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Spatially explicit population estimates of African leopards and spotted hyenas in the Queen Elizabeth Conservation Area of southwestern Uganda

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Abstract

African leopards (*Panthera pardus pardus*) and spotted hyenas (*Crocuta crocuta*) are data deficient across much of Africa, and there are only a handful of recent population estimates for these species from Uganda. This has conservation ramifications, as both species are important for wildlife tourism, and leopards are hunted for sport in several regions adjacent to national parks as part of a government-led revenue-sharing scheme to foster increased tolerance of wildlife. We ran a single-season camera-trap survey in each of the northern and southern sections of the Queen Elizabeth Conservation Area (2400 km^2), Uganda's second largest national park. We applied spatially explicit capture–recapture (SECR) models to estimate the population density and abundance of leopards and spotted hyenas in the northern Mweya and Kasenyi plains area, and the southern Ishasha sector. Leopard densities were estimated to be 5.03 (95% Highest Posterior Density, HPD = 2.80–7.63) and 4.31 (95% HPD = 1.95–6.88) individuals/100 km^2 for the north and south of the conservation area, respectively, while spotted hyena densities were 13.44 (95% HPD = 9.01–18.81) and 14.07 individuals/100 km^2 (95% HPD = 8.52–18.54) for the north and south, respectively. Leopard densities were in the middle range of those recorded in the literature, while sex ratios were what would be expected for this polygamous felid. Spotted hyena densities were on the higher end of those recorded for the species using spatially explicit capture–recapture (SECR) methods. Our work provides the first robust population estimate of leopards and spotted hyenas in the Queen Elizabeth Conservation Area of western Uganda.

Keywords Bayesian spatially explicit capture–recapture (SECR) model · Big cat · *Crocuta crocuta* · Density · East Africa · Felids · Hyaenids · *Panthera pardus* · Population size · Uganda

Introduction

Robust estimates of animal densities over time and space are critical for developing species threat assessments (e.g., Jacobson et al. 2016), setting harvest quotas (e.g., Balme et al. 2009b), targeting management actions (Balme et al.

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2010a, b), gauging the viability of individual animal populations, and evaluating management effectiveness (e.g., Sollmann et al. 2011). Measures of animal abundance and density are especially valuable for species that are exposed to significant anthropogenic pressures such as legal and illegal hunting (Balme et al. 2009b), are constrained to small habitat patches (Wibisono et al. 2018), and are important to the economies of developing nations through tourism or the ecosystem services they provide (Braczkowski et al. 2018; O'Bryan et al. 2018). Reliable estimates of abundance and densities of entire guilds of large carnivores have been difficult, owing to logistical (Long et al. 2008) and analytical constraints (Williams et al. 2002). Thus, baseline estimates of population abundance are lacking for many of the world's carnivores across their ranges.

In Uganda, African leopards (*Panthera pardus*; hereafter leopards) and spotted hyenas (*Crocuta crocuta*) are examples

of species whose population status is poorly known. While leopards and spotted hyenas are key tourism species (Di Minin et al. 2013; Lindsey et al. 2007) on the one hand, they are also both the most significant predators of small and medium livestock on farms located inside and on the edge of the Queen Elizabeth (Sheppard 2014), Lake Mburo (Braczkowski et al. 2020a), and Murchison Falls National Parks (Mudumba 2011). Such livestock depredation causes damage to human livelihoods (Ochieng et al. 2015), and consequently, leopards and spotted hyenas are often killed in retaliation for stock raiding through poisoning, trapping, and shooting. Leopards in Uganda are also hunted for sport (country-wide annual CITES quota: 28 leopards; Braczkowski et al. 2015). The current status of both species is poorly understood in the country, and sustainability of the current levels of retaliation and sport-hunting and their impacts on populations within protected areas are unknown.

Interspecific interactions between members of large carnivore guilds may also drive density patterns. For example, a reduction in the density of African lions (*Panthera leo*; hereafter lions) could provide a more favourable environment for sympatric species, like spotted hyenas and leopards. Lions and spotted hyenas have been shown to exert considerable pressure on each other mainly through interference competition (Kruuk and Turner 1967; Hayward 2006), and kleptoparasitism. Much of this is owed to their strong degree of dietary overlap, and direct competition over the same food resources (Kruuk and Turner 1967; Hayward 2006). Similarly, leopards appear to avoid spotted hyenas temporally in some landscapes, avoiding peak spotted hyena activity periods (Havmøller et al. 2020). However, how these behavioural interactions translate to population regulation remains unclear. The evidence for lion pressure on leopards at the population level appears to be mixed. In the Sabi Sands Game Reserve of South Africa, which is relatively a larger and an open system, Balme et al. (2017) found no clear evidence for suppression of leopards by lions, either in their distribution or population density. However, Ramesh et al. (2017) in a study from July 2013 to April 2014 did find that leopard densities decreased in the smaller, fenced protected areas of northern KwaZulu-Natal (Ndumu and Tembe) where lion densities were high. Moreover, leopards appear to avoid spotted hyenas temporally in some landscapes, avoiding peak spotted hyena activity periods (Havmøller et al. 2020).

In this study, we aimed to estimate the abundance and density of leopards and spotted hyenas across in the Queen Elizabeth Conservation Area (QECA), Uganda. We used remote camera trapping and Bayesian spatially explicit capture–recapture (SECR) to assess the densities of both species in the QECA. In an earlier study, the lion density was found to be low (2.70 individuals/100 km^2) relative to other similar systems (Braczkowski et al. 2020b). Consequently, we predicted that densities of spotted hyenas and leopards would be higher than in other, similar savannah

systems due to lower levels of interference competition with lions and mesopredator release-like effects (Ramesh et al. 2017).

Methods

Study area

We surveyed leopards and spotted hyenas in the QECA, southwestern Uganda (0.1641º S, 30.0203 º E; 2056 km^2; Fig. 1). This area falls within the Albertine Rift Valley, a global biodiversity hotspot and known to be the most species-rich area in continental Africa (Plumptre et al. 2007). The QECA is comprised of the Queen Elizabeth National Park and two nearby protected systems, the Kyambura wildlife reserve in the north (154 km^2) and the Kigezi Wildlife Reserve in the south (265 km^2), together adding up to an area of 2400 km^2. The QECA is contiguous with Virunga National Park (7900 km^2) in the Democratic Republic of Congo (DRC), and collectively, these reserves are a part of the greater Virunga landscape (Jones et al. 2016). The region has an elevation ranging from 900 to 1300 m asl (Salerno et al. 2017) with two short rainy seasons, in March–May and September–November, totalling 600–1400 mm per year (Chritz et al. 2016).

The QECA is essentially split by two lake systems (Lake Edward in the West, and Lake George to the East) with the small Kazinga channel between these. The most detailed habitat map created for the QECA using ENSO MOSAIC identified 21 habitat types (Plumptre et al. 2010). The area north of the Kazinga channel is dominated by grasslands and wooded grasslands, characterized by giant rat's tail (*Sporobolus pyramidalis*) grassland and African caper (*Capparis tomentosa*), Candelabra tree (*Euphorbia candelabra*) thicket clumps (Wronski and Plath 2006), with dense thickets of sickle bush (*Dichrostachys cinerea*) and Candelabra trees extending towards the western park edge in Mweya and Katwe. The area south of the Kazinga channel is characterized by wooded grasslands comprised of open grasslands belonging to the *Themeda* and *Hyparrhenia* genera as well as *Acacia* and *Ficus* woodlands (Mudumba et al. 2015), and a large patch of tropical high forest characterized by woody plants such as the jumping seed tree (*Sapium ellipticum*), Uganda ironwood (*Cynometra alexandri*), African crabwood (*Carapa grandiflora*), Guinea plum (*Parinari excelsa*), and Sangow (*Newtonia buchananii*). This forest area is known as the Maramagambo forest (Tumwesigye et al. 2000). The main prey species likely to be predated by leopards and/or spotted hyenas include African buffalo (*Syncerus caffer*), Uganda kob (*Kobus kob*), topi (*Damaliscus lunatus*), warthog (*Phacochoerus africanus*), and waterbuck (*Kobus*

Fig. 1 Our density assessments of leopards and spotted hyenas were implemented in the Queen Elizabeth Conservation Area (QECA). Our study area comprised the Queen Elizabeth National Park and the Kyambura and Kigezi Conservation areas. The dotted line represents the 25 km buffer placed around the QECA border for our SECR density analysis. The 25 km buffer area was used to estimate densities in our study area, while posterior abundance of density was estimated only limited to the immediate boundaries of Queen Elizabeth National Park, Kyambura, Ishasha and Kigezi
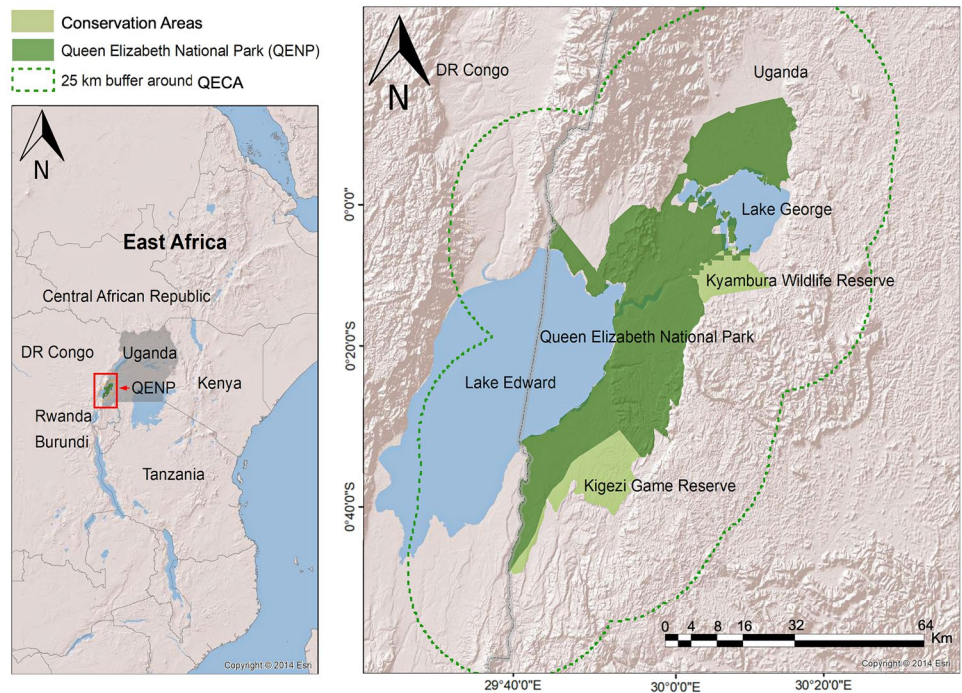
ellipsiprymnus), and these are distributed across both the northern and southern extents of the park (Mudumba et al. 2015). The QECA is one of Uganda's most-visited eco-tourism reserves, but also suffers high rates of conflict between large carnivores and livestock inside the fishing villages, inside the national park and along the park boundaries (Sheppard 2014).

Field methods

We conducted two camera-trap surveys in the QECA from 8 March 2018 to 24 June 2018 using Cuddeback™ 20-megapixel Long Range IR camera traps. The first survey ran from 8 March to 25 April 2018 in the northern section of the park and encompassed 44 camera-trap sites distributed across the Mweya, Kasenyi plains and crater lakes regions. The second survey was conducted approximately 70 km south, across 30 locations in the Ishasha sector from 27 April 2018 to 24 June 2018. These two regions differ markedly (the north being characterized by open grasslands and sickle bush and candelabra tree thickets, and the south being comprised of open grasslands and *Acacia* and *Ficus* woodlands; Mudumba et al. 2015). Each camera-trap site consisted of two camera traps, each mounted to a 1-m steel pole 40 cm from the ground. We positioned camera-trap stations on vehicle tracks and roads, as these are favoured travelling and hunting routes of leopards and spotted hyenas (Balme et al. 2009a; O'Brien and Kinnaird 2011). We positioned each camera station perpendicular to a vehicle track or game trail at a 60–75 degree angle to trigger a detection

on our camera traps early enough and to obtain at least one useable flank for the analysis. We checked each site at least once every 7–10 days to repair damages caused by animals, replace memory cards, and check battery functionality. We set cameras to burst mode (5 images taken every time the infrared sensor was triggered).

Although spatial capture–recapture analyses do not require all animals to have non-zero probability of being detected, we set camera stations at a spacing of ~2 km, a distance shorter than the smallest leopard home-range radius recorded in the literature (30 km^2; Bailey 1993; and 23 km^2 Fattebert et al. 2016), to ensure that individuals could be detected at multiple sites. This spacing of camera traps also allows for the sampling of spotted hyena populations, as typical clan home ranges are between 30 and 56 km^2 in similar (Braczkowski unpublished data), but more productive savannah environments of the Maasai Mara of Kenya and Serengeti, Tanzania (Hofer and East 1993a, 1993b; Boydston et al. 2003). These represent some of the most ecologically analogous savanna varieties to what is found in the Mweya and Ishasha ecosystems of Queen Elizabeth (Braczkowski unpublished data).

We identified individual leopards and spotted hyenas by observing their unique rosette and spot patterns, respectively, from the camera-trap images (Miththapala et al. 1989; O'Brien and Kinnaird 2011; see Appendix Figs. A1, A2, and Supplementary Material 5 Fig. S1 and S2). For leopards, we were able to classify the sex of individuals using distinctive morphological cues such as the presence of a scrotum and the enlarged dewlap and sagittal crest in males (Balme et al.

2012). We used two assessors to assign individual identity to unique photographs from image bursts (i.e., one individual identified from multiple bursts, each with 5 images). We only included in the analysis individuals for which there was consensus between the two assessors (Bahaa-el-din et al. 2016). For spotted hyenas, to avoid mismatching flanks and mistakenly double-counting individuals, we chose the flank of the animal with the highest number of photographs recorded during our survey (Henschel et al. 2014a). We did this as spotted hyenas often walked around cameras and did not present a clear flank on both of their body sides, and several individuals moved around a single camera at the same time. For leopards, we omitted the individuals for which we did not have at least one representation from both flanks. We only noted an individual spotted hyena or leopard once during a 24 h period to maintain temporal independence between camera-trap detections (Thorn et al. 2009).

Analytical methods

We estimated leopard and spotted hyena densities in the QECA by analysing their detections using Bayesian spatially explicit capture–recapture (SECR) models (Royle et al. 2009). This is a hierarchical model consisting of two processes, the state process and the observation process. The state process models how animals are distributed over a given region (called the state space) and the observation process describes how data from these animals are collected during the survey.

The state space encompassed our camera-trap polygon of the QECA and a buffer of 25 km around it (including the eastern section of Virunga National Park and the southwest of Kibale National Park; Fig. 1). We then generated equally spaced pixels (0.158 km^2) across this area to describe a discrete state space. The centres of these pixels represented potential activity centres of the animals (leopards or spotted hyenas). We masked out all highly modified agricultural areas (mainly banana plantations, bare ground, and open fields) within the state space as leopards and spotted hyenas are unlikely to use intensive agricultural lands in their home ranges (Fattebert et al. 2015a, b). This state space size (total size = 13,434 km^2; of which 5960 km^2 deemed suitable) was larger than several previous studies in similar habitats (e.g., Strampelli et al. 2018 used a 10 km buffer and Braczkowski et al. 2016 used a 15 km buffer). We did this to account for the possibility that leopards and spotted hyenas would move greater distances in the QECA due to poaching pressure recorded in Critchlow et al. (2017). There is no cost in making the state space too large, except increased computation time when running the model. However, if the state space size is too small, density estimates will likely be positively biased (Gopalaswamy et al. 2012). The statistical

expressions for describing the state process in the context of such discrete spaces are defined in Royle et al. (2013), and more recently in the context of lions, in Elliot et al. (2020).

We used a standard spatial capture–recapture matrix (trap locations, individual animals, and sampling occasions, all input files are provided in Supplementary Material 1) to record our data. A sampling occasion was defined by a single 24 h cycle. We also incorporated trap malfunctions into our matrix of sampling occasions recorded during the survey (Gopalaswamy et al. 2012).

Large terrestrial carnivores typically differ in their home-range sizes, movement patterns, and capture probability (Palomares et al. 2012; Srbek-Araujo 2018), which can affect the observation process (Sollmann et al. 2011). SECR is considered a robust method for calculating animal densities, because it accounts for individual heterogeneity in detection probability on account of an individual's location and other covariates. Since male and female leopards usually have different home-range sizes, we also included sex as a covariate in the observation process. We did not do this for spotted hyenas as the visibility of testes was often obscured by the large tail of individuals, and because female spotted hyenas feature a pseudo scrotum which makes identification of sex from camera-trap images unreliable (Muller and Wrangham 2002).

In SECR modelling, σ is the scale parameter, representing the rate of decline in the detection rate as the location of the animal's activity centre moves away from a camera-trap station. λ_0 is the basal encounter rate, which is the encounter rate of an animal whose activity centre lies exactly at a camera-trap station. θ defines the shape of the detection function. If this parameter is estimable from the given data, the shape of the detection function could define the manner in which an animal utilises space or resources (Elliot and Gopalaswamy 2017). Therefore, in our models, the probability of detecting a leopard or spotted hyena i in pixel j is defined by a complementary log–log function.

Model 1 estimated the detection function (defined by θ) and assumed that detection probability is sex-specific:

$$cloglog(\pi_{ij}) = log(\lambda_0) + \beta_{sex} - f\left[dist(i,j|\theta, \sigma_{sex})\right],$$

where π_{ij} describes the detection probability on a given sampling occasion, which is a function of the basal encounter rate λ_0 and distance between the activity centre of individual i and pixel j, θ and sex-specific σ_{sex}. The cloglog function is the complementary log–log transformation applied on the detection probability π_{ij}. By doing this, the components of π_{ij} can be represented as additive terms in a generalized linear model (Royle et al. 2009; see Table 1). The specific form of this detection function is

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

In all, we assessed seven a priori models for leopards and two for spotted hyenas (Table 2). The shape of the detection function may inform us about the manner in which leopards and spotted hyenas utilise space. However, obtaining adequate sample sizes to estimate this parameter is difficult (Elliot et al. 2017, Broekhuis et al. 2020, Braczkowski et al. 2020a), so we fixed the value of this parameter in some models. The most common detection function (the half-normal) in SECR studies, for us to compare our results with, requires that $\theta = 1$. However, Elliot et al. (2017) found that the estimated value of θ was found to be close to 0.5 for lions. Therefore, we considered a few models by fixing θ at 0.75 as a trade-off value. We estimated a continuous θ parameter, which defines the shape of the detection function for leopards and spotted hyenas in some models, and also fixed θ at specific values in some models (Elliot and Gopalaswamy 2017). The detection function takes on a version of the negative exponential form (i.e., when $\theta = 0.5$) and a Gaussian form ($\theta = 1$). In this version of the negative exponential form, only the power term in the numerator changes and not the denominator. As we could not accurately ascertain sex in spotted hyenas, we only ran the first and seventh models for this species, allowing the model to estimate θ in one case and by fixing it at 1 in the other.

We used a modified version of the package SCRbayes (https://github.com/jaroyle/SCRbayes) as available in Elliot and Gopalaswamy (2017) in the R environment (R Development Core Team 2018), which implements Bayesian Markov chain Monte Carlo (MCMC) methods using the Metropolis–Hastings algorithm (Tierney 1994) for analyses (all model definitions and code are provided in Supplementary Material 2 and 3). We set 4 chains to analyse each model and set them to initially run for 50,000 iterations with a burn-in of 2000 iterations. However, if the chains did not converge, we further discarded initial iterations until our chains converged. The total number of posterior samples for each chain are noted in (Table 3). All datasheets and accompanying code are provided in Supplementary Material 1 of this paper. Each camera-trap survey was analysed separately using the above criteria. Our Bayesian SECR approach uses data augmentation, which adds to a dataset of known leopards with an enlarged set of all zero-encounter histories

Table 1 Parameter definitions for the SECR models applied for our leopard and spotted hyena surveys in the QECA in 2018

Parameter	Definition
n	Total number of leopards or spotted hyenas detected during the survey period
n_z	Number of leopards or spotted hyenas augmented to n, so $M = n + n_z$ represents the maximum number of leopards or hyenas in the large state space
σ_F	Rate of decline in detection rate with increasing distance between the activity centre of a female leopard and a trap location
σ_M	Rate of decline in detection rate with increasing distance between the activity centre of a male leopard and a trap location
β_{sex}	The difference of the complementary log–log value of detection rate between a male and female leopard
λ_0	Basal encounter rate of a leopard or spotted hyena whose activity centre is located exactly at a trap location
ψ	Ratio of the true number of individuals in the population compared with the data-augmented population M
N_{super}	Estimated total number of leopards or spotted hyenas in the larger state space
ψ_{sex}	Proportion of the population which are males. Sex ratio (females:males) $= (1 - \psi_{sex}) / \psi_{sex}$
θ	Determines the shape of the estimated detection function; value θ ranges from 0.5 (a version of the exponential form) to 1 (Gaussian)
D	Estimated density of leopards or spotted hyenas per 100 km^2

Note we did not use sex as a parameter in the spotted hyena density models due to inability to accurately identify the sex of individual spotted hyenas

Table 2 Model definitions of SECR density models used to estimate leopard and spotted hyena densities in the Queen Elizabeth Conservation Area (QECA) in 2018

Model	Key model assumption	Detection function (θ) value
1	Basal detection rate is sex-specific	Model estimated θ
2	Basal detection rate is independent of sex	Model estimated θ
3	Basal detection rate is independent of sex	$\theta = 0.75$
4	Basal detection rate is sex-specific	$\theta = 0.75$
5	Basal detection rate is sex-specific, but rate of decline in detection rate is independent of sex	$\theta = 0.75$
6	Basal detection rate and rate of decline in detection rate are independent of sex	$\theta = 0.75$
7	Basal detection rate is sex-specific	$\theta = 1$

Table 3 The number of iterations, Bayesian *p* values, and the natural logarithm of marginal likelihood scores for our leopard and spotted hyena SECR density estimate models

Species and location of survey	Model number	Bayesian *p* value	Natural logarithm of marginal likelihood	Total iterations	Burn-in required to reach convergence
Leopards—northern survey (Mweya–Kasenyi)	1	0.68	− 56,574.18	48000	2000
	2	0.66	− 54,444.49	48,000	2000
	3	0.68	− 58,564.83	48,000	2000
	4	0.69	− 58,672.64	48,000	2000
	5	0.71	− 59,593.86	48,000	2000
	6	0.65	− 59,596.09	48,000	2000
	7	0.69	− 61,506.91	48,000	2000
Leopards—southern survey (Ishasha)	1	0.68	− 42,457.08	100,000	2000
	2	0.56	− 42,447.54	48,000	2000
	3	0.58	− 42,309.97	48,000	2000
	4	0.57	− 42,361.41	48,000	2000
	5	0.58	− 42,372.92	48,000	2000
	6	0.51	− 42,470.70	48,000	2000
	7	0.59	− 42,464.77	48,000	2000
Spotted hyenas—northern survey (Mweya-Kasenyi)	1	0.62	− 90,072.07	48,000	2000
	2	0.61	− 88,146.85	48,000	2000
Spotted hyenas—southern survey (Ishasha)	1	0.59	− 79,958.28	48,000	2000
	2	0.57	− 77,860.06	48,000	2000

(Gopalaswamy et al. 2012). We set this augmentation value to 1500 for both leopards and spotted hyenas.

Model choice was determined by examining, simultaneously, three criteria: (1) we used the Bayesian p value based on individual encounters (Royle et al. 2009) to discard models that did not fit the data (a p value close to 0 or 1 indicates a poor fit), (2) we assessed correlations visually between posterior parameters to assess issues of parameter identifiability, and (3) we examined the natural logarithm of the marginal likelihood using the harmonic mean estimator (L-MLHM; Dey et al. 2019) to identify the top model to identify the top model after they passed the above tests. MCMC chain convergence was assessed using the Gelman–Rubin statistic (Gelman and Rubin 1992).

Modern Bayesian SECR also allows for the computation of area-specific densities and abundance (Elliot and Gopalaswamy 2017). We therefore also computed posterior mean abundance across the northern and southern study areas and posterior standard deviation of abundance (Broekhuis and Gopalaswamy 2016; Elliot and Gopalaswamy 2017). In the northern survey, this comprised the area immediately inside a 5 km buffer of our camera traps, and within the boundaries of the park (431 km²). For the southern survey, this also represented the area within a 5 km buffer around our camera traps, within the boundaries of the park (316 km²). For all iterations of the MCMC output, we took the sum of all pixels within each area of interest (Figs. 2, 3). We limited our abundance estimates to these regions as our northern and southern areas were characterized by different habitats and are a significant distance

apart (~ 42 km linearly from the southern and northern most extents of these two survey areas). Model results are presented as summary statistics including posterior mean, posterior standard deviation (posterior SD), and a 95% Highest Posterior Density (HPD) interval, which is similar to a 95% confidence interval commonly used in frequentist statistics. Finally, because we were able to identify the sex of individuals and sex-based movement parameters for male and female leopards (sigma, σ), we could estimate the sex ratio of leopards in our study. We did this through the following formula: $(1 - \psi_{sex})/(\psi_{sex})$ which provides an estimate of the female:male sex ratio.

Results

After accounting for camera-trap malfunctions (mainly due to animal disturbance), the northern survey included 2065 trap nights of survey effort while the southern survey included 1661 nights. We identified 42 individual spotted hyenas (22 individuals recaptured at least once) in the northern survey and 38 (21 recaptures) in the south, while 19 (14 recaptures) and 12 (11 recaptures) individual leopards were recorded, respectively (Table 4). Of the leopards identified in our study in the northern survey, 8 were males and 11 were females, while in the southern survey, we identified three males and nine females. Total percentage of useable images for leopards was 97% for both surveys, while for spotted hyenas, this was 47% across both surveys (Table 4).
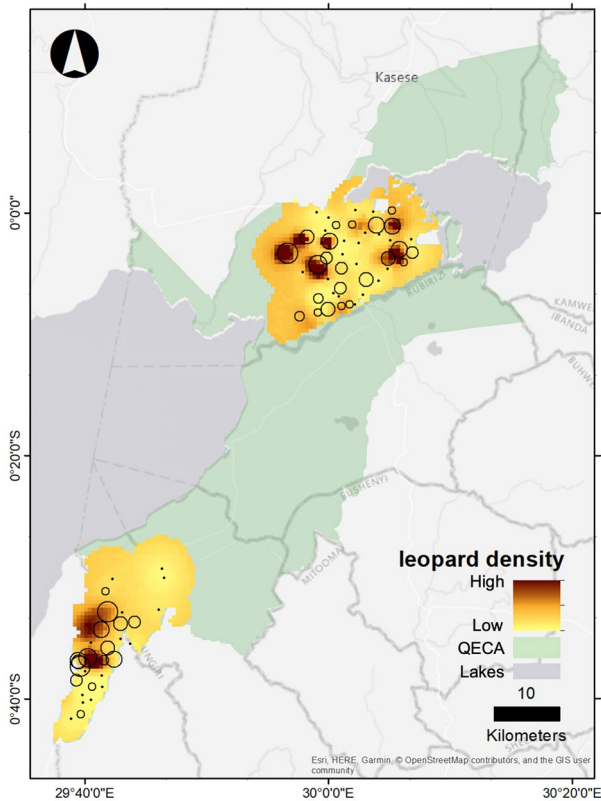
Fig. 2 A pixelated density map showing leopard densities across the north and south of the QECA, respectively, as calculated in 2018 using a Bayesian SECR model from Royle et al. (2009). This map reports estimated leopard densities per 0.158 km² pixel. The number of individual leopard detections at each camera-trap station is also denoted by the size of circles at camera locations
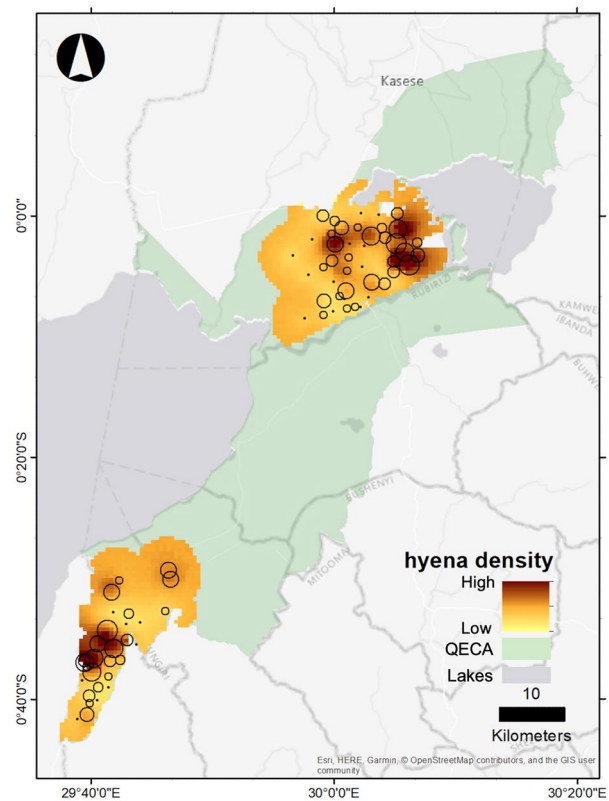
Fig. 3 A pixelated density map showing spotted hyena densities across the north and south of the QECA, respectively, as calculated in 2018 using a Bayesian SECR model from Royle et al. (2009). This map reports estimated spotted hyena densities per 0.158 km² pixel. The number of individual spotted hyena detections at each camera-trap station is also denoted by the size of circles at camera locations

Model diagnostics and model choice

Bayesian p values for all of our leopard density models ranged from 0.52 to 0.71, indicating an adequate model fit (relative to extremities: 0.10–0.90). Convergence of MCMC chains was indicated by a Gelman–Rubin statistic (PSRF < 1.20) for each parameter for each model (Gelman and Rubin 1992; Supplementary Material 2). MCMC chains of models estimating spotted hyena density also converged and models adequately fit the data (Bayesian p value range = 0.57–0.62 and Gelman–Rubin statistic

for all parameters < 1.20; Supplementary Material 3). Model selection for our leopard survey using the natural logarithm of marginal likelihood of data within each model, Bayesian p values, and examination of parameter covariance plots indicated that our second model (which assumes basal detection rate is independent of sex and θ is estimated by the model) gained most support for the northern (L-MLHM = − 54,444.49; Table 4) survey, while model 3 (which assumes basal detection rate is independent of sex and θ is estimated is fixed at 0.75) gained most support for the southern survey

Table 4 Body flanks, unique individuals, and recaptured individuals identified in our two 2018 SECR density surveys in the QECA

Species	Survey locality	Left flanks	Right flanks	Useable flanks in final analysis	Unique individuals	Individuals recaptured
Spotted hyena	Mweya-Kasenyi	178	156	90	42	22
	Ishasha	185	132	80	38	21
Leopard	Mweya-Kasenyi	64	62	61	19	14
	Ishasha	43	44	43	12	11

Table 5 Parameter estimates with accompanying posterior SD from the leopard and spotted hyena SECR density surveys implemented in the QECA in 2018

Species and location of survey	Model number	Sigma (σ_m)		Sigma2 (σ_f)		Lam0 (λ_0)		Beta sex (β_{sex})		Psi (ψ)		ψ_{sex}		N_{super}		Theta (θ)		Density	
		Post. Est	PSD	Post. Est	PSD	Post. Est	PSD	Post. Est	PSD	Post. Est	PSD	Post. Est	PSD	Post. Est	PSD	Post. Est	PSD	Post. Est	PSD
Leopards—northern survey (Mweya–Kasenyi)	1	0.95	0.15	1.06	0.23	0.06	0.02	−0.94	0.52	0.21	0.06	0.61	0.14	311.12	83.42	0.54	0.04	5.22	1.40
	2	1.00	0.13	0.94	0.14	0.04	0.01	0.00	0.00	0.20	0.05	0.60	0.14	300.00	75.85	0.53	0.03	5.03	1.27
	3	1.55	0.19	2.03	0.33	0.03	0.01	−1.12	0.49	0.18	0.05	0.58	0.17	270.48	71.37	0.75	0.00	4.54	1.20
	4	1.73	0.21	1.81	0.30	0.02	0.01	0.00	0.00	0.17	0.04	0.56	0.14	261.62	64.57	0.75	0.00	4.39	1.08
	5	1.70	0.16	1.70	0.16	0.03	0.01	−0.76	0.41	0.19	0.05	0.63	0.13	295.05	78.86	0.75	0.00	4.95	1.32
	6	1.75	0.19	1.75	0.19	0.02	0.01	0.00	0.00	0.17	0.04	–	–	258.02	65.05	0.75	0.00	4.33	1.09
	7	2.74	0.02	4.20	0.8	0.02	0.01	−1.21	0.45	0.17	0.04	0.58	0.14	252.94	64.70	1.00	0.00	4.24	1.08
Leopards—southern survey (Ishasha)	1	3.16	1.87	1.98	0.56	0.02	0.02	0.27	0.84	0.17	0.05	0.80	0.14	253.95	81.33	0.84	0.12	4.26	1.36
	2	2.70	1.13	2.00	0.55	0.02	0.01	0.00	0.00	0.16	0.05	0.79	0.13	247.03	76.75	0.84	0.12	4.14	1.29
	3	2.29	0.84	1.63	0.25	0.02	0.03	0.22	0.86	0.17	0.06	0.79	0.14	256.60	83.29	0.75	0.00	4.31	1.40
	4	2.06	0.49	1.63	0.22	0.02	0.01	0.00	0.00	0.16	0.05	0.79	0.13	246.80	75.61	0.75	0.00	4.14	1.27
	5	1.73	0.23	1.73	0.22	0.03	0.03	−0.29	0.71	0.16	0.05	0.75	0.14	242.75	76.33	0.75	0.00	4.07	1.28
	6	1.72	0.22	1.72	0.22	0.02	0.01	0.00	0.00	0.15	0.05	–	–	232.49	70.01	0.75	0.00	3.90	1.17
	7	4.86	3.16	2.64	0.45	0.02	0.00	0.32	0.78	0.17	0.05	0.80	0.14	251.00	80.22	1.00	0.00	4.21	1.35
Spotted hyenas—northern survey (Mweya–Kasenyi)	1	2.62	0.27	2.62	0.27	0.008	0.00	0.00	0.52	0.72	0.09	–	–	797.99	143.21	1.00	0.00	13.39	2.40
	2	1.39	0.43	1.39	0.43	0.01	0.01	0.00	0.00	0.52	0.10	–	–	800.87	149.53	0.68	0.13	13.44	2.51
Spotted hyenas—southern survey (Ishasha)	1	3.63	0.45	3.63	0.45	0.006	0.00	0.00	0.00	0.47	0.10	–	–	720.20	145.49	1.00	0.00	12.08	2.45
	2	1.27	0.34	1.27	0.34	0.01	0.00	0.00	0.00	0.55	0.11	–	–	838.59	166.55	0.60	0.08	14.07	2.79

Post. Est indicates the posterior estimate, while PSD indicates the posterior standard deviation

(L-MLHM = − 42,309.97). This was after they passed the above tests. For spotted hyenas, a model, which estimated basal detection rate being independent of sex and allowed the estimation of θ, garnered most support for both the northern and southern surveys.

Density estimates

Leopard densities

Under the top model, leopard density for the northern section of the QECA was estimated at 5.03 leopards/100 km^2 (posterior SD 1.27; 95% HPD 2.80–7.63; Table 5), while for the southern section, density was estimated at 4.31 leopards/100 km^2 (posterior SD 1.40; 95% HPD 1.95–6.88). The range of posterior density estimates per pixel for the two survey regions and greater state space (0.158 km^2) was 0.004–1.30 leopards (Fig. 2). The scale parameter for males was 1.00 km (posterior SD 0.13; 95% HPD 0.79–1.27; Table 5) and 0.93 km for females (posterior SD 0.14; 95% HPD = 0.72–1.20; Table 5) in the northern survey. For the southern survey, we estimated a scale parameter of 2.29 km for males (posterior SD 0.84; 95% HPD 1.22–3.82; Table 5) and 1.63 km for females (posterior SD 0.25; 95% HPD 1.17–2.10; Table 5). The female-to-male sex ratio for the north was 1:0.66 (posterior SD 0.25; 95% HPD 1:0.79–1:0.18 females to males), while for the south, this was 1 female leopard: 0.27 males (posterior SD 0.25; 95% HPD 1:1–1:0.01 females to males). The posterior abundance estimate for leopards in the northern survey area (431 km^2) was 20.51 individuals (posterior SD 6.06), while in the south (316 km^2), this value was 12.88 individuals (posterior SD 4.97).

Spotted hyena densities

Under the top model, spotted hyena density for the northern survey was estimated at 13.44 individuals/100 km^2 (posterior SD 2.51; 95% HPD 9.01–18.81), while the density estimate for the southern survey was 14.07 individuals/100 km^2 (posterior SD 2.79; 95% HPD 8.52–18.54). The range of posterior density estimates per pixel across the QECA (0.158 km^2) ranged from 0.04 to 0.60 spotted hyenas (Fig. 3). The spotted hyena scale or movement parameter σ for both sexes combined was 1.4 km in the northern survey (posterior SD 0.43; 95% HPD 0.84–2.27; Table 5), and 1.27 km in the southern survey (posterior SD 0.34; lower 95% HPD 0.88–2.03; Table 5). The posterior abundance estimate for spotted hyenas in the northern survey (431 km^2) area was 59.06 individuals (posterior SD 11.66), while in the south (316 km^2), this value was 44.70 individuals (posterior SD 10.18).

Discussion

Our density estimates fill an important gap for two regionally important higher order predators with significant ecological and tourism value in southwestern Uganda. We estimated leopard densities to be 5.03 and 4.31 individuals/100 km^2 for the northern and southern sections of the QECA, respectively. These density estimates fall approximately in the midrange of recently published leopard densities from SECR methods (mean density from 17 studies in 20 locations was 5.0 individuals/100 km^2; range = 0.62–11.80 individuals/100 km^2; Table S1 in Supplementary Material 4). SECR estimates of spotted hyena populations have to date been rare in the peer-reviewed literature, and direct comparisons to estimates from spoor counts and call up surveys are not appropriate, due to inherently high levels of sampling-based overdispersion present in these methods (see Gopalaswamy et al. 2015a, b; Elliot and Gopalaswamy 2017). Compared to the five known studies that employed closed SECR models and remote camera trapping to estimate spotted hyena densities, our estimates of 13.44–14.07 spotted hyenas/100 km^2 were the highest in the recorded literature (Table S2 in Supplementary Material 4), for both the northern and southern sections of the QECA.

Leopard densities

Our study provides a baseline leopard density for the QECA, one of Uganda's largest national parks, which, together with Virunga in the neighbouring Democratic Republic of Congo, forms part of a globally significant wilderness block (Watson et al. 2016). The only previous population estimate for leopards in Uganda was based on a calculation that correlated leopard density to rainfall and habitat productivity (Martin and de Meulenaer 1988). Although Uganda is estimated to hold only 1% of the African leopard sub-species' range, it is important regionally, in that it encompasses nearly 10% of the leopard's potential range in East Africa (Jacobson et al. 2016).

Importantly, because we had only a single snapshot in time, it was impossible for us to assess whether the leopard population in the QECA is stable, decreasing or increasing. The fact that the estimated densities are within the average of other protected populations in Africa tends to indicate that there is no release of the leopard population as a consequence of the relatively low lion population (2.70 lions/100 km^2, Braczkowski et al. 2020b), with leopards possibly being kept in check by the relatively high density of spotted hyenas (see below). The system supports similar densities of leopards in the north and south of the Kazinga channel in the QECA, suggesting that these two subpopulations function as a single population. In both areas, sex ratio was female biased,

indicating a healthy population structure for this polygynous species. Indeed, we expect more females than males in a population given the leopard socio-spatial structure, with males with large home ranges overlapping several females with smaller home ranges (Fattebert et al. 2016). As a point of comparison, in the Sabi-Sands Game Reserve of South Africa, arguably one of the best-protected and prey-rich protected areas in Africa, Balme et al. (2019) estimated a ratio of 1 adult male: 1.8 adult females in a stable leopard population.

Hyena densities could reflect competitive release

Spotted hyenas are the most successful of Africa's large carnivores, in that they are widespread, and highly adaptable (Mills and Harvey 2001; Hayward 2006). This is due to their generalist diet and ability to access a variety of prey sizes, mainly resultant of both group and solitary foraging (optimal prey range of 56–182 kg). They also have the ability to scavenge (Hayward 2006), and their exceptionally large premolars allow them to access nutrients from bone material in ways inaccessible to sympatric carnivore species (Werdelin, 1989; Binder and Valkenburgh 2000; Tanner et al. 2008).

The high density of spotted hyenas lends some support to our a priori hypothesis that they may have experienced a degree of competitive release, resultant of a decrease in lion density in the QECA (this decrease over a 10-year period is described in Braczkowski et al. 2020b). This is one possible explanation for our results. Creel and Creel (1996) estimate spotted hyenas to outnumber lions in some of Africa's largest and most pristine protected area systems (Kruger National Park in South Africa, Selous Game Reserve/Nyerere National Park, Ngorongoro Conservation Area and Serengeti National Park in Tanzania) on average by a ratio of 1 spotted hyena: 0.30 lions (range=1:0.20–1:0.80). Spotted hyenas also outnumbered lions in the QECA, however more prolifically. Lion densities in this system are estimated to be 2.70 individuals/100 km^2 (posterior SD=0.47; Braczkowski et al. 2020b), translating into a ratio of approximately 1 spotted hyena: 0.15 lions in the north of the QECA, and 1:0.20 in the south.

Lions are an important source of interference competition for spotted hyenas, and pressure from lions (mainly through kleptoparasitism) was shown to outweigh prey availability as a limiting factor of spotted hyena densities in Amboseli National Park, Kenya (Watts and Holekamp 2008, 2009). Trinkel and Kastberger (2005) showed spotted hyenas in Etosha National Park, Namibia could not prevent lion stealing their kills, nor could they themselves steal lion kills unless they outnumbered lions by a factor of >3. Watts and Holekamp (2008) showed that lower lion densities in Amboseli compared to the Maasai

Mara led to a 24% greater lifetime reproductive success in spotted hyenas in Kenya's Amboseli ecosystem compared to those in the Masaai Mara. They showed that lower lion densities allowed for increased food intake, more scavenging of lion kills and higher body condition scores, despite overall prey densities being lower in Amboseli. High spotted hyena-to-lion ratios also mean that they can successfully deter lions from killing cubs at den sites through aggressive mobbing behaviour (Kruuk 1972). However, in other systems, spatio-temporal interactions could facilitate carnivore sympatry (Karanth et al. 2017), and in that context, the idea of competitive release may be only be temporarily relevant.

The high spotted hyena densities in the QECA could also be explained by the species' resilience to human persecution (e.g., poisoning and other forms of killing in retaliation to livestock depredation) and disturbance (e.g., snaring and spearing of prey). Henschel et al. (2014b), in their surveys of lions in west African protected areas, showed spotted hyenas continued to persist in 3 of the 10 national parks where lions had been extirpated. Green et al. (2018) suggested that spotted hyenas were not as affected by the edge effects (namely killing by cattle herders) that impacted lions in the Talek area of the Masaai Mara. They attributed this to the fact that spotted hyenas were less likely to kill cattle during the day (compared to lions, which were more likely to kill cows during the day, and were targets of retaliatory killing). Similarly, M'soka et al. (2018) found an inverse relationship between spotted hyena and lion densities in the Liuwa Plains National Park of Zambia and argued that spotted hyenas can compensate for anthropogenic disturbances if prey density remains high and competition from lions is low.

Importantly, spotted hyenas tend to form clans and may move as groups; however, they regularly undergo a fission–fusion structure, with certain individuals leaving and re-joining the clan on a temporary basis (Smith et al. 2008). It remains to be explored if this tendency may induce biases in estimates of density and sex ratios based on our sampling situation. However, López-Bao (2018) show that wolf social structure (a group, pack-living structure) does not majorly impact the density estimates of wolves from SECR. Similarly, Bischof et al. (2020) suggest that if low-to-moderate levels of gregariousness are observed in group living individuals, there is little overdispersion that occurs on the detection function and scale parameter. Contrastingly, if gregariousness is high, high rates of overdispersion may be observed in confidence intervals around parameter estimates, potentially leading to spurious estimates. These aspects of SECR require further investigation, ideally through a combination of simulations and ground-based exercises.

Implications for conservation

Species conservation policies and decisions are largely guided by population numbers. Hence, reliable estimation of animal density over time and space becomes vital, especially under continued anthropogenic pressures (see numerous examples in Karczmarski et al. 2022). Using the SECR approach, we have attempted to address this knowledge gap for leopards and spotted hyenas. There are more advanced models now available to deal with partial identity data (e.g., SPIM model, Augustine et al. 2018; Dey et al. 2019) within the SECR framework and these can be considered for future analyses, especially when we can also apply them on discrete state spaces such as ours and treat them as candidate models within a Bayesian model selection framework (Dey et al. 2019) for purposes of formal inference.

Alongside a separate estimate of lion density in the same region (Braczkowski et al. 2020a), these estimates of leopards and spotted hyenas present an important baseline on the status of three large carnivore species in one of Uganda's largest national parks, and a globally significant wilderness area. However, single snapshot density estimates as provided by our study do not inform the dynamics of population trends and status. Future repeated, annual surveys could assist in assessing important vital rates of all the three sympatric carnivores. This has been implemented effectively to not only estimate population trends

(e.g., Williams et al. 2017; Balme et al. 2009b), but in estimating birth, death, emigration, and immigration rates (e.g., Karanth et al. 2006; Duangchantrasiri et al. 2016). A recent study on tigers in Rajaji National Park in India demonstrated the conservation importance of estimating vital rates. In their study of tigers in a disturbed and disturbance-free zone, the authors showed that although densities remained consistent over time in these areas, vital rates differed and differences in land tenure of individuals suggested that one population was a potential source, while the other a potential sink (Harihar et al. 2020). This is particularly important for the context of our study as leopards are a utilised species in trophy hunting across Uganda and sink areas are typically the source of leopard declines due to overharvest (Balme et al. 2010a, b).

The window of opportunity for the conservation of Uganda's top terrestrial predators (lions, leopards, and spotted hyenas) is likely shrinking. The disappearance of lions from three large conservation areas in the last 15 years (Toro Sem-Liki, Pain-Upe, and Lake Mburo; UWA 2010) should serve as an important warning that leopards and spotted hyenas too require robust monitoring of their populations.

Appendix

See Appendix Figs. A1, A2.

Fig. A1 Leopard individual #11 captured on sampling occasion #12 at camera site #36. Note the clear rosette pattern located on the left flank and on the left hind leg. This image was captured using a CuddebackTM 20-megapixel Long Range IR camera traps
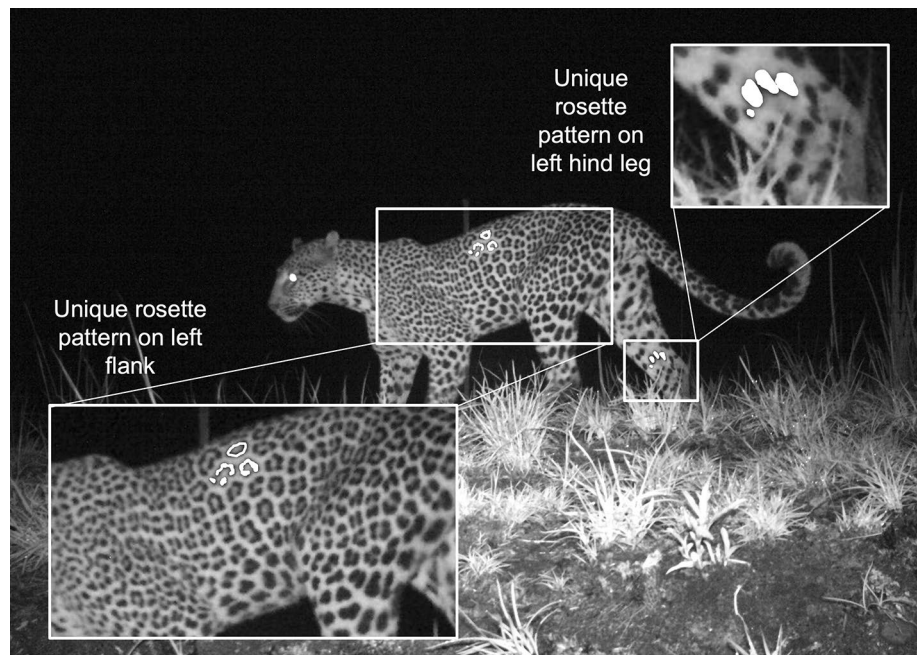
Fig. A2 Spotted hyena individual #8 captured on sampling occasion #13 at camera site #7. This image was captured using a CuddebackTM 20-megapixel Long Range IR camera traps

Declarations

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