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RESEARCH ARTICLE

Adaptive data collection strategies for spatial capture–recapture monitoring: Linking monitoring approaches to seasonal variation in density and space use

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Abstract

1. Effective monitoring of wildlife populations and their changes over time is essential for guiding conservation strategies. For monitoring to fulfil this role, large-scale and long-term resource commitments are required, yet frequently lacking. Consequently, site-based monitoring of key species is often sporadic, inconsistent and disconnected from wildlife agencies, reducing the role of monitoring in adaptive management.
2. To overcome these challenges, Kenya's wildlife management and research agencies coordinated and participated in three surveys that were designed to evaluate adaptable, search–encounter data collection strategies within a spatially explicit capture–recapture (SECR) framework for lions (*Panthera leo*) under real-world monitoring constraints.
3. Three surveys were conducted in Nairobi National Park, which lies in Kenya's capital. The first survey was conducted by a multi-agency team of field biologists during the wet season (2018). The second and third surveys were conducted in the dry season (2021 and 2022) by trained wildlife enthusiasts and by field biologists participating in a SECR training workshop, respectively. The resulting estimates were used to assess their consistency with known spatiotemporal patterns of variation in lion population density.
4. Our results were consistent with those reported in previous studies. Lion density (lions/100 km^2) in the park was higher during the dry season (2021: 26.90, PSD = 6.61; 2022: 27.74, PSD = 6.61), compared with the wet season (2018:

18.52, PSD = 4.62) when prey are dispersed outside the park. Movement for all lions (inferred by sex ratio-weighted spatial scale parameter, σ_w, in km) was largest during the wet season (2018: 3.38, PSD = 0.7) compared with the dry season (2021: 1.38, PSD = 0.2; 2022: 1.44, PSD = 0.2). Lion activity centres were more clustered on the southern boundary of the park during the wet season compared with during dry seasons.

5. *Solution*. Our results support existing evidence that human–lion conflicts are more likely to peak during the wet season, thus providing key insights for the conservation of lions in this ecosystem. Our study demonstrates that monitoring constraints need not preclude adaptability, provided data collection evolves within a robust framework that yields comparable estimates and informs management interventions.

KEYWORDS
abundance, African lion, density, Nairobi National Park, population monitoring, SECR, spatial capture–recapture, spatiotemporal variation

1 | INTRODUCTION

Globally, wildlife populations are undergoing significant declines in abundance, diversity and distribution as a result of unsustainable human activities and environmental changes (Ceballos et al., 2017). These declines threaten ecosystem stability and the essential services that biodiversity provides to humanity (Bagri & Vorhies, 1997). A key response to halting these declines has been the implementation of strategies that focus on managing impacts and interactions between humans and wildlife (Riley et al., 2002). However, good management is integrally linked to well-designed population monitoring programmes that form the basis of improved decision-making in conservation (Gopalaswamy et al., 2022; Stem et al., 2005). These monitoring programmes may play a vital role in guiding adaptive management efforts by providing a platform to track strategy implementation, detect changes in populations and serve as early warning systems (Lindenmayer et al., 2013; Nichols & Williams, 2006; Stem et al., 2005).

Recognising the need for conservation programmes to be coupled with wildlife monitoring, several governments globally adhere to policy frameworks targeting biodiversity loss (Jones et al., 2013). These time-bound policy frameworks, such as those provided by the Convention on Biological Diversity (CBD) and the International Union for the Conservation of Nature (IUCN), emphasise the need for systematic monitoring of wildlife status and trends (Bagri & Vorhies, 1997; Convention on Biological Diversity, 2022, 2024; Tittensor et al., 2014). They foster globally aligned, goal-oriented biodiversity targets to ensure that monitoring programmes drive informed responses to ecological challenges (Jones et al., 2013). However, despite these frameworks, for most wildlife species, population status and trends are inconsistently documented, and often unquantified or poorly understood (Barnes et al., 2016). This is because effective monitoring programmes rely on regular long-term field monitoring, which is often difficult to implement, as they require standardised protocols that should be carried out frequently by well trained personnel (Elliot et al., 2021; Ngene et al., 2023). Moreover, the substantial resources required (i.e. time, money and human capacity) make long-term monitoring difficult to sustain or replicate, resulting in gaps with many sites lacking rigorous long-term data to yield meaningful insights into population dynamics (Rafiq et al., 2019). Lack of consistent and comparable long-term data of key population parameters, such as abundance and space use, limits the role of monitoring in adaptive management as it becomes disconnected from wildlife management agencies. This is especially critical for charismatic species, such as large carnivores, where public and political pressure to provide abundance estimates often leads to speculative or inaccurate estimates (Gopalaswamy et al., 2022). Such estimates may result in undesirable steps in the decision-making process and facilitate inappropriate policy decisions, placing species at risk (Bauer et al., 2015; Gopalaswamy et al., 2022; Nichols & Williams, 2006).

In Kenya, the Wildlife Conservation and Management Act (WCMA) 2013 mandates the submission of biannual wildlife status reports, which assess the status of wildlife populations and guide conservation strategies (Kenya, 2013). To meet this requirement, in 2018 the country's governing wildlife body, Kenya Wildlife Service (KWS), adopted spatially explicit capture–recapture (SECR) methods to monitor key source populations of lions (*Panthera leo*; Ngene et al., 2023). This approach helped the country avoid the shortcomings of methodologies, such as call-in or track/spoor counts that can result in inaccurate estimates with high uncertainty (Belant et al., 2019; Dröge et al., 2020; Elliot & Gopalaswamy, 2017; Gopalaswamy et al., 2015). Initial surveys conducted using SECR provided a baseline for conducting repeat surveys to monitor population trends, thereby facilitating the evaluation of conservation

interventions (Elliot et al., 2021; Gopalaswamy et al., 2022; Ngene et al., 2023).

Over the past 15 years practitioners have developed, adapted and applied SECR models to fit a wide variety of field data collection protocols (Royle et al., 2013; Tourani, 2022). This flexibility, combined with a robust theoretical and statistical foundation, has led SECR models to quickly emerge as the industry standard for large-scale monitoring of large carnivore populations (e.g. Bischof et al., 2020). While SECR models were originally designed for structured data, they were extended to accommodate unstructured data (Royle et al., 2011; Russell et al., 2012), and a wide variety of unstructured spatial sampling protocols have been developed to estimate lion density (Elliot et al., 2021; Elliot & Gopalaswamy, 2017; Ngene et al., 2023; Royle et al., 2011; Russell et al., 2012; Western et al., 2022). While analytical developments have advanced exponentially, developments in field techniques have been slower, making it imperative to find solutions to overcome the challenges of collecting meaningful data, while still producing robust outputs.

To help meet the goals of the WCMA 2013 and Kenya's National Recovery and Action Plan for lions (2020–2030), which emphasise the importance of regular population monitoring (Kenya Wildlife Service, 2020a), we conducted three search–encounter surveys for lions in Nairobi National Park (NNP), Kenya. NNP is a relatively small (~117 km^2), partially fenced peri-urban ecosystem where seasonal prey migrations occur through the unfenced southern section during the wet season (Reid et al., 2008). These migrations create pulses and spatial shifts in ungulate distribution (Chesson et al., 2004), which in turn redistribute resources in space and time, and the resource dispersion hypothesis (RDH) predicts that carnivores will adjust their space use and local density in response (Macdonald, 1983). For instance, Broekhuis et al. (2021) documented seasonal changes in cheetah (*Acinonyx jubatus*) density and movements coincident with large herbivore migrations in Maasai Mara, Kenya. Additionally, because NNP lies at a human–wildlife interface, these shifts are known to intensify human–lion conflicts as a result of depredation of livestock by lions (Lesilau, 2019). Regular monitoring that can detect these shifts and guide management interventions is essential for NNP, yet the park currently lacks a long-term lion monitoring programme.

To lay the groundwork for such an initiative, we employed three alternative data collection strategies under realistic field constraints, and all surveys used the same hierarchical SECR framework; what differed among surveys were the strategies used to collect search–encounter data (i.e. personnel and field logistics). We then discuss these estimates in the context of previous studies that documented spatiotemporal variation in lion density and space use in the park (Chege et al., 2025; Lesilau, 2019). Our objectives were to: (1) to compare density and space use estimates obtained from alternative data collection strategies within a single SECR framework; (2) assess whether these estimates are consistent with the known seasonal ecology of the NNP lion population; and (3) to discuss the implications for practical, management-oriented monitoring.

2 | METHODS

This research was carried out under permits KWS/BRP/5001 and NACOSTI/P/21/8899, granted by the Kenya Wildlife Service and The National Commission for Science, Technology and Innovation (NACOSTI) in Kenya.

2.1 | Study area

Nairobi National Park was established in 1946 and has an area of ~117 km^2 (Owino et al., 2011). It is situated between latitudes 1° 20′ and 1° 26S and longitudes 36° 50′ and 36° 58E. It lies at an altitude ranging from 1500 to 1800 m above sea level, and experiences a mean annual maximum rainfall of ~900 mm in two seasons: March to May (long rains) and November to December (short rains) (Lesilau, 2019). The habitat consists of open savanna grasslands dominated by *Pennisetum mezzianum*, *Themeda triandra* and *Bothriochloa insculpta* interspersed with *Vachellia drepanolobium* trees. The western part is covered by semi-evergreen forest, while riverine vegetation consists of *V. xanthophloea* and *V. mellifera* (Rudnai, 1973). The park is fenced on three sides that border Nairobi city, while the southern section that borders the Athi-Kapiti plains (which includes part of Kitengela), an area of 2456 km^2 pastoralist rangeland, is unfenced (Lesilau et al., 2021; Figure 1). These plains form the wet season dispersal area for blue wildebeest (*Connochaetus taurinus*), Burchell's zebra (*Equus quagga burchellii*), common eland (*Tragelaphus oryx*), Coke's hartebeest (*Alcephalus buselaphus*), Grant's gazelle (*Gazella granti*) and Masai giraffe (*Giraffa camelopardalis tippelskirchi*) (Reid et al., 2008; Wandaka & Francis, 2019). However, the habitat for wildlife both in the park and on the plains is threatened by anthropogenic activities, such as rapid expansion of infrastructure, human settlements and urban centres (Wandaka & Francis, 2019).

2.2 | Lion surveys

Three sightings-based surveys, using alternative data collection strategies, were conducted within the boundary of NNP (Figure 1) during daytime hours. KWS in collaboration with the Wildlife Research and Training Institute (WRTI) coordinated the surveys. The first survey was conducted over 33 days during a wet season of 2018 by a multi-agency team of experienced field biologists from government and non-governmental organisations (Elliot et al., 2021). The second survey was carried out over 46 days in a dry season of 2021 and was overseen by members of the first survey, but fieldwork was conducted by four wildlife enthusiasts (citizen scientists) using their own vehicles. The four citizen scientists underwent a one-day training session on the data collection protocol and were requested to specifically search for lions during their routine park drives. However, unlike in the 2018 survey, they were not permitted to drive off-road. The third survey was carried

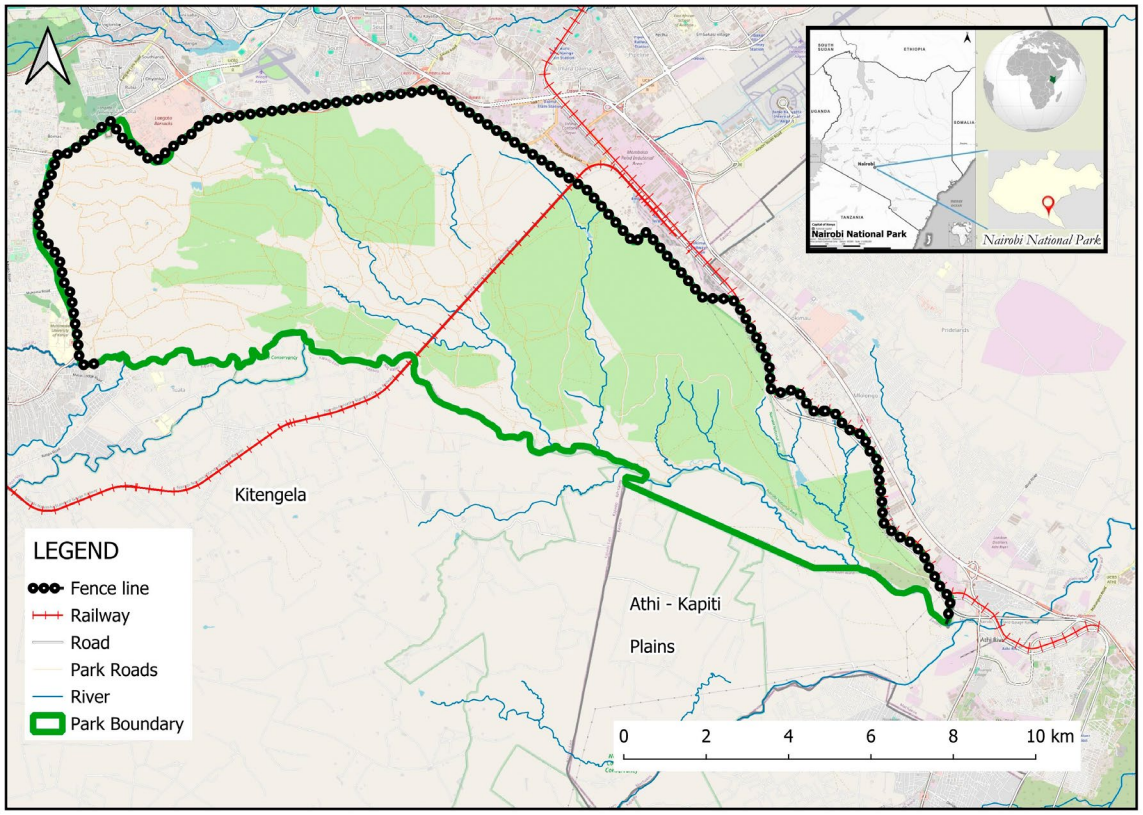

FIGURE 1 Study area—Nairobi National Park.

out over 10 days in a dry season of 2022. This survey was also overseen by members of the first survey and was part of a 10-day training workshop. Consistent with the 2021 survey, participants did not drive off-road. Although the three surveys differed in terms of personnel and fieldwork design, all were conducted using a search–encounter survey approach (Elliot et al., 2020; Elliot & Gopalaswamy, 2017) designed for analysis within an SECR framework (Royle et al., 2009). During all three surveys, when lions were sighted, wherever possible, a series of close-up photographs were taken of each individual from different angles so as to acquire records of their unique whisker vibrissae spots (Pennycuick & Rudnai, 1970). Each individual was then assigned a unique ID. Sex was assigned based on secondary sexual characteristics, and age was estimated based on phenotypic features, such as body size, shoulder height, nose pigmentation and mane development (Miller et al., 2016). Since lion mortality is typically high during the first year (Packer et al., 1988), all individuals estimated to be less than 1 year of age were excluded.

All lion sightings were recorded using an android smartphone installed with a customised application (www.cybertracker.org) set to automatically record a GPS point every 10 s for accurate recording of the search effort. Since the primary objective of the fieldwork was to uniformly cover the study area and individually identify as many lions as possible, as many times as possible (Elliot et al., 2021), teams were regularly advised which area in NNP required more attention given the previous coverage. Figure 2 shows maps of search effort for each survey, illustrating how coverage was distributed across the park and ensuring that effort was not biased towards certain areas. Each team uploaded the data (sightings, search effort and photographs) daily to a central database. Photographs were sorted chronologically and into separate folders for each individual. Individual ID catalogues were created for each individual, and individuals were differentiated based on their whisker spots. For subsequent sightings, if the whisker spots matched an existing ID catalogue, it was classed as a recapture, whereas if the whisker spots did not match any existing ID catalogue, it was classed as a new individual and assigned a new ID and catalogue. To help ensure accuracy of the capture history, each detection was then validated by two observers who worked independently and discussed any discrepancies.

2.3 | Data analysis

For each survey, we estimated the spatial lion density in NNP using a Bayesian SECR model as detailed by Elliot and Gopalaswamy (2017). First, we created a 20 km buffer around NNP. We then generated equally spaced pixels (0.25 km^2) representing potential activity centres across the state space (2494 km^2) and masked out urban areas as unsuitable habitat (Figure S1). The data augmented upper bound of lion abundance (M) was set at 300, representing the maximum number of lions possible within the state space. The state process includes a model component notated as $[N|M,\psi] \sim \text{Binomial}(M,\psi)$ for

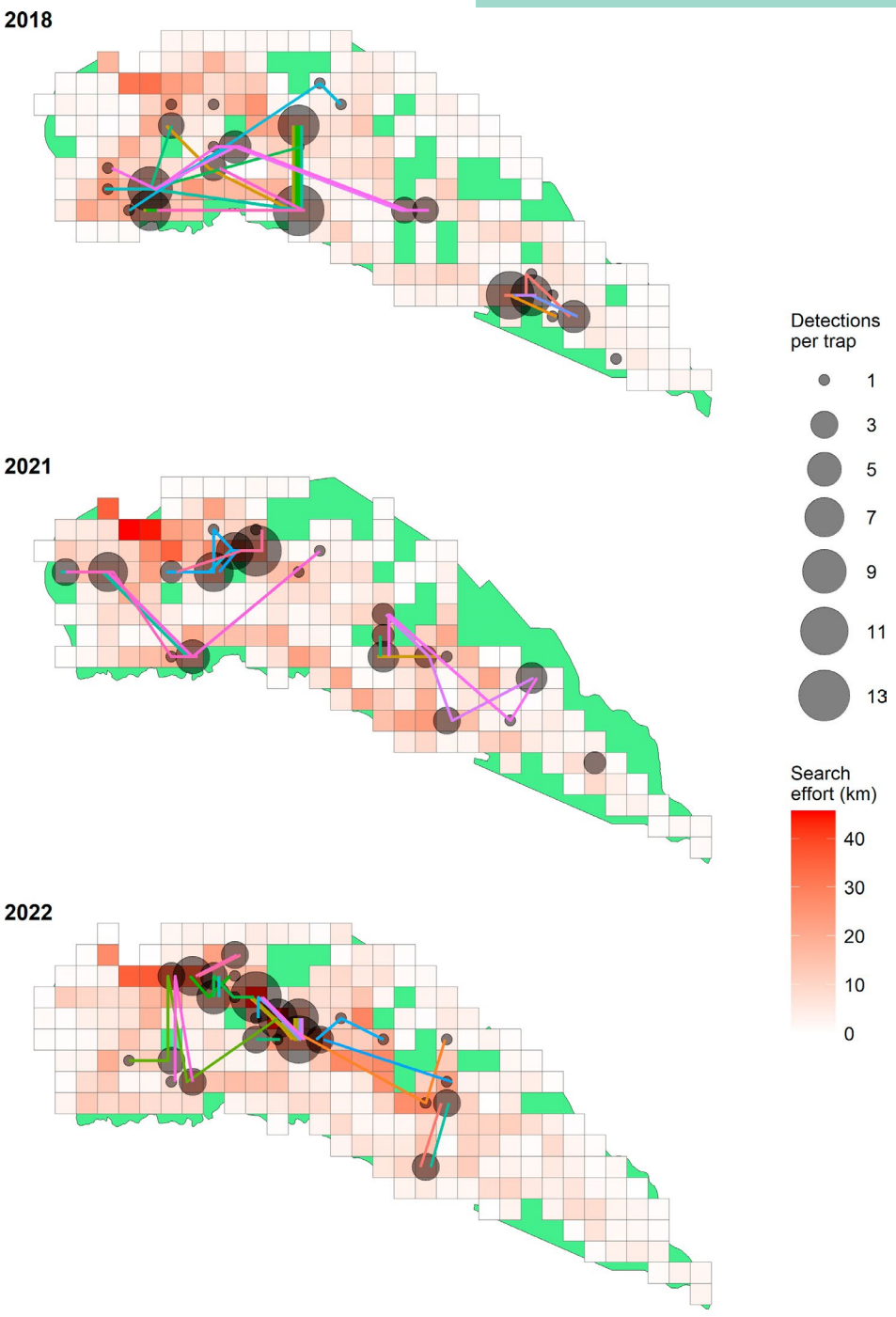

FIGURE 2 Survey effort in Nairobi National Park for 2018, 2021 and 2022, respectively. Unstructured spatial sampling protocol was used to locate and identify individual lions. The spatial capture–recapture sampling design accounted for search effort per grid cell (0.5 km^2 pixels) per sampling occasion (1 day). Coloured lines connecting detections represent spatial recaptures of individual lions.

estimating the abundance of lions (N), where ψ is the probability that an individual chosen from a fixed M is a member of the population. The activity centres of M individuals were assumed to be located within R pixels of suitable habitat following a multinomial distribution. Each individual was assigned a prior occupancy probability of 1/R (Royle et al., 2013).

We followed the methodology detailed in Elliot and Gopalaswamy (2017) to describe how individuals were detected during each of the surveys (observation process). A standard spatial capture–recapture array was compiled (Gopalaswamy et al., 2012) consisting of individuals, trap locations (defined by pixels of 0.5 km^2) and sampling occasions. To account for a potential bias that may arise from uneven sampling of traps, we included an effort covariate (logarithm of kilometres driven) per trap per day. Sex-specific covariates were included when defining the observation process, by specifically accounting for different detection

probabilities between males and females, and we additionally estimated the sex ratio.

2.4 | Candidate models

For each survey four a priori models were defined that assumed (1) the basal encounter rate (λ_0) and the rate of decline in detection (σ) are sex-specific; (2) λ_0 is not sex-specific but σ is sex-specific; (3) neither λ_0 nor σ is sex- specific; and (4) λ_0 is sex-specific but σ is not. The search–encounter protocol (effort) was included in each candidate model, measured on a logarithmic scale. Additionally, the detection function parameter (θ) was fixed to 1, which implies a half-normal detection function. The probability of detecting lion i in pixel j on sampling occasion k (π_{ijk}) is defined by a complementary log–log function of covariates (Elliot & Gopalaswamy, 2017):

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

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

We ran the models using R version 4.2.0 (R Core Team, 2022), using the same priors as Davis et al. (2025) and the code provided by 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. Each model was set to run for four chains, each with 151,000 iterations. We discarded outcomes from the first 1000 iterations as burn-in. We visually inspected trace plots, and assumed models had converged if the mean potential scale reduction factor for each parameter was <1.05 (Gelman & Rubin, 1992), and discarded more initial iterations as burn-in if convergence was not achieved. To select a model for reporting, first we checked each model for adequacy using the Bayesian p-value assessment based on individual encounters (Royle et al., 2009). This tool was used to reject any model whose Bayesian p-value lay outside the extremities (0.15–0.85). Next, to infer upon potential parameter redundancy relating to model overfitting relative to sample size, we visually inspected pairwise correlation plots between estimated parameters, where we were most interested in correlations involving the density parameters. We also estimated the marginal likelihood using the harmonic mean estimator (Dey et al., 2019). However, as recommended by Samarasinghe et al. (2022), we did not rely on the resulting inference since we encountered difficulties in achieving consistency in the Geweke diagnostic.

We inferred movement of lions based on the σ parameter, which is sex-specific. We also calculated the posterior mean and standard deviation of the overall weighted movement parameter (σ_w), weighted by the sex ratio, incorporating both male and female lions. To obtain the posterior draws of σ_w, we used the posterior draw values of male and female movement (σ_{male} and σ_{female}) along with the proportion of males (ψ_{sex}), applying the formula:

$(1-\varphi_{sex})\sigma_{female} + \varphi_{sex}\sigma_{male}$. This approach ensures that the movement parameter is appropriately weighted based on the sex ratio of the population.

2.5 | Posterior mean abundance

For all iterations of the MCMC outputs, we summed all pixels within the NNP boundary and computed posterior mean abundance, standard deviations (PSD) and 95% highest posterior density intervals (HPD). This was possible to do because the Bayesian model we utilised preserved the lion activity centres as latent variables. For each survey, we computed a sex-weighted mean of the estimated movement parameters $(\sigma_{male}, \sigma_{female})$ and multiplied this value by $\sqrt{X^2_{0.05,2}} \times \sigma$, yielding a radius that encompasses approximately 95% of individual movement outcomes around a trap (Royle et al., 2013). All traps were then buffered by this radius, and the union of these buffers was used to define the area over which density was plotted.

3 | RESULTS

All three surveys produced relatively robust datasets for SECR analysis, with high numbers of detections per identified individual and mean spatial recaptures per lion exceeding 2.4 in each survey. Data summaries are provided in Table 1. These data help to identify survey-specific detection parameters separately from density. The mean distance moved and the mean maximum distance moved by lions was higher during the wet season.

3.1 | Model diagnostics

All models converged with 150,000 iterations, except for model 1 of the 2018 survey. For this specific case, an additional post-hoc burn-in of 7000 iterations was required to ensure convergence. The mean potential scale reduction factor for each parameter across all models and surveys was consistently at or below 1.02, suggesting that all models converged. Across all models, the Bayesian p-value ranged 0.45–0.82 reflecting acceptable goodness-of-fit (Table S1). We report posterior parameter estimates for model 2 since visual inspection of the pairwise correlation plots between estimated parameters from the posterior MCMC draws indicated the least parameter redundancy for this model across the surveys (see Appendix 3).

3.2 | Lion density and movement

The mean lion density (lions/100 km^2) inside the park was considerably higher during the dry seasons in 2021 (26.90, PSD = 6.61) and 2022 (27.74, PSD = 6.61) compared with the wet season in 2018 (18.52, PSD = 4.62). Consequently, mean lion abundance within the

TABLE 1 Summary of the data collected during three lion surveys in Nairobi National Park. All surveys were conducted using a search–encounter protocol designed to find and identify individual lions so that the resulting data could be used in spatially explicit capture–recapture (SECR) models. These summaries relate only to lions over the age of 1 year.

	2018	2021	2022
Season	Wet	Dry	Dry
Prey	Dispersed	Concentrated	Concentrated
Survey dates	08 October–09 November 2018	08 July–22 August 2021	7–14 November 2022[a]
Survey length	33 days	46 days	8 days
Search–encounter effort	1377 km	1548 km	1822 km
Individual lions identified	22	20	20 (2 unknown sex)
Males	8	5	9
Females	14	15	9
Lion detections	63	69	57
Km driven per detection	22	22	32
Number of recaptures	41	49	37
Individuals recaptured	18	12	20
Individuals at >1 trap	18	11	20
Males at >1 trap	6	5	9
Females at >1 trap	12	6	9
Avg. spatial recaptures	2.64	2.35	2.70
Mean distance moved (MDM)	3608 m	1873 m	1614 m
Mean Max distance moved (MMDM)	4929 m	3386 m	2048 m

[a]In 2022 the rains began after the survey ended hence the classification as dry season.

park was also higher during the dry seasons (Table 2) when lion activity centres were more centrally located within the park boundary (Figure 3), indicating notable temporal variation.

Overall, σ_w (which is indicative of within-season movement, in km) was largest during the wet season (2018: 3.38, PSD = 0.7) compared with the dry season (2021: 1.38, PSD = 0.2; 2022: 1.44, PSD = 0.2; Figure 4). Similarly, for females, movement was greater in the wet season of 2018 (3.01; PSD = 0.82) than in the dry seasons of 2021 (1.18; PSD = 0.17) and 2022 (1.6; PSD = 0.25). Males also had larger movement in the wet season of 2018 (4.62; PSD = 0.99) compared with the dry seasons of 2021 (2.52; PSD = 0.41) and 2022 (1.34; PSD = 0.23; Table 2 and Figure 4).

The sex ratio varied across the years with the highest female to male ratio being in 2021 (5.6♀: 1♂, Table 2).

4 | DISCUSSION

Our study demonstrates the potential of using SECR to generate robust and comparable estimates that are ecologically meaningful and relevant to management, even when using different data collection strategies. This is important since limited resources often mean that survey timing is opportunistic and having flexibility in data collection strategies creates more opportunities for conducting surveys. However, this flexibility should be accompanied by scientific oversight to ensure that survey design and data quality remain rigorous and comparable across sites and years. This further strengthens the case for the use of the SECR framework as a national monitoring strategy for lions (Ngene et al., 2023).

Our study was limited by the number of seasonal surveys (i.e. one wet and two dry seasons), which may constrain the strength of inference about seasonal dynamics and conflict risk, and additional seasonal replication would be required to conclusively disentangle seasonal effects from inter-annual variation. Nevertheless, the available data support our interpretations, and because detection is allowed to vary among surveys, it is unlikely that systematic biases in density estimates are driven solely by data collection strategy. Our SECR results show an inverse relationship between estimated density and lion movement (σ), that is when density within the park is low, σ is relatively high, and when density increases, σ decreases. Therefore, we do not attribute the low density and abundance observed in 2018, and the considerably higher estimates in 2021 and 2022 to an increase in the lion population. Instead, we interpret these differences in density and space use as consistent with previous GPS telemetry studies that found seasonal changes in lion home-range size and movements (Lesilau et al., 2021).

During the wet season, lions increased their movement, often leaving the park and venturing into neighbouring community lands (Chege et al., 2025; Lesilau et al., 2021). Furthermore, our results show that lion movement was substantially larger in the wet season than in the dry season. This is reflective of the seasonal dynamics of the ecosystem: large herbivores concentrate inside the park during the dry season, while during the wet season, the emergence of seasonal wetlands and the presence of more productive and nutrient-rich grasses drive the herbivores to disperse towards the southern boundary and further beyond the park boundaries (Owino et al., 2011). During these wet periods, lion home ranges expand to accommodate the distribution of prey. This phenomenon is evident in our estimates of sigma, which were larger during the wet season, and also in the observed seasonal shifts in lion activity centres. Lesilau (2019) found that when these shifts occur and when lions follow prey beyond the park boundaries, during the wet season, they may encounter livestock, which can lead to livestock depredation. These depredation events are more common during the wet season (Lesilau, 2019) and often result in the retaliatory killing of lions, and in this ecosystem more than 20 cases have been reported over an 11 year period between 2011 and 2022 (KWS, unpublished records). Negative interactions between people and lions pose an ongoing threat to this lion population, which is further threatened

TABLE 2 Posterior estimates of parameters estimated by Model 2 [$\beta_{sex} = 0$ (fixed), $\theta = 1$(fixed)], HPD = 95% highest posterior density intervals for each estimate, PSD = posterior standard deviation. These results relate only to lions over the estimated age of 1 year.

		2018 (wet season)			2021 (dry season)			2022 (dry season)		
Parameter	Definition	Posterior mean	PSD	95% HPD	Posterior mean	PSD	95% HPD	Posterior mean	PSD	95% HPD
σ_F	Rate of decline in detection probability with increasing distance between a female lion's activity centre and the centroid of a sampled grid cell	3.01	0.82	1.83–4.71	1.18	0.17	0.87–1.53	1.6	0.25	1.16–2.1
σ_M	Rate of decline in detection probability with increasing distance between a male lion's activity centre and the centroid of a sampled grid cell	4.62	0.99	2.91–6.61	2.52	0.41	1.81–3.34	1.34	0.23	0.93–1.8
β_{eff}	The rate of change in the complementary log–log value of detection probability as the (log) effort changes by one unit, where effort is measured in kilometres	2.09	0.26	1.58–2.61	1.66	0.21	1.26–2.07	1.67	0.22	1.24–2.11
λ_0	The basal encounter rate of a lion whose activity centre is located exactly at the centroid of a grid cell	0.0057	0.0015	0.0030–0.0086	0.0098	0.0028	0.0048–0.0154	0.0043	0.0017	0.0015–0.0078
ψ	The ratio of the true number of individuals in the population compared with the data augmented population *M*	0.3	0.08	0.15–0.46	0.44	0.11	0.24–0.66	0.45	0.11	0.26–0.67
N_{super}	The total number of lions in the larger state space *S*	90.32	22.53	48–133	131.21	32.24	72–194	135.30	32.24	76–198
ψ_{sex}	The proportion of lions that are male	0.28	0.11	0.08–0.50	0.15	0.07	0.03–0.29	0.54	0.14	0.28–0.8
D	Estimated density of lions >1 yr. /100 km^2	18.52	4.62	10.25–27.68	26.90	6.61	14.76–39.77	27.74	6.61	15.58–40.59
Abundance	Number of lions within Nairobi National Park	19.52	4.97	8–28	30.44	6.13	20–42	32.64	6.032	22–44
Sex ratio	Derived from ψ *sex* (1- ψsex/ψsex)	2.6♀: 1♂			5.6♀: 1♂			1♀: 1♂		

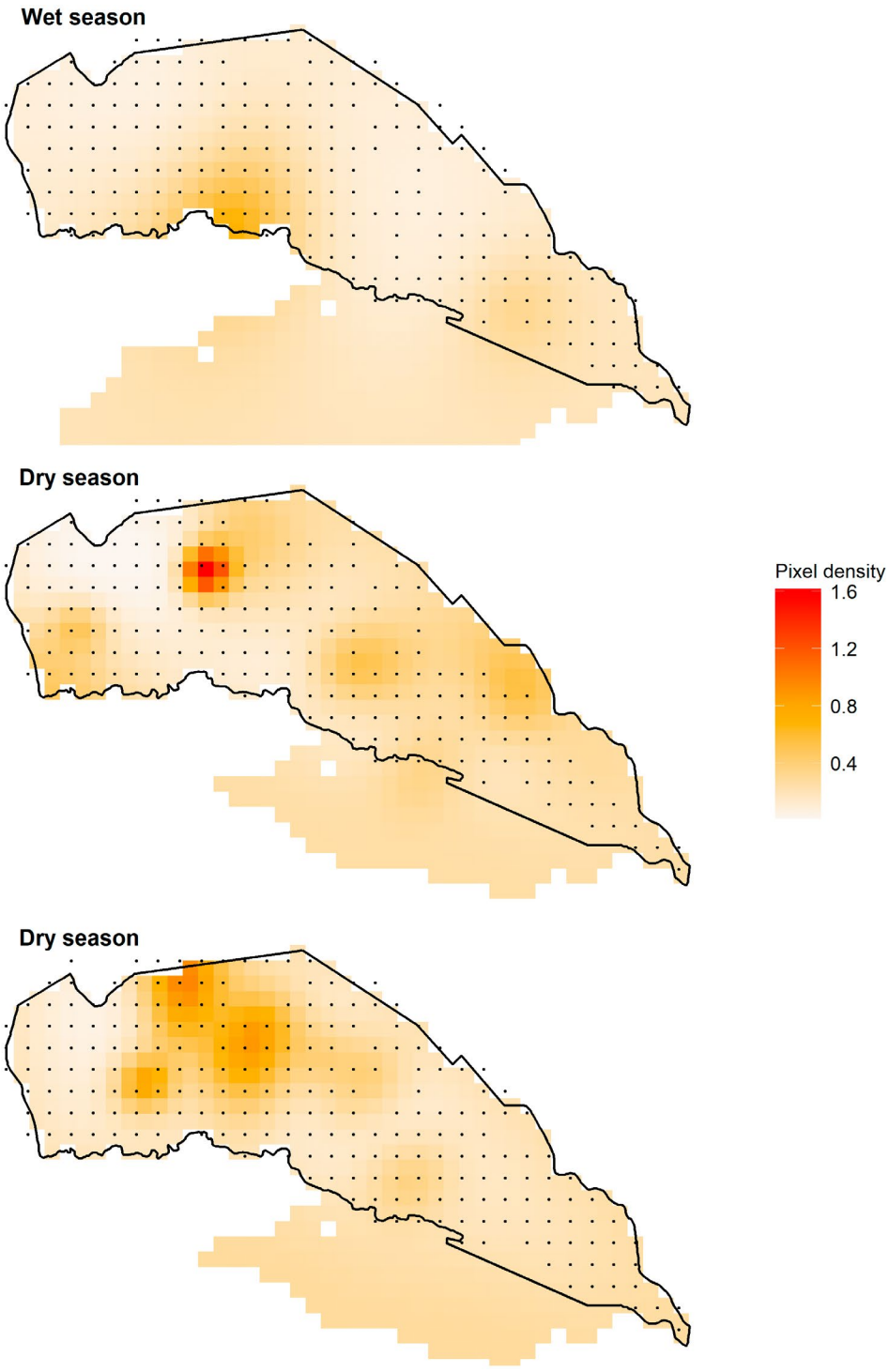

FIGURE 3 Pixel-specific lion density in Nairobi National Park, Kenya, derived from model 2 for 2018 (wet season), 2021 and 2022 (dry seasons), respectively. NB: For each survey, density was plotted within a buffer equal to 2.44 times the sex-weighted sigma; pixels outside buffer were omitted.

by habitat loss driven by the expansion of human settlements and development activities both inside and outside the park (Mwangi et al., 2022; Wandaka & Francis, 2019). It is worth noting that the lion population has remarkably remained stable for almost six decades. Similar to our survey, previous studies have estimated the lion population to oscillate between 25 and 35 individuals (Lesilau, 2019; Rudnai, 1973). Since the previous studies were simply a tally of all known individuals, and did not account for imperfect detection or measure their search effort, we cannot directly compare our estimates to theirs, but suggest that their figures are credible given the small size of NNP and the intensive nature of those studies. While this is remarkable given the enormous growth that Nairobi city has

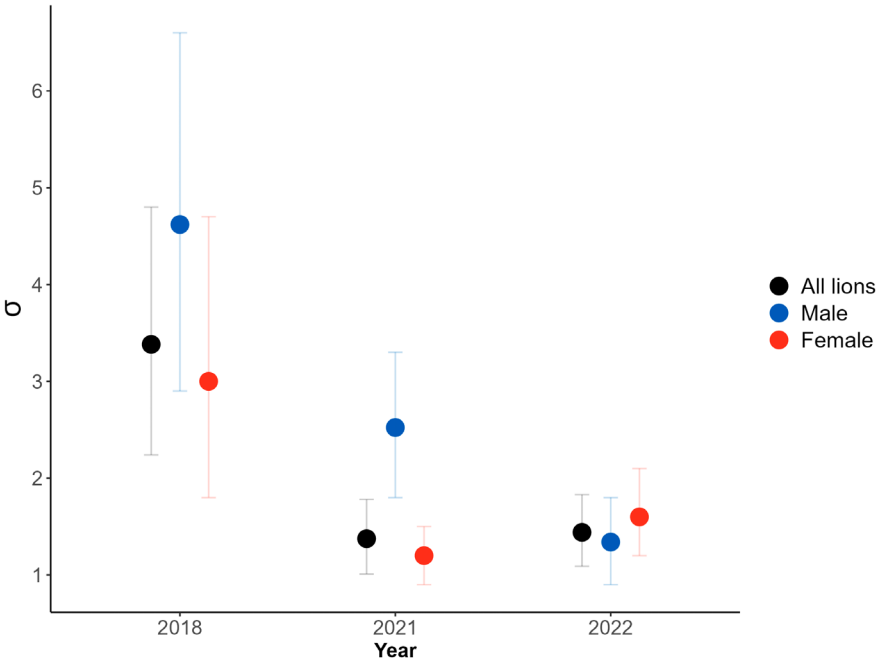

FIGURE 4 Plot showing the variation in σ (related to lion movement) across the three surveys for all lions, male and female lions. Error bars represent the 95% Highest Posterior Density intervals.

experienced during this period, a recent study found signs of genetic degradation due to the increasing movement restriction (Chege et al., 2024), further highlighting the vulnerability of this population, despite stable population numbers.

The Athi-Kapiti plains (Figure 1) were once vital to the health and stability of wildlife populations in the park (Owino et al., 2011); however, persistent land-use changes and increased human activities have transformed the plains into a high-risk area for both wild herbivores and lion populations due to conflicts and poaching (Kenya Wildlife Service, 2020b; Reid et al., 2008). Our results, which are supported by previous studies, suggest that lion activity centres shift seasonally, and that for some lions these plains may be vital for movement and survival. The NNP management plan 2020–2030 recommends securing dispersal areas outside the park and increasing community partnerships (Kenya Wildlife Service, 2020b). The plan proposes fencing sections close to high-density residential areas and, where land uses are compatible, establishing a buffer zone along the open southern section by fencing in willing private landowners. The plan also proposes providing support to the community to create viable community conservancies in the remaining dispersal areas. Therefore, noting the importance of these plains for the lion population, management efforts should prioritise efforts that facilitate lion movement and connectivity. This will also be critical for maintaining the genetic diversity of this lion population (Chege et al., 2024). We also recommend the establishment of a well-equipped and strategically placed conflict response unit during the wet seasons, an early warning system (conflict) through use of animal tracking technologies, and a regular long-term lion monitoring programme that will evaluate the effectiveness of implemented measures.

We note that the sampling period for the 2022 survey was substantially shorter than the first two surveys, and that estimates of σ are relative to this. Additionally, we found that male lions covered larger distances than females. However, in 2022, the movement of female lions was larger than that of males, but this is largely because six of the nine males detected during this survey were dependent offspring (See Table S2). Generally, male lion movements are larger as their movement is dependent on both food resources and the need to access and defend female prides, while female movements are influenced by access to resources (Schaller, 1972). Chege et al. (2025) and Lesilau et al. (2021) fitted GPS collars to lions in the same ecosystem and reported similar seasonal and sex-specific variation in lion movement. Similar patterns have been reported for lions in Amboseli NP, Kenya (Tuqa et al., 2014) and in Hwange NP, Zimbabwe (Loveridge et al., 2009). In Kenya's Maasai Mara, cheetahs displayed a similar pattern where sex-specific densities and space use varied according to large herbivore seasonal migrations (Broekhuis et al., 2021).

The estimated sex ratio fluctuated drastically across the surveys (2018: 2.6♀: 1♂, 2021: 5.6♀: 1♂, 2022: 0.8♀: 1♂), and it is important to note that these quite closely mirrored the shifts in our observed sex ratios (2018: 1.8♀: 1♂, 2021: 3♀: 1♂, 2022: 1♀: 1♂). In a small population such as Nairobi's, such variation is expected, because a single cohort or litter with a skewed sex ratio can strongly influence the population-level ratio. Our counts also include all individuals older than 1 year, rather than only fully adult animals, so they are not directly comparable to a 'typical' adult lion sex ratio (often ~2 females: 1 male). As visible in Table S2, the 2018 and 2021 surveys include several female-heavy cohorts in the Northern (KIN) pride, whereas the 2022 survey adds multiple young males from the KINe and EASM male groups, plus a mixed-sex litter in the Southern pride. In a population of this size, the appearance or disappearance of such cohorts readily shifts the apparent sex ratio without implying a strong directional demographic trend. In addition, since sample sizes

are modest relative to all the parameters being estimated, we emphasise that the model-based sex ratios should be interpreted with caution.

Detection rates and the spatial scale parameter showed significant variation across the three surveys. This highlights the importance of using SECR models, which hierarchically separate the state process from the observation process. Such models provide a robust framework for directly inferring density and space use, enabling researchers to estimate animal populations more accurately, regardless of the data collection method employed (Elliot et al., 2021; Royle & Converse, 2014). The adaptability of this framework allowed us to use the three alternative data collection strategies that were convenient at the time of undertaking each survey. However, it is worth noting that SECR models rely on sufficient spatial recaptures to provide reliable estimates of detection parameters, movement and ultimately animal density (Borchers & Efford, 2008). When recaptures are sparse, for example, due to low population density, limited survey effort or uneven spatial coverage, estimates of movement and detection probability can become imprecise and biased, which in turn affect density estimates (Schmidt et al., 2022). Additionally, in closed populations, SECR models assume demographic closure during each survey period and consistent detection processes across survey areas. Violations of these assumptions compromise inference, particularly when spatial recaptures are few (Schmidt et al., 2022; Tourani, 2022). Therefore, in areas where population data may be low or in poorly designed sampling situations, SECR-derived density estimates should be interpreted with caution. In our study, despite having a small population, all three surveys produced relatively strong data (mean spatial recaptures per individual >2.4 and high detections per identified lion), which increases confidence in the resulting estimates. In a recent study, Ball et al. (2023) conducted post-hoc analyses to guide the minimum resource requirements for future search–encounter–based SECR surveys in Pilanesberg (South Africa) aimed at obtaining accurate and precise estimates of the principal parameters of interest. These recommendations were subsequently implemented by Davis et al. (2025) using a reduced search–encounter effort. However, because the strength of inference in our study was only marginally adequate, we do not expect a comparable reduction in effort to improve sampling efficiency unless λ_0 can be lowered.

Furthermore, we clarify that the observed variations in Nsuper (Table 2) do not necessarily reflect a true increase in lion population abundance across the larger state space. Instead, this variation is likely a result of our sampling area being restricted to within the park boundary; therefore, it may largely reflect the changes in local abundance and density within the park. We anticipate that we will observe stability in global abundance if we include spatial covariates in the model and sample outside the park in the future.

Many protected areas in Kenya and across Africa are underfunded and lack long-term monitoring programmes (Lindsey et al., 2018). We therefore propose adaptive options for establishing such programmes for lions and other species that are driven by partnerships between government agencies, conservation organisations and local communities. By involving wildlife enthusiasts, expenses for equipment (e.g. cameras) and operational costs (e.g. fuel) were minimised, as participants conducted the surveys during their routine game viewing activities thus reducing the financial burden on management. Similarly, the first survey shared costs through collaboration with NGOs and the third combined a robust monitoring exercise with capacity building through a training workshop. By harnessing public support and resources alongside scientific leadership, managers and researchers in parks, such as NNP, that have a high number of tourists can generate accurate wildlife population estimates, monitor trends, while also encouraging public participation and transparency in conservation activities (Dagorne et al., 2020; Rafiq et al., 2019). In areas with fewer tourist visitations, regular programmes with local communities, education institutions and conservation stakeholders can be incorporated to contribute to wildlife population monitoring (Dagorne et al., 2020).

To ensure accurate and reliable data collection, regular training sessions are essential for effective implementation of monitoring programmes. Small parks such as NNP provide an ideal training ground to conduct workshops and our 2022 survey serves as an example of how to meet the dual needs of regular training and regular monitoring. As such, we anticipate that an annual workshop in NNP would be instrumental in knowledge growth and that this model could be replicated in other similar small parks.

AUTHOR CONTRIBUTIONS

Mumbi Chege, Nicholas B. Elliot, Elphas Bitok, Linus Kariuki, Femke Broekhuis and Arjun M. Gopalaswamy conceived and designed the study. Mumbi Chege, Nicholas B. Elliot, Elphas Bitok, Nadia de Souza and Femke Broekhuis led data collection and management, with Mumbi Chege, Nicholas B. Elliot, Femke Broekhuis and Arjun M. Gopalaswamy analysing the data. Laura D. Bertola, Hans H. de Iongh and Geert R. de Snoo supervised the process. Mumbi Chege led the writing, with all authors providing input and contributions.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

All input files and R scripts to reproduce our analysis are available at: https://doi.org/10.5061/dryad.vt4b8gv6t (Chege et al., 2026).

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SUPPORTING INFORMATION

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

Figure S1. The state space (2494 km^2). Map showing the 20 km buffer created around the survey area to demarcate the state space. Potential activity centres were represented by equally spaced pixels (0.25 km^2) – suitable lion habitat. Areas of unsuitable for lions were masked prior to analysis (grey area).

Table S1. Model specification and diagnostics for Models 1–4 years 2018, 2021 and 2022.

Table S2. Number of individual lions recorded per sampling year in Nairobi National Park.

Figure S2. (I–IV). Correlation plots for 2018 – wet season survey.

Table S3. (i–iv). Posterior estimates of parameters for Models 1–4 for 2018 survey (wet season).

Figure S3. (V–VIII). Correlation plots for 2021 – dry season survey.

Table S4. (v–viii). Posterior estimates of parameters for Models 1–4 for 2021 survey (dry season).

Table S5. (ix–xii). Posterior estimates of parameters for Models 1–4 for 2022 survey (dry season).

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