Leopard and spotted hyena densities in the Lake Mburo National Park, southwestern Uganda

Aleksander Braczkowski Corresp., [1, 2], **Ralph Schenk** [3], **Dinal Samarasinghe** [4], **Duan Biggs** [1], **Allie Richardson** [5], **Nicholas Swanson** [3], **Merlin Swanson** [3], **Arjun Dheer** [6], **Julien Fattebert** [7, 8]

[1] Resilient Conservation Group, Centre for Planetary Health and Food Security, Griffith University, Nathan, Queensland, Australia

[2] School of Natural Resource Management, Nelson Mandela University, George Campus, George, Western Cape, South Africa

[3] Mihingo Lodge, Kampala, Uganda

[4] Wildlife Research and Nature Conservation Foundation (WRNCF), Colombo, Sri Lanka

[5] School of Biological Science, The University of Queensland, Brisbane, Queensland

[6] Department of Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany

[7] Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, United States

[8] Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Durban, KwaZulu-Natal, South Africa

Corresponding Author: Aleksander Braczkowski
Email address: a.braczkowski@griffith.edu.au

Robust measures of animal densities are necessary for effective wildlife management. Leopards (*Panthera pardus*)and spotted hyenas (*Crocuta Crocuta*) are higher order predators that are data deficient across much of their East African range and in Uganda, excepting for one peer-reviewed study on hyenas, there are presently no credible population estimates for these species. A lack of information on the population status and even baseline densities of these species has ramifications as leopards are drawcards for the photo-tourism industry, and along with hyenas are often responsible for livestock depredations from pastoralist communities. Leopards are also sometimes hunted for sport. Establishing baseline density estimates for these species is urgently needed not only for population monitoring purposes, but in the design of sustainable management offtakes, and in assessing certain conservation interventions like financial compensation for livestock depredation. Accordingly, we ran a single-season survey of these carnivores in the Lake Mburo National Park of south-western Uganda using 60 remote camera traps distributed in a paired format at 30 locations. We analysed hyena and leopard detections under a Bayesian spatially explicit capture-recapture (SECR) modelling framework to estimate their densities. This small national park (370 km^2) is surrounded by Bahima pastoralist communities with high densities of cattle on the park edge (with regular park incursions). Leopard densities were estimated at 6.31 individuals/100 km^2 (posterior SD = 1.47, 95% CI = 3.75 – 9.20), and spotted hyena densities were 10.99 individuals/100 km^2, but with wide confidence intervals (posterior SD = 0.33, 95% CI = 5.63 – 17.37). Leopard and spotted hyena abundance within the boundaries of the national park were 24.87 (posterior SD 7.78) and 39.07 individuals (posterior = SD 13.51) respectively. Leopard densities were on the middle end of SECR studies published in the peer-reviewed literature over the last five years while spotted hyena densities were some of the first reported in the literature using SECR, and similar to a study in Botswana which reported 11.80 spotted hyenas/100 km^2. Densities were not noticeably lower at the park edge, and in the southwest of our study site, despite repeated cattle incursions into these areas. We postulate that the relatively high densities of both species in the region could be owed to impala *Aepyceros melampus* densities ranging from 16.6 – 25.6 impala/km^2. Another, potential explanatory variable (albeit a speculative one) is the absence of interspecific competition from African lions (*Panthera leo*), which became functionally extinct (there is only one male lion present) in the park nearly two decades ago. This study provides the first robust population estimate of these species anywhere in Uganda and suggests leopards and spotted hyenas continue to persist in the highly modified landscape of Lake Mburo National Park.

Leopard and spotted hyena densities in the Lake Mburo National Park, southwestern Uganda

Alexander Braczkowski[1,2,*], Ralph Schenk[3], Dinal Samarasinghe[4], Duan Biggs[1], Allie Richardson[5], Nicholas Swanson[3], Merlin Swanson[3], Arjun Dheer[6], Julien Fattebert[7,8]

[1]Resilient Conservation Group, Environmental Futures Research Institute, Griffith University, 170 Kessels Road, Nathan, Queensland 4111, Australia

[2]School of Natural Resource Management, Nelson Mandela University, George Campus, George 6530, South Africa

[3]Mihingo Lodge, P.O. Box 28142, Kampala, Uganda

[4]Wildlife Research and Nature Conservation Foundation (WRNCF), 487/4 old road Kottawa, Pannipitiya, 10230 Sri Lanka

[5]School of Biological Sciences, The University of Queensland, St. Lucia, Queensland 4067, Australia

[6]Department of Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research, Berlin 10315, Germany

[7]Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA

[8]Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Durban 4000, South Africa

*Corresponding Author: alexander.braczkowski@gmail.com

Short Title: Leopard and spotted hyena densities in Lake Mburo

Words in Abstract: 409

Word count: 4922 excluding references

Number of figures: 3

Number of tables: 5

KEYWORDS

Panthera pardus, *Crocuta crocuta*, spatially explicit capture-recapture, population size, East Africa, human-carnivore conflict

ABSTRACT

Robust measures of animal densities are necessary for effective wildlife management. Leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*) are higher order predators that are data deficient across much of their East African range and in Uganda, excepting for one peer-reviewed study on hyenas, there are presently no credible population estimates for these species. A lack of information on the population status and even baseline densities of these species have ramifications as leopards are drawcards for the photo-tourism industry, and along with hyenas are often responsible for livestock depredations from pastoralist communities. Leopards are also sometimes hunted for sport. Establishing baseline density estimates for these species is urgently needed not only for population monitoring purposes, but in the design of sustainable management offtakes, and in assessing certain conservation interventions like financial compensation for livestock depredation. Accordingly, we ran a single-season survey of these carnivores in the Lake Mburo National Park of south-western Uganda using 60 remote camera traps distributed in a paired format at 30 locations. We analysed hyena and leopard detections under a Bayesian spatially explicit capture-recapture (SECR) modelling framework to estimate their densities. This small national park (370 km^2) is surrounded by Bahima pastoralist communities with high densities of cattle on the park edge (with regular park incursions). Leopard densities were estimated at 6.31 individuals/100 km^2 (posterior SD = 1.47, 95% CI = 3.75 – 9.20), and spotted hyena densities were 10.99 individuals/100 km^2, but with wide confidence intervals (posterior SD = 0.33, 95% CI = 5.63 – 17.37). Leopard densities were on the middle end of SECR studies published in the peer-reviewed literature over the last five years while spotted hyena densities were some of the first reported in the literature using SECR (n=5 studies since 2011), and similar to a study in Botswana which reported 11.80 spotted hyenas/100 km^2. Densities were not noticeably lower at the park edge, and in the southwest of our study site, despite repeated cattle incursions into these areas. We postulate that the relatively high densities of both species in the region could be owed to impala *Aepyceros melampus* densities ranging from 16.6 – 25.6 impala/km^2. Another, potential explanatory variable (albeit a speculative one) is the absence of interspecific competition from African lions (*Panthera leo*), which became functionally extinct (there was only one male lion present) in the park nearly two decades ago. This study provides the first robust population estimate of these species anywhere in Uganda and suggests leopards and spotted hyenas continue to persist in the highly modified landscape of Lake Mburo National Park.

INTRODUCTION

Precise measures of animal densities represent one of the most fundamental precursors for effective wildlife management (Karanth 1995, White and Burnham 1999, Duangchantrasiri et al. 2015, Rayan and Linkie 2015). Density estimates assist *inter alia* with species assessments (Jacobson et al. 2016), the setting of harvest quotas (Balme et al. 2009b), and in gauging the viability of individual populations (Sollmann et al. 2011). Measures of animal abundance and density are becoming increasingly critical for species that are exposed to significant anthropogenic pressures, are constrained to small habitat patches, and are important to the economies of developing nations (O'Bryan et al. 2018).

Large carnivores naturally occur at relatively low densities and have large space requirements (Balme et al. 2009b, Gopalaswamy et al. 2012b). Anthropogenic sources of mortality at the edges of small reserves can therefore depress carnivore densities, even within protected areas because animals move beyond their boundaries and are killed (e.g. Balme et al. 2009b, Woodroffe and Ginsberg 1998). In Uganda, most protected areas are relatively small, isolated and have high human pressures at their edges (Venter et al. 2016). Additionally, most Ugandan national parks and wildlife reserves are bordered by livestock rearing communities, and large carnivores regularly kill livestock in these areas (Ochieng et al. 2015). Consequently, large carnivores are often killed in retaliation for livestock killing, and damage through poisoning, trapping or shooting (Tweheyo et al. 2012).

Leopard (*Panthera pardus*) and spotted hyena (*Crocuta crocuta*) are examples of species which have impacts on the livelihoods of local communities in Uganda (Ochieng et al. 2015). Both species were responsible for 1,102 attacks on cattle, sheep and goats on the edge of Lake Mburo National Park (hereafter LMNP) (spotted hyenas n=762 or 69%, leopards n=340 or 31% between January 2009–December 2018, Braczkowski et al. 2020c). Consequently, at least 19 leopards were killed on the boundary of LMNP in a 4-year period from 2003–2006 (CITES CoP 14 Proposal 3), and two hyena clans (each >14 individuals in size) that were regularly viewed by tourists were poisoned in 2007 (Ralph Schenk pers.comm). However, both species are also important for the wildlife-viewing tourism (Van der Meer et al. 2016) and in Uganda in 2018 alone, 1 585 people purchased a night game drive permit for leopard viewing in LMNP, equating to US$47 550 in revenue for the Ugandan Wildlife Authority (A. Kule pers. comm.). This often leads to contradictory management goals, where one entity seeks higher densities to maximize tourism revenue, and the other seeks lower densities due to livelihood loss from conflict. However, a lack of robust information on the population status of leopards and spotted hyenas inhibits the design of sustainable management offtakes and also in assessing the impact of conservation interventions on carnivores and communities (e.g. Financial compensation, the erection of livestock protection bomas etc.).

To address these concerns, we sought to estimate the population abundance and densities of leopards and spotted hyenas in the LMNP, south-western Uganda. LMNP is a small, protected area that lacks much of the charismatic megafauna found elsewhere in the country e.g. mountain gorillas (*Gorilla beringei beringei*), chimpanzees (*Pan troglodytes*), African elephants (*Loxodonta africana*) and lions (*Panthera leo*). Consequently, leopards and spotted hyenas are important tourism draws for the region. This is even more important as African lions became functionally extinct in LMNP in the early 2000's (Uganda Wildlife Authority 2010). There is also legal trophy hunting of leopards on LMNP's edge and high rates of human-leopard conflict on its boundary (Braczkowski et al. 2020c). This study represents the first assessment of leopards undertaken in a protected area system in Uganda and provides one of the first spatially explicit estimates of spotted hyena densities in the literature. This study produces a baseline single season snapshot into the population densities for both species to inform conservation management in the region and to better track the impacts of conservation interventions.

STUDY AREA

We studied leopards and spotted hyenas in the LMNP (370 km^2), Kiruhura district, Western Uganda (30° 47' – 31° 04'E, 00° 30' – 0° 30' S, Figure 1). The LMNP forms part of the Akagera savanna ecosystem which extends from Rwanda and north-western Tanzania down into south-western Uganda (Menaut 1983, Van de Weghe 1990). LMNP experiences a bimodal annual rainfall pattern (October – December and February – June) and annual rainfall and temperatures average 800 mm and 28° C, respectively (Moe et al. 2016). The woody vegetation in the park is characterized by dry *Acacia* savanna dominated by *Acacia hockii*, woodlands, thickets and swamps which occur on the edges of Lake Kachera and Mburo (Rannestad et al. 2006). The most common grasses include (*Loudetia kagerensis*), (*Chloris gayana*), and (*Sporobolus pyramidalis*). LMNP supports one of two remaining population of impala (*Aepyceros melampus*) in Uganda, the most common and preferred prey of the African leopard (Hayward et al. 2006). The park also harbours Plains zebra (*Equus quagga*) , Cape buffalo (*Syncerus caffer*), Defassa waterbuck (*Kobus ellipsiprymnus defassa*), bushbuck (*Tragelaphus* scriptus) and warthog (*Phacochoerus africanus*, Rannestad et al. 2006). There is only one male lion (≥ 10 years old) in LMNP (a vagrant thought to have come from Akagera National Park, in neighbouring Rwanda). LMNP is bordered by a matrix of small human settlements, small-scale subsistence crops, dairy ranches and communal grazing lands (Ochieng et al. 2015).

Park history, introduction of trophy hunting and human-carnivore conflict

Although the national park itself is small, much of the former park area - which is now mainly used as cattle rangeland - still has considerable woodlands, thickets and natural vegetation and Rannestad et al. (2006) noted higher densities of bushbuck, impala, reedbuck (*Redunca redunca*), waterbuck and zebra outside of the national park's borders during the wet season. The region surrounding LMNP has a trophy hunting scheme which was initiated due to increasing complaints by communities, stating that the increasing wildlife was a nuisance (Ochieng et al. 2015). The leopard is only allowed to be hunted when a problem animal tag is made available by Ugandan Wildlife Authority (hereafter UWA) attributed to repeated stock killing and damage. Although harvests of leopards since 2007 have been low in Uganda (17 skins, skulls and trophies exported from 2009–2017), attempts were made to have the species downgraded from CITES Appendix 1 to Appendix 2 and proposed a quota of 50 leopards annually (despite the lack of even a single abundance estimate anywhere in the country, CITES CoP 14 Proposal 3). Currently, 28 leopards are available annually on quota country-wide. Contrastingly, in Africa, hyenas are often taken opportunistically by trophy hunters rather than as prized trophy animals and we could not find any evidence that they are an actively hunted species in Uganda (see for example: http://www.uganda-wildlife-safaris.com).

METHODS

Camera trapping

This research was granted approval by the Uganda Wildlife Authority under permit number: UWA/COD/96/05 as approved by the Executive Director Mr Stephen Masaba. We implemented one single season camera-trap survey for 53 days in the LMNP from 26 July 2018 – 16 September 2018 using Cuddeback™ 20-megapixel Long Range IR camera traps (powered by 8 AA batteries each) set in a paired format. The survey encompassed 30 camera trap sites distributed across the national park (Figure 1), but we omitted camera traps in the far western sector of the park due to a lack of road access. Each camera trap site consisted of two camera traps, each mounted to a 1 m steel pole 40 cm from the ground. We positioned each camera perpendicular to a vehicle track or game trail at a 60 – 75°-angle to facilitate early detection of leopards and spotted hyenas. We set our camera traps on roads, vehicle tracks, trails and drainage lines, as these are regularly used by leopards and spotted hyenas as travel and hunting routes

(Balme et al. 2009a, Balme et al. 2009b, Henschel et al. 2014). We checked traps every 4 – 7 days to correct for animal damage, replace memory cards and to assess battery functionality (Braczkowski et al. 2016). Camera traps were set to burst mode and took five images every time the infrared sensor was triggered. We set camera traps in a way as to ensure that at least one camera-trap site was present in an area corresponding to the smallest female leopard home-range recorded in the literature (30 km^2; Bailey 1993, and 23 km^2 in Fattebert et al. 2016), as these are smaller than male leopards and spotted hyenas. Our camera spacing was 2.1 km (5-7 camera stations per female home range). We did choose this camera spacing in order to ensure that no animal had a zero probability of capture (Karanth and Nichols 1998). The identity of individual leopards and spotted hyenas was determined by their unique rosette and spot patterns (Miththapala et al. 1989, O'Brien and Kinnaird 2011). For leopards, we were able to classify the sex of individuals by using distinctive morphological cues such as the presence of testes and the enlarged dewlap and sagittal crest in males (Balme et al. 2012, Braczkowski et al. 2015a).

The first and eighth author assigned individual identity to temporally unique photographs and only included into the final density estimation process individuals for which there was consensus (Bahaa-el-din et al. 2016). We excluded images that were blurred, were too far away from the camera trap and those where observers could not agree on identity. For the purpose of building capture histories with known unique individual identities, we used both flanks of leopards in our analysis (Figure 2). Spotted hyenas, however, often walked around cameras and did not present a clear flank on both sides of a single animal, and several individuals moved around a single camera at the same time. To avoid mismatching flanks and mistakenly double-count individuals, we chose the flank of hyenas with the highest number of photographs recorded during our survey (Henschel et al. 2014).

SECR modelling

We estimated leopard and spotted hyena densities and abundance in LMNP using Bayesian spatially explicit capture re-capture modelling. By incorporating spatial information into the detection process, the method does not suffer from the "edge effects" common to non-spatial estimators (Gopalaswamy et al. 2012a). The modelling approach uses a state (leopard and spotted hyena population size and locations in the landscape) and observation process (Royle et al 2009, Gopalaswamy et al 2012b). To accurately estimate the densities and home-range centres of both species we generated potential activity centres across our study area (370 km^2) in the form of 0.336 km^2 (i.e. 580 m x 580 m, Gopalaswamy et al. 2012a) equally spaced pixels. This state-space assumes the number of leopards and spotted hyenas found in these pixels are defined by a binomial process, but because spotted hyenas are often found in groups, the state process allows for ≥ 2 spotted hyenas to have an activity centre in the same pixel (Gopalaswamy et al. 2012a). The state space encompassed the LMNP, and a buffer of 25 km around it (including the eastern rangelands bordering the park, Kanyaryeru and the southern farmlands). We masked out all human settlements and water bodies inside and surrounding the national park, as leopards and spotted hyenas are unlikely to have their home-range centres directly in such unsuitable habitats (Royle et al. 2009, Gopalaswamy et al. 2012a, Braczkowski et al. 2016). We used a classical capture re-capture sampling design and created a standard capture re-capture matrix (trap locations, individual leopards or hyenas and sampling occasions, e.g., du Preez et al. 2014, Braczkowski et al. 2016, Williams et al. 2017). Large terrestrial carnivores regularly feature differences at the sex-level in their home-range sizes and capture probability (Gopalaswamy et al. 2012b, Braczkowski et al. 2016). Differences in movements of animals based upon sex can affect the observation process in spatial capture-recapture (Sollmann et al. 2011). To factor this into our models, we included a sex-specific covariate in the observation process and accounted for different capture probability for leopards. We did not do this for hyenas as the female spotted hyenas feature a pseudo-scrotum which makes sexing difficult, and the visibility of males' testes was often obscured by their large tail (Hamilton et al. 1986).

In SECR modelling, σ is the scale parameter, and represents the rate of decline in the detection rate as the location of the animal's activity centre moves away from a camera trap station. $\lambda 0$ is the basal encounter rate and can be defined as the encounter rate of an animal whose activity centre lies exactly at a camera trap station. The detection rates of an individual animal decline with increasing distance between its activity centre and camera trap location (Borchers and Efford 2008, Royle et al., 2009) and the parameter θ defines the shape of the detection function. If this parameter is estimated from the given data, the shape of the detection function could define how an animal utilizes space or resources in its environment (Elliot and Gopalaswamy 2017). In practice, since encounter rates are so small, they are approximately equal to detection probabilities (Efford 2019). We either used a fixed θ at 0.75 (Elliot and Gopalaswamy 2017) and 1 (Gaussian form, Royle et al., 2009) or estimated a continuous θ parameter from the data. The complementary log-log link was used to convert encounter rates to Bernoulli detections, therefore, in our models, the probability of detecting a leopard or hyena i in pixel j is defined by a complementary log-log function of covariates.

We assessed six *a priori* models for leopards, and two for spotted hyenas (parameter definitions are presented in Table 1). Model 1 estimated the detection function (this is defined by θ) and assumed that detection probability is sex specific:

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

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 center of individual *i* and pixel *j*, θ and sex-specific σ_{sex}. The specific form of this detection function is:

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

Model 2 was based on the assumption that detection probability is not dependent on sex, (i.e., βsex was fixed at 0). The rate of decline in detection probability (σ) however, remained sex specific because this parameter is also linked to the movement of animals.

Model 3 as with model 2, had βsex set at 0 while the detection function was set at $\theta = 0.75$

Model 4 was based on the assumption that basal encounter rate is dependent on sex, thus, βsex 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 the same as model 1 but the detection function parameter (θ) was fixed at 1.

For the spotted hyenas' density assessment, we only used model 1 and model 6 due to the lack of a sex covariate.

We used Bayesian Markov Chain Monte Carlo (MCMC) simulation and the Metropolis-Hastings algorithm (Tierney 1994) to run our models in the package SCRbayes (https://github.com/jaroyle/SCRbayes) in the programming environment R Version 3.6.1 (R Development Core Team 2019). We set each model to run 8862-Table_5_REVISED.docx for 20,000 iterations including a burn-in of 5,000 iterations but we adjusted this further if we did not arrive at a standing distribution, (refining burn-in period and initial iterations further). Each model was set to run for 4 chains (Elliot and Gopalaswamy 2017). Model adequacy was determined by examining the Bayesian *p*-value on individual encounters (Royle et al. 2009). MCMC convergence was assessed using the Gelman–Rubin diagnostic (Gelman & Rubin 1992). The five input files necessary to run these analyses and accompanying R scripts are provided in the supporting information section of this manuscript (Supporting information 3). Although we were principally interested in estimating density, we also computed posterior mean abundance across the study area of the greater LMNP system.

RESULTS

We recorded a total of 1,444 trap nights during the 53-day survey period. Cameras were not functional due to animal interference and battery failures for 146 trap nights, and these were not included in the SECR analysis. We recorded a total of 61 temporally independent (ie. animals counted only once in a 24-hour period) detections of leopards during our camera trap survey, and 51 spotted hyena detections (Table 2). From these we recorded 112 and 42 useable flanks for leopards and hyenas respectively (51 right hyena flanks vs 32 left flanks; 9 excluded due to not identifiable or juvenile hyena). We identified 20 unique leopards (six adult males and 14 adult females), and 27 (no sex noted) spotted hyenas. This equates to a detection rate of 1.38 leopards and 1.87 spotted hyenas per 100 trap-nights.

Density estimates and Model diagnostics

Bayesian p-values for all our leopard density models ranged from 0.61– 0.76 (Supporting Information 1), indicating an adequate model fit (extremities 0.15 – 0.85). Convergence of models was indicated by a mean potential shrink reduction factor of <1.2 for each parameter for each model (Gelman and Rubin 1992, Supporting Information 1). The same assessment of model adequacy was recorded for a model where sigma was estimated without a sex effect for the estimates of spotted hyena density (Bayesian p = 0.61 and shrink reduction factor for all parameters <1.2, Supporting Information 2). Model selection using marginal likelihood from Dey et al. (2018) indicated that model 5, which considered basal encounter rate to be dependent on sex but detection probability independent of sex had the highest log likelihood score (log likelihood = -55,615.56, Table 3).

Leopard density estimates

Using model 5, leopard density for LMNP was estimated at 6.31 individuals/100 km^2 (posterior SD 1.47, 95% CI range = 3.75 – 9.20). The posterior mean abundance for the Lake Mburo National Park was 24.87 (posterior SD 7.78) using this model. The leopard movement parameter or sigma σ for males and females from this model was 1.33 km (this movement parameter is a measurement of how far animals travel in the landscape and is related to home range size; Braczkowski et al. 2020b). The next best-ranked candidate model (model number 4) which considered sex as a factor affecting detection probability estimated a movement parameter of 1.60 km for males and 0.59 km for females.

Hyena density estimates

For spotted hyenas, right flanks were recorded with the highest frequency (Table 2).

Spotted hyena density for LMNP was estimated at 11.00 individuals/100 km^2 (posterior SD = 0.32, 95% CI range = 5.57 – 17.09) using model 1. The spotted hyena movement parameter σ for both sexes combined was 3.15 km. The posterior mean abundance for the entire state space buffer was 39.07 spotted hyenas (posterior = SD 13.51, Table 3).

DISCUSSION

We provide a robust estimate of leopard densities and abundance in the LMNP ecosystem, southwestern Uganda, and also the first SECR assessment for spotted hyenas in Uganda as a whole (however these had wider confidence intervals when compared to leopards). These estimates are important baselines for the future monitoring of leopard and spotted hyena populations in the LMNP, one which experiences both significant levels of human-carnivore conflict and trophy hunting (Braczkowski et al. 2020c). Robust estimates of population abundance and densities are a critical cornerstone for tracking changes and trends in carnivore populations over time (e.g. Balme et al. 2009b, Williams et al. 2017). In this human-carnivore conflict-prone area, it is unknown whether retaliatory killings following depredation on livestock are sustainable in the long term, especially as the LMNP is small and isolated from other larger protected areas. Previous research has shown that carnivore populations in small, isolated national parks cannot withstand the edge effects from human-carnivore conflict (e.g. from cattle farming) and trophy hunting (Woodroffe and Ginsberg 1998, Balme et al. 2009b).

Possible explanations for observed leopard and hyena densities

Leopard densities in LMNP were on the mid-tier of estimates recorded in the recent literature using SECR studies (n=15 studies from 2013 – 2018, Table 4). The leopard densities we observed at 6.31 individuals/100 km^2 are somewhat surprising given a) the small size of LMNP, and b) the high levels of conflict between these two carnivores and the livestock rearing communities on the park edge (Braczkowski et al. 2020c). Contrastingly, the hyena densities were similar to a SECR study in uMkhuze Game Reserve, northern Kwa-Zulu Natal, South Africa (a savanna system) which estimated a density of 10.59 individuals/100 km^2 (posterior SD = 2.10, De Blocq 2014), and a study in Botswana's Moremi estimated 11.80 (posterior SD = 2.60, Rich et al. 2019). We postulate that three factors may be contributing to these densities, namely 1) the availability of preferred prey, 2) the existence of a compensation scheme that reimburses ranchers after depredation events on the LMNP edge (Braczkowski et al. 2020c), and 3) the functional extinction of lions in the region dating back to over a decade ago (at the time of publication there was only one male lion (≥ 10 years old) in this ecosystem, a vagrant thought to have come from Akagera National Park, in neighbouring Rwanda). LMNP is one of only two protected areas in Uganda with a population of impala, the most preferred prey of leopards (Hayward et al. 2006). The most recent studies implemented using distance sampling by Rannestad et al. (2006) and Kisame et al. (2018) found significant populations of impala within LMNP and on the adjacent cattle farmlands at 25.6 ± 4.8 individuals/km^2 in the 2003 study of Rannestad et al. (2006), and 15.3 and 16.6 individuals/km^2 in the 2014 and 2016 sampling periods of Kisame et al. (2018). Importantly Rannestad et al. (2006) also found a higher number of impala groups (80 vs 58) and total individuals (348 vs 255) in the community lands adjoining the park than within the national park in the wet season of 2003. Similarly, Kisame et al. (2018) estimated that nearly half of the impala population in the LMNP and surrounding ranches was found on non-protected land. Other densities of key leopard prey species estimated in this study included 3.8 ± 0.8 individuals/km^2 for bushbuck (higher densities outside) and warthogs (12.3 ± 2.9 individuals/km^2, densities lower outside national park, Rannestad et al. 2006). The availability of these species at relatively high densities both inside and beyond the edge of LMNP could be one reason for the densities of leopards and hyenas we observed in our study. It also remains unclear whether the functional extinction of lions in the LMNP has contributed to some level of release of leopards and spotted hyenas. For example, from their study of leopard densities in three Kwazulu-Natal Parks, South Africa, Ramesh et al. (2016) found that where lion distribution overlapped spatially with leopards, densities of leopards decreased drastically. However this pattern of leopard suppression by lions was not observed in the Sabi Sand Game Reserve, a protected area system adjacent to the Kruger National Park where leopard-lion observations have been recorded since the 1970's (Balme et al. 2017b).

Spotted hyenas and lions have an intricate relationship of facilitation and competition (Périquet et al. 2015). Unlike leopards, spotted hyenas do not show a negative correlation with lion presence in Africa (Périquet et al. 2015) despite intraguild predation and the negative impact that lions can have on hyena reproduction (Watts and Holekamp 2008). Spotted hyenas may benefit from the presence of lions – and vice versa – due to the high dietary overlap between the species leading to scavenging and kleptoparasitic opportunities (Hayward 2006, Davidson et al. 2019). Observed positive correlations in lion and spotted hyena density in many parts of Africa may also be a result of their similar preferred prey base. In Zambia, M'soka et al. (2016) found a high density of spotted hyenas in a lion-depleted ecosystem, though it was suggested that the observed density was driven by the availability of wildebeest, as in Höner et al. (2005). The spotted hyena densities we observed in our study were similar to an unpublished SECR study from uMkhuze Game Reserve, KwaZulu-Natal, South Africa (De Blocq 2014), and a study from Botswana's Moremi (Rich et al. 2019). Estimates of spotted hyena densities using non-SECR methods, from African savanna sites range widely from 2 – 20 individuals/100 km^2 in the Kruger National Park, South Africa (Mills et al. 2001) to over 100 individuals/100 km^2 in the Ngorongoro Crater, Tanzania (Kruuk, 1972; Höner et al. 2005). The spotted hyena density from this study is similar those from protected areas in southern Africa but lower than those in other East African savannas (Holekamp and Dloniak 2010). It is important to note that the majority of previous estimates have been produced using non-spatial methods (e.g. call-ups and mark-resight), and to our knowledge our study is one of the first to use a SECR approach for spotted hyena density estimation (Table 5). SECR densities are typically lower for large carnivores due to other methods making more generalized extrapolations over a given unit area (Noss et al. 2012) which may explain the difference between our results and those from other savanna systems in East Africa where non-spatial methods were used.

It is noteworthy that areas of high density between the species do not appear to overlap (Figure 3). Previous studies have suggested that spotted hyenas can be significant kleptoparasites of leopard kills, forcing them to cache or avoid areas with high hyena density (Balme et al. 2017a; Davis et al., 2021). Similarly, another study detected low temporal overlap between leopards and spotted hyenas in Tanzania, which was postulated to be due to the avoidance of kleptoparasitism (Havmøller et al. 2020).

Therefore, the avoidance of kleptoparastism may drive the differences in space use between the species we detected in LMNP but would require further investigation.

Limitations and future monitoring of large carnivores in LMNP

Our study is limited by a lack of temporal replication. This is important as we could not generate critical population parameters such as emigration, immigration, birth and death (e.g. Karanth et al. 2006). These parameters are indicators of population trend and are ultimately required to ascertain the true trajectory of a given population. It should also be remembered that spotted hyenas live in fission-fusion clans and may move together in groups or singularly. It remains to be seen if this clan-living structure may cause biases in estimates of density and other parameters in our sampling situation. For example, López-Bao (2018) show that wolf densities are not significantly affected by group living. Similarly, Bischof et al., (2020) suggest that if there are low to moderate levels of gregariousness observed in group living individuals, there is little overdispersion that occurs in the estimation of the detection function and scale parameter. However, if gregariousness is high, overdispersion may be observed in confidence intervals around parameter estimates, affecting the veracity of estimates. Although our study represents the first snapshot of this leopard and spotted hyena population, it is important as a baseline estimate from which future estimates can be made against (eg. Balme et al. 2009b). Our study also failed to quantify any relationships between hyenas and leopards, which in some sites have been shown to positively influence one another's occupancy in a landscape (Comley et al. 2020).

There is a growing conflict between large carnivores and humans in the greater LMNP ecosystem (Braczkowski et al. 2020c). The impacts of spotted hyenas and leopards on cattle, sheep and goats in the Bahima pastoral lands adjacent to LMNP are significant, and leopards and spotted hyenas were the source of 98% (n=1102) of depredation events recorded between January 2009 – December 2018 in the region (Braczkowski et al. 2020c). Other studies have highlighted spotted hyenas as a primary source of livestock loss, which combined with their negative public image, makes them vulnerable to retaliatory killing (Kissui 2008; Holmern et al.2007). While spotted hyenas are behaviourally flexible, populations are slow to recover following even moderate reduction (Benhaiem et al. 2018). This pattern has also been observed for African leopards (e.g. Balme et al. 2009b). For this reason, the continued monitoring of the LMNP spotted hyena and leopard population is crucial from a human-carnivore conflict perspective. Continued population monitoring of leopards is also critical in the context of trophy-hunting of leopard and leopard prey, which is allowed on properties adjoining the LMNP. Even though legal harvests of leopards in Uganda since 2007 have been low (17 skins, skulls and trophies exported from 2009 – 2017), and 28 leopards are available on quota country-wide annually (Braczkowski et al. 2015b), it is critical to monitor these populations annually or biannually as they can rapidly decline under even modest harvest pressures (Balme et al. 2010). The way in which quotas have been set in Uganda for leopards was also done using a non-robust method which related rainfall to leopard densities (CITES CoP 14 Proposal 3).

CONCLUSION

We aimed at providing the first leopard and spotted hyena population density estimates for the Lake Mburo ecosystem in Uganda, a small but regionally important national park with significant cattle farming on its edge. We found that leopard occur at a relatively high density of 6.3 individuals/100 km^2, probably due to a combination of factors such a high local prey density and an absence of lions. Spotted hyena densities of were also relatively high, with several factors putatively at play, including abundance of prey including livestock, the absence of lions, and the general tolerance of hyenas for human disturbance. Our estimates form a robust baseline for future population monitoring to inform both the design of sustainable management offtakes, and conservation interventions for the two species in the region.

ACKNOWLEDGEMENTS

We are grateful to the Ugandan Wildlife Authority for their support in the implementation of this study, particularly Aggrey Rwetsiba and Kule Asa Musinguzi. The Scientific Exploration Society, Rufford Foundation, Mihingo Lodge, and the Siemiatkowski Foundation are thanked for their help with funding and supporting Alex Braczkowski while he was in the field.

REFERENCES

Bailey, T.N. (1993). The African leopard. Columbia University Press, New York.

Bahaa-el-din, L., Sollmann, R., Hunter, L. T., Slotow, R., Macdonald, D. W., & Henschel, P. (2016). Effects of human land-use on Africa's only forest-dependent felid: The African golden cat Caracal aurata. Biological Conservation, 199, 1-9.

Balme, G.A., Hunter, L.T.B. & Slotow, R. (2009a). Evaluating methods for counting cryptic carnivores. J. Wildl. Mgmt. 73, 433–441.

Balme, G.A., Slotow, R. & Hunter, L.T.B. (2009b). Impact of conservation interventions on the dynamics and persistence of a persecuted leopard population. Biol. Conserv. 142, 2681–2690.

Balme, G.A., Slotow, R.O.B. and Hunter, L.T. (2010). Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda–Mkhuze Complex, South Africa. *Animal conservation*, *13*(3), pp.315-323.

Balme, G.A., Hunter, L. and Braczkowski, A.R. (2012). Applicability of age-based hunting regulations for African leopards. *PloS one*, *7*(4).

Balme, G. A., Miller, J. R., Pitman, R. T., & Hunter, L. T. (2017a). Caching reduces kleptoparasitism in a solitary, large felid. *Journal of Animal Ecology*, *86*(3), 634-644.

Balme, G. A., Pitman, R. T., Robinson, H. S., Miller, J. R., Funston, P. J., & Hunter, L. T. (2017b). Leopard distribution and abundance is unaffected by interference competition with lions. Behavioral Ecology, 28(5), 1348-1358.

Benhaiem, S., Marescot, L., East, M. L., Kramer-Schadt, S., Gimenez, O., Lebreton, J. D., & Hofer, H. (2018). Slow recovery from a disease epidemic in the spotted hyena, a keystone social carnivore. *Communications biology*, *1*(1), 1-12.

Bischof, R., Dupont, P., Milleret, C., Chipperfield, J., & Royle, J. A. (2020). Consequences of ignoring group association in spatial capture–recapture analysis. Wildlife Biology, 2020(1).

Borchers, D. L., & Efford, M. G. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. Biometrics, 64(2), 377-385.

Braczkowski, A.R., Balme, G.A., Dickman, A., Macdonald, D.W., Fattebert, J., Dickerson, T., Johnson, P. and Hunter, L. (2015a). Who bites the bullet first? The susceptibility of leopards Panthera pardus to trophy hunting. *PloS one*, *10*(4).

Braczkowski, A. R., Dickman, A., Macdonald, D. W., Johnson, P. J., Balme, G. A., Lindsey, P. A., & Hunter, L. T. (2015b). Rosettes, Remingtons and Reputation: Establishing potential determinants of leopard (Panthera pardus) trophy prices across Africa. African Journal of Wildlife Research, 45(2), 158-168.

Braczkowski AR, Balme GA, Dickman A, Fattebert J, Johnson P, Dickerson T, Macdonald DW, Hunter L. (2016). Scent Lure Effect on Camera-Trap Based Leopard Density Estimates. *PLoS One*: e0151033.

Braczkowski, A., Gopalaswamy, A. M., Nsubuga, M., Allan, J., Biggs, D., & Maron, M. (2020b). Detecting early warnings of pressure on an African lion (Panthera leo) population in the Queen Elizabeth Conservation Area, Uganda. *Ecological Solutions and Evidence*, *1*(1), e12015.

Braczkowski, A., Fattebert, J., Schenk, R., O'Bryan, C., Biggs, D., & Maron, M. (2020c). Evidence for increasing human-wildlife conflict despite a financial compensation scheme on the edge of a Ugandan National Park. Conservation Science and Practice, 2(12), e309.

Comley, J., Joubert, C. J., Mgqatsa, N., & Parker, D. M. (2020). Lions do not change rivers: complex African savannas preclude top-down forcing by large carnivores. *Journal for Nature Conservation*, 125844.

Davidson, Z., Dupuis-Desormeaux, M., Dheer, A., Pratt, L., Preston, E., Gilicho, S., Mwololo, M., Chege, G., MacDonald, S., Doncaster, C. P. (2019). Borrowing from Peter to pay Paul: managing threatened predators of endangered and declining prey species. *PeerJ*, *7*, e7916.

Davis, R. S., Yarnell, R. W., Gentle, L. K., Uzal, A., Mgoola, W. O., & Stone, E. L. (2021). Prey availability and intraguild competition regulate the spatiotemporal dynamics of a modified large carnivore guild. *Ecology and Evolution*.

De Blocq, A.D. (2014). *Estimating spotted hyaena (Crocuta crocuta) population density using camera trap data in a spatially explicit capture-recapture framework* (Doctoral dissertation, University of Cape Town).

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

Duangchantrasiri, S., Umponjan, M., Simcharoen, S., Pattanavibool, A., Chaiwattana, S., Maneerat, S., Kumar, N.S., Jathanna, D., Srivathsa, A. and Karanth, K.U. (2016). Dynamics of a low-density tiger population in Southeast Asia in the context of improved law enforcement. *Conservation Biology*, *30*(3), pp.639-648.

du Preez, B.D., Loveridge, A.J. and Macdonald, D.W. (2014). To bait or not to bait: a comparison of camera-trapping methods for estimating leopard Panthera pardus density. *Biological Conservation*, *176*, pp.153-161.

Efford, M. G. (2019). Non-circular home ranges and the estimation of population density. Ecology, 100(2), e02580.

Elliot, N.B. and Gopalaswamy, A.M. (2017). Toward accurate and precise estimates of lion density. *Conservation Biology*, *31*(4), pp.934-943.

Fattebert, J., Robinson, H.S., Balme, G., Slotow, R. and Hunter, L. (2015). Structural habitat predicts functional dispersal habitat of a large carnivore: how leopards change spots. *Ecological Applications*, *25*(7), pp.1911-1921.

Fattebert, J., Balme, G. A., Robinson, H. S., Dickerson, T., Slotow, R., & Hunter, L. T. (2016). Population recovery highlights spatial organization dynamics in adult leopards. *Journal of Zoology*, *299*(3), 153-162.

Gelman, A. and Rubin, D.B. (1992). Inference from iterative simulation using multiple sequences. *Statistical science*, *7*(4), pp.457-472.

Gopalaswamy, A.M., Royle, J.A., Delampady, M., Nichols, J.D., Karanth, K.U. and Macdonald, D.W. (2012a). Density estimation in tiger populations: combining information for strong inference. *Ecology*, *93*(7), pp.1741-1751.

Gopalaswamy, A.M., Royle, J.A., Hines, J.E., Singh, P., Jathanna, D., Kumar, N.S. and Karanth, K.U. (2012b). Program SPACECAP: software for estimating animal density using spatially explicit capture–recapture models. *Methods in Ecology and Evolution*, *3*(6), pp.1067-1072.

Hamilton, W.J., Tilson, R. L., & Frank, L. G. (1986). Sexual monomorphism in spotted hyenas, Crocuta crocuta. *Ethology*, *71*(1), 63-73.

Havmøller, R. W., Jacobsen, N. S., Scharff, N., Rovero, F., & Zimmermann, F. (2020). Assessing the activity pattern overlap among leopards (Panthera pardus), potential prey and competitors in a complex landscape in Tanzania. *Journal of Zoology*, *311*(3), 175-182.

Hayward, M. W. (2006). Prey preferences of the spotted hyaena (Crocuta crocuta) and degree of dietary overlap with the lion (Panthera leo). *Journal of Zoology*, *270*(4), 606-614.

Hayward, M.W., Henschel, P., O'brien, J., Hofmeyr, M., Balme, G. and Kerley, G.I.H. (2006). Prey preferences of the leopard (Panthera pardus). *Journal of Zoology*, *270*(2), pp.298-313.

Henschel, P., Malanda, G. A., & Hunter, L. (2014). The status of savanna carnivores in the Odzala-Kokoua National Park, northern Republic of Congo. *Journal of Mammalogy*, *95*(4), 882-892.

Holekamp, K. E., & Dloniak, S. M. (2010). Intraspecific variation in the behavioral ecology of a tropical carnivore, the spotted hyena. In *Advances in the Study of Behavior* (Vol. 42, pp. 189-229). Academic Press.

Holmern, T., Nyahongo, J., & Røskaft, E. (2007). Livestock loss caused by predators outside the Serengeti National Park, Tanzania. *Biological conservation*, *135*(4), 518-526.

Höner, O. P., Wachter, B., East, M. L., & Hofer, H. (2002). The response of spotted hyaenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. *Journal of Animal Ecology*, *71*(2), 236-246.

Höner, O. P., Wachter, B., East, M. L., Runyoro, V. A., & Hofer, H. (2005). The effect of prey abundance and foraging tactics on the population dynamics of a social, territorial carnivore, the spotted hyena. *Oikos*, *108*(3), 544-554.

Jacobson, A. P., Gerngross, P., Lemeris Jr, J. R., Schoonover, R. F., Anco, C., Breitenmoser-Würsten, C., ... & Laguardia, A. (2016). Leopard (Panthera pardus) status, distribution, and the research efforts across its range. *PeerJ*, *4*, e1974.

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

Karanth, K. U., & Nichols, J. D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. Ecology, 79(8), 2852-2862.

Karanth, K. U., Nichols, J. D., Kumar, N. S., & Hines, J. E. (2006). Assessing tiger population dynamics using photographic capture–recapture sampling. *Ecology*, *87*(11), 2925-2937.

Kisame, F.E., Wanyama, F., Buhanga, E. & Rwetsiba, A. (2018). Ground Counts for medium to large mammals in Lake Mburo Conservation Area. Uganda Wildlife Authority, Kampala, Uganda. Available at: https://www.ugandawildlife.org/phocadownload/conservation-publications/survey-reports/Ground-counts-for-LMNP-2018.pdf

Kruuk, H. (1972). *The spotted hyena: a study of predation and social behavior* . University of Chicago Press.

López-Bao, J. V., Godinho, R., Pacheco, C., Lema, F. J., García, E., Llaneza, L., ... & Jiménez, J. (2018). Toward reliable population estimates of wolves by combining spatial capture-recapture models and non-invasive DNA monitoring. Scientific reports, 8(1), 1-8.

Martin, R.B. and de Meulenaer, T. (1988). Survey of the status of the leopard *Panthera pardus* in sub-Saharan Africa. CITES, Geneva, Switzerland.

Menaut JC (1983) The Vegetation of African Savannas. In: Bourlière F (ed) Tropical savannas, vol 13. Elsevier, Amsterdam, pp 109–150.

Miller, J.R., Pitman, R.T., Mann, G.K., Fuller, A.K. and Balme, G.A. (2018). Lions and leopards coexist without spatial, temporal or demographic effects of interspecific competition. *Journal of Animal Ecology*, *87*(6), pp.1709-1726.

Miththapala, S., Seidensticker, J., Phillips, L.G., Fernando, S.B.U. and Smallwood, J.A. (1989). Identification of individual leopards (Panthera pardus kotiya) using spot pattern variation. *Journal of Zoology*, *218*(4), pp.527-536.

M'soka, J., Creel, S., Becker, M. S., & Droge, E. (2016). Spotted hyaena survival and density in a lion depleted ecosystem: The effects of prey availability, humans and competition between large carnivores in African savannahs. *Biological Conservation*, *201*, 348-355.

Mills, M. G. L., Juritz, J. M., & Zucchini, W. (2001). Estimating the size of spotted hyaena (Crocuta crocuta) populations through playback recordings allowing for non-response. In Animal Conservation forum (Vol. 4, No. 4, pp. 335-343). Cambridge University Press.

Moe, S. R., Loe, L. E., Jessen, M., & Okullo, P. (2016). Effects of mammalian herbivores and termites on the performance of native and exotic plantation tree seedlings. *Journal of applied ecology*, *53*(2), 323-331.

Noss, A. J., Gardner, B., Maffei, L., Cuéllar, E., Montaño, R., Romero-Muñoz, A., ... & O'Connell, A. F. (2012). Comparison of density estimation methods for mammal populations with camera traps in the K aa-I ya del G ran C haco landscape. *Animal Conservation*, *15*(5), 527-535.

O'Brien, T.G. and Kinnaird, M.F. (2011). Density estimation of sympatric carnivores using spatially explicit capture–recapture methods and standard trapping grid. *Ecological Applications*, *21*(8), pp.2908-2916.

O'Bryan, C. J., Braczkowski, A. R., Beyer, H. L., Carter, N. H., Watson, J. E., & McDonald-Madden, E. (2018). The contribution of predators and scavengers to human well-being. Nature ecology & evolution, 2(2), 229-236.

Ochieng, A., Ahebwa, W.M. and Visseren-Hamakers, I.J. (2015). Hunting for conservation? The re-introduction of sport hunting in Uganda examined. In *Institutional Arrangements for Conservation, Development and Tourism in Eastern and Southern Africa* (pp. 139-155). Springer, Dordrecht.

Périquet, S., Fritz, H. and Revilla, E. (2015). The Lion King and the Hyaena Queen: large carnivore interactions and coexistence. *Biological reviews*, *90*(4), 1197-1214.

Ramesh, T., Kalle, R., Rosenlund, H. and Downs, C.T. (2017). Low leopard populations in protected areas of Maputaland: a consequence of poaching, habitat condition, abundance of prey, and a top predator. *Ecology and evolution*, *7*(6), pp.1964-1973.

Rannestad, O.T., Danielsen, T., Moe, S.R. and Stokke, S. (2006). Adjacent pastoral areas support higher densities of wild ungulates during the wet season than the Lake Mburo National Park in Uganda. *Journal of tropical ecology*, *22*(6), pp.675-683.

Rayan, D.M. and Linkie, M. (2015). Conserving tigers in Malaysia: A science-driven approach for eliciting conservation policy change. *Biological Conservation*, *184*, pp.18-26.

R Development Core Team. (2019). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rich, L. N., Miller, D. A., Muñoz, D. J., Robinson, H. S., McNutt, J. W., & Kelly, M. J. (2019). Sampling design and analytical advances allow for simultaneous density estimation of seven sympatric carnivore species from camera trap data. *Biological Conservation*, *233*, 12-20.

Royle, J.A., Karanth, K.U., Gopalaswamy, A.M. and Kumar, N.S. (2009). Bayesian inference in camera trapping studies for a class of spatial capture–recapture models. *Ecology*, *90*(11), pp.3233-3244.

Sollmann, R., Furtado, M.M., Gardner, B., Hofer, H., Jácomo, A.T., Tôrres, N.M. and Silveira, L. (2011). Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biological Conservation*, *144*(3), pp.1017-1024.

Tierney, L. (1994). Markov chains for exploring posterior distributions. *The Annals of Statistics*, pp.1701-1728.

Tweheyo, M., Tumusiime, D. M., Turyahabwe, N., Asiimwe, A., & Orikiriza, L. (2012). Wildlife damage and control methods around Lake Mburo National Park, Uganda. *International journal of pest management*, *58*(1), 25-31.

Uganda Wildlife Authority (2010). Strategic action plan for large carnivore conservation in Uganda 2010–2020. Kampala, Uganda.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M. and Levy, M.A. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature communications*, *7*(1), pp.1-11.

Vissia, S., Wadhwa, R., & van Langevelde, F. (2021). Co-occurrence of high densities of brown hyena and spotted hyena in central Tuli, Botswana. Journal of Zoology.

Van der Meer, E., Badza, M. N., & Ndhlovu, A. (2016). Large carnivores as tourism flagship species for the Zimbabwe component of the Kavango Zambezi Transfrontier Conservation Area. *African Journal of Wildlife Research*, *46*(2), 121-134.

Van de Weghe, J.P. (1990) *Akagera, Land of Water, Grass and Fire*. WWF, Brussels.

Watts, H. E., & Holekamp, K. E. (2008). Interspecific competition influences reproduction in spotted hyenas. *Journal of Zoology*, *276*(4), 402-410.

White, G.C. and Burnham, K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird study*, *46*(sup1), pp.S120-S139.

Williams, P.J., Hooten, M.B., Womble, J.N. and Bower, M.R. (2017). Estimating occupancy and abundance using aerial images with imperfect detection. *Methods in Ecology and Evolution*, *8*(12), pp.1679-1689.

Woodroffe, R. and Ginsberg, J.R. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, *280*(5372), pp.2126-2128.

Figure 1

Study area map of the Lake Mburo National Park

Study area map of the Lake Mburo National Park

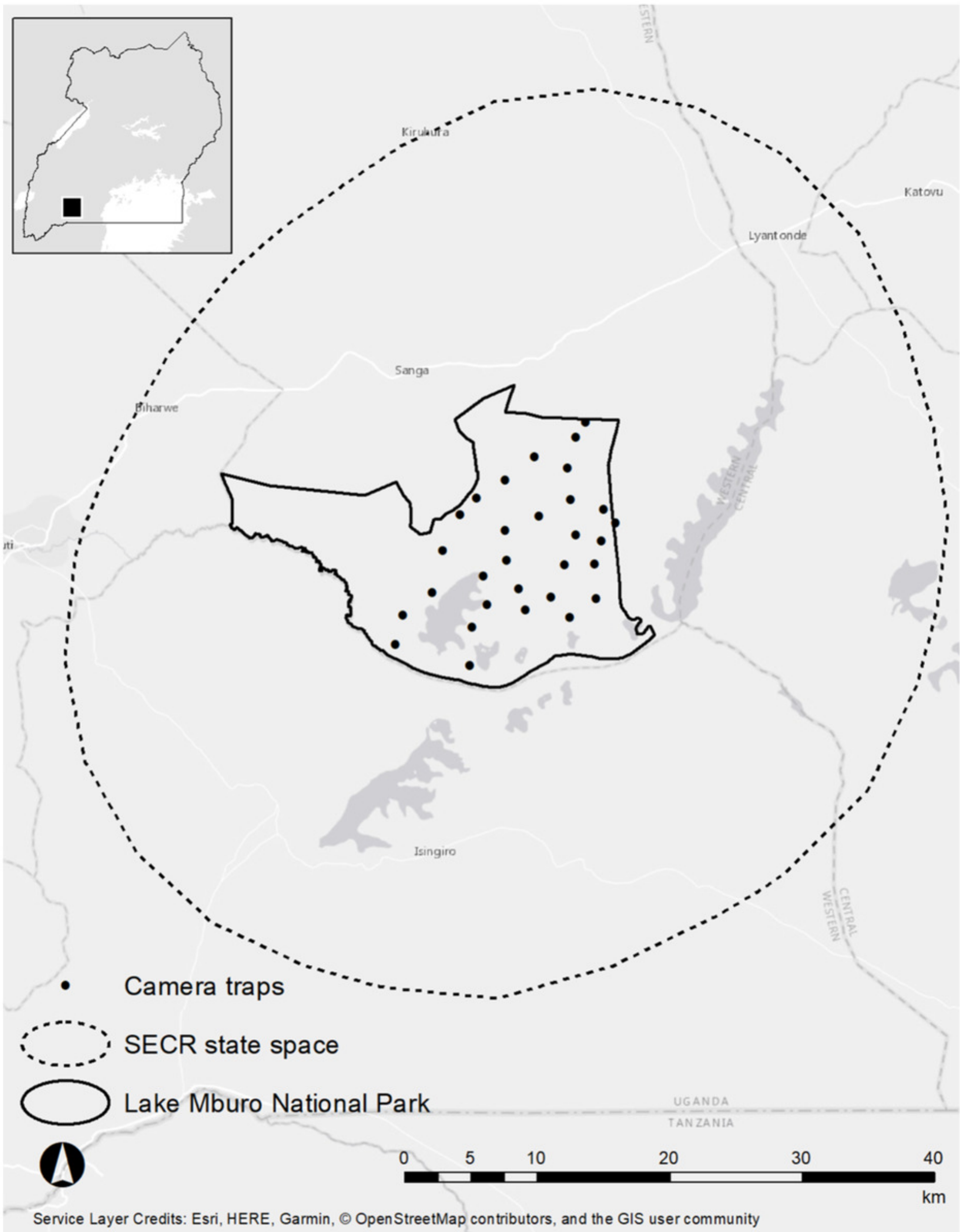
Kiruhura
Katovu
Lyantonde
Sanga
Biharwe
Isingiro
UGANDA
TANZANIA
Camera traps
SECR state space
Lake Mburo National Park
0 5 10 20 30 40
km
Service Layer Credits: Esri, HERE, Garmin, © OpenStreetMap contributors, and the GIS user community

Figure 2

Individual Identification of spotted hyenas and leopards from camera traps

Individual identification information extracted from leopards and spotted hyenas in the LMNP, 2018. Slide 1 (top) denotes a female leopard captured at trap location five on sampling occasion two and ten respectively. Rosette patterns and facial spots were extracted during these two occasions. Slide 2 (bottom) denotes the spot pattern extracted from a spotted hyena captured at location 12 and 27 on sampling occasions 5 and 22 respectively.

Figure 3

Densities of leopards and hyenas in Lake Mburo

African leopard and spotted hyena detection frequencies (denoted in frequency by the size of spheres) and density estimates from our SECR models, LMNP, Uganda.

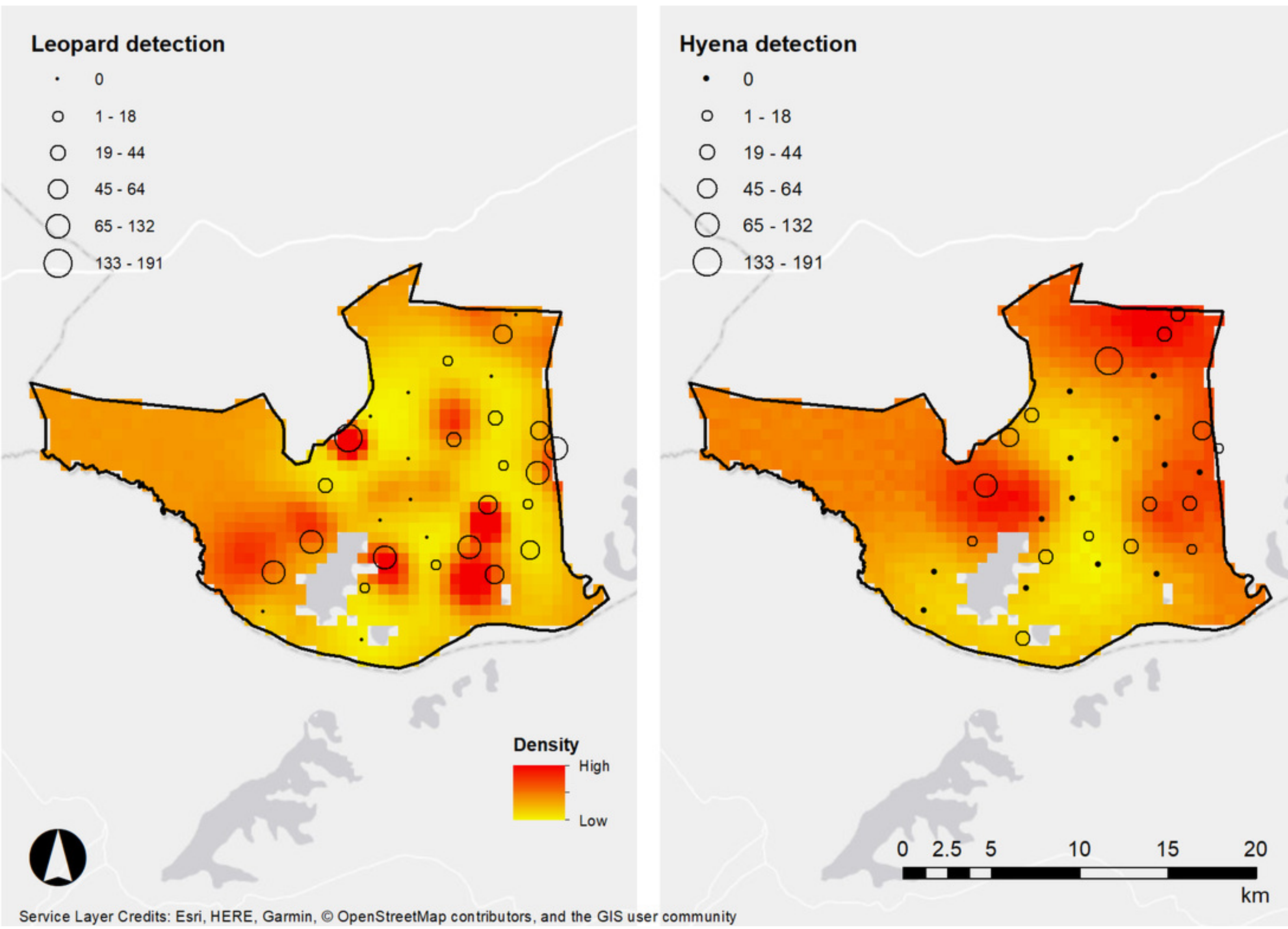

Table 1 (on next page)

Model components for secr analysis of leopard and hyena population densities

Model components for secr analysis of leopard and hyena population densities

Parameter	Definition
n	total number of leopards or hyenas detected during the survey period
nz	number of leopards augmented to n, so M = n+nz represents the maximum number of leopards in the large state space S
σF	rate of decline in detection probability with increasing distance between the activity center of a leopardess and the location at which she was found
σM	rate of decline in detection probability with increasing distance between the activity center of a leopard and the location at which he was found
βsex	difference of the complementary log-log value of detection probability between a male and female leopard
λ0	basal encounter rate of a leopard whose activity center is located exactly at the centroid of a grid cell
ψ	ratio of the true number of individuals in the population compared with the data-augmented population *M*
*N*super	total number of leopards in the larger state space *S*
ψsex	proportion of leopards that are female (1-psi.sex/psi.sex)
θ	determines the shape of the estimated detection function, value θ ranges from 0.5 (exponential form) to 1 (Gaussian)
D	estimated density of leopards per 100 km^2

1

Table 2(on next page)

Number of flanks of hyenas and leopards recorded during camera trapping in LMNP with total recaptures

Number of flanks of hyenas and leopards recorded during camera trapping in LMNP with total recaptures

Species	Number of left flanks	Number of right flanks	Number of useable flanks for analysis	Unique individuals identified	Unique individuals recaptured
Spotted hyena	32	51	42	27	8
Leopard	57	55	112	20	13

Table 3 (on next page)

SECR models from the Lake Mburo survey

Models used to generate our density analyses for leopards and spotted hyenas in the LMNP, Uganda, 2018. We present the model number, Bayes p-value to signify model adequacy and the marginal likelihood values used to select our models, and number of iterations used to achieve convergence.

Species	Model number	Bayes p-value	Marginal likelihood	Total iterations	Burn in required to reach convergence
Leopards	1	0.71	-62893.814	52000	42000
	2	0.71	-62885.778	50000	20000
	3	0.72	-62784.534	80000	2000
	4	0.71	-62729.456	50000	20000
	5	0.61	-55615.556	50000	20000
	6	0.76	-62985.962	50000	20000
Spotted Hyenas	1	0.62	-41030.296	11000	6000
	2	0.64	-41045.548	11000	1000

Table 4(on next page)

Literature review of recent SECR leopard studies

A review of 17 recent SECR studies performed on leopards in the last 5 years from the peer-reviewed literature. Some studies used a combination of maximum likelihood and Bayesian-based modelling approaches and therefore contain 2 or more estimates. We excluded the following studies for the following reasons:Goswami and Ganesh 2014 – no error reporting around estimatesKittle et al. 2017 – SECR results of tracks places results in contentionRich et al. 2019 – estimate is not directly reported only a figure is present*We examined the first ten pages of Google Scholar and limited the studies in this table to a) those using SECR and b) being published in the last 5 years.

Study name	Location	Habitat type	Model used to estimate density	Density estimate (leopards/100 km2)	SD (SE)
Balme et al. 2019	Sabi-Sands Game Reserve, South Africa	Semi-wooded savanna	Borchers and Efford 2008	11.80	2.60
Borah et al. 2014	Manas National Park, India	Tropical forest and mountains	Borchers and Efford 2008	3.40	0.82
Braczkowski et al. 2016	Phinda Private Game Reserve, South Africa	Savanna	Royle et al. 2009a	3.55	1.04
Braczkowski et al. 2016	Phinda Private Game Reserve, South Africa	Savanna	Borchers and Efford 2008	3.40	1.20
Devens et al. 2018	Baviaanskloof mountains, South Africa	Mountain fynbos and forest	Royle et al. 2009a	0.24	0.10
Devens et al. 2018	Langeberg mountains, South Africa	Mountain fynbos and forest	Royle et al. 2009a	1.89	0.30
Du Preez et al. 2014	Bubye Valley Conservancy, Zimbabwe	Mopane woodland (savanna)	Borchers and Efford 2008	5.28	0.89
Du Preez et al. 2014	Bubye Valley Conservancy, Zimbabwe	Mopane woodland (savanna)	Royle et al. 2009a	5.46	1.14
Hedges et al. 2015	Kenyir Wildlife Corridor, Malaysia	Dipterocarp forest	Borchers and Efford 2008	3.30	1.28
Hedges et al. 2015	Kenyir Wildlife Corridor, Malaysia	Dipterocarp forest	Royle 2011	3.06	0.91
Kittle and Watson 2017	Horton Plains, Sri-Lanka	Montane forest	Borchers and Efford 2008	13.40	6.3
Ngoprasert et al. 2017	Ban Krang, Kaeng Krachan National Park, Thailand	Evergreen forest	Borchers and Efford 2008	2.50	1.20
Qi et al. 2015	Laoye mountains, China	Deciduous forest	Royle et al. 2009a	0.62	0.15
Rahman et al. 2018	Ujong Kulon National Park, Java, Indonesia	Tropical forest	Borchers and Efford 2008	12.80	1.99
Rahman et al. 2018	Ujong Kulon National Park, Java, Indonesia	Tropical forest	Royle et al. 2009a	11.54	1.22
Ramesh et al. 2017	Ndumo Game Reserve, South Africa	Woodland savanna	Royle et al. 2009a	1.60	-
Ramesh et al. 2017	Western Shores, South Africa	Coastal savanna	Royle et al. 2009a	8.40	-
Rostro Garcia et al. 2018	Srepok wildlife sanctuary, Cambodia	Dry deciduous forest	Royle et al. 2009a	1.00	0.40
Selvan et al. 2014	Pakke Tiger Reserve, India	Tropical forest	Borchers and Efford 2008	2.82	1.20
Strampelli et al. 2018	Xonghile Game Reserve, Mozambique	Woodlands and thickets (savanna)	Borchers and Efford 2008	2.59	0.96

Swanepoel et al. 2015	Farming matrix, Waterberg, South Africa	Livestock and game farms	Borchers and Efford 2008	6.59	5.20
Swanepoel et al. 2015	Lapalala Game Reserve, South Africa	Mountain bushveld (dystrophic savanna)	Borchers and Efford 2008	5.35	2.93
Swanepoel et al. 2015	Welgevonden Game Reserve, South Africa	Mountain bushveld (dystrophic savanna)	Borchers and Efford 2008	4.56	1.35
Thapa et al. 2014	Parsa Wildlife Reserve, Nepal	Dry deciduous forest	Efford et al. 2004	3.78	0.85
Thapa et al. 2014	Parsa Wildlife Reserve, Nepal	Dry deciduous forest	Royle et al. 2009a	3.48	0.83
Williams et al. 2017	Soutpansberg mountains, South Africa	Matrix of livestock farms, nature reserves, mountains	Royle et al. 2009a	5.34	0.02

Table 5(on next page)

Spotted hyena densities recorded in the literature

Spotted hyena density estimates using SECR and camera trapping in six locations across sub-Saharan Africa.

Study name	Location	Habitat type	Model used to estimate density	Density estimate (hyenas/100 km2)	SD (SE)
Vissia et al. 2021	Central Tuli, Botswana	Riverine woodland and shrub savanna	Borchers and Efford 2008	14.90	2.23
Rich et al. 2019	Moremi Game Reserve and cattle matrix, Botswana	Semi-wooded savanna	Borchers and Efford 2008	11.80	2.60
Briers-Louw 2017	Majete Game Reserve, Malawi	Tropical dry woodland/miombo savanna woodland	Royle et al. 2009	2.69	0.48
De Blocq 2014	uMhkhuze Game Reserve, South Africa	Semi-wooded savanna	Royle et al. 2009	10.59	2.1
O'Brien and Kinnaird 2011	Mpala Ranch, Kenya	Semi-wooded savanna/cattle ranch	Borchers and Efford 2008	4.93	1.7