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ORIGINAL PAPER

# Potential for camera-traps and spatial mark-resight models to improve monitoring of the critically endangered West African lion (*Panthera leo*)

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**Abstract** West African lions are critically endangered throughout their range. Recent monitoring efforts focused on determining where remaining populations persist and obtaining preliminary population estimates to assess status across the region. However, current monitoring methods do not result in estimates that can be easily compared across sites or over time. Thus, there is a need to develop methods that allow for unbiased and precise comparable population parameter estimates for baseline and long-term monitoring. Spatial mark-resight models offer the ability to estimate lion density for a site over a standardized unit of area making estimates comparable. In addition, Bayesian inference is not constrained by asymptotic assumptions and allows for unbiased and precise estimates even with small sample sizes and low detection rates. We demonstrate the utility of Bayesian inference of a spatial mark-resight model for West African lion populations using a single-season camera trap survey at a study site in Niokolo-Koba National Park, Senegal. We estimated a site specific density of 3.02 lions/100 km$^2$ (1.72–5.57/100 km$^2$) based on trap-specific relocations of individuals with unique identifying natural marks, and counts of unmarked individuals at each trap. We conclude with a discussion of limitations of the current study and possible improvements on this method. We suggest immediate action including site specific monitoring within protected areas to conserve lions in this most northern part of their range. This monitoring approach can provide useful estimates over

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large areas providing an easily implemented and repeatable methodology for local and regional monitoring of critically endangered lion populations.

## Introduction

Across the range of the African lion (*Panthera leo*), West Africa is thought to hold the most critical lion population, classified as "Endangered" in the IUCN Red List (Bauer and Van Der Merwe 2004; IUCN 2013), and more recently identified as "Critically Endangered" (Henschel et al. 2014), and they are believed to be restricted exclusively to protected areas. Knowledge of West African lion ecology and population status is crucial in managing protected areas as they are considered indicators of ecosystem health due to their trophic position and vulnerability to ecosystem perturbations at any level (Mills 1991).

Although there are many studies on lions in Africa, there is a strong geographic bias, with most studies occurring in southern and eastern Africa (Ray et al. 2005). Thus, there is an urgent need to intensify lion research in West Africa in order to better protect its relict population from extinction. A recent publication has brought attention to the critical situation concerning lions in this region (Henschel et al. 2014). Henschel et al. (2014) combined various types of data from 21 protected areas across West Africa and attempted to confirm the presence of lion populations in these areas, and produce preliminary estimates of abundance based primarily on call-up surveys and a common track count methodology (Funston et al. 2010). Initial lion population estimates were alarmingly low, finding lion populations persisting in only four of the 21 previously assumed occupied sites (Henschel et al. 2014). There is conservation value in attempts to estimate the total number of individuals across the entirety of their range as it highlights the critical status of the West African lion population. However, to identify specific conservation priorities more detailed ecological information is needed about how the species is using their range, and we need baseline demographic monitoring to compare population status in different parts of the range or over time.

The accuracy of abundance estimates from index-based surveys can be misleading (McKelvey and Pearson 2001; Sollmann et al. 2013a; Tobler and Powell 2013), and such surveys require calibration, which has not been done for lions in this region (Henschel et al. 2014). The use of indices as a surrogate for abundance is commonly questioned as indices often do not account for variability and biases in detection (Sollmann et al. 2013a; Hayward and Marlow 2014). In addition, the precision of such estimates can be poor, resulting in large intervals of possible abundances, which can hinder their use in assessing population status and trends. Despite these problems, monitoring of carnivores in Africa still often relies on attempts to locally calibrate counts or indices (Funston et al. 2010; Thorn et al. 2010; Bauer et al. 2014; Henschel et al. 2014; Midlane et al. 2015), even though there is a strong record of failure with track index validation for multiple species across many regions (Ruscoe et al. 2001; Blackwell et al. 2002; Jhala et al. 2011; Karanth et al. 2011; Katzner et al. 2011; Watts et al. 2011; Sollmann et al. 2013a), and especially for carnivores with typically very low detection rates (Royle et al. 2008). In Africa in particular, track indices are considered ineffective at estimating absolute abundance (Balme et al. 2009;

Thorn et al. 2010). Furthermore, even estimates of abundance that account for imperfect detection can be difficult to compare because the size of the area surveyed is unknown and may change over time or between study areas (Borchers and Efford 2008). Thus, researchers are often interested in estimating population density, as this parameter is standardized across a given area and is therefore comparable between studies and over time.

The objective of this study was to demonstrate the utility of the spatial capture-recapture (SCR) framework to estimate density of West African lions in one previously assessed area in its range. SCR models (Royle and Young 2008) are hierarchical models that account for both the spatial organization and movement of individuals (the process model) in relation to the placement and effectiveness of the detection devices (the observation model). Thus, SCR models directly estimate space use of animals and density simultaneously while accounting for imperfect detection (Royle et al. 2013a, Royle et al. 2013b). As a result estimates from SCR models from different sites, times, and detection methods are comparable over the same unit of area. In addition, SCR models are easily integrated across sites or stratified populations (Royle and Converse 2014), and can integrate multiple monitoring methods within the same modeling framework (Gopalaswamy et al. 2012; Sollmann et al. 2011), making SCR models a flexible and versatile tool for effective monitoring across regions and over time.

Camera trap data is often used with capture-recapture models when all animals in a population are individually identifiable by natural markings such as spots and/or stripes. However, when only a subset of the animals photographed are uniquely identifiable from unique marks, as with African lions, recently developed mark-resight models may be employed to estimate abundance and density by combining information about captures of
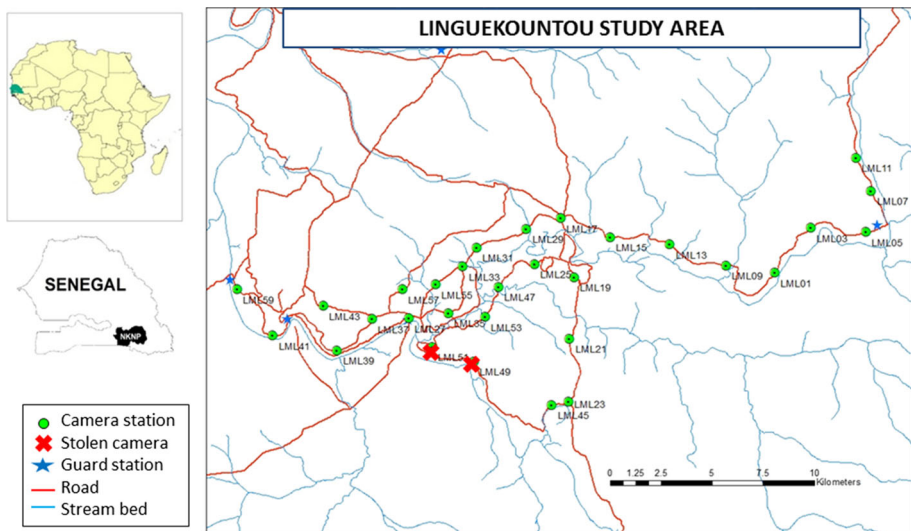


**Fig. 1** Study area in the Niokolo Koba National Park (NKNP), Senegal. Location of the study area outlined in black with the 30 camera stations in black dots placed along trails. Mean camera spacing was 2.5 km (SE = 0.68). Camera trap locations were selected to maximize detection of carnivores, including siting cameras along roads, in optimal habitat, and micrositing on sections of roads where lion sign was detected when possible. Background habitat generated from a 2012 USGS land use –land cover map of NKNP (Tappan 2012)

marked individuals with counts of unmarked individuals (White and Shenk 2001; McClintock et al. 2009; Chandler and Royle 2013; Sollmann et al. 2013b; Rich et al. 2014). This joint-model approach often allows for better precision compared to models that only consider detection of unmarked individuals because it includes information on detection rates of known individuals and shares parameters between the marked and unmarked populations (Chandler and Royle 2013, Rich et al. 2014). We demonstrate the application of a spatial mark-resight model (SMR) to estimate lion density from camera-trap data collected in Niokolo-Koba National Park (NKNP) in Senegal. This modeling framework, coupled with camera trap survey techniques, allows for relatively precise and unbiased estimates of African lion density at the study site in NKNP. In addition, we argue that with increased sampling sites and survey intensity, this modeling method can be improved upon and provide even more precise estimates over larger areas providing an easily implemented and repeatable methodology for broader local and regional monitoring of critically endangered lion populations.

## Methods

### Study site

Niokolo Koba National Park (NKNP) in Senegal is one of the largest protected areas in West Africa (9130 km$^2$). NKNP was created in 1954 and is located in south-eastern Senegal, between 12°30′ and 13°20′ North and 18°30′ and 13°42′ West, in a well-watered region, unlike most parts of the country (Fig. 1). It is a non-fenced area that covers 9130 km$^2$ and contains heterogeneous vegetation types, generated by complex soil and geologic formations that are distributed in three types of terrain: valleys, plateaus, and hills with the highest elevation at Mount Assirik at 311 meters. The climate is of Sudanian type with a rainy season from May to October. Average annual rainfall ranges from 900 to 1200 mm and temperature ranges from 25 °C in December to 33 °C in May (DPNS 2000). The climate creates a transitional vegetation between Sudano-Guinean savanna and Guinean savanna, with wooded savannah composing nearly 69 % of the habitat types (Tappan 2012). All the streams of the park belong to the catchment of the Gambia River, which crosses the park from southeast to northwest. The main tributaries are Niokolo Koba, Koulountou, and Nieriko. In addition to these streams, some permanent and temporary ponds and pools play an important role in supplying water and fresh grass for wildlife.

### Field methods

We received research permission from the Senegalese Department of National Parks and established camera trap locations for West African lions within NKNP after consultation with the park managers and a pilot study in 2012. Based on carnivore detections during a 44-night pilot study we decided to place all cameras used for this study on human surveillance and tourist trails (Foster and Harmsen 2012). Before setting up a station, we first searched the designated study area for lion signs such as tracks and scats to microsite camera placement in areas with the highest potential for photo-capture (Meek et al. 2014).

We deployed 30 camera-traps from February 4 to April 23, 2013 spaced across the dense network of human trails, from 5 km north of the old guard post of Linguekountou to the guard post of Gué Damantan (Fig. 1), resulting in a minimum convex polygon

surrounding cameras of 285.4 km$^2$. This area of the park was selected because previous research indicated this may be the last remaining portion of the park to support populations of large carnivores (Renaud et al. 2006), and lions in particular (Ndao and Henschel 2011). The less frequently used and bushy trails were cleared out before setting up a station. Two stations were stolen during the first two weeks without replacement. The average distance between two consecutive cameras was 2.5 km (SD = 0.68; min = 0.82; max = 3.2 km). Cameras were mounted on trees at 30–40 cm above the ground and consisted of two cameras at each station placed on the opposing side of a trail or road (mean road/trail width = 3 m), with a slight offset to avoid mutual flash interference. Each station comprised at least one digital and one film camera to capture both flanks of passing animals and to ensure that stations would still be functional even if analog cameras—which are more prone to failure—ran out of film or batteries. Eight stations consisted of two digital cameras. Digital cameras were set to take two consecutive photos for each trigger event with a delay of 1 min between events while the film cameras were adjusted to take one picture per trigger event, with a delay of 30 s between events. Cameras were checked every 13–15 days to replace batteries, film, memory cards or malfunctioning cameras.

## Data analysis

Photographs of distinct individual animals taken within a 30 min-time interval were only recorded once (i.e. as a single capture event), regardless of the number of photographs in calculating trap success (O'Brien et al. 2003). Trap success was calculated for lions caught at each station as the number of capture events of a given species per 100 trap-nights, following Dillon and Kelly (2007). A trap-night is defined as a 24-h period where the station is fully active (at least one of the 2 cameras is functional). While some lions do not have clear natural markings, three investigators worked separately and compared results based on obvious marks such as mane size, shape and color, and more subtle marks such as scars, missing tail tips, and markings on the interior side of hind legs, following Kelly et al. (2008).

We used a hierarchical spatial mark-resight model (SMR) to estimate lion density (Chandler and Royle 2013; Sollmann et al. 2013a, b, c). The SMR model consists of two separate component models, a SCR model for marked individuals (Royle et al. 2013a), and a spatial model for unmarked individuals (Chandler and Royle 2013; Royle et al. 2013a). Both component models consist of encounter histories of animals at specific trap locations ($J$) over a repeated number of sampling occasions ($K$). The process model for both components is the same, and assumes that individual animals use space around an individual activity center ($s$), and that detection decreases with distance away from activity centers, represented by a scaling parameter ($\sigma$). However, the observational model for each component is different. We used an SCR$_0$ model (Royle et al. 2013a) for the marked individual component, where we consider identifiable individuals most likely to be detected at activity center $s$, and estimate an expected encounter rate ($\lambda_0$), if a camera was located at the hypothetical activity center of an individual. We then assumed detection decreases with distance from the activity center and this decrease follows a bivariate Gaussian (half-normal) distribution according to scaling parameter ($\sigma$). The model for unmarked individuals also assumed detection is highest at individuals' activity centers. However, because individuals are not identifiable in this component model, we use a latent data model and sum the counts of detections ($n$), assuming greater numbers of detections in space are correlated with a greater density of individual activity centers (Chandler and Royle 2013; Royle et al. 2013a).

Due to the small sample size and low detection rates of individuals and counts of unmarked individuals, we opted to analyze the model using Markov chain Monte Carlo (MCMC) because Bayesian analysis allows for estimation of detection rates that are close to the bounds of 0 and 1, and inference is free from asymptotic assumptions problematic with small sample sizes (Kéry and Schaub 2012). For each model component, we used data augmentation to account for individuals present but not detected during the study (Royle and Young 2008). This approach sets a maximum number of possible activity centers within the state space ($S$), and then uses an indicator variable ($z_i$, a Bernoulli trial), associated with each possible unobserved activity center, to estimate whether those possible activity centers are actual individuals with a capture history consisting of all zeros, or whether they are not actual individuals (structural zeros), with a binomial distribution of all trials ($\psi_m$ for the marked component model and $\psi_u$ for the unmarked component model).

To estimate density, all activity centers for detected individuals and all undetected activity centers determined to be representative of actual individuals are summed (marked plus unmarked). Density is derived by dividing the sum of activity centers within the state space by the total area of the state space. While the model assumes independent activity centers, the model is known to be robust to this assumption (Russell et al. 2012). Moreover, an equivalent view of the uniformity assumption is that it implies a lack of specific information about each activity center, similar to an uninformed prior. Thus, the possible non-independence of individual lion activity centers is not expected to bias estimates of density.

By using a hierarchical approach, we are able to combine the dataset consisting of marked captures and recaptures with the data set of counts of unmarked individuals at camera trap locations by sharing the scaling parameter ($\sigma$) in a joint model. Thus, the process model describing individual home range movements around an activity center is shared between the two component models and we assume the distance an individual moves from the hypothetical home range center is similar, whether an animal is marked or unmarked. In addition, as with other mark-resight models, detection rates of marked individuals and unmarked individuals are assumed to be the same ($\lambda_0$). This allows for the model for marked individuals to be integrated with the model for unmarked individuals with a shared parameter for the expected encounter rate at activity centers ($\lambda_0$), and is expected to improve estimation of $\psi_u$ in the unmarked model component by providing more specific information on detection from the marked model component (Chandler and Royle 2013; Sollmann et al. 2013b; Royle et al. 2013a). In both model components, we accounted for non-operational occasions (i.e. camera malfunctions) during camera deployment when estimating $\lambda_0$.

Although the parameter $D$ is estimated by dividing the sum of activity centers found ($N$) by the prescribed state space, the choice of $S$ is not arbitrary, but is a prior of the binomial point process model and is determined by testing the sensitivity of resulting parameter estimates to changes in the size of $S$. The estimate of $N$ scales with the state space size and is invariant to the state space size as long as the size is sufficiently large (Royle et al. 2013a). However, if the state space size is too small, then $D$ will be sensitive to its size. When the state space size is too large, computation time increases dramatically as possible individuals represented by activity centers 2–3 times the distance of $\sigma$ from the trap array will have zero probability of being captured. For computation time, the ideal size for $S$ is equivalent to a representative buffer around the trap array at least 2–3 times the estimate for $\sigma$. For our final model, we selected a state space area of 1687.20 km$^2$ which represents an approximate 12 km distance surrounding the camera

trap array, greater than three times the final estimates of $\sigma$ and sufficiently large so $D$ is not sensitive to the size of $S$.

We formatted data in R (R Core Team 2013) using the SCR23darray() function in the analysis package scrbook (Royle et al. 2014), and implemented the SMR model in R using the rjags (Plummer 2014), and coda (Plummer et al. 2006) packages. We ran the model with three MCMC chains with 100 adaptations for the Metropolis-within-Gibbs algorithm, and then used coda to sample 200,000 iterations from the posterior distributions of each monitored parameter ($\lambda_0$, $\sigma$, $\psi_u$, $\psi_m$, $m$, and $N$) at a thinning rate of 1, including a burn-in of 100,000 iterations. We assessed MCMC convergence by visually inspecting trace plots for each monitored parameter, and $\hat{R}$ statistics $\leq 1.1$ (Gelman and Rubin 1992). For all parameters, we reported the posterior means and standard deviation, posterior modes, medians and 95 % credible intervals. We derived density by dividing the posterior modes for N (the sum of the estimated marked and unmarked population) by the area of the state space, as the posterior mode is an unbiased estimate of abundance compared to the posterior mean in SCR models (Chandler and Royle 2013). Finally, we decomposed the SMR model into the two components, a model for marked individuals, and a model for unmarked individuals. We used the same data set to estimate population density with all detections considered unmarked (a spatial aggregate count model, Chandler and Royle 2013), and a SCR model only including detections of marked individuals. This comparison allowed us to determine if the SMR approach did improve parameter estimation and precision of estimates. The same settings and priors were used for all three models.

# Results

The 78 days of camera-trapping at 28 stations resulted in a sampling effort of 2014 effective trap-nights. The total number of capture events was 5121 and consisted of 3432 photos of mammals. We obtained 43 independent captures of lions, resulting in a mean (SE) trap success of 2.06 (0.72) lions per 100 trap-nights. Most of the lion captures occurred at 6 of the 8 stations where both digital cameras were present. Most lion individuals were relatively easy to distinguish from each other by the presence of subtle scars, spots and dark coloration on their hind legs, mane development and shape, and missing tail

**Table 1** Lion trap rates and total marked and unmarked individuals for the Linguekountou study area in NKNP from February 4, 2013 to April 23, 2013 (78 days) for 28 camera stations (2 of 30 cameras were stolen)

| All lion trap rates | Lion capture demographics | Number of individually marked lion captures | Number of individually marked lions (recaptures) | Number of unmarked (unidentifiable) lions |
|---|---|---|---|---|
| 2.06/100 trap-nights (0.72) | Adult males | 4 | 4 (12) | 4 |
| | Subadult males | 1 | 1 | 0 |
| | Adult females | 4 | 4 (2) | 2 |
| | Subadult females | 0 | 0 | 0 |
| | Sex undetermined | 0 | 0 | 1 |

There was a total of 2014 trapping nights. Camera traps/day = 25.81, and mean trap-nights per camera = 71.89. Mean trap spacing = 2.5 km (SD = 0.68) resulting in a trap array with a minimum convex polygon area of 285.40 km$^2$. Four lion photo-captures were discarded due to poor image quality

tips (Online Resource 1). The three investigators who examined lion photographs agreed on 7 of the 9 individual lions in 32 photographs and came to consensus on the final 2 individuals, while 7 other photographs were considered unmarked. The remaining 4 photographs were discarded due to poor quality (Table 1).

Based on the SMR posterior mode and 95 % credible intervals (Table 2), the estimated lion density for the study site in NKNP is 3.02 lions/100 km$^2$ (1.72–5.57/100 km$^2$). This credible interval can be interpreted as a 95 % probability that the density of lions is between 1.72 and 5.57 lions per 100 km$^2$ in the study area. The data augmentation parameter for the unmarked component is much smaller than the marked model component in the SMR model, which agrees with our observation that a greater proportion of the population appears to have some sort of highly identifiable natural mark.

The SCR model including only detections of marked individuals converged and produced estimates with similar precision to the SMR model that also included counts of unmarked individuals (Table 2). However, the estimate of density for the SCR model (2.07 lions/100 km$^2$, 1.25–4.62/100 km$^2$) was lower than the estimate for the SMR model, as the SCR model only includes detections for the marked portion of the population and does not include the unmarked portion of the population. The unmarked model was unable to produce a converged estimate for baseline encounter probability ($\hat{R}$ for $\lambda_0 < 1.24$), and the standard errors and range between 95 % credible interval estimates for the remaining

**Table 2** Posterior summary statistics for the Spatial Mark-Resight (SMR) model for African lions at Niokolo-Koba National Park, and the same parameter estimates for a model considering all detections as unmarked individuals (unmarked), and a spatial capture-recapture model considering only marked individuals (marked)

| Model/Parameter | Mean | SE | Mode | Q 0.025 | Q 0.50 | Q 0.975 |
|---|---|---|---|---|---|---|
| SMR $\sigma$ | 1.72 km | 0.26 | 1.65 | 1.34 | 1.68 | 2.35 |
| SMR $\lambda_0$ | 0.038 | 0.02 | 0.031 | 0.017 | 0.036 | 0.075 |
| SMR $\psi_u$ | 0.091 | 0.05 | 0.06 | 0.02 | 0.08 | 0.22 |
| SMR $\psi_m$ | 0.320 | 0.11 | 0.29 | 0.15 | 0.31 | 0.56 |
| SMR $D$ | 3.32/100 km$^2$ | | 3.02/100 km$^2$ | 1.72/100 km$^2$ | 3.20/100 km$^2$ | 5.57/100 km$^2$ |
| Unmarked $\sigma$ | 2.35 km | 1.02 | 2.12 | 1.37 | 2.19 | 4.79 |
| Unmarked $\lambda_0$ | <0.01 | 0.01 | <0.01 | <0.01 | <0.01 | 0.01 |
| Unmarked $\psi$ | 0.15 | 0.11 | 0.07 | 0.02 | 0.12 | 0.45 |
| Unmarked $D$ | 8.30/100 km$^2$ | 6.54 | 4.17/100 km$^2$ | 1.19/100 km$^2$ | 6.52/100 km$^2$ | 26.08/100 km$^2$ |
| Marked $\sigma$ | 1.79 km | 0.32 | 1.71 | 1.30 | 1.75 | 2.52 |
| Marked $\lambda_0$ | 0.04 | 0.02 | 0.04 | 0.02 | 0.04 | 0.09 |
| Marked $\psi$ | 0.30 | 0.10 | 0.25 | 0.13 | 0.28 | 0.53 |
| Marked $D$ | 2.61/100 km$^2$ | 0.87 | 2.07/100 km$^2$ | 1.25/100 km$^2$ | 2.49/100 km$^2$ | 4.62/100 km$^2$ |

For all models, the detection model is comprised of $\sigma$ (the scaling parameter) and $\lambda_0$ (expected encounter rate if a camera was located at the hypothetical activity center of an individual), which are shared parameters for marked and unmarked individuals in the SMR model. For the SMR model and the data augmentation parameter ($\psi$) is estimated for both the marked population ($m$) and the unmarked population ($u$), where there is a single $\psi$ estimated for the unmarked and marked only models. Density ($D$) = activity centers/area of state space, and is invariant to the size of the state space because $N$ scales to the state space (Royle et al. 2014). When the state space is sufficiently large (at least 2–3 times the estimate of $\sigma$), $N$ will increase with increase in the size of the state space, but $D$ will remain approximately the same

estimates including density (4.17 lions/100 km$^2$, 1.19–26.08 lions/100 km$^2$) were much wider and less precise than the estimates produced by the SMR model (Table 2).

## Discussion

African lion populations represent two different stories across the continent. Although classified as "Vulnerable" by the IUCN Red List (2013), lions in southern and eastern Africa have more genetically diverse and demographically stable populations compared to the geographically isolated populations in western Africa (Nowell and Jackson 1996; Chardonnet 2002; Bertola et al. 2011). Lions in the western portion of the range are believed to face even greater threats due to increased habitat loss and fragmentation, illegal hunting, and depletion of their prey base (Bauer and Van Der Merwe 2004; Sogbohoussou 2011; Henschel et al. 2014).

Because of its location in the extreme west of Africa and on the northern edge of the sub-Sahelian woodland belt, NKNP harbors many mammal populations including lions that are at the northern extreme of their distribution (Sillero-Zubiri et al. 1997). As an area that has a national park status in the Senegalese Forestery Act, no hunting is allowed. However, poaching is one of the main threats and mainly targets lion prey species such as antelopes. Carnivores and specifically lions are poorly studied in NKNP, and there have been very few attempts to estimate population size and distribution since its creation in 1954. We used camera trapping, a targeted carnivore-specific methodology (Balme et al. 2009) to obtain a population estimate of local lion density (3.02 lions/100 km$^2$, 1.72–5.57/100 km$^2$) for an area of NKNP (the Linguekountou study area), and to demonstrate how SCR methods can provide improved baseline monitoring information for future conservation actions. Our study indicates that NKNP still harbors a population of critically endangered West African lions at the northern edge of their range, and protection of lions in this area should be a priority.

Camera-trapping techniques using a capture-recapture framework (O'Connell et al. 2010) have proven very effective in estimating population size and density of elusive and cryptic large carnivores such as tigers (*Panthera tigris*) in India (Karanth 1995; Karanth and Nichols 1998) and Sumatra (Sunarto et al. 2013), jaguars (*Panthera onca*) in Belize (Silver et al. 2004) and Brazil (Silveira et al. 2010), and leopards (*Panthera pardus*) in Nepal (Thapa et al. 2014) and South Africa (Balme et al. 2009). Camera trapping for carnivores, especially felids, is now widely used for abundance and density estimation and greatly improves our understanding of wildlife population status (Meek et al. 2014). In Africa, camera trapping has been used in several studies targeting elusive species including carnivores (Kauffman et al. 2007; Marnewick et al. 2008; Balme et al. 2010; Henschel et al. 2010; Pettorelli et al. 2010), but most of these studies occurred in southern and eastern Africa, further illustrating the strong bias in geographic regions for carnivore research in Africa (Ray et al. 2005; Henschel et al. 2014).

To our knowledge, this study is the first to use camera-trap data and Bayesian analysis of a SMR model to estimate African lion density. Even with a limited study site and small number of cameras (28) and occasions (78), the model produced relatively precise estimates of lion density (between 1.72 and 5.57/100 km$^2$). This estimate is far more precise than the previous estimates from NKNP for an undetermined sized area (16 lions, 95 % confidence intervals between 0 and 54 lions; Henschel et al. 2014). These results suggest the SMR model with camera trap data can produce useful baseline estimates of lion density

for study sites within NKNP, and that this methodology can be easily implemented across other study sites to provide comparable unbiased and relatively precise estimates. Our estimate of density suggests there are about 1–6 lions using areas of 100 km$^2$ in size at this study site. This is not unreasonable considering we detected at least 9 individuals with a camera array encompassing approximately 285 km$^2$. Thus, this method holds promise to considerably improve our ability to monitor West African lion population status in different regions and over time.

Assessment of population sizes and densities of wildlife populations, specifically for large carnivore species, is crucial for effective, science-based management (Krebs 2001; Kéry and Schaub 2012; Balme et al. 2009; Midlane et al. 2015; Hayward et al. 2015). In addition, knowledge of carnivore population trends can aid in implementing broader impact conservation management actions that will benefit other species (Estes et al. 2011; Ripple et al. 2014). Because of the position of NKNP at the most northern limit of distribution of lions, losing large predator populations such as West African lions would be detrimental to biodiversity and global conservation efforts. We selected our study site specifically because it was thought to contain optimal lion habitat and possibly support a higher lion density than the remainder of the park. However density estimates even for this optimal habitat area are still very low. This begs for future research in NKNP expanding over greater areas of the park and into other protected areas in West Africa. As suggested by Henschel et al. (2014) immediate action including sound population sampling and analysis is required to direct and inform conservation actions.

## Limitations and recommendations to improve future monitoring

This study represents a way forward in rigorous population monitoring for West African lions. West Africa has seen little use of systematic, standardized camera-trap surveys for wildlife. Our study confirms the feasibility of using camera-trapping in a landscape dominated by wooded savannah (69 % cover at our study site) to estimate lion density. Many other elusive mammals were catalogued during this study (Kane 2014), suggesting this method may be useful in estimating population and species parameters such as density and occupancy for other species in West Africa. Some species such as elephants (*Loxodonta africana*), African wild dogs (*Lycaon pictus*), and caracals (*Caracal caracal*) have not been photographed in NKNP for at least a decade, and this short, single-season study provided proof of their presence. Placement of cameras on human trails and roads was advantageous as lion captures occurred on heavily used trails, as confirmed by the high concurrent human trap rate (36.16/100 trap-nights). Population estimation from camera surveys could be expanded to other species, although caution should be exercised when using cameras spaced and sited for large carnivores to detect other non-target or secondary target species (Meek et al. 2014; Mann et al. 2014). Increased camera surveys in the region could allow for baseline population estimates of many mammalian species from a common survey effort, and thus a better understanding of community interactions such as competition between predator populations and predator–prey dynamics (Yackulic et al. 2014).

Interestingly, most lion individuals were relatively easy to distinguish from each other by their subtle and distinct marks, making the local lion population an ideal candidate for density estimation using Bayesian inference of an SMR model (Royle et al. 2009). Bayesian implementations of SCR models, such as the SMR model, provide a flexible platform to generate unbiased estimates of density comparable across different study sites and over time. The modeling approach allows for joint estimation with shared parameters, so survey types and can be alternated across sites and in different years depending on

specific research objectives and costs constraints (Gopalaswamy et al. 2012; Sollmann et al. 2013c). For example, if it was desirable to collect DNA from fecal samples or hair snares, a method identified as a promising direction in African carnivore monitoring (Thorn et al. 2010), the SCR structure can be used with fecal genotype mark-recapture data or incorporated as an additional survey type into the larger camera survey study design (Kéry et al. 2011; Nichols et al. 2011; Sollmann et al. 2011; Gopalaswamy et al. 2012; Sollmann et al. 2013c). Regardless of model integration or survey type, if SCR methods are utilized, the resulting density estimates will be comparable for equal units of area. Furthermore, recent research has identified fragmentation and resulting metapopulation dynamics as vital conservation considerations for eastern lion populations in Kenya and Tanzania (Dolrenry et al. 2014). It is likely these considerations would be even more important for West African lion populations with high levels of habitat loss, lower densities, and reductions in prey base (Nowell and Jackson 1996; Chardonnet 2002; Bauer and Van Der Merwe 2004; Sogbohoussou 2011; Henschel et al. 2014). A structured stratified SCR sampling strategy (Royle and Converse 2014) could allow for monitoring of different subpopulations at different survey intensities, depending on site specific research priorities.

The SMR approach utilizes two types of data of different qualities (marked and unmarked populations). As we demonstrated with the model considering all individuals as unmarked, there were an insufficient number of detections of this cryptic carnivore to allow for parameter estimate convergence for baseline detection without the added information from the marked recaptures (Table 2), and precision of estimated parameters was poor (see also Chandler and Royle 2013). Conversely, the model that only estimated density of marked individuals was easy to fit and resulted in similar precision to the SMR model. However, accuracy is biased and density underestimated as the model only estimates the density of marked individuals and while the unmarked population is ignored (Rich et al. 2014). Thus, the SMR approach incorporating unmarked counts for which there is little information, with marked individuals for which there is greater movement and detection information, resulted in improved parameter estimation and greater precision.

While the estimates from the SMR model are unbiased (Chandler and Royle 2013) and more precise than previous estimates (Henschel et al. 2014), there are many ways to improve upon study design and the modeling method. First, increases in the number of cameras (or detectors) will increase precision, and increases in camera trap array size will improve inference to a greater area. While our study only included cameras placed in similar habitat selected to produce the best detection rate with limited cameras, study designs incorporating multiple habitat types could not only improve inference to a larger population and area, but provide estimates of density surfaces and would allow for inference about resource selection (Royle et al. 2013b). Incorporating trap specific covariates such as habitat, resource selection functions (Royle et al. 2013b), individual covariates such as sex (Sollmann et al. 2011), and site and survey specific covariates (Tobler and Powell 2013) when appropriate, can also increase accuracy and precision in estimates.

There is often sex determined differences in movement of large carnivores that may affect estimates of $\sigma$ and $\lambda_0$, and potentially bias $D$ (Sollmann et al. 2011). However, it is often difficult to determine sex with certainty for some species from camera images. While we may be confident in assignment of males, we cannot always confirm an individual is not male, and therefore female. The sexual dimorphism of African lions presents an interesting possible exception, and it would be wise to consider a sex covariate in future monitoring efforts employing the SMR approach with a more extensive camera-trap survey. Accounting for sex bias in movement in a larger scale study can improve precision and

inference about specific habitat selection, and this information could be particularly useful as barriers to female dispersal were recently determined to be a limiting factor in eastern African lion subpopulation persistence (Dolrenry et al. 2014). It would follow that consideration of age or stage as an individual covariate in a large scale application of an SMR approach may also elucidate conservation priorities to maintain population persistence and genetic connectivity in an increasingly fragmented landscape (Royle et al. 2015).

Future research including continued monitoring over time could allow for determination of trends in lion populations (Gardner et al. 2010). The use of Bayesian analysis of the SMR model allows for updates with additional data from new sites and years, continuing to improve estimate accuracy and precision, and our overall understanding of lion population status and population ecology. Relatively easy to gather information on West African lions such as that provided by the camera survey in this study is essential for effective conservation of this dwindling, threatened and endangered top predator in Senegal. The SMR model demonstrated here (Online Resource 2) provides a versatile and relatively easily implemented monitoring strategy and provides useful estimates of an elusive, low density population. We hope the method and recommendations outlined here will encourage new directions in rigorous and thoughtful design of studies and methods of analysis to improve conservation efforts of the critically endangered lions in West Africa (Hayward et al. 2015).

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