

Numbers count: Reliable estimates of lion density

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Introduction

Population density estimates are indispensable to our understanding of ecological processes, population dynamics and conservation biology (May 1999). That density estimates are accurate is vital to wildlife managers 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. 2015b) 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. 2012a). 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. 2012a; Russell et al. 2012).

Peculiarly, such methods have not been widely adapted to African species. The African lion (*Panthera leo*) epitomizes this paradigm: they are one of the most extensively studied large mammals on earth 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. Bauer et al. 2015b; Bauer et al. 2015a; Packer et al. 2013; Périquet et al. 2014). 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

46 site specific density estimates and none for the presented trends (Packer et al. 2013). These
47 data, supplemented by additional unpublished data were later used to justify the lions
48 continued classification as ‘vulnerable’ by the IUCN (Bauer et al. 2015a). The same data
49 were then used in a population viability analysis in a study that garnered much media
50 attention, due to alarming conclusions of widespread population declines (Bauer et al.
51 2015b). In the most recent continent-wide assessment of lion numbers, where population
52 sizes were mapped and ‘strongholds’ delineated (Riggio et al. 2013), the authors
53 supplemented previous continent-level assessments (Bauer & van der Merwe 2004;
54 Chardonnet 2002) with conservation strategies, action plans, expert opinion and a few
55 published surveys.

56 An array of methods have been used to estimate lion density, including long-term
57 studies combined with telemetry data (e.g. Mosser et al. 2009), camera trapping (e.g. Cusack
58 et al. 2015), distance sampling (e.g. Durant et al. 2011) and genetic surveys (e.g. Creel &
59 Rosenblatt 2013). Since these techniques are costly and impractical in many sites, track
60 surveys (e.g. Funston et al. 2010) and call-up surveys (e.g. Ogotu & Dublin 1998) are the
61 most commonly used techniques to assess lion density (Midlane et al. 2015), and hence it is
62 worth examining them in more detail.

63 In experiments such as track surveys, it is assumed that animal abundance is estimated
64 reliably at a small scale. Simultaneously, an index of abundance (derived from track surveys)
65 is gathered under the presumption that the estimated abundance and the putative index can be
66 fit by linear regression-based approaches using ordinary least square (OLS) solutions. When
67 index data are accumulated over larger scales, it should be possible to predict density at those
68 scales (Eberhardt & Simmons 1987). The utility of such abundance indices has been widely
69 criticized over the past two decades (see Anderson 2001 and references therein), culminating
70 in a statistical examination of the approach that concluded that index-calibration experiments

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

80 Call-up surveys present similar concerns. In this method loud noises are used to attract
81 lions to a station in order to count them. Prior to the survey a calibration experiment is (not
82 always) conducted in order to assess response likelihood and time and area sampled per
83 station. This approach generally abides by the principles of the ‘canonical estimator’
84 (Williams et al. 2002) where we have the relation $\hat{N} = C / \hat{p}\hat{\alpha}$, where \hat{p} is the estimate of
85 detection probability, $\hat{\alpha}$ is the proportion of the area sampled and C is the count. In call-up
86 surveys response likelihood is equivalent to \hat{p} in the canonical estimator and $\hat{\alpha}$ is the total
87 sampling area (area sampled per station multiplied by the number of stations) divided by the
88 larger area of inference. The product of $\hat{\alpha}\hat{p}$ then is essentially the probability of observing an
89 individual lion within a given area. However, variation in $\hat{\alpha}$ or \hat{p} between call-in stations
90 spatially and within call-in stations temporally, will produce considerable variation in the
91 observed count, which will also be the case if the product of $\hat{\alpha}\hat{p}$ is very low. As such, all the
92 statistical conclusions about induced overdispersion in abundance estimation will occur
93 (Gopalaswamy et al. 2015; Gopalaswamy 2015) and the confidence intervals will frequently
94 be too large to enable meaningful assessment of trends over time (e.g. Ogutu et al. 2005).

More recently, surveys of other African predators (O'Brien & Kinnaird 2011), African lions (Rosenblatt et al. 2014; Blackburn et al. 2016) 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) and Blackburn et al. (2016) utilized a mark-recapture framework to produce estimates of African lions over a 4-5 year period 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 fails to characterize the spacing rules governing carnivore populations (Sandell 1989) despite Blackburn et al. (2016) specifically recognizing that lions are territorial); (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.

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 ($\sim 2,398 \text{ km}^2$) 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 characterised 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. Mean annual rainfall is variable across the study area, with the eastern edge of the study area receiving $\sim 877 \text{ mm}$ compared to $\sim 1300 \text{ mm}$ on the western edge (Ogutu et al. 2011). 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.

Data collection

Five observers in vehicles intensively patrolled the study area for 92 days (01 August 2014 - 31 October 2014), during which time they recorded all lion sightings and their exact locations. 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. Wherever possible, great care was taken to individually identify all lions at each sighting using whisker vibrissae spots and other distinguishing marks (Pennycuick & Rudnai 1970). Cub mortality is highest during the first year in the

Mara-Serengeti ecosystem (Packer et al. 1988), and thus all lions under the estimated age of one year were excluded from analysis since their inclusion may violate closure. In many instances we first sighted cubs while very young and could accurately determine age, while in other cases we used described field methods (Whitman & Packer 2007). Our 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

We employed a Bayesian spatial capture-recapture model for our analysis (Royle et al. 2009; Gopalaswamy et al. 2012b). Accordingly, we defined a large statespace S , of $\sim 10,400\text{km}^2$, represented in discrete form by pixels (0.3975km^2). Unsuitable habitat within this statespace was masked out for analysis (Royle et al. 2009; Gopalaswamy et al. 2012b). The statespace 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 value of M (the data-augmented value of abundance in the larger statespace) was set at 1,653 ($\eta = 203$ and $\eta_z = 1,450$), which represents the maximum number of lions possible within the statespace. Our expectation was that the estimate of ψ lie between 0.2-0.8 for reliable estimation of the binomial proportion (Gopalaswamy et al. 2012a), since,

$$[N_{\text{sup } er} | M\psi] \square \text{Bin}[M, \psi].$$

Observation process

We envision a standard spatial capture-recapture data set (See Gopalaswamy et al. 2012b for a full example) that is a 3-dimensional matrix, consisting of individuals ($i = 1, 2, 3 \dots N$) x trap locations ($j = 1, 2, 3 \dots J$) x sampling occasions ($k = 1, 2, 3 \dots K$). In our sampling situation, the trap locations are defined by the pixels themselves and we account for

search effort (logarithm of kilometers driven) invested in each pixel per sampling occasion (one day). Since investing more effort in certain pixels compared to others could yield an increased number of detections in highly sampled pixels, we incorporate an additional covariate of search effort per pixel per sampling occasion. 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 (Macdonald 1983), which is likely to influence the observation process in spatial capture-recapture models (Sollmann et al. 2011). We therefore incorporate sex-specific covariates in defining the observation process.

Spatial capture-recapture models employ a variety of detection function models (Royle et al. 2011; Buckland et al. 2001) to define the mechanism of decline in detection probability with increasing distance between the activity center of an animal and a trap location (in our case, the centroid of a search pixel). Rather than testing various detection function models we explicitly estimate parameter θ and consider an infinite number of possibilities between a perfect Gaussian detection function ($\theta = 1$) and a perfect negative exponential detection function ($\theta = 0.5$; Royle et al. 2009). Thus, θ defines the shape of the detection function, and is indicative of resource utilization.

Hence, 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. The below represents the full model in our analysis (see section on Candidate models below).

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

Candidate models

We defined the following *a priori* models.

Model 1: $[\beta_{\text{sex}}, \theta(\cdot)]$ - Full model assumes that detection probability is sex-specific and the detection function is estimated (defined by θ)

194 Model 2: $[\beta_{sex} = 0(fixed), \theta(.)]$ - Assumes detection probability is independent of sex. Rate
195 of decline in detection probability (σ) remains sex-specific, since this parameter is also
196 related to animal movement.

197 Model 3: $[\beta_{sex} = 0(fixed), \theta = 0.75(fixed)]$ - Detection probability is independent of sex
198 and detection function shape, defined by θ , is fixed to a certain value.

199 Model 4: $[\beta_{sex}, \theta = 0.75]$ – Detection probability is sex-specific but the shape of the
200 detection function is fixed.

201 *Implementation of the model*

202 The above set of models were implemented using an adaptation of the package
203 SCRbayes (<https://github.com/jaroyale/SCRbayes>) in the programming environment R (R-
204 Development-Core-Team 2015). The models were implemented using the Bayesian Markov
205 Chain Monte Carle (MCMC) simulation using the Metropolis-Hastings algorithm (Tierney
206 1994). We set each model for 11,000 iterations with a burn-in period of 1,000 iterations. We
207 refined the burn-in period during later stages of an analysis if we found evidence that we had
208 not arrived at a stationary distribution. As a result we had 10,000 posterior samples for each
209 chain. A total of four chains were set to run for each model.

210 *Model checking*

211 Each model was subsequently checked for adequacy utilizing the Bayesian p-value
212 assessment (Royle et al. 2009; Gopalaswamy et al. 2012a). Although there are a few different
213 test statistics available for the Bayesian p-value assessment (Gopalaswamy et al. 2012a;
214 Royle et al. 2009; Royle et al. 2013), we implemented the test statistic based on individual
215 encounters as suggested in Royle et al. (2009). All R scripts for our analyses can be found in
216 the supplementary materials (S1).

Posterior mean abundance

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

Results

During the 92 days of sampling we drove a total of 8,397kms and recorded 817 captures (sightings) of individual lions. It was not always possible to identify every individual at each sighting due to environmental variables and 165 lion captures could not be identified and thus were excluded from the 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 was estimated between 0.6-0.7 for all models, thus indicating that they were all adequate, since this value lies well within the extremities (0.15-0.85). We assessed the MCMC chain convergence for all the models using the Gelman-Rubin diagnostic (Gelman & Rubin 1992) and all models had a shrink reduction factor of less than 1.2 for each parameter. Furthermore, all four models produced very similar posterior mean estimates and levels of precision. Since there was such little variation between the models, and the full model contained the most information, we report the posterior

estimates of the parameters in Model 1 here (Table 1), with the remaining models reported in the supplementary materials (S2).

Posterior mean density estimates

Lion density within our study area was estimated at 16.85 (PSD = 1.30) individuals >1yr per 100km². The posterior density estimates for each pixel (0.3975km²) ranged from 0.0003 to 4.011 lions/km², revealing the heterogeneous distribution of lions across space (Fig. 2). Mean pixel density for all the conservancies combined (0.175) was higher than that of the MMNR (0.167), illustrating the conservation importance of these newly established protected areas. The 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 a breakdown of 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 over time, thereby identifying spatial areas of concern and demographics of concern. However, our methodology would benefit from the following improvements: (a) incorporate how an individual is found; (b) build in those individuals that were not identified, which may not necessarily change the density estimate, but will reduce the variance; (c) split the demographics to include sub-adults; (d) account for opportunistically detected mortalities.

Although lion sex ratios are frequently equal at birth (Schaller 1972), our estimates show that by one year the ratio was $2.2\text{♀}:1\text{♂}$. 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 ($2.33\text{♀}:1\text{♂}$) 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. Although a previous study reported larger differences in movement between demographics (Elliot et al. 2014), that study utilized data over a five year period, compared to three months in the current study. It is therefore likely that while male lions do move more than females, as they more actively patrol their larger territories (Schaller 1972), this becomes increasingly evident over larger time scales. 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 extremely high relative to the estimate, making inference problematic. It is also noted that additional information went into some sightings, which was not accounted for in the models. For instance, if a field observer followed up on a report of a lion

or spotted tourist vehicles grouped around a sighting, this would influence the effort in that cell. Future models should have a conditional probability built in to account for this.

Two previous surveys (Dloniak 2006; Ogutu & Dublin 1998) 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. 2015a; Bauer et al. 2015b). Ogutu & Dublin (1998) and Dloniak (2006) provided estimates for those studies 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. 2015b), which were later contested (Bauer et al. 2015c; Riggio et al. 2015). The same data were used in another paper highlighting the costs of lion conservation and concluding that fences are the best means of conserving lions (Packer et al. 2013). These data were 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 (Dloniak 2006; Ogutu & Dublin 1998), 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; Bauer et al. 2015c), while the 2005 survey took place over 10 months – both time frames potentially violate assumptions of closure (Karanth & Nichols 1998). Given that the first survey was 20 months and the second was 10 months, it is not surprising that a longer survey would yield higher

numbers, since greater effort should return more sightings and more birth, death, immigration and emigration will occur at longer intervals. To illustrate the point, our monitoring data shows that during ten months (January-August 2013) we recorded 197 unique individuals >1yr within MMNR, while we recorded 337 individuals during 20 months (January 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, using 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 100km², 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 fluctuating, 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 et al. 2005; Blackburn et al. 2016; Ogutu & Dublin 1998; Dloniak 2006) or 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.

While we acknowledge that the Maasai Mara is unique in that it is possible to sight 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, estimated 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 back surveys where individuals are recognizable. Our methods are therefore applicable to a wide range of species, including Asiatic lions.

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-back surveys (unless utilized within a mark-recapture framework), be abandoned for estimating density at all important lion source populations. We also discourage extrapolations based on faulty predictions from linear regression based index-calibration experiments.

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503 Table 1. Posterior summaries from Bayesian spatially explicit capture-recapture (SECR) of
 504 parameters estimate using Model 1 [$\beta_{sex}, \theta (\cdot)$]. Number of posterior samples used was 10,000.
 505 Bayesian P-value = 0.6397.
 506

Parameter	Posterior mean	Posterior standard deviation	Definition
σ_F	0.700	0.044	Rate of decline in detection probability as a female lion's activity center increases as a function of her distance from the centroid of a grid cell
σ_M	0.790	0.059	Rate of decline in detection probability as a male lion's activity center increases as a function of his distance from the centroid of a grid cell
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

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

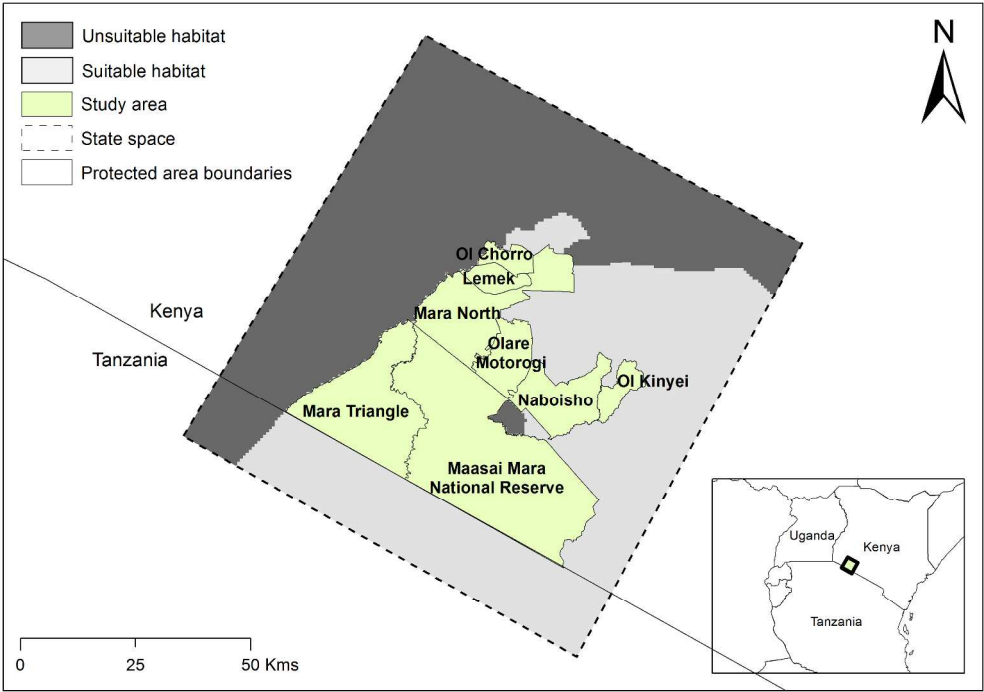
Protected Area	Posterior mean abundance	Posterior standard deviation	Posterior mean density	Posterior standard deviation
Olare Motorogi	44.51	3.29	32.11	2.38
Olare (excluding Motorogi)	29.80	3.01	31.27	3.16
Oi Chorro	11.22	3.02	20.96	5.64
Oi Kinyei	14.33	2.43	22.50	3.81
Lemek	10.66	2.95	17.15	4.75
MMNR	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

508 Figure Legends

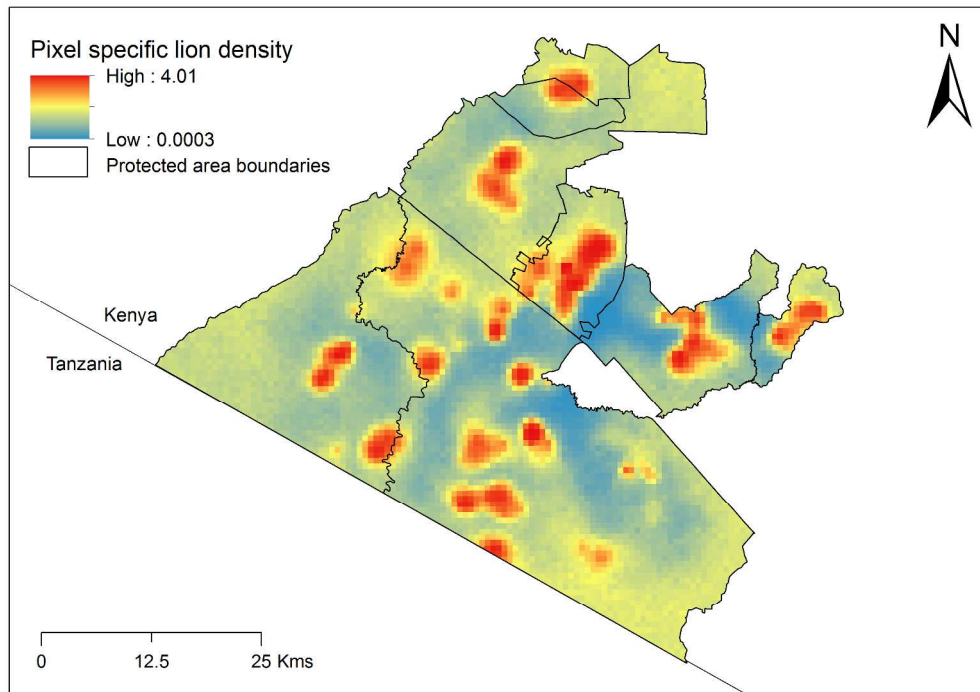
509 Fig. 1. The larger states space ($\sim 10,400\text{km}^2$) was defined by a 15km buffer around the study
510 area ($2,398\text{km}^2$). Unsuitable habitat was masked out prior to analysis. Names of each
511 protected area under different management regimes are included for reference.

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

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