The importance of reliable monitoring methods for the management of small, isolated populations

Nicholas B. Elliot¹² | Alice Bett³ | Monica Chege³ | Kasaine Sankan² | Nadia de Souza⁴ | Linus Kariuki³ | Femke Broekhuis¹ | Patrick Omondi³ | Shadrack Ngene³ | Arjun M. Gopalaswamy⁵⁶

¹Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxfordshire, OX13 5QL, UK
²Kenya Wildlife Trust, P.O. Box 86-00502 Karen, Nairobi, Kenya
³Kenya Wildlife Service, Box 40241-0100, Nairobi, Kenya
⁴Lion Guardians, P.O. Box 15550-00509, Langata, Nairobi, Kenya
⁵Statistics and Mathematics Unit, Indian Statistical Institute—Bangalore Centre, Bengaluru, 560059, India
⁶Wildlife Conservation Society, Global Conservation Programs, 2300, Southern Boulevard, Bronx, New York, 10460

Abstract
To effectively manage wildlife populations, it is essential to reliably estimate their abundance. This is particularly the case for small, isolated populations, which are vulnerable to extirpation. Lake Nakuru National Park in Kenya is one such small, isolated area where an introduced population of African lions (*Panthera leo*) is vulnerable to genetic degradation and catastrophic events. A founder population of six individuals was introduced between 1984 and 1992, with no further recorded immigration. We used Bayesian spatially-explicit capture–recapture models to estimate lion density and abundance based on unstructured spatial sampling. For individuals over the age of 1 year, posterior mean lion density was estimated to be 6.75 (mode = 5.93, posterior SD = 0.92) individuals/100 km², with a mean abundance of 11.37 (mode = 10, posterior SD = 1.54), and a sex ratio of 1.38♀:1♂. Previous reports provided abundance figures much higher than ours. However, our estimates are the result of the first scientifically robust survey and we discuss why they should be viewed as a baseline rather than being suggestive of population decline, and how the discrepancy highlights the need for regular systematic surveys using a standardized framework. Given the small population size and prolonged genetic isolation, we provide long-term management recommendations to secure this lion population.

KEYWORDS
abundance, African lion, density, isolated populations, Lake Nakuru National Park, SCR, spatial capture–recapture

INTRODUCTION
Small, isolated populations are vulnerable to extirpation due to environmental, demographic and genetic stochasticity (Lande, 1993; Saccheri et al., 1998). To minimize these risks, intensive management is often required and wildlife managers increasingly attempt to mimic natural metapopulation dynamics in efforts to maintain genetic diversity (Miller, Harper, Bloomer, Hofmeyr, & Funston, 2015). However, it is likely that...
environmental and demographic events will cause extinctions long before the effects of decreased genetic diversity are experienced (Lande, 1988). To effectively manage small populations it is therefore essential to obtain reliable estimates of population parameters such as abundance. Yet even in small, isolated ecosystems, abundance estimation is problematic, particularly in the case of large carnivores which typically occur at low density, are elusive and exhibit heterogeneous detection probabilities (Karanth, 1995). As a result, in most instances abundance estimates are nonexistent, forcing managers to rely on local knowledge and perceptions of abundance, which may be vastly inflated (Moqanaki, Jiménez, Bensch, & López-Bao, 2018). Where abundance estimates of large carnivores do exist they are frequently derived from abundance indices, such as spoor counts or raw counts, which give rise to concerns over their accuracy and precision (Elliot & Gopalaswamy, 2017; Gopalaswamy, Delampady, Karanth, Kumar, & Macdonald, 2015). Inaccurate abundance estimates, and especially those that are inflated, may lead to management decisions that further jeopardize threatened wildlife (Loveridge, Searle, Murindagomo, & Macdonald, 2007).

Large carnivores across the world are numerically and geographically declining (Ripple et al., 2014). African carnivores are no exception: African lions (*Panthera leo*) for example have lost 90% of their historic range (Jacobson & Riggio, 2018), and may have experienced a decrease of 43% between 1993 and 2014 (Bauer et al., 2015), resulting in an IUCN classification of “Vulnerable” (Bauer, Packer, Funston, Henschel, & Nowell, 2016). Extensive prey depletion, habitat loss and human–lion conflict mean that fencing certain populations may be an effective way of conserving them (Packer et al., 2013). While fenced lion populations may flourish (Bauer et al., 2015), small populations require intensive and costly management to prevent a variety of undesired outcomes (Miller et al., 2013). At a population level, both rapid growth (Miller & Funston, 2014) and persistent declines perhaps associated with inbreeding depression (Trinkel et al., 2008) have been reported, necessitating a range of management interventions including translocation, lethal management, and birth control (see Miller et al., 2013 for an assessment and guidelines on managing lions in small fenced reserves in South Africa where at least 44 such populations exist).

Lake Nakuru National Park (LNNP) contains one such small, fenced lion population in Kenya. LNNP was gazetted in 1968 and is encompassed by a chain-link fence (1976) and an electric fence (1986). Between 1984 and 1992, a founding population of six lions (one male and three females from Aberdare National Park, one male from Nairobi National Park, and one female from Tsavo National Park) were introduced to LNNP (Waweru, 1995; M. C. Ngige, personal communication, November 2010). Assuming the three females from Aberdare National Park were related (possibly also to the male), it is likely that this translates to three or four founder lineages. No known immigration has since occurred. In June 2014, two adult females breached the fence and settled in neighboring Soysambu Conservancy. These lionesses occasionally return to LNNP and mate with the resident males. At the time of our survey, Soysambu was thought to contain 14 individuals (eight >1 year old; K. Combes, personal communication, September 2017). In recent times, lions originating from LNNP that have engaged in livestock depredation either within Soysambu or outside LNNP have occasionally been translocated to other wildlife areas (four lions in 2016, two lions in 2017 and two lions in 2018; A. Bett, unpublished data). While no systematic or published surveys have been conducted, reports suggest a population of 65 lions in 2002 (Kenya Wildlife Service, 2002) and 56 lions in 2010 (Bett, Omengo, & Mungai, 2010). However, both figures were based on raw counts without systematic individual identification of lions, and routine ground counts between 2010 and 2017 recorded opportunistic sightings of between six and 16 individuals (A. Bett, unpublished data). To obtain reliable estimates of lion abundance and density, which is critical to managing this small, isolated population, we used unstructured spatial sampling (Russell et al., 2012) combined with a spatially explicit capture–recapture (SECR) analysis (Royle, Chandler, Soliman, & Gardner, 2013) and laid the foundation for long-term monitoring.

## 2 METHODS

### 2.1 Study area

Lake Nakuru National Park (LNNP, centered at 0.39°S, 36°E) in Kenya’s Rift Valley is approximately 188 km², and completely encloses a soda lake (Figure 1). LNNP is uniquely important in Kenya as it is a Ramsar Site, World Heritage Site, a Rhino Sanctuary and one of Kenya’s most visited National Parks (Kenya Wildlife Service, 2018). In recent years, the lake water level has risen dramatically: in 2010, it occupied 31.8 km² rising to 53.3 km² in 2017. Thus, total land area during this survey was ~134.7 km². Long-term mean annual precipitation is 869 mm/year with peaks in rainfall between April–May, August, and November (Ogutu, Owen-Smith, Piepho, Kuloba, & Edebe, 2012). The study area is bordered by Nakuru city (north), intensive agricultural lands (west and south) and Soysambu Conservancy (east). Due to its status as a rhino sanctuary, it is completely enclosed by an electric fence.
which is designed to prohibit wildlife movement and deter poaching, but is occasionally breached by lions and other carnivores (KWS, unpublished data). However, such breaches are rare as the fence is patrolled and maintained on a daily basis by park fence attendants. The resulting genetic isolation of LNNPs wildlife, together with the nearby large city, intensive agriculture, altered physiochemical characteristics of the lake water, invasive plants and historic heavy metal dumping have resulted in various threats to wildlife (Brenneman, Bagine, Brown, Ndetei, & Louis Jr, 2009; Jumba, Kisia, & Kock, 2007; Kairu, 1996; Kenya Wildlife Service, 2018; Kiprutto, Kangogo, & Kiage, 2018; Kisia, Jumba, & Kock, 2002; Kock et al., 1994; Ng’weno, Mwasi, & Kairu, 2010; Wambui, Opere, Githaiga, & Karanja, 2018).

2.2 | Field methods

Fieldwork was conducted by observation teams in two vehicles that intensively patrolled the study area for 21 days (September 11, 2017–October 2, 2017) during daylight hours, using the unstructured, search encounter techniques outlined by Elliot and Gopalaswamy (2017) that consists of recording drive effort and the location and sampling occasion for each lion sighting (Figure S1). Whenever possible, a series of close-up photographs were taken of each individual from multiple different angles in order to obtain records of their vibrissae spots. The pattern of these spots is unique to each individual (Pennycuick & Rudnai, 1970), and was used in combination with other distinguishing features, such as ear tears and dental wear, to create ID cards for different individuals. Each individual was assigned a unique ID and a gender based on secondary sexual characteristics and estimated to be under or over the age of 1 year based on phenotypic features such as body size, shoulder height, nose pigmentation, and mane development (Miller et al., 2016; Whitman & Packer, 2007). Photographs taken at subsequent sightings were then visually compared to existing ID cards and if these photographs matched existing ID cards, this was considered a recapture, whereas if they did not match, a new ID card was created (see Figure S2 for more details and an example ID card). Since lion mortality is highest during the first year (Packer et al., 1988), we excluded all individuals estimated to be less than 1 year of age, as including them would likely violate the population closure assumption of mark-recapture models (Otis, Burnham, White, & Anderson, 1978).

2.3 | Analytical framework

To model the spatial distribution of lions (state process) we followed the recommended approach by first generating a state-space that would be larger than 2.5 times the expected spatial scale parameter sigma (σ) (Royle, Chandler, Sollmann, & Gardner, 2013). Thus, we defined a 15 km buffer around the sampled area. Next, we generated potential activity centers across the 2,356 km² state-space, represented by equally spaced pixels (0.25 km²). Thereafter we masked out pixels that were deemed to be unsuitable habitat (Nakuru city to the North and agricultural lands to the West and South) or suitable but inaccessible habitat (Soysambu Conservancy). Thus, we made the explicit assumption that the LNNP population was geographically closed during our survey and masked out all pixels that fell outside LNNP and those that fell within the lake itself. Although Soysambu Conservancy is known to be suitable lion habitat, the electric fence separating the two areas precludes movement except on rare occasions when a hole appears briefly (e.g., from animals digging) before being fixed by park fence attendants who regularly patrol the fence while undertaking routine fence maintenance. The value of M (the data-augmented

---

**FIGURE 1** The lion state-space (~2,356 km²) as defined by a 15 km buffer around the study area, Lake Nakuru National Park (188 km²) in Kenya. Areas unsuitable for lions were masked prior to analysis. Soysambu Conservancy was masked out since an electric fence encompasses Lake Nakuru National Park thereby restricting movement.
value of abundance in the larger state-space) was set at 90 (comprising of the number of individuals observed during the survey \( n = 10 \) and the number of individuals augmented for the analysis \( n_z = 80 \)), which represents the maximum number of lions possible within the state-space.

We note that in our particular set up, owing to fencing, the abundance (\( N \)) in the study area is equal to the (\( N \)) estimate within the larger state-space and often called \( N_{\text{super}} \) in the Bayesian spatial capture–recapture literature (Royle, Karanth, Gopalaswamy, & Kumar, 2009). The state process involved a model component to estimate abundance (\( N \)) and this is defined by \([N|M, \psi]\sim\text{Binomial}(M, \psi)\), where \( \psi \) is the probability that an individual chosen from \( M \) is a member of the population. If \( R \) is the total number of pixels defined in the state-space, the animals occupy the pixels according to \((c_1, c_2, \ldots, c_R) \mid (p_1, p_2, \ldots, p_R) \sim \text{Multinomial}[N, (p_1, p_2, \ldots, p_R)]\), where \((c_1, c_2, \ldots, c_R)\) represents the number of animals at each pixel and \((p_1, p_2, \ldots, p_R)\) represents the pixel occupancy probabilities of the \( R \) pixels.

Prior to confrontation with the data, we may consider \( p_1 = p_2 = \ldots = p_R \), so that the prior probability of an individual occurring at a randomly selected pixel is \( 1/R \) (Royle, Chandler, Sollmann, & Gardner, 2013).

To describe the manner in which individuals were detected during the survey (observation process) we followed all steps outlined by Elliot and Gopalaswamy (2017) and compiled a standard spatial capture–recapture array (Gopalaswamy et al., 2012) consisting of individuals, trap locations (defined by pixels of 0.25 km\(^2\)), and sampling occasions. Since highly sampled traps might increase the number of detections, we included an effort covariate (logarithm of kilometers driven) per trap per day. The inclusion of the effort covariate generalizes the SECR model to accommodate unstructured sampling (see Gogoi, Kumar, Banerjee, & Jhala, 2020 where effort is assumed to be constant). In addition, we included sex-specific covariates when defining the observation process. By explicitly accounting for different detection probabilities between males and females we additionally estimated the sex ratio.

### 2.4 Candidate models

We defined a set of five a priori models and compared their outputs (see Table 1 for parameter definitions). Due to the small sample size, we fixed the detection function parameter (\( \theta \)) to 1, which implies a fixed, half-normal detection function. The probability of detecting lion \( i \) in pixel \( j \) on sampling occasion \( k \) (\( \pi_{ijk} \)) is defined by a complementary log–log function of covariates (Elliot & Gopalaswamy, 2017):

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

| Parameter       | Definition                                                                 |
|-----------------|-----------------------------------------------------------------------------|
| \( \sigma_F \)  | 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 sampled grid cell |
| Posterior mean  | 1.897                                                                      |
| Posterior mode  | 2.518                                                                      |
| Posterior SD    | 0.300                                                                      |
| \( \sigma_M \)  | 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 sampled grid cell |
| Posterior mean  | 1.592                                                                      |
| Posterior mode  | 2.164                                                                      |
| Posterior SD    | 0.285                                                                      |
| \( \beta_{\text{eff}} \) | The rate of change in the complementary log–log value of detection probability as the (log) effort changes by one unit (1 km of drive effort) |
| Posterior mean  | 3.769                                                                      |
| Posterior mode  | 2.153                                                                      |
| Posterior SD    | 0.541                                                                      |
| \( \lambda_0 \) | The basal encounter rate of a lion whose activity center is located exactly at the centroid of a grid cell |
| Posterior mean  | 0.018                                                                      |
| Posterior mode  | 0.034                                                                      |
| Posterior SD    | 0.004                                                                      |
| \( \psi \)      | The ratio of the true number of individuals in the population compared to the data augmented population \( M \) |
| Posterior mean  | 0.134                                                                      |
| Posterior mode  | 0.152                                                                      |
| Posterior SD    | 0.039                                                                      |
| \( N_{\text{super}} \) | The total number of lions in the larger state-space \( S \) |
| Posterior mean  | 11.371                                                                     |
| Posterior mode  | 10                                                                         |
| Posterior SD    | 1.544                                                                      |
| \( \psi_{\text{sex}} \) | The proportion of lions that are male |
| Posterior mean  | 0.421                                                                      |
| Posterior mode  | 0.566                                                                      |
| Posterior SD    | 0.151                                                                      |
| \( D \)         | The estimated density of lions/100 km\(^2\) > 1 year of age |
| Posterior mean  | 6.748                                                                      |
| Posterior mode  | 5.935                                                                      |
| Posterior SD    | 0.916                                                                      |

Note: Number of posterior samples used was 50,000. Maximum value of potential scale reduction factor = 1. Bayesian \( p \)-value = .794. See Figure S4 for pairwise plots between parameters, Figure S5 for posterior distributions of abundance and density, and Table S2 for detailed summaries of posterior estimates for each model.
where \( f(\text{dist}(i,j) \mid \theta, \sigma_{\text{sex}}) \) describes how detection rate is a function of distance between the activity center of individual \( i \) and pixel \( j \), which are conditional on \( \theta \) and \( \sigma_{\text{sex}} \). We ran five variations of this general model as follows:

Model 1: \( N(.), \lambda_{0}(\text{sex + effort}), \sigma(\text{sex}) \)—based on the assumption that basal encounter rate and the rate of decline in detection probability are sex-specific.

Model 2: \( N(.), \lambda_{0}(\text{effort}), \sigma(\text{sex}) \)—based on the assumption that basal encounter rate is independent of sex and the rate of decline in detection probability is sex-specific.

Model 3: \( N(.), \lambda_{0}(\text{effort}), \sigma(.) \)—based on the assumption that basal encounter rate and the rate of decline in detection probability are independent of sex.

Model 4: \( N(.), \lambda_{0}(\text{sex + effort}), \sigma(.) \)—based on the assumption that basal encounter rate is sex specific and the rate of decline in detection probability is independent of sex.

Model 5: \( N(.), \lambda_{0}(\text{effort}) \)—due to the small, fenced nature of our study area, we ran a conventional nonspatial capture–recapture model (e.g., Otis et al., 1978), corrected for effort (see Royle et al., 2009) to assess whether this would be more appropriate.

The models were implemented in the programming environment R (R Core Team, 2019), using the same priors as Broekhuis and Gopalaswamy (2016) and the code provided in Elliot and Gopalaswamy (2017). This code implements a Bayesian Markov Chain Monte Carlo (MCMC) approach using the Metropolis-Hastings algorithm (Tierney, 1994) to fit the models. We set four chains to run for each model, with each chain defined to initially be 51,000 iterations long. We discarded outcomes from the first 1,000 iterations as burn-in. We assessed the MCMC convergence for all models using the Gelman-Rubin diagnostic (Gelman & Rubin, 1992), and discarded more initial iterations as burn-in if convergence was not achieved. If nonconvergence persisted, we re-ran the analysis with longer chain lengths until convergence was achieved.

We used the following approach to draw inference on model choice: First, we checked each model for adequacy using the Bayesian \( p \)-value assessment based on individual encounters (Royle et al., 2009). We employed this tool as a model rejection tool, rather than a model selection tool; second, we created pair-wise correlation plots between estimated parameters from the posterior MCMC draws. These were visually inspected to infer upon parameter redundancy issues relating to model overfitting relative to sample size. We were particularly concerned to explore if any correlation was influencing the abundance parameters; Finally, although there is no established model selection method proven to work well for Bayesian SECR models such as ours, a recent development using simulations shows promise (see equation 2.6, Dey, Delampady, & Gopalaswamy, 2019, noting that the SECR models used by them were different from ours). We considered the adequate models obtained from the first step and, as recommended in Dey et al. (2019), we applied the harmonic mean estimator of the marginal likelihood using the MCMC draws to finally select the model generating the highest value for the logarithm of the marginal likelihood. As such, our model choice was influenced by all the criteria described above.

2.5 Posterior mean abundance

Since the state space was restricted to our study area, we make use of the \( N_{\text{super}} \) estimate to provide posterior mean and posterior SD of abundance (\( N \)). All R scripts, functions, and data for our analyses are in Supporting Information.

3 RESULTS

During the 21-day survey, we drove 2,579 km in search of lions and recorded 54 detections of 16 individuals (Figure S1). Six of these were estimated to be <1 year old and were excluded (see Figure S3 for encounter history plots).

3.1 Model diagnostics

To achieve convergence (mean potential scale reduction factor of <1.05 for each parameter), the number of iterations for Model 1 was increased to 250,000 (with a post hoc burn of 5,000 iterations), while Models 2–5 converged with 50,000 iterations. Bayesian \( p \) value for Model 2 (0.794) and Model 3 (0.792) lay within the extremities (0.15–0.85) indicating that the models were adequate, while Models 1 (0.933), 4 (0.912) and 5 (0.971) indicated a poor goodness of fit, and thus were rejected. Models 2 and 3 displayed the least parameter redundancy and covariance (Figure S4). Finally, the marginal likelihood estimate for Model 2 was highest. Taking these evidences together, we therefore report the posterior parameter estimates from Model 2 (Table 1) and use this model for inference. We provide parameter estimates (Table S1) and display the posterior distribution of abundance and density for all models in the supplementary materials (Figure S5). We note that the posterior distributions of density and \( N_{\text{super}} \) across all models are generally skewed (Figures S4 and S5), owing to small sample size. While
the choice of a posterior summary statistic (mean, median, or mode) is somewhat arbitrary, given the skewed posteriors the mode may be less biased (Marques, Thomas, & Royle, 2011). We also note that there is greater congruence between the models when comparing the mode as opposed to the mean. Hence, we report both the posterior mean and the mode. Posterior distributions for Model 1 and 4 are particularly skewed, indicating greater uncertainty in parameter estimates from these models.

3.2 Posterior density and abundance estimates

Model 2 estimated mean lion density within our study area to be 6.75 (mode = 5.93, posterior SD = 0.92, 95% highest posterior density [HPD] interval = 5.93–8.31) individuals >1 year old/100 km². Posterior density estimates for each 0.25 km² pixel indicate two main “hotspots” of lion activity (Figure 2). The sex ratio, as estimated by ψsex, was 1.38♀:1♂. Posterior mean abundance for LNNP was estimated at 11.37 (mode = 10, posterior SD = 1.54, 95% HPD interval = 10–14) lions >1 year old.

4 DISCUSSION

Our estimated abundance of essentially 11 lions (in two distinct social groups) is consistent with recent opportunistic ground counts of between six and 16 individuals (A. Bett, unpublished data), but considerably lower than previous unpublished reports of 65 lions in 2002 (Kenya Wildlife Service, 2002) and 56 lions in 2010 (Bett et al., 2010). Rather than suggesting a decline of lions, we argue that a more likely scenario is that the previous reports and field effort likely led to double counting and that high basal encounter rates in LNNP (λ0 = 0.02), comparable in magnitude to the high density lion population in Kenya’s Maasai Mara (λ0 = 0.03) (Elliot & Gopalaswamy, 2017) created a perception that lions were more numerous than they actually were (e.g., Moqanaki et al., 2018). The 2010 figure was based on a “rapid survey” over 11 days during November 2010, where a total of 56 lions in 13 social groups were reported while randomly searching for lions. However, individual lions were not systematically identified and no repeat sightings were documented (Bett et al., 2010). It is therefore likely that double counting of individuals occurred, which appears to be corroborated by similar group sizes being seen in similar locations. For example, in southern LNNP, a total of 15 adult males were recorded in an area of 29 km², with no sighting of more than three adult males on a single day and short distances (mean = 3.89 km) between sightings (Bett et al., 2010). Given this, we posit that perhaps only three males occurred within a biologically meaningful home range for lions. This would be comparable to our estimate of σ = 1.59 for males which translates to an approximate home range of 48 km² using a bivariate normal kernel estimator (Calhoun & Casby, 1958; see page 157 of Royle, Chandler, Sollmann, & Gardner, 2013) during our 3-week survey.

We therefore speculate that the earlier number of 56 represents lion detections and not lion abundance. Our confidence in the abundance estimates presented in the current study were strengthened after a subsequent 3-month study in LNNP, where lions were searched for daily and individually identified, revealed only one individual that we had not observed (M. Chege, personal communication, November 2018). It is our contention therefore that the estimates previously provided should not be considered abundance estimates and our results serve as a baseline of lion abundance within LNNP.

Since our study area was relatively small and fenced, we were interested to corroborate our SECR results by

**FIGURE 2** Pixel-specific lion density expressed in units of individual lion activity centers per state-space pixel (0.25 km²) in Lake Nakuru National Park, Kenya. Estimated by Model 2, two clear hotspots of lion activity are revealed: one bordering on Soysambu Conservancy, and the other to the north-east.
comparing the estimates of our reported model (Model 2) to those of a conventional capture–recapture model (Model 5) (e.g., Otis et al., 1978) and note that the estimates are similar (Table S1). However, the SECR approach is applicable in such a fenced situation because the estimated $\sigma$ is relatively small compared to park area size. A relatively large $\sigma$ may demand consideration of conventional capture–recapture in fenced circumstances, since animals may now be considered as freely “mixing.” Therefore, we advocate the use of SECR in such situations since we obtain an estimate of the ecologically informative parameter $\sigma$ and it permits the use of spatial covariates (Royle, Chandler, Sun, & Fuller, 2013).

An additional modeling decision we made was to exclude Soysambu Conservancy from the analysis, thus assuming that our study population was geographically closed during the survey period. We justify this decision due to the electric fence that separates LNNP from Soysambu thus prohibiting free movement. On rare occasions, holes in the fence do appear, but not to the extent that would uphold the assumption of conventional SECR analysis with bivariate normal distributions around activity centers. An analytical alternative was to employ the Royle, Chandler, Gazenski, and Graves (2013) SECR model which permits non-Euclidean distances using a defined covariate habitat layer. However, we rejected this option since we were not confident of estimating an additional resistance parameter with our small sample size and obtaining a measurable covariate to define the degree of fence permeability was not straightforward. Furthermore, we did not have sufficient evidence of regular fence breaches or their locations to justify the use of this complex model.

While our estimated mean density of 6.75 lions >1 year old/100 km², compares favorably to other productive ecosystems (Périquet, Fritz, & Revilla, 2014) and small reserves in South Africa (Miller & Funston, 2014), their low abundance and complete isolation is cause for concern. Although there is occasional intermixing with lions in Soysambu, they originate from the same founders. Furthermore, while at the time of our survey neighboring Soysambu Conservancy was thought to contain eight lions >1 year the Soysambu population is now thought to only consist of five individuals >1 year and only one of which is a breeding age female (K. Combes, personal communication, December 2019). Although the LNNP lion population has little ecological significance to a country that contains two lion strongholds (Serengeti-Mara and Tsavo-Mkomazi, Riggio et al., 2013), they have significant tourism value as LNNP is one of Kenya’s most visited National Parks (Kenya Wildlife Service, 2018) and lions are a major attraction due to their charisma (Macdonald et al., 2015). As such, there is substantial will to conserve this small lion population and we discuss the possible ecological mechanisms at play and long-term management options, with emphasis on proactive methods designed to target causal mechanisms (Miller et al., 2013).

Small, isolated lion populations tend to have three ecological characteristics in common: overpopulation, genetic degradation and increased susceptibility to catastrophic events (Miller et al., 2013). Prey abundance is thought to be high in LNNP particularly for key lion-prey species such as buffalo (Syncerus caffer) and zebra (Equus quagga) (Ogutu et al., 2012), and given that lion overpopulation is a common occurrence, our population estimate was lower than expected. While we have no estimate of lion carrying capacity in LNNP it is possible that the population experienced a typical boom early on (in 2002 the population must have exceeded 37 lions, since this is the number that were euthanized, 29 of which were adults or subadults, after lions killed two rangers (Ogutu et al., 2012)), and that the population is now suppressed, perhaps due to genetic degradation. Prolonged genetic isolation in lions is known to lower fecundity, and increase sperm abnormalities, juvenile mortality and susceptibility to disease (Atkinson, Kitchener, Tobe, & O’Donoghue, 2018; Kissui & Packer, 2004; Packer et al., 1991; Trinkel et al., 2008).

Given the small founder population in LNNP (N = 6) and the fact that no known immigration has occurred since 1992, the genetic integrity of this population should be explored as a priority. In particular, genetic testing of a sample of the population will be useful to determine current levels of inbreeding and the best source for potential future translocations into LNNP. For example, microsatellite data from a sample of the LNNP population could be used to assess their genetic distinctiveness and diversity relative to other lion populations in Kenya to determine the best source for potential future translocations into LNNP (Antunes et al., 2008). Thereafter management interventions can be designed to mimic natural processes such as male tenure length over prides, dispersal and mortality by translocating selected lions into and out of LNNP. However, as advised by Miller et al. (2013), translocated lions should be vaccinated against key diseases such as canine distemper to avoid a population crash as experienced recently in Welgevonden Game Reserve, South Africa (Davidson-Phillips et al., 2019). Translocation of dispersal-aged lions away from LNNP may even have the added benefit of reducing human–lion conflict in the area, since this demographic is most prone to conflict (Elliott, Cushman, Macdonald, & Loveridge, 2014), potentially even more so in small ecosystems. In addition, programs should be implemented to limit human–lion conflicts. The same would apply to the small population in neighboring Soysambu Conservancy.
and an additional course of action could be to maintain fence gaps that allow for lion movement between LNNP and Soysambu, thereby increasing the space and effective population size. A potential side effect of these interventions is that lion numbers rise beyond desired levels and so intensive management informed by regular population monitoring (using SECR) may be required in the long-term.

Our results add further evidence to studies such as Elliot and Gopalaswamy (2017), Broekhuis and Gopalaswamy (2016) and Rafiq et al. (2019) which demonstrated that SECR can produce precise and statistically robust population estimates for a variety of large African carnivores while accounting for variation in detection probability, even where sample sizes are small. They also lend further weight to the call by Elliot and Gopalaswamy (2017) for a unified framework to estimate lion numbers in all important lion populations. Indeed, prompted by the preliminary findings of this study, the Kenya Wildlife Service as part of implementation of its national strategy for lions, has adopted SECR as a standardized framework to monitor all source populations in the country (Kenya Large Carnivore Taskforce, 2009). Given that it usually takes considerable time for new methods to be absorbed by state agencies, we offer specific hypotheses as to how this occurred based on our collective experience: (a) charismatic species such as lions generate global interest and the need for reliable estimates of population trends is understood by a broad spectrum of society, thus motivating the application of cutting-edge science to inform conservation; (b) the rigorous fieldwork (extensive search effort coupled with individual identification) imparts intuitive understanding of the outputs compared to index-based approaches; (c) confidence was gained by the extensive peer-reviewed literature, which reinforces the robustness of the approach and highlights the wider applications, such as estimation of vital rates (Ergon & Gardner, 2014) and the ability to test a range of spatial process hypotheses relating to resource selection (Royle, Chandler, Sollmann, & Gardner, 2013), movement (Royle, Fuller, & Sutherland, 2016), spatial distribution (Elliot & Gopalaswamy, 2017), home-range size (Balme et al., 2019) and connectivity (Fuller, Sutherland, Royle, & Hare, 2016) at a population level; (d) since SECR models can accommodate a wide variety of observation methods and data types (Royle, Chandler, Sollmann, & Gardner, 2013), they provide an appropriate standardized framework to monitor species such as lions that occur in diverse habitats, at varying densities and with changeable behavior.

In summary, even in small, isolated wildlife areas estimating abundance can be problematic yet it is critical that estimates are accurate, precise and regular since these populations require intensive management, and management strategies are frequently based on population size (Miller et al., 2013). However, within such areas, scientific monitoring techniques are frequently replaced by expert opinion or routine monitoring by wildlife managers (Miller & Funston, 2014). Our study shows that relying on such monitoring may misinform management and that scientific sampling techniques, though expensive, should be an integral component of small reserve management.

ACKNOWLEDGMENTS
We are grateful to the leadership of Kenya Wildlife Service for supporting this study, which was a collaborative venture between the Kenya Wildlife Trust, Lion Guardians, and the Kenya Wildlife Service. We thank Julius Kabete, Anita Kiplagat, Christine Ong’iro, Everline Silali, Benard Olume, Kathryn Combes, and Rowena White for diligent assistance with fieldwork, as well as drivers John Momanyi and George Obuya. We thank the KWS Central Rift Conservation Area and Park Management team led by Agrrey Maumo, Samuel Tokore and Haron Sang for logistical support while undertaking the survey. We acknowledge the use of the University of Oxford’s Advanced Research Computing (ARC) facility in carrying out this work (https://doi.org/10.5281/zenodo.22558). A. M. G. thanks Mohan Delampady for helpful conversations about Bayesian statistics and statistical theory. This survey was supported by the kind generosity of ICEA Lion Insurance Group, Kenya.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
Nicholas B. Elliot, Alice Bett, Monica Chege, Linus Kariku, Femke Broekhuis, and Arjun M. Gopalaswamy conceived and designed the study. Nicholas B. Elliot, Alice Bett, Monica Chege, Kasaine Sankan, Nadia de Souza, and Femke Broekhuis led data collection and management, with Nicholas B. Elliot, Monica Chege, Femke Broekhuis and Arjun M. Gopalaswamy analyzing the data. Nicholas B. Elliot led the writing with all authors providing input and contributions.

DATA AVAILABILITY STATEMENT
All input files and R scripts to reproduce our analysis are available in the Supporting Information.

ETHICS STATEMENT
No ethics approval was required for this research. Our fieldwork consisted of finding and photographing lions and did not involve any handling of animals.

ORCID
Nicholas B. Elliot  https://orcid.org/0000-0001-5364-545X
Femke Broekhuis https://orcid.org/0000-0002-4216-
REFERENCES

Antunes, A., Troyer, J. L., Roelke, M. E., Pecon-Slattery, J., Packer, C., Winterbach, C., ... Standen, P. (2008). The evolutionary dynamics of the lion (Panthera leo) revealed by host and viral population genomics. *PLOS Genetics*, 4(11), e1000251.

Atkinson, K. E., Kitchener, A. C., Tobe, S. S., & O’Donoghue, P. (2018). An assessment of the genetic diversity of the founders of the European captive population of Asian lion (Panthera leo aka), using microsatellite markers and studbook analysis. *Mammalian Biology*, 88, 138–143. https://doi.org/10.1016/j.mambio.2017.10.001

Balmé, G., Rogan, M., Thomas, L., Pitman, R., Mann, G., Whittington-Jones, G., ... Hunter, L. (2019). Big cats at large: Density, structure, and spatio-temporal patterns of a leopard population free of anthropogenic mortality. *Population Ecology*, 61(3), 256–267. https://doi.org/10.1002/1438-390X.1023

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T., ... Packer, C. (2015). Lion (Panthera leo) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences*, 112(48), 14894–14899.

Bauer, H., Packer, C., Funston, P. F., Henschel, P., & Nowell, K. (2016). *Panthera leo*. (Errata version published in 2017). IUCN red list of threatened species. International Union for Conservation of Nature, Gland, Switzerland. December 1, 2015. https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T15951A79929984.en

Bett, A., Omongo, F., & Mungai, S. (2010). Rapid survey of lions (Panthera Leo) in Lake Nakuru National Park. Nairobi, Kenya: Kenya Wildlife Service.

Brenneman, R. A., Bagine, R. K., Brown, D. M., Ndetei, R., & Louis, E. E., Jr. (2009). Implications of closed ecosystem conservation management: The decline of Rothschild's giraffe (Giraffa camelopardalis rothschildi) in Lake Nakuru National Park, Kenya. *African Journal of Ecology*, 47(4), 711–719.

Broekhuis, F., & Gopalaswamy, A. M. (2016). Counting cats: Spatially explicit population estimates of cheetah (Acinonyx jubatus) using unstructured sampling data. *PLoS One*, 11(5), e0153875. https://doi.org/10.1371/journal.pone.0153875

Calhoun, J. B., & Casby, J. U. (1958). *Calculation of home range and density of small mammals*. Washington, DC: US Department of Health, Education, and Welfare, Public Health Service.

Davidson-Phillips, S., Davidson-Phillips, P., Canning, G., Schroder, B., Swart, J., & Burger, A. (2019). Canine distemper virus management in lions (Panthera leo) on Welgevonden Game Reserve. *African Journal of Wildlife Research*, 49(1), 155–166.

Dey, S., Delampady, M., & Gopalaswamy, A. M. (2019). Bayesian model selection for spatial capture–recapture models. *Ecology and Evolution*, 9(20), 11569–11583.

Elliot, N. B., Cushman, S. A., Macdonald, D. W., & Loveridge, A. J. (2014). The devil is in the dispersers: Predictions of landscape connectivity change with demography. *Journal of Applied Ecology*, 51(5), 1169–1178. https://doi.org/10.1111/1365-2664.12282

Elliot, N. B., & Gopalaswamy, A. M. (2017). Towards accurate and precise estimates of lion density. *Conservation Biology*, 31(4), 934–943. https://doi.org/10.1111/cobi.12878

Ergon, T., & Gardner, B. (2014). Separating mortality and emigration: Modelling space use, dispersal and survival with robust-design spatial capture–recapture data. *Methods in Ecology and Evolution*, 5(12), 1327–1336.

Fuller, A., Sutherland, C., Royle, J. a., & Hare, M. (2016). Estimating population density and connectivity of American mink using spatial capture–recapture. *Ecological Applications*, 26, 1125–1135. https://doi.org/10.5061/dryad.s7ph4

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, 7, 457–472.

Gogoi, K., Kumar, U., Banerjee, K., & Jhala, Y. V. (2020). Spatially explicit density and its determinants for Asiatic lions in the Gir forests. *PLoS One*, 15(2), e0228374. https://doi.org/10.1371/journal.pone.0228374

Gopalaswamy, A. M., Delampady, M., Karanth, K. U., Kumar, N. S., & Macdonald, D. W. (2015). An examination of index-calibration experiments: Counting tigers at macroecological scales. *Methods in Ecology and Evolution*, 6(9), 1055–1066. https://doi.org/10.1111/2041-210x.12351

Gopalaswamy, A. M., Royle, J. A., Hines, J. E., Singh, P., Jathanna, D., Kumar, N. S., & Karanth, K. U. (2012). Program SPACECAP: Software for estimating animal density using spatially explicit capture-recapture models. *Methods in Ecology and Evolution*, 3(6), 1067–1072. https://doi.org/10.1111/j.2041-210X.2012.00241.x

Jacobson, A., & Riggio, J. (2018). Big cats in Africa: Status update of the African lion, cheetah and leopard, with recommendations for effective big cat conservation funding. Report prepared for National Geographic Society.

Jumba, I., Kisia, S., & Kock, R. (2007). Animal health problems attributed to environmental contamination in Lake Nakuru National Park, Kenya: A case study on heavy metal poisoning in the waterbird (Kobus ellipsiprymnus defassa) (Ruppell 1835). *Archives of Environmental Contamination and Toxicology*, 52 (2), 270–281.

Kairu, J. K. (1996). Heavy metal residues in birds of Lake Nakuru, Kenya. *African Journal of Ecology*, 34(4), 397–400.

Karanth, K. U. (1995). Estimating tiger (Panthera tigris) populations from camera-trap data using capture-recapture models. *Biological Conservation*, 71(3), 333–338.

Kenya Large Carnivore Taskforce. (2009). Conservation and management strategy for lion and spotted hyena in Kenya. Retrieved from http://www.kws.go.ke/content/species-status-wildlife-report-2015-2017

Kenya Wildlife Service. (2002). *The status of Rothschild’s giraffe (Giraffa camelopardalis rothschildi) in Lake Nakuru National Park*. Nairobi, Kenya: Kenya Wildlife Service.

Kenya Wildlife Service. (2018). The National Wildlife Conservation Status Report 2015–2017. Retrieved from http://www.kws.go.ke/content/status-wildlife-report-2015-2017

Kiprutto, N., Kangogo, C. M. J. N. M., & Kiage, E. (2018). Tracing the possible root causes for fleeing flamingos in Kenya’s Lake Nakuru National Park. *Biological Conservation*, 215, 10–16.

Kisia, S., Jumba, I., & Kock, R. (2008). The waterbuck (Kobus ellipsiprymnus defassa) (Ruppell 1835) as an indicator of ecosystem
health in the Central Rift Valley lake systems of Kenya. *African Journal of Ecology*, 40(4), 390–392.

Kissui, B. M., & Packer, C. (2004). Top-down population regulation of a top predator: Lions in the Ngorongoro crater. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1550), 1867–1874.

Kock, R., Jamba, I., Wambua, J., Mwanza, J., Siagi, A., & Kisia, S. (1994). Status of some trace elements in waterbuck (*Kobus ellipsiprymnus defassa*) (Rupell 1835) in relation to soil and forage composition and implications for animal health in Lake Nakuru National Park. In *Proceedings of Research and Planning Workshop on use of research findings in the conservation and management of biodiversity (Nakuru)*. Nairobi: Kenya Wildlife Services.

Lande, R. (1988). Genetics and demography in biological conservation. *Science*, 241(4872), 1455–1460. https://doi.org/10.1126/science.3420403

Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist*, 142(6), 911–927.

Loveridge, A. J., Searle, A. W., Murindagomo, F., & Macdonald, D. W. (2007). The impact of sport-hunting on the lion population in a protected area. *Biological Conservation*, 134(4), 548–558.

Macdonald, E. A., Burnham, D., Hinks, A. E., Dickman, A. J., Malhi, Y., & Macdonald, D. W. (2015). Conservation inequality and the charismatic cat: *Felis felis*. *Global Ecology and Conservation*, 3, 851–866.

Marques, T., Thomas, L., & Royle, J. a. (2011). A hierarchical model for spatial capture-recapture data: Comment. *Ecology*, 92, 526–528. https://doi.org/10.2307/41151161

Miller, J. R., Balme, G., Lindsey, P. A., Loveridge, A. J., Becker, M. S., Begg, C., ... Jansson, I. (2016). Aging traits and sustainable trophy hunting of African lions. *Biological Conservation*, 201, 160–168.

Miller, S., Bissett, C., Burger, A., Courtenay, B., Dickerson, T., Druce, D., ... Kilian, P. (2013). Management of reintroduced lions in small, fenced reserves in South Africa: An assessment and guidelines. *South African Journal of Wildlife Research*, 43(2), 138–154.

Miller, S. M., & Funston, P. J. (2014). Rapid growth rates of lion (*Panthera leo*) populations in small, fenced reserves in South Africa: A management dilemma. *African Journal of Wildlife Research*, 44(1), 43–55.

Miller, S. M., Harper, C. K., Bloomer, P., Hofmeyr, J., & Funston, P. J. (2015). Fenced and fragmented: Conservation value of managed metapopulations. *PLoS One*, 10(12), e0144605.

Moqanaki, E. M., Jiménez, J., Bensch, S., & López-Bao, J. V. (2018). Counting bears in the Iranian Caucasus: Remarkable mismatch between scientifically-sound population estimates and perceptions. *Biological Conservation*, 220, 182–191.

Ng’weno, C. C., Mwasi, S. M., & Kairu, J. K. (2010). Distribution, density and impact of invasive plants in Lake Nakuru National Park, Kenya. *African Journal of Ecology*, 48(4), 905–913.

Ogutu, J. O., Owen-Smith, N., Piepho, H.-P., Kuloba, B., & Edebe, J. (2012). Dynamics of ungulates in relation to climatic and land use changes in an insularized African savanna ecosystem.
Estimating abundance of mountain lions from unstructured spatial sampling. *The Journal of Wildlife Management*, 76(8), 1551–1561.

Saccheri, I., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W., & Hanski, I. (1998). Inbreeding and extinction in a butterfly metapopulation. *Nature*, 392(6675), 491–494.

Tierney, L. (1994). Chains for Exploring posterior distributions. *Annals of Statistics*, 22(4), 1701–1728.

Trinkel, M., Ferguson, N., Reid, A., Reid, C., Somers, M., Turelli, L., ... Haverman, P. (2008). Translocating lions into an inbred lion population in the Hluhluwe-iMfolozi Park, South Africa. *Animal Conservation*, 11(2), 138–143.

Wambui, M. B., Opere, A., Githaiga, J. M., & Karanja, F. K. (2018). Assessing the impacts of climate variability and climate change on biodiversity in Lake Nakuru, Kenya. *Bonorowo Wetlands*, 8(1), 13–24.

Waweru, F. K. (1995). Translocations and introduction of animals in Lake Nakuru National Park. In *Proceedings of workshop on use of research findings in management and conservation of biodiversity* (pp. 77–81). Nakuru, Kenya: Lake Nakuru National Park.

Whitman, K. L., & Packer, C. (2007). *A hunter’s guide to aging lions in eastern and Southern Africa*. Long Beach, CA: Safari Press.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of this article.

---

**How to cite this article:** Elliot NB, Bett A, Chege M, et al. The importance of reliable monitoring methods for the management of small, isolated populations. *Conservation Science and Practice*. 2020;2:e217. [https://doi.org/10.1111/csp2.217](https://doi.org/10.1111/csp2.217)