

RESEARCH ARTICLE

Detecting early warnings of pressure on an African lion (*Panthera leo*) population in the Queen Elizabeth Conservation Area, Uganda

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Abstract

1. African lions are declining across much of their range, yet robust measures of population densities remain rare. The Queen Elizabeth Conservation Area (QECA; 2,400 km²) in East Africa's Albertine Rift has potential to support a significant lion population. However, QECA lions are threatened, and information on the status of lions in the region is lacking.
2. Here, we use a spatially explicit search encounter approach to estimate key population parameters of lions in the QECA. We then compare home range sizes estimated from our models to those from a radio-collaring study implemented a decade earlier.
3. We recorded 8,243.5 km of search effort over 93 days, detecting 30 individual lions (16 female and 14 male) on 165 occasions at a rate of 2 lion detections/100 km². Lion density in the QECA was 2.70 adult lions/100 km² ($SD = 0.47$), while mean abundance was 71 individuals ($SD = 11.05$).
4. Worryingly, the movement parameter for male lions was 3.27 km and 2.22 km for females, suggesting > 400%, and > 100% increases in home range size, respectively, compared to a decade earlier. Sex ratio of lions in the QECA was lower (1 male: 0.75 females), when compared to a previously published review (mean = 1:2.33).

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5. The large movements and skewed sex ratios we report on in this paper are likely a result of human-driven prey depletion. Our results suggest lions in the QECA are in a precarious state, and the lion densities are significantly lower than what they could be.
6. As lions are under pressure throughout much of Africa, our study presents the utility of a census technique that could be used elsewhere as an early warning of lion declines.

KEYWORDS

Bayesian spatially explicit capture-recapture, big cat, density, East Africa, felid, lion, *Panthera leo*, population size, Uganda

1 | INTRODUCTION

The African lion (*Panthera leo*) is listed as an Appendix II species under both the Convention on the International Trade of Endangered Species (CITES; Bauer, Packer, Funston, Henschel, & Nowell, 2016) and Convention on the Conservation of Migratory Species of Wild Animals (CMS). Estimates place the continental population at ~25,852 individuals (range 20,000–30,000) in 102 populations residing in approximately 2.5 million km² (along with 628 in fenced reserves across South Africa; IUCN SSC, 2018). The key threats to African lion populations include (1) habitat degradation and modification, (2) reduction of lion prey through ‘bushmeat’ poaching and (3) human–lion conflict mainly between lions and cattle farmers who kill lions in retaliation for stock depredation (IUCN SSC, 2018). These threats are amplified through weak governance and in many places a lack of resources, which may be both human and financial (Lindsey, Balme, Funston, Henschel, & Hunter, 2016, 2018).

The East African state of Uganda, and its lions, serves as an important case study of the challenges facing the species in many parts of the continent. Lions are listed as critically endangered on the national red list of Uganda (WCS, 2016) and are known to occur in three of its largest national parks (Murchison Falls, Queen Elizabeth and the Kidepo Valley; Omoya, Mudumba, Buckland, Mulondo, & Plumptre, 2014; Uganda Wildlife Authority, 2010). The Queen Elizabeth Conservation Area (comprising the National Park and the Kyambura and Kigezi Game Reserves) has been viewed as one of Uganda’s lion strongholds (Omoya et al., 2014). The park was gazetted in 1952, and large mammal surveys in the 1960–1970s revealed it had the densest herbivore biomass on earth (18,800–19,928 kg/km²), being ranked first out of 24 African sites (Bourlière, 1965; Coe, Cumming, & Phillipson, 1976). However, after Uganda gained independence, state-level resource management declined rapidly, and the Idi Amin and Milton Obote regimes (1971–1985) brought on widespread political instability and poaching, which decimated much of the regions’ wildlife (Edroma, 1986; Lamprey & Michelmore, 1996). Political stability returned to Uganda in 1986, but years of poaching and unrest seemed to have contributed to a large mammal collapse in the park (Chritz, Blumenthal, Cerling, & Klingel, 2016; 1980, 1980). A radio-

collaring study implemented from 2006 to 2011 showed that the home range sizes of lions had expanded, and pride size had decreased in the Queen Elizabeth Conservation Area (QECA) since the 1970s, suggesting that lions were moving further in search of food (Mudumba, Omoya, Mustafa Nsubuga, & Plumptre, 2015). This suggested lions too were impacted by the large-scale decimation of prey species during the period of political instability. However, recent aerial census data suggest that prey populations have been slowly recovering since 1986 (Lamprey, 2018; Plumptre, 2012; Plumptre et al., 2010, 2014).

Despite being appreciated as a flagship species that generates significant revenue for the tourism sector (lions in the QECA each generate at least US\$ 14,000 annually from ecotourism revenue; Plumptre & Roberts, 2006), lion populations in Uganda have not been monitored consistently over time. The history of monitoring lion populations in the park has ranged from total counts of lion sightings from intensive field surveys (e.g. Driciru, 1999; Van Orsdol, Hanby, & Bygott, 1985), expert elicitation (Bauer & Van Der Merwe, 2004) to audio lure counts (Omoya et al., 2014). Moreover, the unusually high detection rates of lions in the QECA, due to their culture of climbing *Euphorbia candelabrum* and sycamore fig *Ficus sycamorus* trees, may have led field workers to be satisfied in applying less-robust lion monitoring methods in the QECA. The use of these different enumeration methods, which often have underestimated and wide confidence intervals, makes robust inference about population trends difficult (Elliot & Gopaldaswamy, 2017).

In this study, we sought to assess the status of African lions in the QECA using rigorous population estimation methods. We directly estimate lion density and other relevant state variables of interest using a newly developed Bayesian spatially explicit capture-recapture (SECR) approach (Royle, Chandler, Sollmann, & Gardner, 2013; Russell et al., 2012), which involves a search-encounter technique to locate and identify individual lions in the landscape, to estimate lion abundance (see Elliot & Gopaldaswamy, 2017). This hierarchical model (see Royle and Dorazio, 2008) helps us jointly estimate key state variables of interest (namely lion density, abundance, sex ratio and sex-specific movement), all in the face of imperfect detection. We then compare the findings from our study to the intensive radio-collaring study by Mudumba et al. (2015). We hypothesised that (1) if lion populations

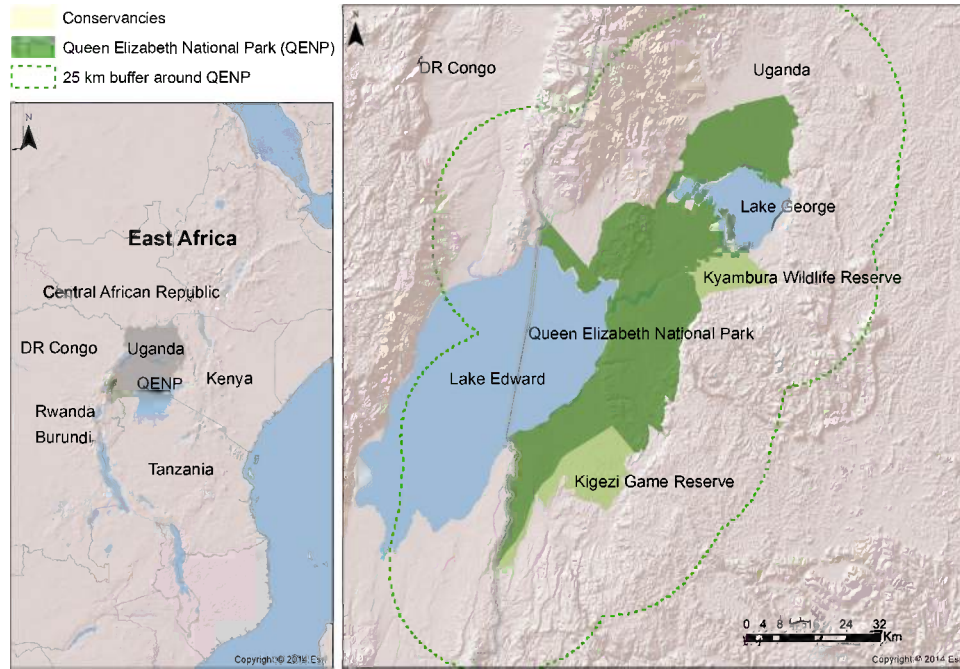


FIGURE 1 The Queen Elizabeth National Park and adjacent Kyambura Wildlife Reserve and Kigezi Game Reserve, collectively representing the QECA. The dashed line represents the 25-km buffer around the QECA

were stable or increasing in the QECA since the study, we would observe similar or decreased home range sizes in our study. However, (2) if lions were declining due to anthropogenic pressures such as prey depletion, home range sizes would increase, and sex ratios of lions would be skewed towards males (when compared to a review of sex ratios by Périquet, Fritz, & Revilla, 2015). Our study highlights the utility of SECR-based search-encounter techniques for assessing the status of African lions, especially where historical information on lion home ranges and movements exist. We suggest this could be used in other African protected areas as an early warning to estimate threats to lions and other individually recognisable species.

2 | MATERIALS AND METHODS

2.1 | Study area

The Queen Elizabeth National Park is in south-western Uganda (Figure 1). It falls within the Albertine Rift Valley, a part of the Eastern Afromontane hotspot, and has the highest diversity of vertebrate species in continental Africa (Plumptre et al., 2007). Queen Elizabeth (1,977 km²) is connected to two nearby protected systems, the Kyambura wildlife reserve in the north (154 km²) and the Kigezi Wildlife Reserve in the south (269 km²), collectively making up the QECA (2,400 km²). The southwest of the QECA and the area north of Lake Edward is also contiguous with Virunga National Park (7,800 km²) in the Democratic Republic of the Congo, and collectively eight national parks, five of which are reserves (Semuliki, Rwenzori, Kibale, Mgahinga, Volcanoes National Park, Bwindi as well as Queen Elizabeth

and Virunga National Park, Kyambura, Kigezi, Kalinzu and Kasyoha-Kitomi) comprise the greater Virunga landscape (Jones et al., 2016), and a globally significant wilderness block (10,000 km²; Allan, Venter, & Watson, 2017). The region has an elevation ranging from 700 to 5,100 m above sea level (Salerno et al., 2018), and two rainy seasons occur in March–May and September–November, totalling 600–1,400 mm per year (Chritz et al., 2016).

The QECA is bisected by the small Kazinga channel, which connects two lake systems (Edward in the west, and George to the east). The area north of the Kazinga channel is dominated by grasslands and wooded grasslands (Wronski, Apio, & Plath, 2006), with dense thickets extending towards the western most park edge. The area south of the Kazinga channel is characterised by wooded grasslands and acacia woodlands (Mudumba et al., 2015) and a large patch of tropical high forest (termed the Maramagambo forest). The main lion prey in the park include Cape buffalo *Syncerus caffer*, Uganda kob *Kobus kob thomasi*, topi *Damalisca lunatus*, warthog *Phacochoerus africanus* and waterbuck *Kobus ellipsiprymnus* (Mudumba et al., 2015).

2.2 | Field methods

Two observers intensively searched the study area for African lions over a 93-day period (10 November 2017 to 10 February 2018). Searches were done daily in a 4 × 4 vehicle. Driving was done on roads and also off-road where access was permitted (Figure 2). The 3-month survey period has previously been used to balance the requirements of population closure and obtaining enough detections for density estimation using spatial capture–recapture (du Preez, Loveridge, &

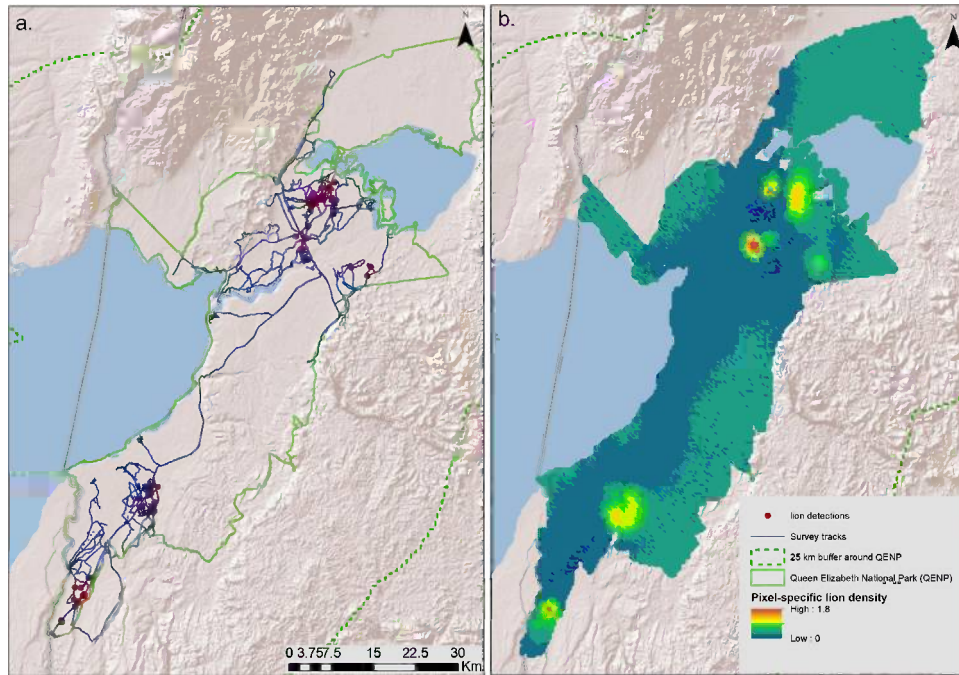


FIGURE 2 Search effort tracks, lion detections and pixel-specific lion densities generated from the search encounter lion survey 10 November 2017–10 February 2018 in the QECA

Macdonald, 2014; Elliot & Gopalaswamy, 2017; Karanth & Nichols, 1998). To measure search effort while driving, we used smartphones loaded with the open source application MapMyDrive (Ring, 2017), which created GPX files of the total kilometres driven per day (all data available online at <https://doi.org/10.5061/dryad.pg4f4qrkn>). Lions in the study area exhibit a rare culture of regular tree-climbing, and rest in the canopy of *Acacia* spp, *Candelabra Euphorbia candelabra* and Sycamore fig *Ficus sycamorus* trees from the early morning till dusk (Mudumba et al., 2015). We therefore searched the study area, scanning both the ground and the upper canopy of the trees with binoculars. When a lion was sighted we collected its GPS location, the time and date it was sighted and the habitat type it was found in. Every lion was photographed with a RED™ EPIC-W video camera or Canon™ 5D Mark III high-resolution camera equipped with a 70–300 mm Canon™ telephoto lens. We took photos of the left and right side of each individual for whisker spot id (Pennycuik & Rudnai, 1970; Figure 3) and also noted ear tears, large scars and for males, their mane development (Miller et al., 2016; Whitman, Starfield, Quadling, & Packer, 2004). We excluded all lions that were evidently < 1 year of age (based on facial scarring, body size and mane development) due to the high mortality in this age class (Packer et al., 1988).

2.3 | Data analyses

We estimated African lion densities and abundance in QECA using our individually identified lion sighting data in a Bayesian SECR modelling framework (Royle et al., 2013). To estimate lion densities over specific sub-regions, we used the posterior distribution of lion activity centres

across our study area defined by equally spaced pixels (centroids being 0.3,975 km apart), resulting in a fine-resolution discrete state space. Thus, a lion's activity centre is defined by a multinomial prior distribution and allows for more than one lion to have its activity centre located at a pixel (see Royle et al., 2013). We used the spatial analyst tool of Arc GIS 9.3 to create a 25-km buffer around the borders of the QECA. This was done to ensure inclusion of all individual lion home ranges within our sampled grid. These were described by 85,028 equally spaced pixels, each representing an area of 0.158 km² within a total state space area of 13,434 km². Areas judged as non-suitable lion habitat (large human settlements, crop-lands and water bodies) were excluded from the buffer (Braczkowski et al., 2016; Mudumba et al., 2015). The remaining, potentially suitable, habitat was hence represented by 37,603 pixels (5,941 km²). The resultant state space was over larger than that used by Elliot and Gopalaswamy (2017) in the Maasai Mara, as we hypothesised lion densities would be lower than the Maasai Mara, and lions would move greater distances in the habitats of the QECA. We used an unstructured spatial capture–recapture sampling design (Russell et al., 2012) and created a standard capture–recapture matrix (trap locations, individual lions and sampling occasions). This allowed us to model the way in which individuals were detected in our lion survey. The ‘traps’ in our study area were represented by 0.158 km² grids of the study area available for searching. We included a covariate to account for search effort per trap per day (natural logarithm of kilometres driven), as some traps with intensive search effort could increase lion detection rates (Elliot & Gopalaswamy, 2017).

Large terrestrial carnivores, including lions, regularly feature individual or group differences in their behaviours. This is most pronounced between the sexes and can affect home range size and

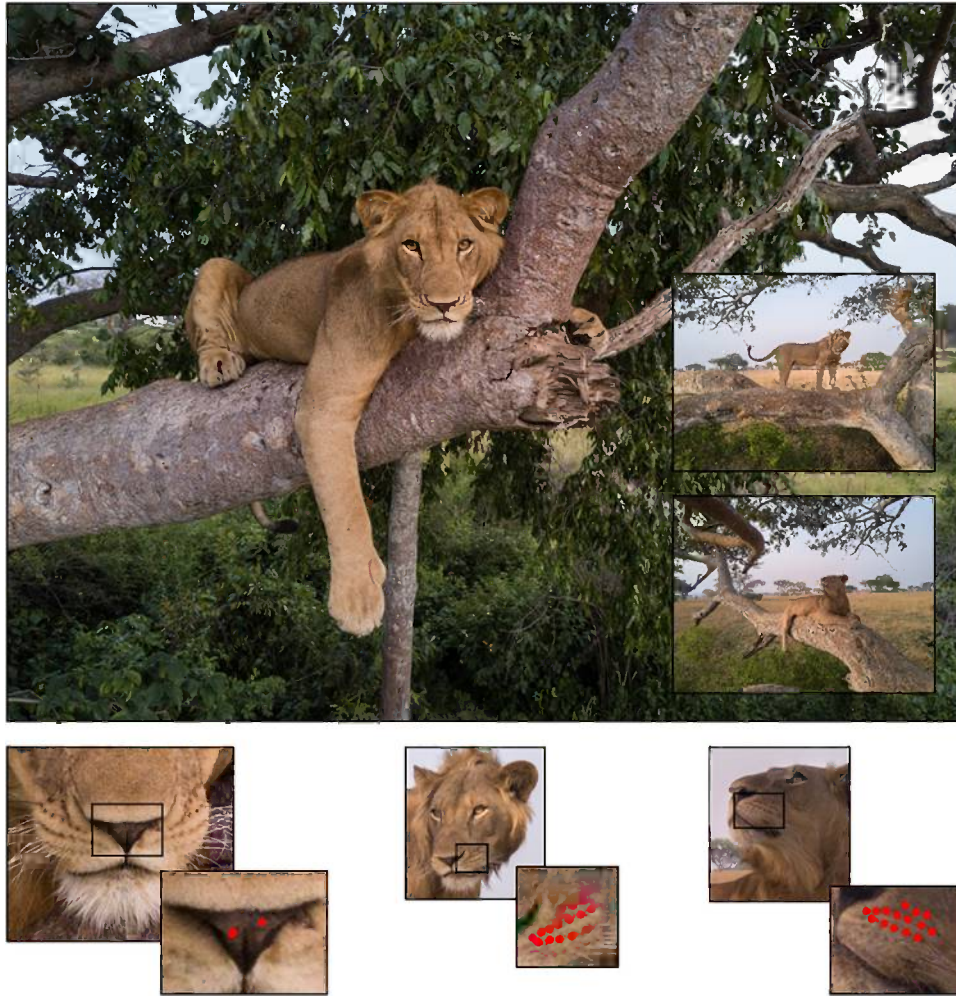


FIGURE 3 Three separate photographs of a young 3–3.5-year old male lion (Jacob – M1) taken in Queen Elizabeth National Park during our 93 day lion survey. We used nose pigmentation and patterning (Whitman et al., 2004), scars, whisker spots (Pennycuik & Rudnai, 1970) and mane development (Miller et al., 2016) to assign individual identities to each of the lions photographed in our survey

capture probability (Karanth & Nichols, 1998) and can affect inference from SECR (Sollmann et al., 2011). To factor this into our modelling, we included a sex-specific covariate in the observation process and accounted for different encounter probability for males and females. Because detection probability of an individual animal declines with increasing distance between its activity centre and the searched pixel, largely due to animal movement, the rate of decline in detection probability σ could be used as a surrogate for movement range. The ϑ (theta parameter), which defines the functional form of the detection function, can be used to infer resource selection for African lions. In our analysis, we estimated ϑ and also fixed it at certain fixed values in our candidate model set. The detection function takes on a negative exponential form when $\vartheta = 0.5$ and a Gaussian form when $\vartheta = 1$. Therefore, in our models, the probability of detecting a lion i in pixel j on sampling occasion k is defined by a complementary log– function of covariates.

To estimate African lion density and abundance, we created seven a priori models and assessed their results (parameter definitions are presented in Table 1). Model 1 was the full model, and it estimated the

detection function (defined by θ) and was based on the assumption that detection probability is sex specific:

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

where $f[\text{dist}(i, j) | \vartheta, \sigma_{\text{sex}}]$ describes how a 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} . The specific form of this detection function is

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

Model 2 was based on the assumption that basal encounter rate is independent of sex; thus, β_{sex} was fixed at 0. Rate of decline in detection probability (σ) remained sex specific (i.e. dependent on sex) because this parameter is also related to animal movement.

TABLE 1 Model parameters, definitions and posterior summaries from our Bayesian SECR density model of African lion density in the QECA where was the full model, and it estimated the detection function (defined by θ) and was based on the assumption that detection probability is sex specific

Parameter	Posterior mean	Posterior SD	Definition
n	30 ^a	-	Total number of lions detected during the survey period
n_z	400 ^b	-	Number of lions augmented to n , so $M = n + n_z$ represents the maximum number of lions in the large state space S
σ_F^c	0.88	0.12	Rate of decline in detection probability with increasing distance between the activity centre of a lioness and the location at which she was found
σ_M^c	1.08	0.14	Rate of decline in detection probability with increasing distance between the activity centre of a lion and the location at which he was found
β_{sex}	0.56	0.32	Difference of the complementary log--log value of detection probability between a male and female lion
β_{eff}	0.99	0.22	Rate of change in the complementary log--log value of detection probability as the (log) effort changes by 1 unit (1 km of drive effort)
λ_0	0.02	0.005	Basal encounter rate of a lion whose activity centre is located exactly at the centroid of a grid cell
ψ	0.37	0.07	Ratio of the true number of individuals in the population compared with the data-augmented population M
N_{super}	160.98	28.05	Total number of lions in the larger state space S
ψ_{sex}	0.57	0.11	Proportion of lions that are female
θ	0.55	0.04	Determines the shape of the estimated detection function; value θ ranges from 0.5 (exponential form) to 1 (Gaussian)
D	2.70	0.47	Estimated density of lions per 100 km ²

^a16 females and 14 males.

^bThe data augmentation value was reduced to 400 after an initial run of 1,500 showed no improvement in estimation of parameters.

^cNote that for comparison of home ranges between the Mudumba study we fitted a model where θ was 1 – we did this as this best approximates the 95% kernel distribution in home-range studies. All raw model results are provided in Supplementary Information 2. When we reran our highest ranked candidate model (i.e. Model 1) setting θ at 1 the male sigma was 3.27 km and 2.22 km for females.

Model 3 was identical to Model 2, but the detection function parameter θ was fixed at 0.75.

Model 4 was based on the assumption that basal encounter rate is dependent on sex; thus, β_{sex} was fixed at 1. Rate of decline in detection probability (σ) also remained sex specific. The detection function parameter θ was fixed at 0.75.

Model 5 assumed basal encounter rate is dependent on sex, but rate of decline in detection probability was independent of sex. The detection function parameter was fixed at $\theta = 0.75$.

Model 6 was based upon the assumption that detection probability is independent of sex and that the rate of decline in detection probability was also independent of sex. The detection function parameter was fixed at $\theta = 0.75$.

Model 7 was the same as model 1, but the detection function parameter was fixed at 1.

To run these models, we used the package SCRbayes (<https://github.com/jaroyale/SCRbayes>) in the programming environment R (R Development Core Team, 2015). We used Bayesian Markov chain Monte Carlo (MCMC) simulation and the Metropolis--Hastings algorithm (Tierney, 1994) to run our models. We set each model to run for 11,000 iterations with a burn-in of 1,000 iterations. Each model was set to run for four chains (Elliot & Gopalaswamy, 2017). If we did not arrive at a stationary distribution, we refined the burn-in period further. MCMC convergence was assessed using the Gelman--Rubin diagnostic (Gelman & Rubin, 1992).

Model adequacy and model selection were determined by examining the Bayesian p -value on individual encounters (Royle, Karanth, Gopalaswamy, & Kumar, 2009), assessing correlations between posterior parameters from the MCMC draws and by examining the Harmonic Mean (HM) estimator of the marginal likelihood of each model (Dey, Delampady, & Gopalaswamy, 2019). As such we did not entirely rely on the marginal likelihood estimate to perform model selection but used this in addition to the model adequacy test and inspection of correlation plots to make decisions on model choice. The five input files necessary to run these analyses and the accompanying R scripts are provided at <https://doi.org/10.5061/dryad.pg4f4qrkn>.

Finally, we utilised the information on lion movements from our models to determine a crude measure of sex-specific lion home range size. We then compared these to the estimates from Mudumba et al. (2015). To do this, we converted the movement parameters (σ) for males and females from the model that gained most support from our model selection process. However, as we wanted to compare range size with that of Mudumba et al. (2015), which represented a 95% kernel distribution, we reran the highest ranked candidate model, setting the θ parameter to 1. This enabled us to make comparisons of home-range estimates with the 95% kernel distribution estimated in Mudumba et al. (2015). To convert sex-specific σ to a measure of home-range size, we used the formula from Calhoun and Casby (1958):

$$\pi(\sigma\sqrt{5.99})^2$$

TABLE 2 African lion detections recorded during the 93-day African lion survey in the QECA

Number of lions in group (or alone)	Number of times detected	Total detections
1	25	25
2	6	12
3	7	21
4	8	32
5	9	45
10	3	30

We used this formula as felid home ranges (and animal species more broadly) approximately assume a circular or semi-circular shape (Bunnfeld et al., 2011; Calhoun and Casby, 1958; Fattebert, Robinson, Balme, Slotow, & Hunter, 2015). We could reasonably assume that this could serve as a minimum home-range estimate. 5.99 is the value from the chi-square table corresponding to an alpha (α) level of 0.05 and 2 degrees of freedom. Two degrees of freedom are considered because movements are represented now by a 'bi-variate' normal distribution, implying movement of lions along both X and Y axes.

Although we were principally interested in estimating density, we also computed posterior mean abundance (i.e. total number of lions) across the QECA alone.

3 | RESULTS

We recorded 70 lion sightings during the 93-day survey period (34 sightings of lion groups and 36 sightings of single lions) totalling 165 lion detections (Figure 2) of 30 individuals (16 female and 14 male). These detections were made after 8,243.5 km of search effort resulting in 2 lion detections/100 km². Due to high cub mortality, all lions judged to be < 1 year of age detected were excluded when found with their natal prides ($n = 9$ cubs in two prides). One lion was detected 13 times (Table 2), five lions were detected nine times, four lions were detected eight times, three lions were detected seven times, one lion was detected six times, one lion was detected five times, two lions were detected four times, 10 lions were detected three times, two lions were detected two times and one lion was detected once. Based on these lion detections, we found mean female pride size was 3.2 individuals (only including adult females, $n = 5$ prides) and mean total pride size was 6.2 individuals (including adult males, $n = 5$ prides).

3.1 | Lion density, abundance, movement and home range size

Lion density for the QECA was estimated at 2.70 individuals/100 km² (posterior SD 0.47; range 1.83–3.62). The range of posterior density estimates per pixel (0.158 km²) was 0.0002–1.89 lions per km², showing a wide regional range in lion densities across the QECA. We note,

however, that since multiple individuals in lion prides will have the same activity centre during such discrete state space implementations, this range may be exaggerated. The lion movement parameter (σ) estimated from our highest ranked model (model 1, with θ set to 1), for males was 3.27 km and 2.22 km for females (Table 3). When this was converted to an approximate estimate of minimum average home range size (i.e. $\pi(\sigma\sqrt{5.99})^2$), the average home range size for male lions was 203.66 km² (range 130.57–285.07), and 93.79 km² (range 64.20–128.80) for females. The male to female sex ratio in our study estimated by ψ_{sex} was 1:0.75. The posterior mean abundance for the QECA was 71 lions (posterior SD 11.05).

3.2 | Model diagnostics

Bayes p -value was estimated at 0.70–0.78 (Table 4), which were within the bounds of the extremities to gauge model adequacy (0.15–0.85). All shrink reduction factors generated using the Gelman–Rubin diagnostic statistic were < 1.10 (Table 5), indicating satisfactory convergence. The lowest marginal likelihood recorded for our seven models (Supplementary Information 1) was our first model, which assumed detection probability, and the rate of decline in detection probability was dependent on sex (Table 1).

4 | DISCUSSION

4.1 | African lion density and movement in the QECA

Our results represent the first attempt at estimating lion densities through a SECR approach in the QECA, and the first estimate of lion abundance there in a decade since the call-up surveys of Omoya et al. (2014) done in November–December 2008. We found lion density to be 2.70 individuals/100 km², and approximate minimum home ranges were 203.66 km² and 93.79 km² for male and female lions respectively – much larger than those estimated by Mudumba et al. (2015). This implies that home ranges have increased considerably over just a decade. Our results also show a lower than expected number of female lions in the QECA system. Collectively the apparent increase in range sizes and skewed sex ratio lends support to our second hypothesis that African lions in the QECA are in a state of decline and require urgent conservation attention. These lines of evidence suggest that potential lion densities in the QECA could be considerably higher.

The most striking result of our survey was the average home range sizes generated from the sex-specific movement parameters (σ) for males and females in this study. When these are compared to those recorded in an intensive radio-collaring exercise implemented by Mudumba et al. (2015) in QECA from 2006 to 2011, they reveal that range size estimates have increased by over 414% for males ($n = 5$ individuals averaged 39.64 km² in Mudumba et al., 2015) and, by ~106% for females ($n = 4$ individuals averaged 45.58 km² in Mudumba et al., 2015). The estimates of home ranges generated from our movement

TABLE 3 Model parameters for our seven candidate models assessing African lion population state variables in the QECA

Model	σ_M		σ_F		λ_0		β_{eff}		β_{sex}		ψ		ψ_{sex}		N_{super}		θ		Density	
	Estimate	SD	Estimate	SD	Estimate	SD	Estimate	SD	Estimate	SD	Estimate	SD	Estimate	SD	Estimate	SD	Estimate	SD	Estimate	SD
1	1.08	0.14	0.88	0.10	0.02	0.005	0.99	0.22	0.56	0.32	0.37	0.07	0.57	0.11	160.98	28.05	0.55	0.04	2.70	0.47
2	1.02	0.15	0.93	0.12	0.02	0.005	0.99	0.22	0	0	0.38	0.07	0.57	0.11	161.66	28.31	0.55	0.05	2.71	0.48
3	1.79	0.12	1.34	0.1	0.01	0.002	1	0.22	0.58	0	0.37	0.07	0.57	0.11	156.96	28.14	0.75	0	2.63	0.5
4	1.65	0.11	1.42	0.1	0.01	0.002	0.99	0.22	0.00	0.00	0.37	0.07	0.57	0.11	157.07	27.28	0.75	0	2.64	0.44
5	1.55	0.09	1.55	0.09	0.01	0.002	1	0.22	0.12	0.21	0.35	0.07	0.53	0.11	150.64	27.24	0.75	0	2.52	0.46
6	1.55	0.08	1.55	0.08	0.01	0.002	1	0.21	0	0	0.35	0.06	0.0007	0.002	148.48	25.48	0.75	0	2.49	0.43
7	3.27	0.33	2.22	0.20	0.07	0.001	1.02	0.22	0.57	0.26	0.37	0.07	0.57	0.11	157.74	27.19	1	0	2.65	0.46

TABLE 4 Bayes p -values for our seven candidate models assessing lion density in the QECA created to assess African lion density in the QECA

Model number	Bayes p -value	Natural logarithm of marginal likelihood
1	0.74	-158,020.56
2	0.75	-161,676.60
3	0.74	-163,470.45
4	0.78	-165,528.85
5	0.73	-161,916.87
6	0.70	-162,227.85
7	0.75	-172,241.9

parameters are an under-representation of their true size, due to limited detections over a 3-month sampling period. This means they are all the more pertinent. Recent satellite collar data from 10 individual lions across two prides (including one male coalition) from June–September 2018 averaged 292.43 km² and showed even higher increases in range size (Mustafa Nsubuga, WCS unpublished data, 2018). The range size study of Mudumba et al. (2015) is unlikely to have suffered from significant range size underestimation as only lions with 102–634 GPS locations were used in the analysis of home ranges, well above the recommended 30–100 location point threshold for accurate seasonal home-range estimation (Girard, Ouellet, Courtois, Dussault, & Breton, 2002). Importantly, the Mudumba study utilised VHF collar data of individuals; therefore, there may be some underestimation artefacts, particularly at the extremities of these lion ranges. However, even if these ranges were underestimated by 50% (i.e. ~60 km² for males and ~67 km² for females), the minimum range sizes estimated from our SECR analysis still show significant range expansions. This is backed up by WCS unpublished data ($n = 10$ individuals, June–September 2018, averaged 292.43 km²; Mustafa Nsubuga, WCS unpublished data, 2018).

There are a number of key factors that are important in shaping the density and movements of large carnivores in African savannas, including the availability of prey and the density of competitors. Loveridge et al. (2009) showed that the home-range size of lions in Hwange National Park, Zimbabwe, decreased with increasing prey biomass. Commercial and subsistence poaching of lion prey species is widespread across the QECA, and parts of the Ishasha sector, the park's lake edges and rivers showed the highest poaching pressure from 1999 to 2012 (Critchlow et al., 2015). Furthermore, the commercial, and non-commercial harvest of animals increased during this time. We suggest the increased movements of lions we detected are likely a response to systematic prey depletion in the broader QECA.

The high male to female sex ratio of one adult male to 0.75 adult females in the region is highly unusual. A review of 40 scientific papers reporting adult African lion male to female ratios reported a mean ratio of 1 adult male lion: 2.33 adult females (Périquet et al., 2015). Even the least-productive arid and semi-arid environments (e.g. the Kgala-gadi of Botswana and Namibia's Etosha National Park) where lion home

TABLE 5 Shrink reduction factors for the key parameters from our seven candidate models created to assess African lion density in the QECA

Model number	σ_M		σ_F		λ_0		β_{eff}		β_{sex}		ψ		ψ_{sex}		N_{super}		θ		Density	
	Est	CI	Est.	CI	Est	CI	Est	CI	Est	CI	Est.	CI	Est	CI	Est	CI	Est	CI	Est	CI
1	1.03	1.03	1.01	1.01	1.03	1.02	1	1	1.01	1.01	1.01	1.01	1	1	1.01	1.01	1.02	1.02	1.01	1.01
2	1.02	1.02	1.01	1.01	1	1	1	1	NA	NA	1.01	1.01	1	1	1.01	1.01	1.02	1.02	1.01	1.01
3	1	1	1	1	1	1	1	1	1	1	1.01	1.01	1	1	1.02	1.01	NA	NA	1.02	1.01
4	1	1	1	1	1	1	1	1	NA	NA	1.03	1.02	1	1	1.03	1.03	NA	NA	1.03	1.03
5	1	1	1	1	1.01	1.01	1	1	1.01	1.01	1.02	1.02	1	1	1.03	1.02	NA	NA	1.03	1.02
6	1	1	1	1	1	1	1	1	NA	NA	1.03	1.02	1	1	1.04	1.03	NA	NA	1.04	1.03
7	1	1	1	1	1	1	1	1	1	1	1.01	1.01	1	1	1.01	1.01	NA	NA	1.01	1.01

ranges are large and densities low feature higher adult sex ratios of 1:1.2 and 1:1.4 respectively (Funston, 2011; Stander, 1991). We also found a low mean number of females per pride (mean = 3.2 individuals; $n = 5$ prides), considerably lower than Kgalagadi (female pride size mean = 4.2 ± 0.4 SE individuals; Funston, 2011), and Etosha (female pride size mean = 4.8 ± 0.5 individuals; Stander, 1991). The mean number of females per pride was also lower than recorded for the QECA in 1998 (female pride size mean = 4.8 individuals; Driciru, 1999), and the total number of prides detected was also significantly different (10 prides detected in 1999 vs. five detected in 2017–2018).

It is problematic to compare our lion density and abundance estimates to previous estimates in the QECA, and more broadly in the lion literature, as the methods used differ widely. Unlike non-spatial techniques, SECR methods integrate the individual identity and landscape use of African lions in the density estimation process while explicitly accounting for search effort (Elliot & Gopalaswamy, 2017). We could, therefore, only make direct comparisons to four other African protected area systems, in which a SECR approach has been used to estimate lion densities. Of these, our estimates of African lion density were similar to those found in the Okavango of Botswana (2.5/100 km²; Rafiq et al., 2019) and the Nikolo-Koba National Park, Senegal (3.02/100 km²; Kane, Morin, & Kelly, 2015). They were approximately $\sim 6\times$ lower than the Maasai Mara in Kenya, while movement parameters were $4\times$ and $3\times$ higher for male and female lions respectively. The Maasai Mara harbours plentiful prey, potentially resulting in the shorter movements of lions there (Elliot & Gopalaswamy, 2017). Our estimates of lion density in the QECA were however higher than those estimated in a matrix of mopane woodland *Colophospermum mopane*, savannah floodplains and livestock area in the Ngamiland district of Botswana (1.2/100 km²; Rich et al., 2019). These densities, and those in the Okavango region, are unsurprising due to large swathes of these regions comprising inundated floodplains and stands of mopane, both less-suitable lion habitat than woodland savannas.

4.2 | Conservation implications

Taken together, the reduced home range sizes, and unusually male-biased sex ratios suggest that the population of lions in QECA is under threat and densities are likely to be significantly lower than what is ecologically possible in this area. The low densities of African lions and the larger movement estimates observed in our study may be due to poaching of preferred lion prey in the region. The QECA was historically considered to have some of the highest mammalian biomass in Africa, but it declined from 19,928 to 24,764 kg/km² in the mid-1970s to 8,050 kg/km² by 2009 (Treves, Plumptre, Hunter, & Ziwa, 2009). The SECR parameters generated from our study suggest this downward trend has continued since the study of Mudumba et al. (2015), and recent aerial surveys of preferred lion prey do not appear to accurately capture this.

The skewed sex ratios may be due to direct killing of lions by people living in villages located within and on the boundaries of the QECA. This is because female lions often venture into community

lands to feed on vulnerable livestock, and as their ranges expand so do their contacts with livestock herders (Woodroffe & Ginsberg, 1998). Direct killing of African lions in the system occurs regularly and in the northern section of the park alone, at least 47 adult and sub-adult lions were killed between 2006 and 2012 (Uganda Carnivore Program, unpublished data, 2006–2012, <https://uganda-carnivores.org/field-updates/>), equating to at least seven lions being killed annually. This is directly comparable to the Waza National Park in Cameroon, a similar-sized National Park (1,700 km²) where the estimated annual removal of six lions led to a population collapse (Tumenta et al., 2010). During this collapse, the lions in Waza also increased their home range size (59% increase in range size over a 10-year period), which the authors attributed to poaching of lion prey (Tumenta et al., 2013).

Treves et al. (2009) used predator carrying capacity models to show that if preferred lion prey in the QECA recovered to pre-conflict levels, the region could support approximately 500 lions. However, we recommend the immediate priority for managers in the QECA to secure and stabilise the lion population. Key areas with the highest lion use include the southernmost extent of the Ishasha region, the eastern Kigezi and the savannah plains directly to the west and southwest of the Hamkungu fishing community (a human settlement with over 2000 cattle) (Figure 2). Stemming female mortality is particularly important as prides with ≥ 3 individuals are significantly more successful in raising cubs (Packer et al., 1988). Our abundance estimate of just 71 lions suggests this population is perilously low.

4.3 | Benefits and caveats of the method

Robust lion monitoring in the QECA has been lacking. The last lion survey implemented in 2008 using call-up surveys reported abundance estimates with high margins of error at the regional level (north = 72 ± 49 SE, central = 41 ± 30 and south = 27 ± 25 , Omoya et al., 2014). Moreover, historical lion surveys from the QECA between 1977 and 2008 used a mixture of audio lure surveys, individual id total counts which were divided by region (i.e. n lions/total km² of study area), and expert solicitation to inform densities and abundance estimates over time. This is dangerous, as one can never accurately draw on these estimates to understand lion population trends. Our lion density estimates performed with acceptable levels of precision (2.70 ± 0.47 SD), and it is likely that this would have improved with search effort. Elliot and Gopalaswamy (2017) in the Maasai Mara ecosystem achieved narrow confidence bounds on their density estimates (17.08 ± 1.31 SD) due to a higher number of total detections and individual lions (438 and 203 respectively).

Some parts of the QECA could not be surveyed due to a lack of road and off-road access (namely Pelican Point, Maramagambo forest and the savannah plains southeast of Kasese). Although we did not survey these regions, our modelling framework incorporates this into the overall density and abundance estimation process through the estimation of search effort. We do not feel that our survey would have generated meaningful results in the Maramagambo forest and the region east of Kasese town as (1) lions in the QECA avoid lowland forest and

have clear preferences for grassland and wooded grassland habitats (Mudumba et al., 2015). This is reemphasised by a 2014 camera trap survey in Maramagambo (3,552 trap nights across 36 stations), which yielded only two lion detections at the same station (Mills, 2018), and (2) the plains southeast of Kasese have been identified as having some of the most intense commercial and non-commercial poaching which has increased over time (Critchlow et al., 2015). This being said an adaptation of the method where call-ups are done in regions with limited access, and where individuals are photographed could strengthen inference (Nic Elliot, personal communication, 2019).

The method of Elliot and Gopalaswamy (2017) for surveying African lions considers the entire population when generating estimates of lion movement and their activity centres. Furthermore, it can be used under a citizen-science approach where safari guides and their tourists are used to collect photographs of lions on safari. This could make the costs of such surveys considerably lower than traditional methods (Rafiq et al., 2019).

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AUTHORS' CONTRIBUTIONS

AB and AG conceived the manuscript and experiments. AB, MN and AG performed all fieldwork. AB, AG and JA analysed the data. AB, AG, JA, DB, MM and MN wrote the paper.

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