Leopard and spotted hyena densities in the Lake Mburo National Park, southwestern Uganda (#58862)

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

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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.

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2

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31 human-carnivore conflict

32

33   **ABSTRACT**

34   Robust measures of animal densities are necessary for effective wildlife management. Leopards (*Panthera*

35   *pardus*) and spotted hyenas (*Crocuta Crocuta*) are higher order predators that are data deficient across

36   much of their East African range and in Uganda, excepting for one peer-reviewed study on hyenas, there

37   are presently no credible population estimates for these species. A lack of information on the population

38   status and even baseline densities of these species has ramifications as leopards are drawcards for the

39   photo-tourism industry, and along with hyenas are often responsible for livestock depredations from

40   pastoralist communities. Leopards are also sometimes hunted for sport. Establishing baseline density

41   estimates for these species is urgently needed not only for population monitoring purposes, but in the

42   design of sustainable management offtakes, and in assessing certain conservation interventions like

43   financial compensation for livestock depredation. Accordingly, we ran a single-season survey of these

44   carnivores in the Lake Mburo National Park of south-western Uganda using 60 remote camera traps

45   distributed in a paired format at 30 locations. We analysed hyena and leopard detections under a Bayesian

46   spatially explicit capture-recapture (SECR) modelling framework to estimate their densities. This small

47   national park (370 km^2) is surrounded by Bahima pastoralist communities with high densities of cattle on

48   the park edge (with regular park incursions). Leopard densities were estimated at 6.31 individuals/100

49   km^2 (posterior SD = 1.47, 95% CI = 3.75 – 9.20), and spotted hyena densities were 10.99 individuals/100

50   km^2, but with wide confidence intervals (posterior SD = 0.33, 95% CI = 5.63 – 17.37). Leopard densities

51   were on the middle end of SECR studies published in the peer-reviewed literature over the last five years

52   while spotted hyena densities were some of the first reported in the literature using SECR, and similar to

53   a study in Botswana which reported 11.80 spotted hyenas/100 km^2. Densities were not noticeably lower

54   at the park edge, and in the southwest of our study site, despite repeated cattle incursions into these

55   areas. We postulate that the relatively high densities of both species in the region could be owed to impala

56   *Aepyceros melampus* densities ranging from 16.6 – 25.6 impala/km^2. Another, potential explanatory

57   variable (albeit a speculative one) is the absence of interspecific competition from African lions (*Panthera*

58   *leo*), which became functionally extinct (there is only one male lion present) in the park nearly two

59   decades ago. This study provides the first robust population estimate of these species anywhere in Uganda

60   and suggests leopards and spotted hyenas continue to persist in the highly modified landscape of Lake

61   Mburo National Park.

62

63

64

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 the East African state of Uganda, most protected areas are relatively small, isolated and have high human pressures at their edges (Venter et al. 2016, Plumptre et al. 2017). Additionally, the majority of Ugandan national parks and wildlife reserves are bordered by livestock rearing communities, and large carnivores regularly kill livestock (Ochieng et al. 2015). Consequently, large carnivores are often killed in retaliation for stock 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. in review). 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 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

97 sustainable management offtakes and also in assessing the impact of conservation interventions on
98 carnivores and communities (e.g. Financial compensation, the erection of livestock protection bomas
99 etc.).

100

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

113

114 **STUDY AREA**
115 We studied leopards and spotted hyenas in the LMNP (370 km^2), Kiruhura district, Western Uganda (30°
116 47' – 31° 04'E, 00° 30' – 0° 30' S, Figure 1). The LMNP forms part of the Akagera savanna ecosystem which
117 extends from Rwanda and north-western Tanzania down into south-western Uganda (Menault 1983, Van
118 de Weghe 1990). The park experiences a bimodal annual rainfall pattern (October – December and
119 February – June) and annual rainfall and temperatures average 800 mm and 28° C, respectively (Moe et
120 al. 2016). The woody vegetation in the park is characterized by dry *Acacia* savanna dominated by *Acacia*
121 *hockii*, woodlands, thickets and swamps which occur on the edges of Lake Kachera and Mburo (Rannestad
122 et al. 2006). The most common grasses include *Loudetia kagerensis*, *Chloris gayana*, and *Sporobolus*
123 *pyramidalis*. LMNP supports one of two remaining population of impala *Aepyceros melampus* in Uganda,
124 the most common and preferred prey of the African leopard (Hayward et al. 2006). The park also harbours
125 Plains zebra *Equus quagga* , Cape buffalo *Syncerus caffer*, Defassa waterbuck *Kobus ellipsiprymnus*
126 *defassa*, bushbuck *Tragelaphus scriptus* and warthog *Phacochoerus africanus* (Rannestad et al. 2006).
127 There is only one male lion (≥ 10 years old) in LMNP (a vagrant thought to have come from Akagera

128   National Park, in neighbouring Rwanda). ~~The park~~ is bordered by a matrix of small human settlements,

129   small-scale subsistence crops, dairy ranches and communal grazing lands (Ochieng et al. 2015).

130

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

132   Although the national park itself is small, much of the former park area - which is now mainly used as

133   cattle rangeland - still has considerable woodlands, thickets and natural vegetation and Rannestad et al.

134   (2006) noted higher densities of bushbuck, impala, reedbuck *Redunca redunca*, waterbuck and zebra

135   outside of the national park's borders during the wet season. The region surrounding LMNP has a trophy

136   hunting scheme which was initiated due to increasing complaints by communities, stating that the

137   increasing wildlife was a nuisance (Ochieng et al. 2017). The leopard is only allowed to be hunted when a

138   problem animal tag is made available by Ugandan Wildlife Authority (hereafter UWA) attributed to

139   repeated stock killing and damage. Although harvests of leopards since 2007 have been low in Uganda

140   (17 skins, skulls and trophies exported from 2009–2017), attempts were made to have the species

141   downgraded from CITES Appendix 1 to Appendix 2 and proposed a quota of 50 leopards annually (despite

142   the lack of even a single abundance estimate anywhere in the country, CITES CoP 14 Proposal 3). Currently,

143   28 leopards are available annually on quota country-wide. Contrastingly, in Africa, hyenas are often taken

144   opportunistically by trophy hunters rather than as prized trophy animals and we could not find any

145   evidence that they are an actively hunted species in Uganda (see for example: http://www.uganda-

146   wildlife-safaris.com).

147

148   **METHODS**

149   **Camera trapping**

150   This research was granted approval by the Uganda Wildlife Authority under permit number:

151   UWA/COD/96/05 as approved by the Executive Director Mr Stephen Masaba. We implemented one single

152   season camera-trap survey for 53 days in the LMNP from 26 July 2018 – 16 September 2018 using

153   Cuddeback™ 20-megapixel Long Range IR camera traps (powered by 8 AA batteries each) set in a paired

154   format. The survey encompassed 30 camera trap sites distributed across the national park (Figure 1), ~~but~~

155   ~~we omitted camera traps in~~ the far western sector of the park due to a lack of road access. Each camera

156   trap site consisted of two camera traps, each mounted to a 1 m steel pole 40 cm from the ground. We

157   positioned each camera perpendicular to a vehicle track or game trail at a 60 – 75°-angle to facilitate early

158   detection of leopards and spotted hyenas. We set our camera traps on roads, vehicle tracks, trails and

159   drainage lines, as these are regularly used by leopards and spotted hyenas as travel and hunting routes

160   (Balme et al. 2009a, Balme et al. 2009b, Henschel et al. 2014). We checked traps every 4 – 7 days to correct

161   for animal damage, replace memory cards and to assess battery functionality (Braczkowski et al. 2016).

162   Camera traps were set to burst mode and took five images every time the infrared sensor was triggered.

163   We set camera traps in a way as to ensure that at least one camera-trap site was present in an area

164   corresponding to the smallest female leopard home-range recorded in the literature (30 km^2; Bailey 1993,

165   and 23 km^2 in Fattebert et al. 2016), as these are smaller than male leopards and spotted hyenas. Our

166   camera spacing was 2.1 km (5-7 camera stations per female home range). We did choose this camera

167   spacing in order to ensure that no animal had a zero probability of capture (Karanth and Nichols 1998).

168   The identity of individual leopards and spotted hyenas was determined by their unique rosette and spot

169   patterns (Miththapala et al. 1989, O'Brien and Kinnaird 2011). For leopards, we were able to classify the

170   sex of individuals by using distinctive morphological cues such as the presence of testes and the enlarged

171   dewlap and sagittal crest in males (Balme et al. 2012, Braczkowski et al. 2015).

172

173   The first and eighth author assigned individual identity to temporally unique photographs and only

174   included into the final density estimation process individuals for which there was consensus (Bahaa-el-din

175   et al. 2016). We excluded images that were blurred, were too far away from the camera trap and those

176   where observers could not agree on identity. For the purpose of building capture histories with known

177   unique individual identities, we used both flanks of leopards in our analysis (Figure 2). Spotted hyenas,

178   however, often walked around cameras and did not present a clear flank on both sides of a single animal,

179   and several individuals moved around a single camera at the same time. To avoid mismatching flanks and

180   mistakenly double-count individuals, we chose the flank of hyenas with the highest number of

181   photographs recorded during our survey (Henschel et al. 2014).

182

183   **SECR modelling**

184   We estimated leopard and spotted hyena densities and abundance in LMNP using Bayesian spatially

185   explicit capture re-capture modelling. By incorporating spatial information into the detection process, the

186   method does not suffer from the "edge effects" common to non-spatial estimators (Gopalaswamy et al.

187   2012a). The modelling approach uses a state (leopard and spotted hyena population size and locations in

188   the landscape) and observation process (Royle et al 2009, Gopalaswamy et al 2012b). To accurately

189   estimate the densities and home-range centres of both species we generated potential activity centres

190   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)

191   equally spaced pixels. This state-space assumes the number of leopards and spotted hyenas found in these

192   pixels are defined by a binomial process, but because spotted hyenas are often found in groups, the state
193   process allows for ≥ 2 spotted hyenas to have an activity centre in the same pixel (Gopalaswamy et al.
194   2012). The state space encompassed the LMNP, and a buffer of 25 km around it (including the eastern
195   rangelands bordering the park, Kanyaryeru and the southern farmlands). We masked out all human
196   settlements and water bodies inside and surrounding the national park, as leopards and spotted hyenas
197   are unlikely to have their home-range centres directly in such unsuitable habitats (Royle et al. 2009,
198   Gopalaswamy et al. 2012a, Braczkowski et al. 2016). We used a classical capture re-capture sampling
199   design and created a standard capture re-capture matrix (trap locations, individual leopards or hyenas
200   and sampling occasions, e.g., Du Preez et al. 2014, Braczkowski et al. 2016, Williams et al. 2018). Large
201   terrestrial carnivores regularly feature differences at the sex-level in their home-range sizes and capture
202   probability (Gopalaswamy et al. 2012b, Braczkowski et al. 2016). Differences in movements of animals
203   based upon sex can affect the observation process in spatial capture-recapture (Sollman et al. 2011). To
204   factor this into our models, we included a sex-specific covariate in the observation process and accounted
205   for different capture probability for leopards. We did not do this for hyenas as the female spotted hyenas
206   feature a pseudo-scrotum which makes sexing difficult, and the visibility of males' testes was often
207   obscured by their large tail (Hamilton et al. 1986).
208
209   In SECR modelling, σ is the scale parameter, and ~~this~~ represents the rate of decline in the detection rate
210   as the location of the animal's activity centre moves away from a camera trap station. λ_0 is the basal
211   encounter rate and can be defined as the encounter rate of an animal whose activity centre lies exactly
212   at a camera trap station. θ defines the detection function shape. If this parameter is estimated from the
213   given data, the shape of the detection function could define how an animal utilizes space or resources in
214   its environment (Elliot and Gopalaswamy 2017). The complementary log-log link is used to convert
215   encounter rates to Bernoulli detections. In practice, since encounter rates are so small, they are
216   approximately equal to detection probabilities (Efford 2019). The detection rates of an individual animal
217   decline with increasing distance between its activity centre and camera trap location (Borchers and Efford
218   2008, Royle et al., 2009). We estimated a continuous θ parameter, which defines the shape of the
219   detection function for leopards and spotted hyenas in some models, and also fixed θ at 0.75 (Elliot and
220   Gopalaswamy 2017) and 1 (Royle et al., 2009). The detection function takes on a version of the negative
221   exponential form (i.e., θ = 0.5) and a Gaussian form (θ = 1). Therefore, in our models, the probability of
222   detecting a leopard or hyena i in pixel j is defined by a complementary log-log function of covariates.
223

224 We assessed six *a priori* models for leopards, and two for spotted hyenas (parameter definitions are

225 presented in Table 1). ~~Model 1 estimated the detection function (defined by θ) and assumed that~~

226 ~~detection probability is sex specific:~~

227

228 $$cloglog\,(\pi ij) = \log\,(\lambda_0)\,+\,\beta_{sex}\,-\,f[dist(i,j|\vartheta,\sigma_{sex})]$$

229

230 where, π_{ij} describes the detection probability on a given sampling occasion, which is a function of the basal

231 encounter rate λ_0 and distance between the activity center of individual i and pixel j, θ and sex-specific

232 σ_{sex}. The specific form of this detection function is:

233

234 $$f[dist(i,j)|\vartheta,\sigma sex] = \exp\left|\frac{-\,dist(i,j)^{2\theta}}{2\sigma_{sex}^{2}}\right|$$

235

236 Model 2 was based on the assumption that detection probability is independent of sex, (i.e., βsex was

237 fixed at 0). The rate of decline in detection probability (σ) however, remained sex specific because this

238 parameter is also related to animal movement.

239

240 Model 3 as with model 2, had βsex fixed at 0 while the detection function fixed at θ = 0.75

241

242 Model 4 was based on the assumption that basal encounter rate is dependent on sex, thus, βsex was fixed

243 at 1. Rate of decline in detection probability (σ) also remained sex specific. The detection function

244 parameter θ was fixed at 0.75.

245

246 Model 5 assumed basal encounter rate is dependent on sex but rate of decline in detection probability

247 was independent of sex. The detection function parameter was fixed at θ = 0.75.

248

249 Model 6 was the same as model 1 but the detection function parameter (θ) was fixed at 1.

250

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

252 covariate.

253

254   We used Bayesian Markov Chain Monte Carlo (MCMC) simulation and the Metropolis-Hastings algorithm

255   (Tierney 1994) to run our models in the package SCRbayes (https://github.com/jaroyle/SCRbayes) in the

256   programming environment R Version 3.6.1 (R Development Core Team 2019). We set each model to run

257   for 20,000 iterations including a burn-in of 5,000 iterations but we adjusted this further if we did not arrive

258   at a standing distribution, (refining burn-in period and initial iterations further). Each model was set to

259   run for 4 chains (Elliot and Gopalaswamy 2017). Model adequacy was determined by examining the

260   Bayesian *p*-value on individual encounters (Royle et al. 2009). MCMC convergence was assessed using the

261   Gelman–Rubin diagnostic (Gelman & Rubin 1992). The five input files necessary to run these analyses and

262   accompanying R scripts are provided in the supporting information section of this manuscript (Supporting

263   information 3). Although we were principally interested in estimating density, we also computed posterior

264   mean abundance across the study area of the greater LMNP system.

265

266   **RESULTS**

267   We recorded a total of 1,444 trap nights during the 53-day survey period. Cameras were not functional

268   due to animal interference and battery failures for 146 trap nights and these were not included in the

269   SECR analysis. We recorded a total of 61 temporally independent (ie. Animals counted only once in a 24

270   hour period) detections of leopards during our camera trap survey, and 51 spotted hyena detections

271   (Table 2). From these we recorded 112 and 42 useable flanks for leopards and hyenas respectively (51

272   right hyena flanks vs 32 left flanks; 9 excluded due to not identifiable or juvenile hyena). We identified 20

273   unique leopards (six adult males and 14 adult females), and 27 (no sex noted) spotted hyenas. This

274   equates to a detection rate of 1.38 leopards and 1.87 spotted hyenas per 100 trap-nights.

275

276   **Density estimates and Model diagnostics**

277   Bayesian p-values for all of our leopard density models ranged from 0.61– 0.76 (Supporting Information

278   1), indicating an adequate model fit (extremities 0.15 – 0.85). Convergence of models was indicated by a

279   mean potential shrink reduction factor of <1.2 for each parameter for each model (Gelman and Rubin

280   1992, Supporting Information 1). The same assessment of model adequacy was recorded for a model

281   where sigma was estimated without a sex effect for the estimates of spotted hyena density (Bayesian p =

282   0.61 and shrink reduction factor for all parameters <1.2, Supporting Information 2). Model selection using

283   marginal likelihood from Dey et al. (2018) indicated that model 5, which considered basal encounter rate

284   to be dependent on sex but detection probability independent of sex had the highest log likelihood score

285   (log likelihood = -55,615.56, Table 3).

286

287 **Leopard density estimates**

288 Using model 5, leopard density for LMNP was estimated at 6.31 individuals/100 km² (posterior SD 1.47,

289 95% CI range = 3.75 – 9.20). The posterior mean abundance for the ~~Lake Mburo National Park~~ was 24.87

290 (posterior SD 7.78) using this model. The leopard movement parameter or sigma σ for males and females

291 from this model was 1.33 km (this movement parameter is a measurement of how far animals travel in

292 the landscape and is related to home range size; Braczkowski et al. 2020b). The next best-ranked

293 candidate model (model number 4) which considered sex as a factor affecting detection probability

294 estimated a movement parameter of 1.60 km for males and 0.59 km for females.

295

296 **Hyena density estimates**

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

298 Spotted hyena density for LMNP was estimated at 11.00 individuals/100 km² (posterior SD = 0.32, 95% CI

299 range = 5.57 – 17.09) using model 1. The spotted hyena movement parameter σ for both sexes combined

300 was 3.15 km. The posterior mean abundance for the entire state space buffer was 39.07 spotted hyenas

301 (posterior = SD 13.51, Table 3).

302

303 **DISCUSSION**

304 We provide a robust estimate of leopard densities and abundance in the LMNP ecosystem, southwestern

305 Uganda, and also the first SECR assessment for spotted hyenas in Uganda as a whole (however these had

306 wider confidence intervals when compared to leopards). These estimates are important baselines for the

307 future monitoring of leopard and spotted hyena populations in the LMNP. Robust estimates of population

308 abundance and densities are crucial in tracking changes and trends over time (e.g. Balme et al. 2009b,

309 Williams et al. 2017). In this human-carnivore conflict-prone area, it is unknown whether retaliatory

310 killings following depredation on livestock are sustainable in the long term, especially as the LMNP is small

311 and isolated from other larger protected areas. Previous research has shown that carnivore populations

312 in small, isolated national parks cannot withstand the edge effects from human-carnivore conflict (e.g.

313 from cattle farming) and trophy hunting (Woodroffe and Ginsberg 1998, Balme et al. 2009b).

314

315 **Possible reasons for observed leopard and hyena densities**

316 Leopard densities in LMNP were on the mid-tier of estimates recorded in the recent literature using SECR

317 studies (n=15 studies from 2013 – 2018, Table 4). The leopard densities we observed at 6.31

318   individuals/100 km² are somewhat surprising given a) the limited size of LMNP, and b) the high levels of

319   conflict between these two carnivores and the livestock rearing communities on the park edge

320   (Braczkowski et al. 2020c). Contrastingly, the hyena densities were similar to a SECR study in uMkhuze

321   Game Reserve, northern Kwa-Zulu Natal, South Africa (a savanna system) which estimated a density of

322   10.59 individuals/100 km² (posterior SD = 2.10, De Blocq 2014), and a study in Botswana's Moremi

323   estimated 11.80 (posterior SD = 2.60, Rich et al. 2019). We postulate that three factors may be

324   contributing to these densities, namely 1) the availability of preferred prey, 2) the existence of a

325   compensation scheme that reimburses ranchers after depredation events on the LMNP edge (Braczkowski

326   et al. 2020), and 3) the functional extinction of lions in the region dating back to over a decade ago. LMNP

327   is one of only two protected areas in Uganda with a population of impala, the most preferred prey of

328   leopards (Hayward et al. 2006). The most recent studies implemented using distance sampling by

329   Rannestad et al. (2006) and Kisame et al. (2018) found significant populations of impala within LMNP and

330   on the adjacent cattle farmlands at 25.6 ± 4.8 individuals/km² in the 2003 study of Rannestad et al. (2006),

331   and 15.3 and 16.6 individuals/km² in the 2014 and 2016 sampling periods of Kisame et al. (2018).

332   Importantly Rannestad et al. (2006) also found a higher number of impala groups (80 vs 58) and total

333   individuals (348 vs 255) in the community lands adjoining the park than within the national park in the

334   wet season of 2003. Similarly, Kisame et al. (2018) estimated that nearly half of the impala population in

335   the LMNP and surrounding ranches was found on non-protected land. Other densities of key leopard prey

336   species estimated in this study included 3.8 ± 0.8 individuals/km² for bushbuck (higher densities outside)

337   and warthogs (12.3 ± 2.9 individuals/km², densities lower outside national park, Rannestad et al. 2006).

338   The availability of these species at relatively high densities both inside and beyond the edge of LMNP

339   could be a key reason for the densities of leopards and hyenas we observed in our study. It also remains

340   unclear whether the functional extinction of lions in the LMNP has released spotted hyena density.

341   Spotted hyenas and lions have an intricate relationship of facilitation and competition (Périquet et al.

342   2015). Unlike leopards, spotted hyenas do not show a negative correlation with lion presence in Africa

343   (Périquet, Fritz and Revilla 2015) despite intraguild predation and the negative impact that lions can have

344   on hyena reproduction (Watts and Holekamp 2008). Spotted hyenas may benefit from the presence of

345   lions – and vice versa – due to the high dietary overlap between the species leading to scavenging and

346   kleptoparasitic opportunities (Hayward 2006, Davidson et al. 2019). Observed positive correlations in lion

347   and spotted hyena density may also be a result of their similar preferred prey base. In Zambia, M'soka et

348   al. (2016) found a high density of spotted hyenas in a lion-depleted ecosystem, though it was suggested

349   that the observed density was driven by the availability of wildebeest, as in Höner et al. (2005). There is

350   only one male lion (≥ 10 years old) in LMNP (a vagrant thought to have come from Akagera National Park,

351   in neighbouring Rwanda). From their study of leopard densities in three Kwazulu-Natal Parks, Ramesh et

352   al. (2016) found that where lion distribution overlapped spatially with leopards, densities of leopards

353   decreased drastically.

354

355   **Spotted hyena densities in LMNP and comparisons to other studies**

356   The spotted hyena densities were similar to an unpublished SECR study from uMkhuze Game Reserve,

357   KwaZulu-Natal, South Africa (De Blocq 2014), and a study from Botswana's Moremi (Lindsey et al. 2019).

358   Estimates of spotted hyena densities using non-SECR methods, from African savanna sites range widely

359   from 2 – 20 individuals/100 km² in the Kruger National Park, South Africa (Mills et al. 2001) to over 100

360   individuals/100 km² in the Ngorongoro Crater, Tanzania (Kruuk, 1972; Höner et al. 2005). The spotted

361   hyena density from this study is similar those from protected areas in southern Africa but lower than those

362   in other East African savannas (Holekamp and Dloniak 2010). The majority of previous estimates have

363   been produced using non-spatial methods (e.g. call-ups and mark-resight), and to our knowledge our

364   study is one of the first to use a SECR approach for spotted hyena density estimation (Table 5). SECR

365   densities are typically lower for large carnivores due to other methods making more generalized

366   extrapolations over a given unit area (Noss et al. 2012) which may explain the difference between our

367   results and those from other savanna systems in East Africa where non-spatial methods were used.

368

369   It is noteworthy that areas of high density between the species do not appear to overlap (Figure 3).

370   Previous studies have suggested that spotted hyenas can be significant kleptoparasites of leopard kills,

371   forcing them to cache or avoid areas with high hyena density (Balme et al. 2017; Davis et al., 2021).

372   Similarly, another study detected low temporal overlap between leopards and spotted hyenas in

373   Tanzania, which was postulated to be due to the avoidance of kleptoparasitism (Havmøller et al. 2020).

374   Therefore, the avoidance of kleptoparastism may drive the differences in space use between the species

375   we detected in LMNP but would require further investigation.

376

377   **Limitations and future monitoring of large carnivores in LMNP**

378   Our study is limited by a lack of temporal replication. This is important as we could not generate critical

379   population parameters such as emigration, immigration, birth and death (e.g. Karanth et al. 2006). These

380   parameters are indicators of population trend and are ultimately required to ascertain the true trajectory

381   of a given population. It should also be remembered that spotted hyenas live in fission-fusion clans and

382   may move together in groups or singularly. It remains to be seen if this clan-living structure may cause

383   biases in estimates of density and other parameters in our sampling situation. For example, Lopex-Bao

384   (2018) show that wolf densities are not significantly affected by group living. Similarly, Bischof et al.,

385   (2020) suggest that if there are low to moderate levels of gregariousness observed in group living

386   individuals, there is little overdispersion that occurs in the estimation of the detection function and scale

387   parameter. However, if gregariousness is high, overdispersion may be observed in confidence intervals

388   around parameter estimates, affecting the veracity of estimates. Although our study represents the first

389   snapshot of this leopard and spotted hyena population, it is important as a baseline estimate from which

390   future estimates can be made against (eg. Balme et al. 2009b). Our study also failed to quantify any

391   relationships between hyenas and leopards, which in some sites have been shown to positively influence

392   one another's occupancy in a landscape (Comley et al. 2020).

393

394   There is a growing conflict between large carnivores and humans in the greater LMNP ecosystem

395   (Braczkowski et al. 2020). The impacts of spotted hyenas and leopards on cattle, sheep and goats in the

396   Bahima pastoral lands are significant with leopards and spotted hyenas being the source of 98% (n=1102)

397   of depredation events between January 2009 – December 2018 in the region (Braczkowski et al. 2020c).

398   Other studies have highlighted spotted hyenas as a primary source of livestock loss, which combined with

399   their negative public image, makes them vulnerable to retaliatory killing (Kissui 2008; Holmern et al.2007).

400   While spotted hyenas are behaviourally flexible, populations are slow to recover following even moderate

401   reduction (Benhaiem et al. 2018). This pattern has also been observed for African leopards (e.g. Balme et

402   al. 2009b). For this reason, the continued monitoring of the LMNP spotted hyena and leopard population

403   is crucial from a human-carnivore conflict perspective. Continued population monitoring of leopards is

404   also critical in the context of trophy-hunting of leopard and leopard prey, which is allowed on properties

405   adjoining the LMNP. Even though legal harvests of leopards in Uganda since 2007 have been low (17 skins,

406   skulls and trophies exported from 2009 – 2017), and 28 leopards are available on quota country-wide

407   annually (Braczkowski et al. 2015), it is critical to monitor these populations annually or biannually as they

408   can rapidly decline under even modest harvest pressures (Balme et al. 2010). The way in which quotas

409   have been set in Uganda for leopards was also done using a non-robust method which related rainfall to

410   leopard densities (CITES CoP 14 Proposal 3).

411

412   **CONCLUSION**

413 We aimed at providing the first leopard and spotted hyena population density estimates for the Lake

414 Mburo ecosystem in Uganda, a small but regionally important national park with significant cattle farming

415 on its edge. We found that leopard occur at a relatively high density of 6.3 individuals/100 km², probably

416 due to a combination of factors such a high local prey density and an absence of lions. Spotted hyena

417 densities of were also relatively high, with several factors putatively at play, including abundance of prey

418 including livestock, the absence of lions, and the general tolerance of hyenas for human disturbance. Our

419 estimates form a robust baseline for future population monitoring to inform both the design of

420 sustainable management offtakes, and conservation interventions for the two species in the region.

421

427

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Figure 1

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.

Table 1(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

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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

Figure 2

Study area map of the Lake Mburo National Park
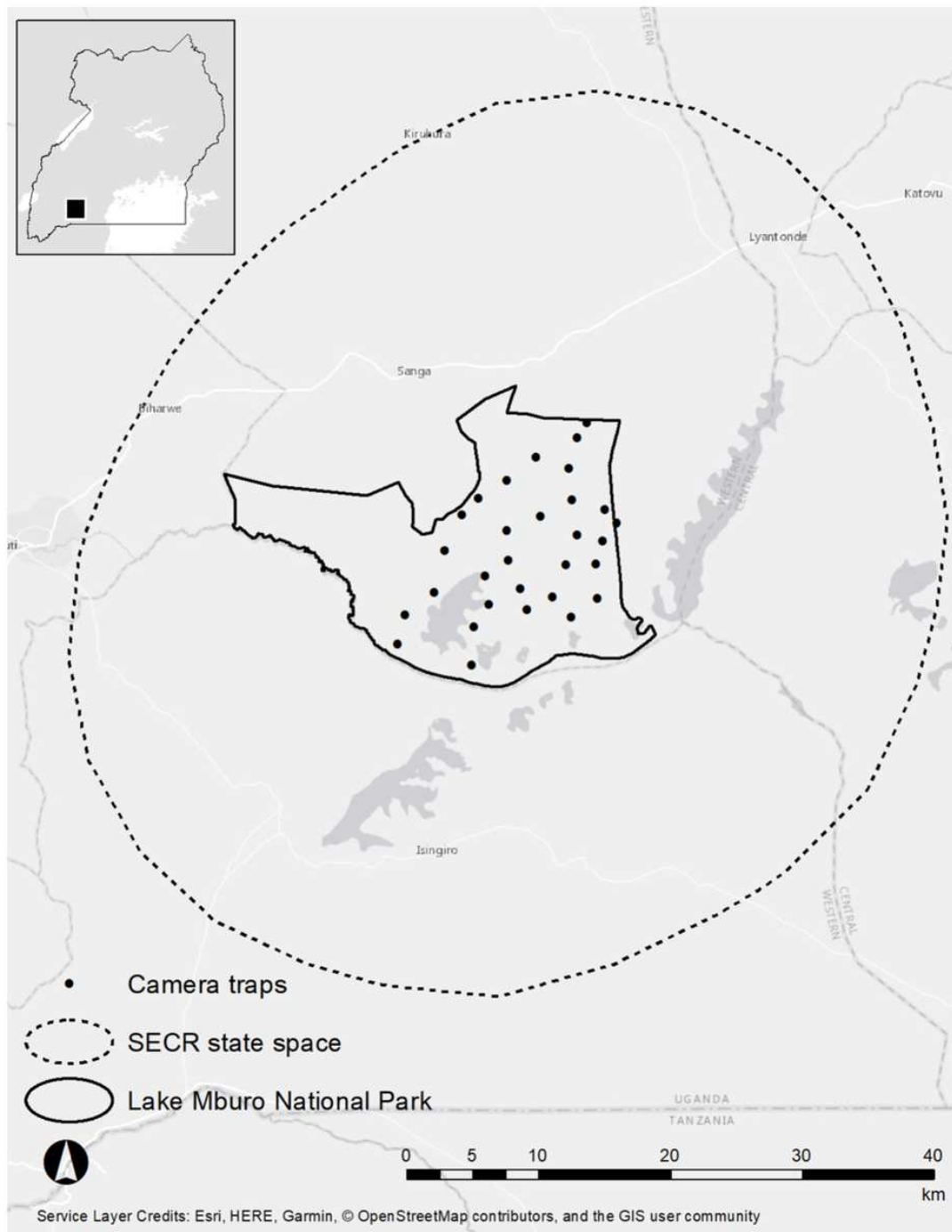
Study area map of the Lake Mburo National Park

Table 2(on next page)

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
$\lambda 0$	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

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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.
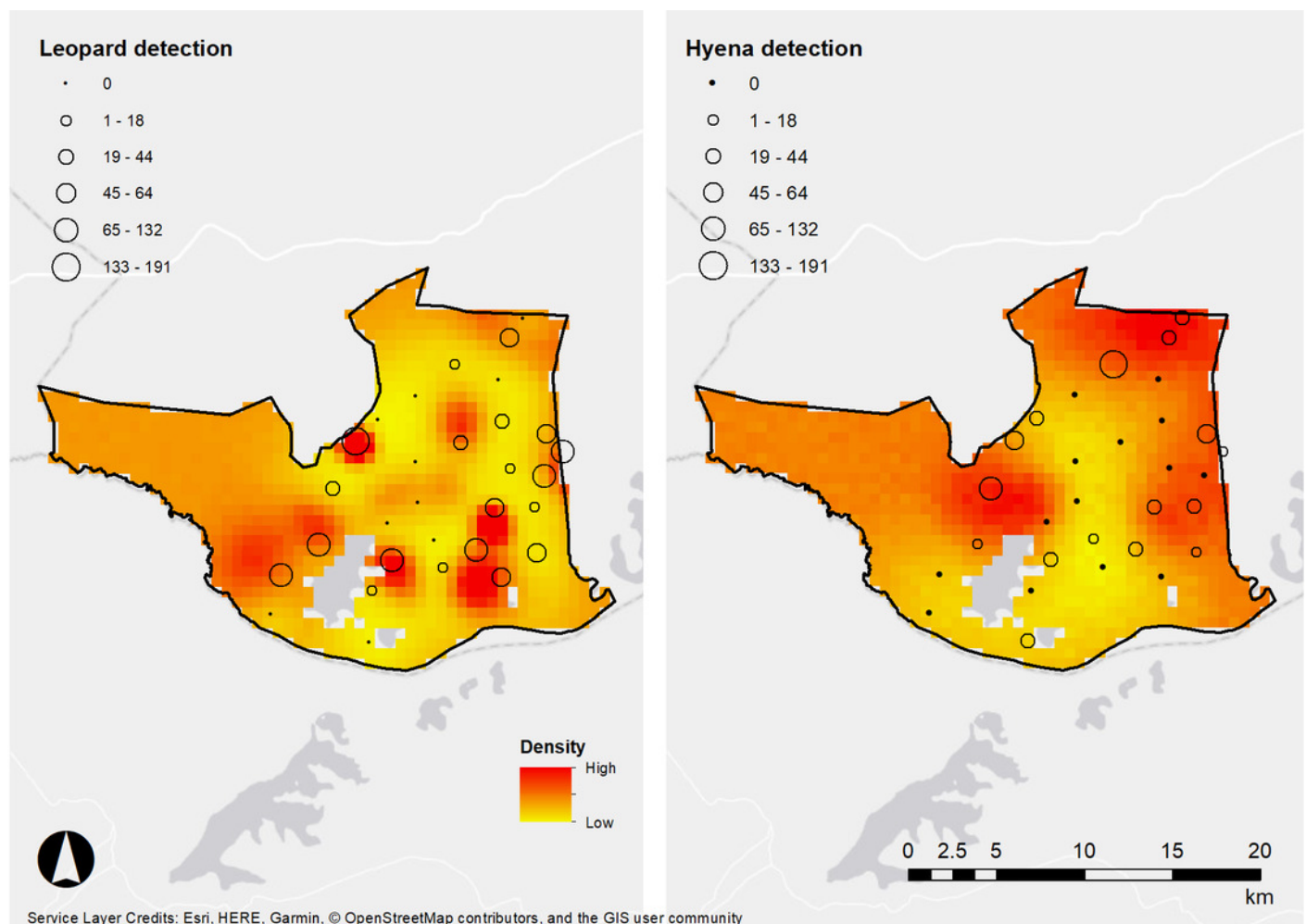
Table 3(on next page)

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

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Table 4(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)
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

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Table 5(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

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