Towards accurate and precise estimates of lion density

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Key Words: Density, Panthera leo, Maasai Mara, precision, spatial capture-recapture, SECR

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/cobi.12878.

Abstract

Reliable estimates of animal density are fundamental to our understanding of ecological processes and population dynamics. Furthermore, their accuracy is vital to conservation biology since wildlife authorities rely on these figures to make decisions. However, it is notoriously difficult to accurately estimate density for wide-ranging species such as carnivores that occur at low densities. In recent years, significant progress has been made in density estimation of Asian carnivores, but the methods have not been widely adapted to African carnivores. African lions (*Panthera leo*) provide an excellent example as although abundance indices have been shown to produce poor inferences, they continue to be used to estimate lion density and inform management and policy. In this study we adapt a Bayesian spatially explicit capture-recapture model to estimate lion density in the Maasai Mara National Reserve (MMNR) and surrounding conservancies in Kenya. We utilize sightings data from a three-month survey period to produce statistically rigorous spatial density estimates. Overall posterior mean lion density was estimated to be 16.85 (posterior standard deviation = 1.30) lions over one year of age per 100km^2 with a sex ratio of 2.2♀:1♂. We argue that such methods should be developed, improved and favored over less reliable methods such as track and call-up surveys. We caution against trend analyses based on surveys of differing reliability and call for a unified framework to assess lion numbers across their range in order for better informed management and policy decisions to be made.

Introduction

Population density estimates are indispensable to our understanding of ecological processes, population dynamics and conservation biology (May 1999). That density estimates are accurate and precise is particularly vital in the case of African lions (*Panthera leo*) since they inform regional strategies (e.g. Kenya Large Carnivore Taskforce 2009), IUCN, ESA and CITES classifications (e.g. Bauer et al. 2015a), trophy hunting quotas (e.g. Croes et al. 2011) and help to define 'conservation units' and 'strongholds' (e.g. Riggio et al. 2013). Density estimates are also used to advocate for controversial management practices such as fencing (e.g. Packer et al. 2013) and culling (Miller & Funston 2014) or to highlight conservation needs (e.g. Bauer et al. 2015c) and successes (e.g. Blackburn et al. 2016). However, obtaining robust and repeatable density estimates of animals in natural settings is often practically and technically difficult (Gopalaswamy et al. 2012b). This is particularly the case for large carnivores, since they naturally occur at low densities, are wide-ranging and often cryptic. In the last two decades, significant progress has been made in density estimation of Asian and American carnivores, particularly within the now well-established, mark-recapture framework (e.g. Karanth & Nichols 1998; Gopalaswamy et al. 2012b; Russell et al. 2012).

Peculiarly, such methods have not been widely adapted to African species. The African lion epitomizes this paradigm: they are extensively studied and study sites dotted throughout their range have provided census figures that have informed three continent-level population assessments (Chardonnet 2002; Bauer & van der Merwe 2004; Riggio et al. 2013) and numerous meta-analyses (e.g. Hayward et al. 2007; Packer et al. 2013; Périquet et al. 2014; Bauer et al. 2015c; Bauer et al. 2015a). However, despite their implications, these studies frequently drew on expert opinion or surveys of debatable reliability. For example, a recent highly publicized study that advocated fencing as the best mechanism to conserve lion populations, cited peer reviewed publications for only three of 42 site-specific density

estimates and none for the presented trends (Packer et al. 2013). These data, supplemented by additional unpublished data, were later used to justify the lion's continued classification as 'vulnerable' by the IUCN (Bauer et al. 2015a). The same data were then used in a population viability analysis in a study that garnered much media attention, due to alarming conclusions of widespread population declines (Bauer et al. 2015c). In the most recent continent-wide assessment of lion numbers, where population sizes were mapped and 'strongholds' delineated (Riggio et al. 2013), the authors supplemented previous continent-level assessments (Chardonnet 2002; Bauer & van der Merwe 2004) with conservation strategies, action plans, expert opinion and a few published surveys.

An array of methods have been used to estimate lion density, including long-term studies combined with telemetry data (e.g. Mosser et al. 2009), camera trapping (e.g. Cusack et al. 2015), distance sampling (e.g. Durant et al. 2011) and genetic surveys (e.g. Creel & Rosenblatt 2013). Since these techniques are costly and impractical in many sites, track surveys (e.g. Midlane et al. 2015) and call-up surveys (e.g. Ogutu & Dublin 1998) are the most commonly used techniques to estimate lion density (Midlane et al. 2015), and hence it is worth examining them in more detail.

In typical track-based index-calibration experiments, it is assumed that animal abundance is estimated reliably at a small scale. Track surveys are conducted within the same area to provide an index of abundance, frequently under the assumptions that there is a consistent relationship between track density and abundance, and that all animals are equally detectable at all sites and across all habitats and substrates. The estimated abundance and the putative index are then fit by linear regression-based approaches using ordinary least square solutions. It should then be possible to predict density based on index data collected in novel areas (Eberhardt & Simmons 1987). The utility of such abundance indices has been widely criticized (see Anderson 2001 and references therein), and a statistical examination of the

approach concluded that index-calibration experiments produce faulty inferences (Gopalaswamy et al. 2015a; Gopalaswamy et al. 2015b). The study statistically demonstrated that principally due to the presence of detection probability (especially when low and variable), there is an overdispersion in the associated relationship between true density and the putative index, and found that the R^2 parameter drops drastically when there is overdispersion. This implies that there is a much larger variance of the parameters than was previously expected. To obtain precise estimates of these overdispersion parameters, a massive sample size must be acquired, and expending substantial resources to obtain vague assessments based on track surveys may not be justified or meaningful for management.

Call-up surveys present similar concerns. In this method an array of sounds (e.g. hyenas (*Crocuta crocuta*) mobbing lions, dying wildebeest calf) are used to attract lions to a station in order to count them (Ogutu & Dublin 1998). Prior to the survey a calibration experiment is (not always) conducted in order to assess response likelihood and time and area sampled per station. This approach generally abides by the principles of the 'canonical estimator' (Williams et al. 2002) where we have the relation $\hat{N} = C / \hat{p}\hat{\alpha}$, where $\hat{p}$ is the estimate of detection probability, $\hat{\alpha}$ is the proportion of the area sampled and C is the count statistic. In call-up surveys the response likelihood is equivalent to $\hat{p}$ in the canonical estimator and $\hat{\alpha}$ is the total sampling area (area sampled per station multiplied by the number of stations) divided by the larger area of inference. The product of $\hat{\alpha}\hat{p}$ then is essentially the probability of observing an individual lion within a given area. However, variation in $\hat{\alpha}$ or $\hat{p}$ between call-in stations spatially and within call-in stations temporally, will produce considerable variation in the observed count, which will also be the case if the product of $\hat{\alpha}\hat{p}$ is very low. As such, all the statistical conclusions about induced overdispersion in abundance estimation will occur (Gopalaswamy et al. 2015a; Gopalaswamy et al. 2015b) and confidence intervals

will frequently be too large to enable meaningful assessment of trends over time (e.g. Ogutu et al. 2005). A recent call-up survey of lions improved upon traditional methodology by using N-mixture models and incorporating covariates to account for variation in detection probability (Belant et al. 2016). However, since they did not identify individuals, it becomes difficult to estimate vital rates in future. Moreover, as with track surveys (e.g. Midlane et al. 2015), the wide confidence intervals produced by Belant et al. (2016) lack the precision needed to detect population change over time.

Other surveys of African predators (e.g. O'Brien & Kinnaird 2011) and Asiatic lions (*P. l. persica*; Banerjee et al. 2013) have made great advancements over traditional approaches, and provide more reliable estimates. Of particular note, Rosenblatt et al. (2014), Blackburn et al. (2016) and Loveridge et al. (2016) utilized a mark-recapture framework to produce estimates of African lions and provide estimates of survival and age-sex structure. In the present study, we aim to improve upon four limitations of those studies: (i) They were not spatially explicit (implying that the estimating model poorly approximates the spacing rules governing carnivore populations); (ii) They did not account for effort (implying that there might be biases associated with individual capture rates); (iii) They were conducted over extended intervals (potentially violating demographic and geographic closure (Karanth & Nichols 1998)); (iv) The conventional capture-recapture models they employed estimate abundance and did not permit them to directly estimate lion density, which is the principal parameter of interest. The first three limitations are particularly severe using conventional capture-recapture approaches as these, essentially multinomial likelihoods (Amstrup et al. 2010), can be very sensitive to model violations. Finally, the use of the Huggins closed-capture estimator (Rosenblatt et al. 2014; Loveridge et al. 2016), in cases where detection probability is higher for certain individuals (e.g. through radio collaring, as evidenced in

Rosenblatt et al. (2014)) may result in a downward bias of population estimates, misleading inferences on demographic trends and artificially narrow confidence intervals.

To improve on these methods we use a repeatable field method, established within a spatially explicit mark-recapture framework (Royle et al. 2013), to provide robust density estimates across the study site. In addition, we estimate parameters such as sex ratios, while accounting for effort and estimating detection probability. This methodology will lay the foundation for long-term, spatially explicit monitoring and allow for an evaluation of ecological determinants of spatial heterogeneity in lion density. Furthermore, our methodology will join seamlessly with long-term, in-depth studies, enabling a better understanding of the link between individuals and populations and is applicable to other study sites and species.

Methods

Study area

The study area (~2,398km^2) was located in southwestern Kenya (centered at 1°S, 35°E), in the MMNR (including the Mara Triangle), Ol Kinyei, Naboisho, Olare Motorogi, Mara North, Lemek and Ol Chorro conservancies (Fig. 1). The area is characterized by open, rolling grasslands interspersed with woodlands and shrublands. Surface water is available from numerous permanent and seasonal rivers that are filled by seasonal rainfall, which is bimodal: a short rainy season between November and December, and a long rainy season between March and June. The ecosystem supports large numbers of resident ungulates, which support high densities of predators. Each year between July and October (or later), large migratory herds of wildebeest (*Connochaetes taurinus*), and zebra (*Equus burchelli*) travel from the Serengeti plains in Tanzania into the study area, resulting in a superabundance of prey.

Field methods

Five observers in vehicles intensively patrolled the study area for 92 days (01 August 2014 - 31 October 2014). We chose 92 days as we deemed this to be a short enough time so as not to violate the assumptions of a closed population (Karanth & Nichols 1998), while long enough to obtain a large amount of data. During this time all lion sightings were recorded by noting their exact location and, wherever possible, lions were individually identified by taking close-up photographs of whisker vibrissae spots and other distinguishing marks (Pennycuick & Rudnai 1970). All lions under the estimated age of one year were excluded from analysis since cub mortality is highest during the first year in the Mara-Serengeti ecosystem (Packer et al. 1988). In many instances we first sighted cubs while very young and could accurately determine age, while in other cases we used described field methods involving mane development, shoulder height and nose pigmentation (Whitman & Packer 2007). Our drive effort was continuously recorded using GPS-enabled smartphones, running a customized CyberTracker (www.cybertracker.org) application, set to take a GPS point every ten seconds.

State process

The state process models the spatial distribution of lions (Royle et al. 2009; Gopalaswamy et al. 2012a). Our aim was to estimate the number of lions and the locations of their activity centers. Accordingly, we generated potential lion activity centers across an area of ~10,400km^2 (the statespace), represented in discrete form by equally spaced pixels (0.3975km^2). While the activity centers are confined to occupying the pixel centers, the small pixel size almost approximates a continuous space. Unsuitable habitat within this statespace was masked out (Royle et al. 2009; Gopalaswamy et al. 2012a) and encompassed our study area, with the addition of a 15km buffer (Fig. 1). While this buffer size may not be adequately

large enough to account for transients, Royle et al. (2016) recently found that spatial capture-recapture density estimates are robust even with a fairly large number of transients during the sampling period. The state process therefore assumes that the number of animals occupying these cells are defined by a binomial process, and that animal activity centers are uniformly distributed (after masking) and independent of one another, but still possible for two or more animals to have their activity center located within the same pixel.

Observation process

The observation process models the manner in which individuals were detected during the survey. In our sampling situation, we recorded which individuals were detected in each pixel on each day. Since highly sampled pixels could increase the number of detections, we included an additional covariate to account for our search effort (logarithm of kilometers driven) per pixel, per day. As such, we utilize an unstructured spatial capture-recapture sampling design (e.g. Russell et al. 2012).

Male and female carnivores often have different home range sizes, which will likely influence the observation process in spatial capture-recapture models (Sollmann et al. 2011). We therefore incorporate sex-specific covariates in defining the observation process. Furthermore, our approach estimates sex ratio by explicitly accounting for varying detection probabilities between males and females owing to behavioral home range differences.

A major advantage of spatial capture-recapture models over traditional capture-recapture methods is that they account for heterogeneity in detection probability. This is important since the probability of detecting an individual declines with increasing distance between its activity center and a searched pixel. Although we do not observe the exact activity centers, our approach accounts for this uncertainty and thus allows us to estimate animal density as opposed to abundance. Rather than testing various detection function

models we estimated a continuous parameter, θ, which estimates a detection function that takes a negative exponential form (when θ=0.5) at one extreme and a Gaussian form (when θ=1) at the other extreme (Royle et al. 2009; Gopalaswamy et al. 2012a). The estimated detection function is therefore indicative of resource utilization. In our models, the probability of detecting a lion *i*, in sampling occasion *k* at pixel *j*, π_{ijk} is defined by a complementary log-log function of covariates (Royle et al. 2009).

Candidate models

There is no general consensus on model selection for Bayesian SECR hierarchical models, such as ours (Gelman & Hill 2006). Nevertheless, we defined the following *a priori* models and compared their results (see Table 1 for parameter definitions).

Model 1: The full model, which estimates the detection function (defined by θ) and assumes that detection probability is sex-specific:

$$c\log\log(\pi_{ijk}) = \log\lambda_0 + \beta_{eff}[\log(EFFORT_{jk})] + \beta_{sex}(SEX_i) - f[dist(i,j)|\theta,\sigma_{sex}]$$

where $f[dist(i,j)|\theta,\sigma_{sex}]$ describes how detection rate is a function of distance between the activity center of individual *i* and pixel *j*, which are conditional on θ and σ_{sex}. The specific form of this detection function is given by:

$$f\left[dist(i,j)|\,\theta,\sigma_{sex}\right] = \exp\left[\frac{-dist(i,j)^{2\theta}}{2\sigma_{sex}^2}\right]$$

Model 2: This model assumes detection probability is independent of sex by fixing $\beta_{sex}=0$. Rate of decline in detection probability (σ) remains sex-specific (i.e. dependent on sex), since this parameter is also related to animal movement.

Model 3: As with model 2, model 3 fixed $\beta_{sex}=0$ but also fixed the detection function shape at $\theta=0.75$.

Model 4: Same as model 1, but the shape of the detection function is fixed at $\theta=0.75$

Implementation of the model

The above set of models were implemented using an adaptation of the package SCRbayes (https://github.com/jaroyle/SCRbayes) in the programming environment R (R-Development-Core-Team 2015). We used Bayesian Markov Chain Monte Carlo (MCMC) simulation and the Metropolis-Hastings algorithm (Tierney 1994) to implement our models. We set each model for 11,000 iterations with a burn-in period of 1,000 iterations. We refined the burn-in period during later stages of an analysis if we found evidence that we had not arrived at a stationary distribution. As a result, we had 10,000 posterior samples for each chain. A total of four chains were set to run for each model.

Model checking

Each model was subsequently checked for adequacy utilizing the Bayesian p-value assessment based on individual encounters (Royle et al. 2009). All R scripts, functions and data for our analyses are provided (Supporting Information).

Posterior mean abundance

While we were principally interested in estimating density, in order to fully discuss our results in the context of previous studies, we computed posterior mean abundance across the study area and within different management areas. For each iteration of the MCMC output, we took the sum of all pixels within each area of interest and computed posterior mean and posterior standard deviation of abundance.

Results

During the 92 days of sampling we drove 8,397kms and recorded 817 captures (sightings) of individual lions. It was not always possible to identify every individual at each sighting and 165 lion captures could not be identified and were excluded from analysis. We then removed 214 captures of lions estimated at <1yr of age, leaving a total of 438 lion

captures. Of these, 203 were unique individuals over the (estimated) age of one year, equating to a capture success rate of 2.4 lions identified per 100km of search effort. Of the 203 individuals, 66 were male and 137 were female. Capture history varied with 77 individuals captured only once, 71 individuals twice, 28 individuals three times, 11 individuals four times, nine individuals five times, three individuals six times and four individuals seven times.

Model diagnostics

Bayesian p-value for all models was estimated between 0.6-0.7, thus indicating that they were all adequate, since this value lies well within the extremities (0.15-0.85). We assessed the MCMC convergence for all the models using the Gelman-Rubin diagnostic (Gelman & Rubin 1992) and all models had a mean potential shrink reduction factor of less than 1.2 for each parameter. Furthermore, all four models produced very similar posterior mean parameter estimates and levels of precision. Since there was such little variation between the models, and there is no consensus on model selection for hierarchical models such as ours (Gelman & Hill 2006), we report the posterior parameter estimates of the model with the most parameters, Model 1 (Table 1, with remaining models reported in Supporting Information).

Posterior mean density estimates

Lion density within our study area was estimated at 16.85 (PSD = 1.30) individuals >1yr per 100km^2. The posterior density estimates for each pixel (0.3975km^2) ranged from 0.0003 to 4.011 lions/km^2, revealing the heterogeneous distribution of lions across space (Fig. 2). It is noteworthy that despite being relatively new protected areas, mean pixel (0.3975km^2) density throughout the conservancies was slightly higher (0.175) than that of the MMNR (0.167). Overall sex ratio, as estimated by ψ_{sex}, was calculated to be 2.2♀:1♂.

Posterior mean abundance estimates

Posterior mean abundance for the entire study area was estimated at 419.89 (PSD=29.25) lions >1yr (see Table 2 for abundance and density estimates per protected area).

Discussion

Our methodology and results demonstrate that an unstructured spatial capture-recapture sampling design can produce tight estimates of population parameters while estimating detection probability. This makes our approach robust in the context of varying detection probabilities (Hayward et al. 2015). By including effort and incorporating a spatial design, we were able to explicitly estimate detection probability and measure density on a fine spatial scale. Furthermore, the estimates were obtained over a relatively short survey period (three months), reducing concerns over population closure (Karanth & Nichols 1998). Our methodology thus improves upon other unstructured designs (e.g. Rosenblatt et al. 2014; Blackburn et al. 2016) and will enable long-term population monitoring with an evaluation of the ecological determinants of lion density at a fine spatial scale. It will also allow for an analysis of spatial demographic trends and vital rates over time, thereby identifying spatial and demographic areas of concern.

Although lion sex ratios are frequently equal at birth (Schaller 1972), our estimates show that by one year the ratio was 2.2♀:1♂. It is likely that the number of male lions decline due to intra-sexual competition for pride tenure and our results are consistent with average sex ratios in lions (2.33♀:1♂) reported in a review of 40 scientific papers (Périquet et al. 2014). The difference between σ_F and σ_M was relatively small (Table 1), indicating that males move slightly more than females. Plentiful prey during the annual Serengeti wildebeest migration could have reduced the larger movements of males seen elsewhere (e.g. Elliot et al. 2014), and could also result in a temporarily high density of lions (Schaller 1972). Future

surveys outside this migration period will be enlightening. Our estimate of θ, which is indicative of resource utilization, was 0.512 (Table 1), a near perfect negative exponential function. This suggests that a negative exponential function may be more appropriate than the traditional Gaussian function when calculating lion home ranges for short time periods. The estimate of parameter β_{eff} was slightly negative (Table 1), which is counter-intuitive since more effort should result in more sightings. However, the posterior standard deviation was high relative to the estimate, making inference problematic. One explanation could be that additional information went into some sightings. For instance, if a field observer followed up on a report of a lion, this would influence the effort in that cell. Future models should have a conditional probability built in to account for this. The negative estimate of β_{eff} could also be indicative of the grid cell sizes we used in combination with lion territoriality. For example, we could have an unoccupied cell neighboring an occupied cell and no amount of effort would result in a lion sighting. Data from a large number of such cells could yield negative estimates of β_{eff}.

Two previous surveys (Ogutu & Dublin 1998; Dloniak 2006) have recently been used in high profile studies that suggest a drastic decline of lions in the MMNR (Packer et al. 2013; Bauer et al. 2015c; Bauer et al. 2015a). Ogutu & Dublin (1998) and Dloniak (2006) provided estimates based on whole counts conducted in 1991-1992 and 2005 respectively. The first survey reported 447 lions >1yr while the second survey reported 269 lions >1yr. These data were utilized in a study that reported rapid declines across Africa (Bauer et al. 2015c), in a paper highlighting the costs of lion conservation and concluding that fences are the best means of conserving lions (Packer et al. 2013) and also used in the most recent IUCN classification, which, based on an inferred population trend, estimated a 54% reduction in lion numbers between 1993 and 2014 (Bauer et al. 2015a). In the present study, our spatially

explicit density estimates translate to an expected abundance of 250 (PSD=19.95) lions >1yr in the MMNR (Table 2). Although this total is similar to Dloniak's (2006) estimate of 269, we argue that this is pure coincidence and it is worth exploring the two previous surveys in more detail. While the two earlier surveys (Ogutu & Dublin 1998; Dloniak 2006), and the current one, relied on individual identification, several fundamental differences exist, making comparisons and analysis of trends problematic: the 1991-1992 and 2005 surveys were whole counts, employed no statistical analysis, estimation of detection probability or of precision; the 1991-1992 survey was conducted over 20 months (not 12 months as recently suggested in Bauer et al. 2015b), while the 2005 survey took place over 10 months – both time frames potentially violate assumptions of closure (Karanth & Nichols 1998). It is perhaps not surprising that a longer survey would yield higher numbers, since more migration and birth will occur at longer intervals. To illustrate the point, our monitoring data shows that during ten months (November 2013-August 2014) we recorded 340 unique individuals >1yr within our study area, while we recorded 429 individuals during 20 months (November 2013-June 2015). Timescale is clearly important and a density estimate should provide a snapshot that indicates the number of animals present in an area at any one time.

More robust estimates, that used mark-recapture, were recently provided for the surrounding conservancies (Blackburn et al. 2016). However, a simple comparison of densities reveals very different estimates compared to ours: If we compute density per conservancy from our spatial analysis (see Table 2) we estimate the following expected density of lions >1yr per 100km^2, compared to that of Blackburn et al. (2016) in brackets – Mara North 16.97 (8.15), Naboisho 14.57 (9.54), Lemek 17.15 (8.62), OOC 31.27 (20.36). However, comparison is problematic since Blackburn et al. (2016) did not account for search effort, the study was not spatially explicit and potentially violated assumptions of closure (Karanth & Nichols 1998). Similarly, comparing our estimates or those of Blackburn et al.

(2016) to those of Ogutu et al. (2005), who estimated lion density within the conservancies from a 2003 call-up survey, despite not seeing a lion in the area, is problematic. This is because fundamental methodological differences exist and therefore fluctuations are not necessarily because the state variable of interest (lion density) is changing, but because we detect lions differentially due to many uncontrollable factors. We therefore caution against comparing our estimates to those of previous surveys in this area (Ogutu & Dublin 1998; Ogutu et al. 2005; Dloniak 2006; Blackburn et al. 2016).

While we acknowledge that the Maasai Mara is unique in that it is possible to observe a large number of lions in a relatively short time period, our approach performs well with small sample sizes and can be used to concurrently estimate density of other species that can be individually identified. For example, the field work presented here was used by Broekhuis and Gopalaswamy (2016) to simultaneously, and accurately, estimate cheetah (*Acinonyx jubatus*) density from just 59 sightings of 25 individuals. In areas where capture success may be even lower, our approach is flexible enough to incorporate data from multiple sources such as camera traps, telemetry, genetics or call-up surveys where individuals are recognizable. Our methods are therefore applicable to a wide range of species, including Asiatic lions, but would benefit from the following improvements: (a) incorporate how an individual is found; (b) build in those individuals that were not identified, which will not necessarily change the density estimate, but may reduce the variance (especially where sample sizes are small) and result in a slightly lower detectability; (c) split the demographics to include sub-adults; (d) account for opportunistically detected mortalities; (e) the state process model used here assumed that activity centers are not clustered, which is contrary to our findings (Fig. 2). Since lions live in fission-fusion groups, it is likely that individuals have the same, or similar, activity centers. Dependence in activity centers is a concern for many spatially explicit models (e.g. Stevenson et al. 2015), and can potentially bias the variance

estimates. Therefore, future work should integrate spatial point processes (see Reich & Gardner 2014 for an example with Strauss process) that are tailor-made for the fission-fusion dynamics of lion prides.

Given the importance of accurate density estimates to our understanding of ecological processes, management decisions and international classification, we recommend that spatially-explicit capture recapture methods are widely adopted to census African carnivores and that more traditional methods, such as spoor and call-up surveys (unless utilized within a mark-recapture framework), be abandoned for estimating density at all important lion source populations. More generally, we discourage pooling of data from differing methodologies in order to inform management and policy decisions. Instead, we call for a unified framework to assess lion densities across their range to allow for accurate population assessments and trend analyses.

Acknowledgements

We are grateful to the authorities of the MMNR, the Kenya Wildlife Service and the Maasai Mara Wildlife Conservancies Association for permission to carry out this research. F. Broekhuis, N. Mogensen, K. Sankan and S. Silantoi are thanked for fieldwork. F. Broekhuis is thanked for helpful comments on this manuscript and for assistance preparing input files. We acknowledge the use of the University of Oxford Advanced Research Computing (ARC) facility in carrying out this work. A. Gopalaswamy was partially supported by Kirk-Turner scholarship and the Indian Statistical Institute and thanks Mohan Delampady on aspects related to statistical theory. The Mara Lion Project/Kenya Wildlife Trust is supported by the very kind generosity of N. Lapham, S. Dunn, A. & M. Earnshaw, N. & B. Dundas in addition to BAND Foundation, Basecamp Foundation, the Delta Trust, the Kenya Wildlife Trust, the African Wildlife Foundation and WWF.

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Tables

Table 1. Posterior summaries from Bayesian spatially explicit capture-recapture (SECR) of parameters estimated using Model 1 [$\beta_{sex}, \theta(.)$]. Number of posterior samples used was 10,000 and Bayesian p-value = 0.6397 thus indicating that the model fit was adequate, since this value lies well within the extremities (0.15-0.85).

Parameter	Posterior mean	Posterior standard deviation	Definition
σ_F	0.700	0.044	Rate of decline in detection probability with increasing distance between the activity center of a lioness and the location at which she was found
σ_M	0.790	0.059	Rate of decline in detection probability with increasing distance between the activity center of a lion and the location at which he was found
β_{sex}	-0.360	0.235	The difference of the complementary log-log value of detection probability between a male and female lion
β_{eff}	-0.0034	0.004	The rate of change in the complementary log-log value of detection probability as the (log) effort changes by one unit (one kilometer of drive effort)
λ_0	0.055	0.008	The basal encounter rate of a lion whose activity center is located exactly at the centroid of a grid cell
ψ	0.590	0.047	The ratio of the true number of individuals in the population compared to the data augmented population *M*
N_{super}	970.7	75.000	The total number of lions in the larger state space *S*
ψ_{sex}	0.314	0.038	The proportion of lions that are female $Sex\,ratio = \frac{1-\psi_{sex}}{\psi_{sex}}$
θ	0.512	0.019	Determines the shape of the estimated detection function. The value of θ ranges from 0.5 (exponential form) to 1 (Gaussian)
D	16.8475	1.3017	The estimated density of lions/100km^2

Table 2. Posterior mean abundance and density estimates split according to protected areas.

Protected Area	Posterior mean abundance	Posterior standard deviation	Posterior mean density	Posterior standard deviation
Olare Motorogi	44.51	3.29	32.11	2.38
Olare (excluding Motorogi)	29.80	3.01	31.27	3.16
Ol Chorro	11.22	3.02	20.96	5.64
Ol Kinyei	14.33	2.43	22.50	3.81
Lemek	10.66	2.95	17.15	4.75
MMNR	174.59	14.17	16.64	1.35
Mara north	58.59	8.04	16.97	2.33
Mara Triangle	75.31	9.32	15.82	1.96
Naboisho	30.69	3.75	14.57	1.78
MMNR + Mara Triangle	249.90	19.95	16.38	1.31
All conservancies combined	170.00	12.79	19.46	1.46

Figure Legends

Fig. 1. The larger states space (~10,400km^2) was defined by a 15km buffer around the study area (2,398km^2). Unsuitable habitat was masked out prior to analysis. Names of each protected area under different management regimes are included for reference.

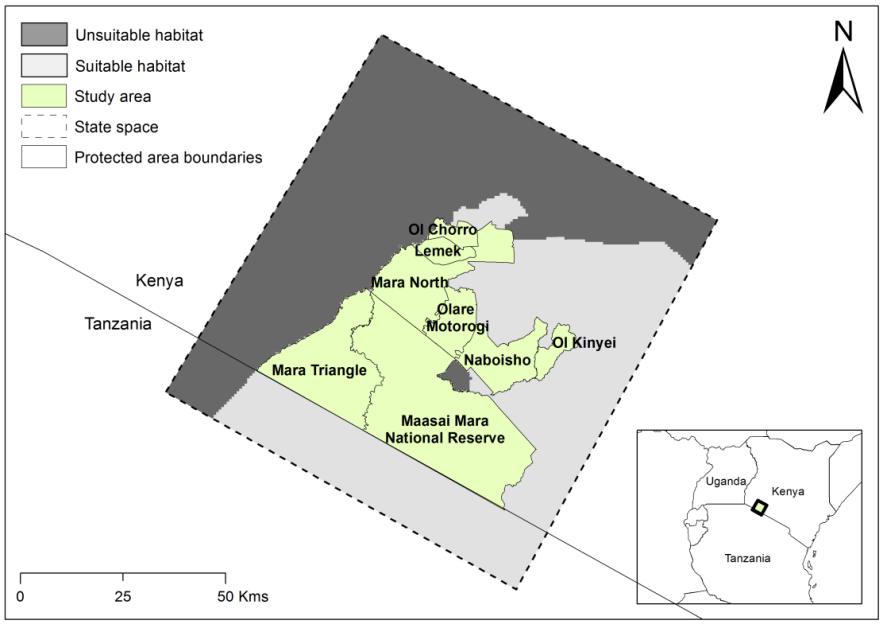

Fig. 2. Pixel specific (0.3975km2) lion density as predicted by Model 1: $[\beta_{sex}, \theta\,(.)]$ - Full model. Our unstructured spatial capture-recapture sampling design accounted for effort (in kilometers) per pixel per sampling occasion (one day). Map depicts the Maasai Mara National Reserve and surrounding conservancies, Kenya.