably track population trends over time, and identify the drivers of change.

The ongoing threats of snaring, poisoning, and poaching exert significant pressure on both lions and anti-poaching teams. Lions inhabiting high-risk areas, such as the northern and western boundary of Kruger National Park, could be equipped with GPS collars to enable rapid

response to threats and aid in locating poisoned animals. While livestock encroachment is minimal due to park fencing along the western boundary, community engagement remains essential for reducing snaring and poisoning of wildlife.

Communities must derive tangible benefits from the park's proximity to their villages to discourage illegal activities, as long as these incentives are lacking, the persistence of such activities by a minority is likely to endure.

Search Encounter

We began the survey on 17th September. In hindsight it would have been preferable to begin one month earlier, due to the high temperatures in October and November. This made it difficult to find lions near to roads as they headed into the thickets early and only provided us with small time gaps to locate and photograph them.

Not being able to drive off road severely limited our ability to take good ID photos of lions during the search encounter protocol. This is evidenced in our data since we recorded 203 detections but were only able to use 91 (45% usable).

However, it should be noted that the vast majority of unusable detections were of the Kanniedood pride (97 detections, or 89% of unusable detections), which consisted of up to 19 individuals (many of which were sub-adults). We repeatedly sighted this pride in the dry Shingwedzi River but frequently were not able to obtain clear photos at each sighting (Figure 6).

Had we been able to identify more individuals during those 203 detections, we would certainly have improved the precision of our results, without necessarily changing the estimates themselves. Our density estimates generally had a Coefficient of Variation of ~20%. While this is within the realms of acceptability, ideally it would have been lower.

A great strength of SCR is that over time, open population models can be run. This will provide the opportunity to assess vital rates and population trend despite these relatively imprecise estimates.

Although there are multiple roads within Nxanatseni North, some were not accessible due to the park closing off several management roads over the years making the road conditions difficult to navigate. From Shingwedzi camp to Pafuri there is not one road that allows tourists to drive east of the main road.

Since there is a limited road network for tourists, some lions do not encounter vehicles often which may contribute to the shy behaviour. Even those prides that do encounter people were sometimes weary of our presence which made it difficult to photograph them, even with a 600 mm lens. At large distances, the image quality was insufficient to discern the whisker spots.

It should be noted that these limitations (no off road driving, and skittish lions) do not call into question the validity of using the search encounter protocol in these conditions. It simply necessitates considerably increased effort and therefore resources.



Figure 6. An example photo taken of four members of the Kanniedood pride. The lions were approximately 100 m away and this photo is not clear enough for ID purposes.

Camera Traps

Our 95 camera trap stations were active for 2,684 trap nights. Our intention was to run the camera traps and the search encounter protocols concurrently for 90 days to allow for direct comparisons and integration. Factoring in the considerable logistics of set-up and retrieval across two grids reduced the total trap nights.

In addition, we had several stations that encountered problems: seven stations were destroyed by elephants, five stations were stolen, and one station completely malfunctioned.

We also had several stations where single cameras stopped working: four due to elephant disturbance, one that simply disappeared, and eight that malfunctioned.

These factors limited the number of trap nights. However, our 2,684 trap nights was comparable to Strampelli et al. (2022) whose four sites consisted of 3,380, 2,172, 2,689 and 3,206 trap nights, while noting our survey area was larger.

The number of captures we recorded (45) was lower than Strampelli et al. (2022), who recorded 390, 67, 53 and 80. However the main difference lay in the number of usable detections. In our study, we could use just 16 (36%) of the detections, whereas Strampelli et al (2022) reported success rates of 90%, 79%, 95%, 83%.

A point of departure between the two studies is that Strampelli et al. (2022) reported using scars and other features to aid identification. We did not use these features in isolation, and in our study a detection was only included if the whisker spots were discernible. The reason we did this is that close inspection of our photos suggested that not all lions had distinguishing scars or marks.

A core assumption of SCR models is that all individuals are available for sampling. Since we are relying on phenotypic features and on natural markings, we are forced to use identifying features that are permanent and unique to every individual. For 16 detections (36%, e.g. Figure 7), despite having clear photos, we could not see the whisker spots, and were not confident we could identify any clear and permanent features to distinguish the individual and that would allow for unambiguous recaptures of these individuals.

With this in mind, we did not include those detections where we could see a distinguishing mark, since we would run the risk of sampling only from a subset of the population (those with distinguishing marks) and therefore providing an estimate for that subset of the population. In other words our estimate would be for the number of lions with distinguishing marks, rather than the number of lions. To avoid this, we focused only on those detections where the whisker spots were visible, since whisker spots are unique to all individuals.

Our final camera trap dataset was therefore very limited, and had no female recaptures. This resulted in a density estimate of very poor precision (CV = 55). The estimate itself (1.08 lions per 100 km^2) was also considerably different (less that half) that estimated from our other, richer datasets, suggesting the camera trap data produced an under-estimate of density, while noting that the HPDs to overlap the estimates from the other datasets (see Appendices).

Our cameras were offset by 1 meter. On several occasions, we obtained a usable photo from the first camera. Presumably, the flash then caused the lion to look at that camera, meaning the second camera captured the back of the head. This limited bilateral identification rates, and resulted in several single-sided detections.

Finally, our mean spacing between stations was 5.5 km. Given that we did not recapture any females, and we had very few spatial recaptures, our spacing may have been too large relative to the home range size of lions in this area.

A similar study compared outputs from search encounter and camera trap data (Briers-Louw et al., 2024), and the two protocols produced similar estimates (albeit with poor precision from camera trap data). Given that capture recapture datasets are often sparse, we encourage the continued use of camera traps, especially in combination with protocols such as search encounter, as this can result in richer datasets. We also encourage the advancement of camera trap technology, to improve the image quality to better aid individual identification of lions.



Figure 7. Example photo. The photo is clear and the camera performed to the best of their ability. However, we were not confident that we could identify any clear and permanent marks or other features that would allow for unambiguous recaptures of this individual.

Combining data and resource selection

We designed this study to produce comparable estimates from search encounter data and camera trap data and since both protocols relied on individually identifying lions and made use of a spatial capture-recapture framework, our expectation was that the two data sources would produce similar estimates.

This was not the case (see Appendices for parameter estimates from all datasets and models). Using the camera trap data we obtained a density estimate of 1.08 (PSD = 0.59), whereas the search encounter dataset provided an estimate of 1.82 (PSD = 0.38) lions per 100 km². The discrepancy (51%) is likely due to the weak camera trap dataset (see Appendix V for data summary and model estimates from the camera trap data).

When we combined the data we obtained an estimate of 1.85 (PSD = 0.31). As expected, combining the datasets gave an estimate comparable to the search encounter data estimate, and improved precision (CV = 21% for search encounter, 17% for the combined dataset).

Large carnivores naturally occur at low densities, and collecting data for estimating population size is challenging. As a result, datasets are frequently sparse and estimates lack precision. In this study, we have provided one solution that allows practitioners to combine data from two widely used field protocols, in a way that improves the precision of estimates.

Future surveys could aim to combine data collection protocols as we have, but would likely have more success using camera traps in a more opportunistic manner, similar to how call-ups were used in Western et al., (2022). With low rates of success in identifying individuals, our results suggest that for camera traps to be used alone in this survey area, we would need many more cameras, and or a longer survey duration to gather a rich dataset that would produce unbiased and precise estimates.

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Appendix I

Camera Trap Protocol

As with the other protocols described in this document, camera traps should be placed in such a way to maximise the chances of being able to individually identify lions through whisker spots.

Selecting a site

Placement of camera traps is not systematic or pre-determined but chosen either when fresh tracks have been found or are used opportunistically, in an attempt to improve detection rates.

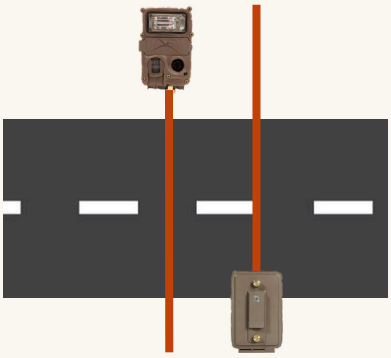
When choosing a site consider the following:

- Select a site where lions are most likely to walk. If there is a fork in the trail/road, place the cameras before the fork.
- Select a site where lions may be 'funnelled' into a relatively narrow path. The cameras should not be placed more than 6 meters apart, so avoid places where this is not possible.

Camera placement

- Always use pairs of camera traps
- Each trap is placed such that the top of the trap is 50 cm above the ground
- When deploying on a road, each trap is placed 2 meters from the centre of the immediate tyre track (distance between the two cameras is 6 meters)
- When deploying on a game trail, each trap is placed 2.5 meters from the centre of the game trail (distance between the two cameras is 5 meters)





- Each trap must be perpendicular to the road/track (facing square on to the road/track)
- The paired traps are offset by 1 meter so that they don't face each other directly

Site preparation

- The site should be cleared of all vegetation
- If appropriate gather vegetation behind the cameras to limit animals moving behind them
- If appropriate place vegetation to funnel the lions through the centre of the camera traps

White Board

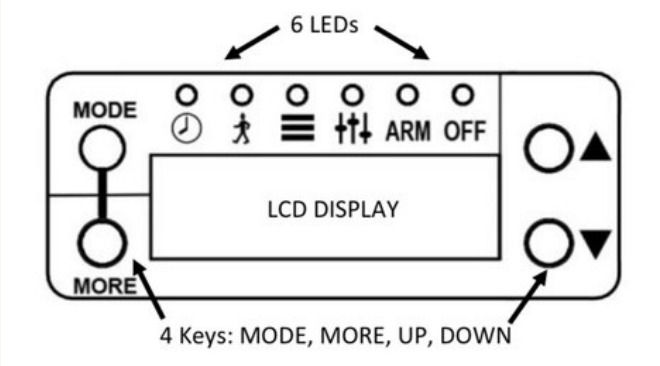
Each time a camera is set up, serviced and taken down, a white board must beheld in front of the camera until an image is taken.

The following details should be written on the white board / piece of paper:

- Station ID
- Camera ID
- Date
- Time



Camera Settings

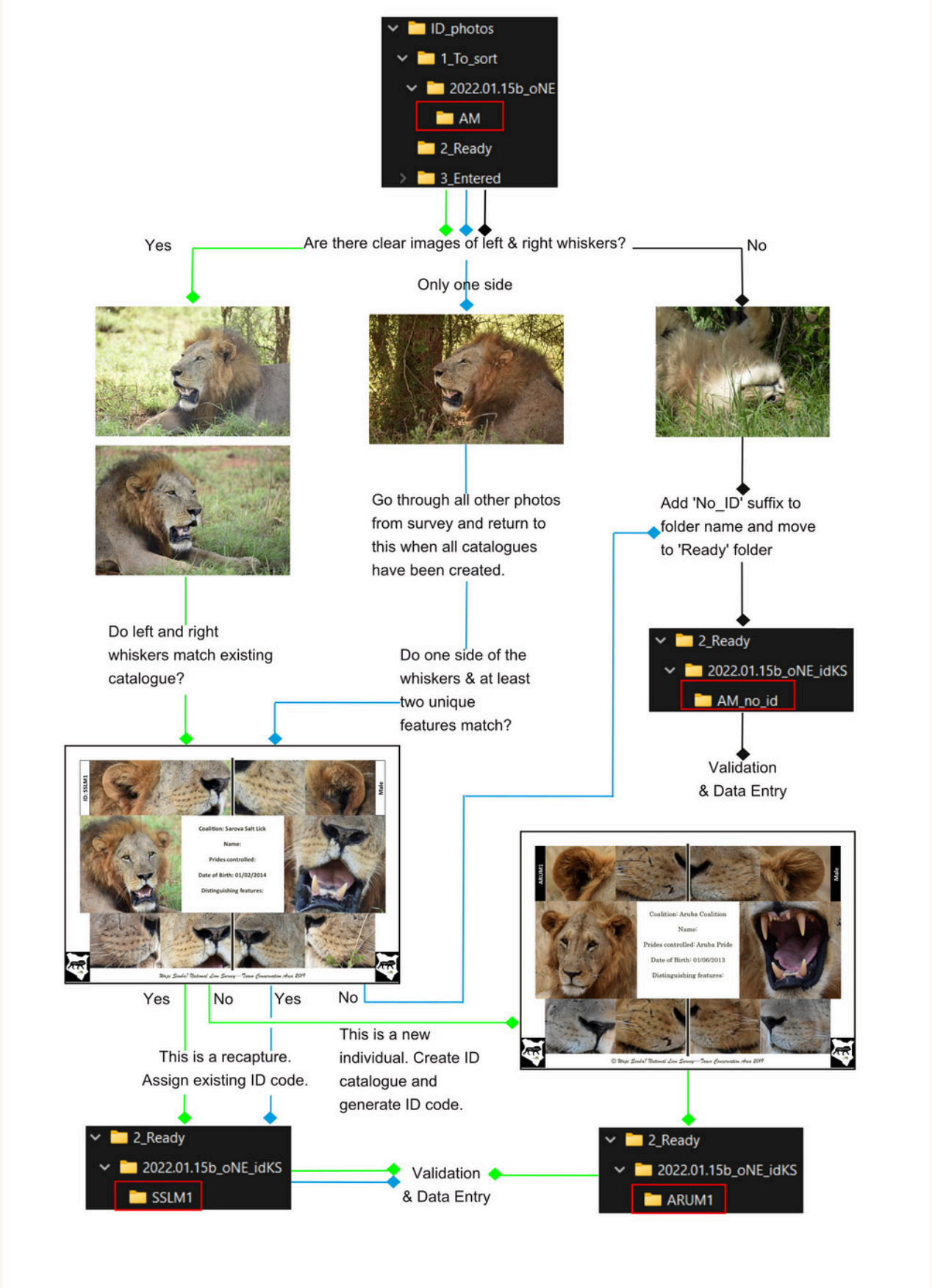


All cameras were cuddeback x-change color model 1279, used with the white flash model. Press the MODE key to change the operating mode. The LED will show which of the six modes is selected. When a mode is enabled, press the MORE key to access additional menus for each mode. Press UP and DOWN keys to alter the setting.

1. **Clock**: set the correct date and time
2. **Commands**:
   - BATTERY - if level is ‘low’ or ‘dead’, replace the batteries
   - CAM ID - set the camera ID according to the camera number
   - ASPECT - set to ‘full’
   - ZONE - set to ‘centred’ and ensure that the front panel zone control shutter is up
   - STRB POWER - set to close
   - IMAGE SZ - set to 20 MP
   - DST mode - set to off
3. **Settings**:
   - Select EZ mode
   - Delay - set to 5 sec
   - Video - set to off
4. **Arm**: This arms the camera so that it will begin taking pictures when triggered

Appendix II

Individual Identification Protocol



Protocol used to identify individual lions. Once the initial IDing had been conducted, all detections were validated by four additional observers who worked independently. If there was disagreement on any detection, it was discussed to see if consensus could be reached. The precautionary principle of 'if in doubt, leave it out' was adopted.

Appendix III

Model estimates derived from camera trap data combined with search encounter data and a resource selection SCR model.

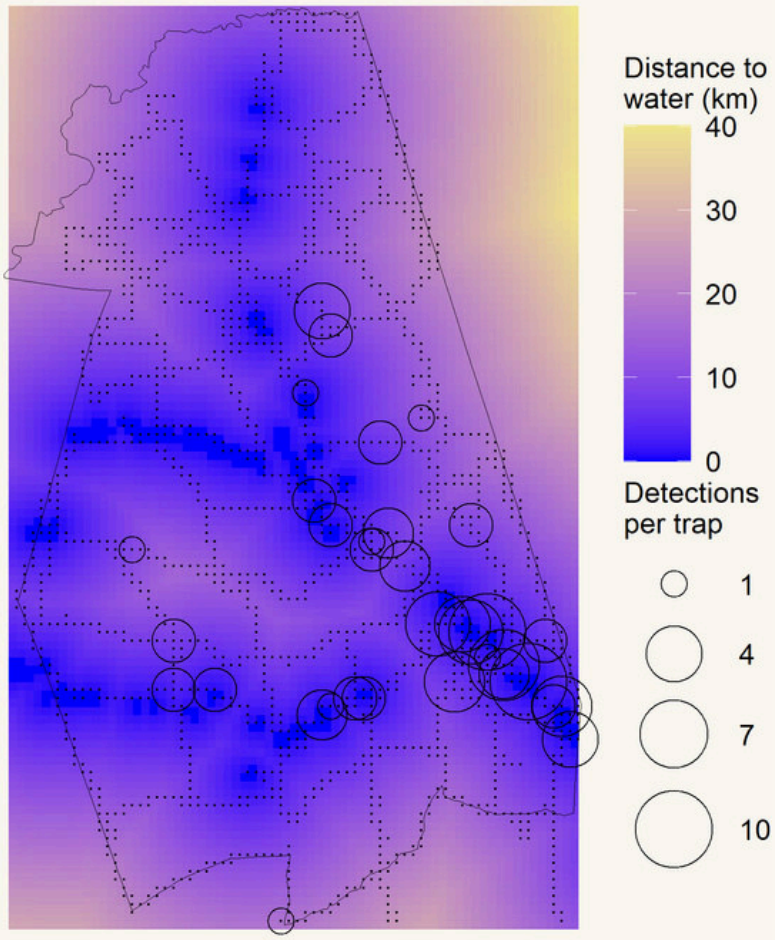


Figure A1. Spider plot depicting detections of lions that were individually identified from their whisker spots during the unstructured search encounter protocol combined with the camera trap protocol. We created cells (traps) of 1 km² around the drive effort. We then totalled up the km driven per trap per day. We then created a camera trap history file which detailed the location of each camera trap station and the days during which it was active. We then created a trap history file which indicated whether a particular trap (defined either by search encounter or a camera trap) was active on a given day (1) or was inactive (0). Finally, we created a capture history detailing which individual lion was detected, in which trap, on which day. This figure is simplified to show the water covariate clearly in relation to the detections. As such, in this figure we depict all traps (black points) regardless of field protocol and do not link recaptures of each individual.

Table A1. Posterior summaries of parameters estimated using Bayesian spatial capture-recapture models to estimate lion density and other state variables in the Nxanatseni North of Kruger National Park, South Africa. Estimates are posterior means and include 95% Highest Posterior Density Intervals in brackets. All estimates pertain to lions estimated to be over the age of one year. Refer to the Methods section for a description of each model. The selected model (Model 4.1) is reported in Results.

Parameter	Model 3.1
σ	6.3 (5.1 - 7.6)
λ0	0.002 (0.001 - 0.003)
β1.eff	0.05 (-0.004 - 0.102)
β2.eff	0.4 (-0.5 - 1.3)
βsex	NA
ψ	0.3 (0.2 - 0.4)
ψsex	NA
Beta.Density	-0.3 (-0.7 - -0.1)
Density	1.8 (1.3 - 2.2)
Abundance	
Nxanatseni North	92 (68 - 114)

Bayesian p-value: 0.57. MLHM: -42,669

Appendix IV

Comparing estimates from different field protocols

Search encounter

Our final dataset for this analysis was made up of 91 detections of 41 individuals.

Initially we obtained 243 detections of lions during the search encounter protocol. Forty detections of at least nine individuals were deemed to be of lions under the age of one year and were removed. Of the remaining 203 detections, 109 were removed because we could not identify the individual using their whisker spots. The vast majority (97) of these 109 detections came from the Kanniedood pride, which were repeatedly seen on consecutive days in a dry river bed too far away to photograph well.

Of the remaining 94 detections, we retained 91 detections of 41 individuals that were bilaterally identified through their unique whisker spots.

All models achieved convergence (mean potential scale reduction factor of <1.05 for each parameter), and no additional initial iterations were discarded post-hoc. Therefore we retained 40,000 iterations for inference from each of the four models we considered.

A goodness-of-fit evaluation using the Bayesian p-value based on individual encounters, (Royle et al. 2009), was used to reject models whose p-value lay outside 0.15-0.85. For all models, Bayesian p-values were between 0.28 and 0.31, indicating all were adequate.

The pair-wise correlation plots showed some parameter redundancy in Models 1 and 2, notably between the sex-specific sigma parameters and density. Model 4 did not contain a sex-specific sigma parameter and indicated the least parameter redundancy in the correlation plots.

Finally, the marginal likelihood estimate for Model 4 was highest (Dey et al. 2019).

Given these evidences, reporting Model 4 is appropriate. However, given our objective of comparing estimates derived from camera traps to those from search encounter to aid direct comparison, we highlight estimates from Model 3. Density was estimated to be 1.82 (PSD = 0.38) lions per 100 km², and lion abundance was estimated to be 96 lions (PSD = 19.4).

All model parameter estimates are in Table A2.

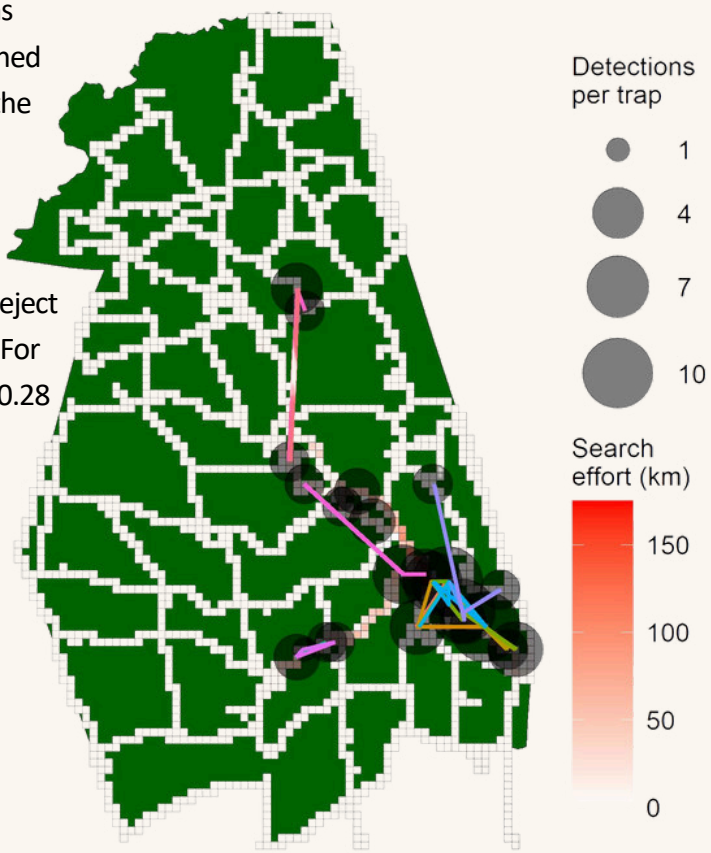


Figure A2. A visual representation of the data collected during the search encounter protocol. We created cells (traps) of 1 km² around the drive effort. We then totalled up the km driven per trap per day. Next, we created a capture history detailing which individual lion was detected, in which trap, on which day. This figure displays our search encounter effort together with the lion detections. Coloured lines link recaptures of individual lions.

Model estimates derived from search encounter data

Table A2. Posterior summaries of parameters estimated using Bayesian spatial capture-recapture models to estimate lion density and other state variables in the Nxanatseni North of Kruger National Park, South Africa. Estimates are posterior means and include 95% Highest Posterior Density Intervals in brackets. All estimates pertain to lions estimated to be over the age of one year. Refer to the Methods section for a description of each model.

Parameter	Model 1	Model 2	Model 3	Model 4
σF	4.8 (3.6 - 6.3)	4.9 (3.7 - 6.2)	6.8 (5.3 - 8.4)	6.6 (5.3 - 8.2)
σM	7.8 (5.6 - 10.1)	8.1 (5.8 - 11.1)		
λ0	0.001 (0.001 - 0.002)	0.001 (0.001 - 0.002)	0.001 (0.001 - 0.002)	0.001 (0.000 - 0.001)
β1.eff	1.5 (1.1 - 1.8)	1.5 (1.2 - 1.8)	1.4 (1.1 - 1.8)	1.4 (1.1 - 1.8)
β2.eff	NA	NA	NA	NA
βsex	-0.1 (-0.9 - 0.8)	NA	NA	0.5 (-0.2 - 1.1)
ψ	0.6 (0.4 - 0.9)	0.6 (0.4 - 0.9)	0.6 (0.3 - 0.8)	0.6 (0.4 - 0.9)
ψsex	0.3 (0.1 - 0.5)	0.3 (0.1 - 0.5)	NA	0.4 (0.2 - 0.6)
Beta.Density	NA	NA	NA	NA
Density	2.5 (1.5 - 3.6)	2.5 (1.5 - 3.6)	1.8 (1.1 - 2.6)	2.0 (1.3 - 2.9)
Abundance				
Nxanatseni North	128 (79 - 183)	128 (78 - 181)	96 (58 - 133)	103 (63 - 142)

Model 1: Bayesian p-value: 0.28. MLHM: -59,944
Model 2: Bayesian p-value: 0.29. MLHM: -57,231
Model 3: Bayesian p-value: 0.29. MLHM: -52,147
Model 4: Bayesian p-value: 0.31. MLHM: -45,845

Parameter definitions

σ	Rate of decline in detection probability (DP) with increasing distance between a lion's activity centre and the centroid of a sampled grid cell, described for F (females) and M (males)
λ0	Basal encounter rate of an individual (female for sex-specific models) lion whose activity centre is located precisely at the centroid of the grid cell
β1.eff	Rate of change in the complementary log-log value of DP as the (log) effort changes by one unit
β2.eff	The change in the complementary log-log value of detection probability when camera traps are included
βsex	Difference of complementary log-log value of detection probability between males and females
ψ	Ratio of true number of individuals in the population compared to the data augmented population M
ψsex	Proportion of lions are male
Beta.Density	Relationship between lion density and distance to water (resource selection model)
Density	Estimated density of adult lion / 100 km²

Appendix V

Comparing estimates from different field protocols

Camera traps

Our final dataset for this analysis was made up of 16 detections of 12 individuals.

We had initially obtained 45 detections of lions from camera trap images, which was reduced as follows: Three of these were estimated to be less than one year old and were removed.

Of the remaining 42, three were classed as 'unusable', 16 were classed as 'unmarked', three were classed as having a 'distinguishing feature', and for 20 we could discern the unique whisker spots.

Of these 20 detections, we obtained bilateral identification for two individuals (four detections), and had five left-side-only detections, and 11 right-side-only detections. We therefore used the bilateral detections and those with the right side.

We also included one detection where we had the left side only, since we had a bilateral ID of this individual from our search encounter dataset.

In this manner, the final camera trap dataset consisted of 16 detections of 12 individuals.

We did not obtain any recaptures of female lions. While we could have used an informed prior, we decided against this owing to the small dataset, and did not attempt to run any sex-specific models using the camera trap data. Instead we ran Model 3 which does not contain any sex-specific parameters.

Model 3 converged (mean potential scale reduction factor of <1.05 for each parameter), and no additional initial iterations were discarded post-hoc. Therefore we retained 200,000 iterations for inference.

A goodness-of-fit evaluation, using the Bayesian p-value based on individual encounters, (Royle et al. 2009), was used to reject any models whose p-value lay outside the extremities (between 0.15-0.85). For Model 3, the Bayesian p-value was 0.6, indicating that it was adequate.

With no alternative models to consider, we highlight the posterior parameter estimates from Model 3. Density was estimated to be 1.08 (PSD = 0.59) lions per 100 km², and lion abundance was estimated to be 55 lions (PSD = 30.3).

All model parameter estimates are in Table A3.

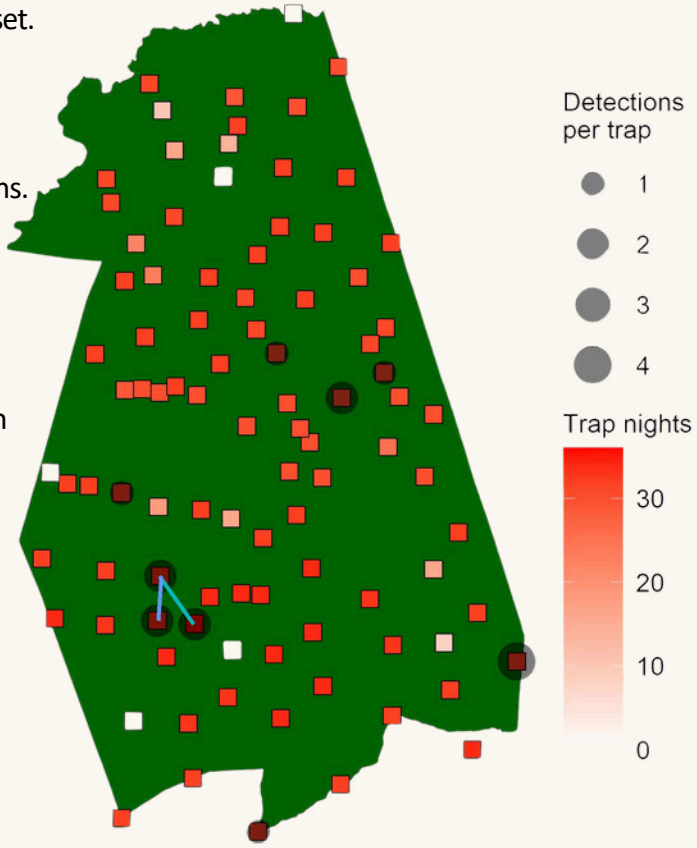


Figure A3. Spider plot depicting identified detections collected using the camera trap protocol. We created a trap history file which detailed the location of each camera trap station and the days during which it was active. Next, we created a capture history detailing which individual lion was detected, in which trap, on which day. Coloured lines link recaptures of individuals.

Model estimates derived from camera trap data

Table A3. Posterior summaries of parameters estimated using Bayesian spatial capture-recapture models to estimate lion density and other state variables in the Nxanatseni North of Kruger National Park, South Africa. Estimates are posterior means and include 95% Highest Posterior Density Intervals in brackets. All estimates pertain to lions estimated to be over the age of one year. Refer to the Methods section for a description of each model.

Parameter	Model 1	Model 2	Model 3	Model 4
σF	NA	NA	3.1 (1.6 - 5.2)	NA
σM	NA	NA		NA
λ0	NA	NA	0.014 (0.001 - 0.035)	NA
β1.eff	NA	NA	NA	NA
β2.eff	NA	NA	NA	NA
βsex	NA	NA	NA	NA
ψ	NA	NA	0.3 (0.1 - 0.7)	NA
ψsex	NA	NA	NA	NA
Beta.Density	NA	NA	NA	NA
Density	NA	NA	1.1 (0.3 - 2.4)	NA
Abundance				
Nxanatseni North	NA	NA	55 (13 - 120)	NA

Model 3: Bayesian p-value: 0.60. MLHM: -15,484

Parameter definitions

σ	Rate of decline in detection probability (DP) with increasing distance between a lion's activity centre and the centroid of a sampled grid cell, described for F (females) and M (males)
λ0	Basal encounter rate of an individual (female for sex-specific models) lion whose activity centre is located precisely at the centroid of the grid cell
β1.eff	Rate of change in the complementary log-log value of DP as the (log) effort changes by one unit
β2.eff	The change in the complementary log-log value of detection probability when camera traps are included
βsex	Difference of complementary log-log value of detection probability between males and females
ψ	Ratio of true number of individuals in the population compared to the data augmented population M
ψsex	Proportion of lions are male
Beta.Density	Relationship between lion density and distance to water (resource selection model)
Density	Estimated density of adult lion / 100 km²

Appendix VI

Comparing estimates from different field protocols

Search encounter combined with camera traps

Our final dataset for this analysis was made up of 107 detections of 52 individuals.

All models achieved convergence (mean potential scale reduction factor of <1.05 for each parameter), after we discarded an additional initial 1,500 iterations post-hoc from Model 1.

Therefore we retained 40,000 iterations for inference (Models 2-4) and 34,000 iterations for Model 1.

A goodness-of-fit evaluation, using the Bayesian p -value based on individual encounters, (Royle et al. 2009), was used to reject any models whose p-value lay outside the extremities (between 0.15-0.85). For all models, Bayesian p-values were between 0.48 and 0.52, indicating all were adequate.

The pair-wise correlation plots showed some parameter redundancy in Models 1 and 2, notably between the sex-specific sigma parameters and density. Model 4 did not a contain sex-specific sigma parameter and indicated the least parameter redundancy in the correlation plots.

Finally, the marginal likelihood estimate for Model 4 was highest (Dey et al. 2019).

Given these evidences, reporting Model 4 is appropriate. However, given our objective of comparing estimates derived from camera traps to those from search encounter, to aid direct comparison we highlight estimates from Model 3.

Density was estimated to be 1.85 (PSD = 0.31) lions per 100 km², and lion abundance was estimated to be 98 lions (PSD = 14.7).

All model parameter estimates are in Table A4.

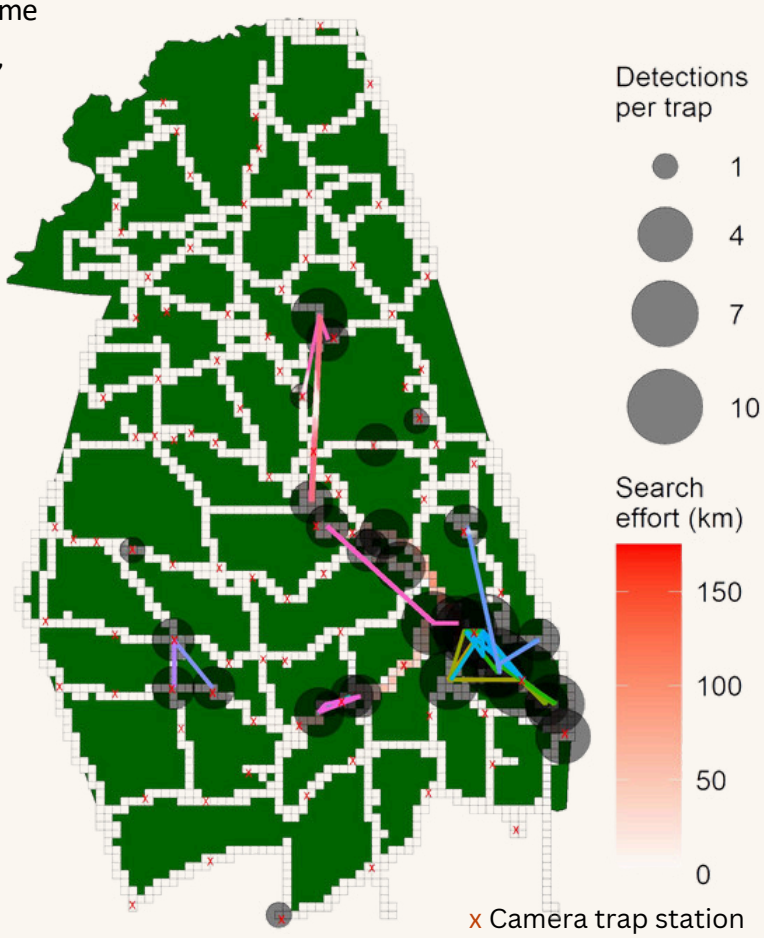


Figure A4. Spider plot depicting identified detections collected using the unstructured search encounter protocol combined with the camera trap protocol. We created cells (traps) of 1 km² around the drive effort. We then totalled up the km driven per trap per day. We then created a camera trap history file which detailed the location of each camera trap station and the days during which it was active. We then created a trap history file which indicated whether a particular trap (defined either by search encounter or a camera trap) was active on a given day (1) or was inactive (0). Finally, we created a capture history detailing which individual lion was detected, in which trap, on which day. Coloured lines link recaptures of individuals.

Model estimates derived from camera trap data combined with search encounter data

Table A4. Posterior summaries of parameters estimated using Bayesian spatial capture-recapture models to estimate lion density and other state variables in the Nxanatseni North of Kruger National Park, South Africa. Estimates are posterior means and include 95% Highest Posterior Density Intervals in brackets. All estimates pertain to lions estimated to be over the age of one year. Refer to the Methods section for a description of each model.

Parameter	Model 1	Model 2	Model 3	Model 4
σF	4.7 (3.5 - 6.0)	4.6 (3.6 - 5.6)	6.0 (5.0 - 7.2)	5.9 (4.9 - 6.9)
σM	6.7 (5.3 - 8.3)	6.9 (5.4 - 8.7)		
λ0	0.002 (0.001 - 0.003)	0.002 (0.001 - 0.003)	0.002 (0.001 - 0.003)	0.002 (0.001 - 0.003)
β1.eff	0.1 (0.0 - 0.1)	0.1 (0.0 - 0.1)	0.1 (0.0 - 0.1)	0.1 (0.0 - 0.1)
β2.eff	0.4 (-0.5 - 1.3)	0.5 (-0.4 - 1.4)	0.5 (-0.4 - 1.3)	0.4 (-0.5 - 1.3)
βsex	0.1 (-0.7 - 0.9)	NA	NA	0.6 (-0.1 - 1.2)
ψ	0.6 (0.4 - 0.8)	0.6 (0.4 - 0.8)	0.5 (0.3 - 0.6)	0.5 (0.3 - 0.7)
ψsex	0.3 (0.2 - 0.5)	0.3 (0.1 - 0.5)	NA	0.4 (0.2 - 0.5)
Beta.Density	NA	NA	NA	NA
Density	2.4 (1.5 - 3.3)	2.4 (1.6 - 3.3)	1.8 (1.3 - 2.5)	2.1 (1.4 - 3.0)
Abundance				
Nxanatseni North	123 (80 - 170)	124 (82 - 168)	98 (69 - 126)	110 (72 - 148)

Model 1: Bayesian p-value: 0.51. MLHM: -69,838
Model 2: Bayesian p-value: 0.49. MLHM: -76,138
Model 3: Bayesian p-value: 0.48. MLHM: -75,049
Model 4: Bayesian p-value: 0.52. MLHM: -63,493

Parameter definitions

σ	Rate of decline in detection probability (DP) with increasing distance between a lion's activity centre and the centroid of a sampled grid cell, described for F (females) and M (males)
λ0	Basal encounter rate of an individual (female for sex-specific models) lion whose activity centre is located precisely at the centroid of the grid cell
β1.eff	Rate of change in the complementary log-log value of DP as the (log) effort changes by one unit
β2.eff	The change in the complementary log-log value of detection probability when camera traps are included
βsex	Difference of complementary log-log value of detection probability between males and females
ψ	Ratio of true number of individuals in the population compared to the data augmented population M
ψsex	Proportion of lions are male
Beta.Density	Relationship between lion density and distance to water (resource selection model)
Density	Estimated density of adult lion / 100 km²