# 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

**Aleksander Braczkowski** [Corresp., 1, 2], **Ralph Schenk** [3], **Dinal Samarasinghe** [4], **Sam Isoke** [5], **Duan Biggs** [1], **Allie Richardson** [6], **Nicholas Swanson** [3], **Merlin Swanson** [3], **Arjun Dheer** [7], **Julien Fattebert** [8, 9]

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

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

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

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

[5] Independent research scientist and field manager, Fort Portal, Uganda, Fort Portal, Uganda

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

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

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

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

Corresponding Author: Aleksander Braczkowski
Email address: alexander.braczkowski@gmail.com

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 both hyenas and leopards are drawcards for the photo-tourism industry, are often responsible for livestock depredations from pastoralist communities, and leopards are 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 30 remote camera traps. We used 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 (0.69 – 22 leopards/100 $km^2$), 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 the protected area in 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 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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[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]Independent research scientist and field manager, Fort Portal, Uganda

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

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

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

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

*Corresponding Author: alexander.braczkowski@gmail.com

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**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 has ramifications as both hyenas and leopards are drawcards for the photo-tourism industry, are often responsible for livestock depredations from pastoralist communities, and leopards are 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 30 remote camera traps. We used 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 (0.69 – 22 leopards/100 $km^2$), 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 the protected area in 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 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.

**KEYWORDS**

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

**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 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 Lake Mburo National Park (hereafter LMNP) in a 4-year period from 2003–2006 (CITES CoP 14 Proposal 3). 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 sustainable management offtakes and also in assessing the impact of conservation interventions on carnivores and communities (eg. 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 (eg. 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 all the more important as African lions became functionally extinct in LMNP in the early 2000's (UWA 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 (*Panthera pardus pardus*) 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). Most of the region is dominated by Pleistocene – recent deposits which mainly give rise to fine sandy loams along ridges and slopes, as well as peat and alluvial clays at the bottom of the valleys (Kamugisha et al. 1997). The LMNP forms part of the Akagera savanna ecosystem which extends from Rwanda and north-western Tanzania down into south-western Uganda (Menault 1983, Van de Weghe 1990). The park 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). The park is bordered by a matrix of small human settlements, small-scale subsistence crops, dairy ranches and communal grazing lands (Ochieng et al. 2015). ~~The dairy ranches and communal grazing lands are owned by Bahima pastoralists belonging to the Ban-yankole tribe.~~

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

~~LMNP forms part of a cattle corridor, which stretches across Tanzania, Uganda and Ethiopia (Tweheyo et al. 2012), and lies in the Ban-yankole tribe lands, surrounded by communities of Bahima patoralists (Tweheyo et al. 2012). In 1933, it was designated as a controlled hunting area before becoming a game reserve in 1962 (Infield et al. 2008). During this period, it was considered one of East Africa's premier wildlife areas (Kingdon 1985). It was designated as a national park in 1982, and at that point covered an area of 650 km$^2$. In 1987, significant tracts of the park were degazetted to its current extent of 370 km$^2$.~~ 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. 2017). ~~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

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). 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, Fattebert et al. 2016), as these are smaller than male leopards and spotted hyenas. We did chose 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. 2015).

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. 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), and right flanks were recorded with the highest frequency for spotted hyenas (Table 1).

**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. 2012). 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. 2018). 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 (Sollman 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).

Because detection probability of an individual animal declines with increasing distance between its activity centre and searched pixel, we could account for this uncertainty (Gopalaswamy et al. 2012a). We estimated a continuous $\theta$ parameter which exhibits the resource use of leopards and spotted hyenas, opposed to testing several detection functions models (Royle et al. 2009, Gopalaswamy et al. 2012b). The detection function takes on a negative exponential form (i.e. $\theta$ = 0.5) and a Gaussian form ($\theta$ = 1). Therefore, in our models, the probability of detecting a leopard or spotted hyena *i* in pixel *j* on sampling occasion *k* is defined by a complimentary log-log function of covariates.

We assessed six *a priori* models for leopards, and two for spotted hyenas (parameter definitions are presented in Table 2). Model 1 estimated the detection function (defined by $\theta$) and assumed that detection probability is sex specific:

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

where, $\pi_{ij}$ describes the detection probability on a given sampling occasion, which is a function of the basal encounter rate $\lambda_0$ and distance between the activity center of individual *i* and pixel *j*, $\vartheta$ and sex-specific $\sigma_{sex}$. 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 independent of 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 related to animal movement.

Model 3 as with model 2, had βsex fixed at 0 while the detection function fixed at $\vartheta = 0.75$

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 $\vartheta$ 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 $\vartheta = 0.75$.

Model 6 was the same as model 1 but the detection function parameter 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 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 detections of leopards during our camera trap survey, and 51 spotted hyena detections (Table 1). 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 young 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 of 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 the model which considered detection probability independent of sex had the highest log likelihood score (log likelihood = -55,615.56, Table 3).

**Leopard density estimates**

Using this model, 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 range of posterior density estimates per pixel (0.336 $km^2$) was 0.0003 – 1.54 leopards showing a wide regional range in leopard densities across the LMNP system. 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 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. The posterior mean abundance for the entire state space buffer of 6,733 km$^2$, which encompassed the LMNP (and the 25 km of suitable habitat immediately around it) was 204.80 leopards (posterior SD = 9.68).

**Hyena density estimates**

Spotted hyena density for LMNP was estimated at 10.99 individuals/100 km$^2$ (posterior SD = 0.33, 95% CI range = 5.63 – 17.37). The range of posterior density estimates per pixel (0.336 km$^2$) was 0.04 – 0.20 spotted hyenas. The spotted hyena movement parameter σ for both sexes combined was 3.22 km. The posterior mean abundance for the entire state space buffer was 357.12 spotted hyenas (posterior = SD 5.75, Table 3). Importantly, the confidence intervals of our density estimate for hyenas was wider than for leopards, despite a higher number of detections.

**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. Robust estimates of population abundance and densities are crucial in tracking changes and trends 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).

**Leopard and spotted hyena densities LMNP**

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 spotted hyena densities 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 (Lindsey et al. 2019). The leopard densities we observed at 6.31

individuals/100 km$^2$ are somewhat surprising given a) the limited 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). We postulate that two factors may be contributing to this, namely the availability of preferred prey, and the functional extinction of lions in the region dating back to over a decade ago. 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).

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), ~~36 individuals/100 km$^2$ in Hluhluwe-Imfolozi, South Africa (Whateley 1981),~~ 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). 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). Another SECR study in uMkhuze Game Reserve, northern Kwa-Zulu Natal, South Africa (a savanna system) estimated a density of 10.59 individuals/100 km$^2$ (posterior SD = 2.10, De Blocq 2014), while a study in Botswana's Moremi estimated 11.80 (posterior SD = 2.60, Rich et al. 2019). 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. Compared to other large carnivores, spotted hyenas have a flexible and unselective diet and are capable of behaving ~~mostly~~ as predators or scavengers (Höner et al., 2002; Hayward 2006). The most common ungulate prey species (both wild and domestic) in and around the LMNP are well within the spotted hyena's preferred prey weight range (56–182 kg, Hayward 2006) and therefore are suitable for its needs. Furthermore, spotted hyenas are known to thrive in human-dominated landscapes (Yirga et al. 2013), so it remains unclear whether the degree of human-carnivore conflict in the LMNP is a limiting factor on spotted hyena density.

It also remains unclear whether the functional extinction of lions in the LMNP has released spotted hyena density. 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, Fritz and Revilla 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 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). There is only one male lion (≥ 10 years old) in LMNP (a vagrant thought to have come from Akagera National Park, in neighbouring Rwanda). From their study of leopard densities in three Kwazulu-Natal Parks, Ramesh et al. (2016) found that where lion distribution overlapped spatially with leopards, densities of leopards decreased drastically.

**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 (eg. Karanth et al. 2006). These parameters are indicators of population trend and are ultimately required to ascertain the true trajectory of a given population. Although our study represents the first snapshot of this leopard and 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. in press). The impacts of spotted hyenas and leopards on cattle, sheep and goats in the Bahima pastoral lands are significant with leopards and spotted hyenas being the source of 98% (n=1102) of depredation events between January 2009 – December 2018 in the region (Braczkowski et al. 2020c). The Mihingo Lodge, a tourist safari lodge situated in the Lake Mburo region has run a voluntary financial compensation scheme over this period with the aim of stemming retaliatory killings after a spurt of leopards were killed in 2003 – 2006 (n=19 individuals killed on the boundary of LMNP during this period). The scheme has spent USD$ 1,623 – 20,546 per annum over this period, yet at this stage it is unknown whether the compensation scheme has led to reduced killings of leopards and spotted hyenas over time. Conservation management decisions should be based upon evidence and should be flexible in their approach, and our density estimates provide a baseline reference for both species for future assessments of conservation interventions (McCarthy and Possingham 2007; Nichols et al. 2007). These data could be used for future comparisons to assess if the compensation scheme is contributing to a reduction in killings of these predators. If the reverse is true where compensation is having a negligible effect on preventing retaliatory killings and is creating an environment for moral hazard (Nyhus 2005), then an alternative conservation mechanism could be trialled, for example the building of livestock protection bomas (Lichtenfeld et al. 2016). 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. 2015), it is critical to monitor these populations annually or biannually as they can rapidly decline under even modest harvest pressures (Balme et al. 2010).

Monitoring of the LMNP spotted hyena population is crucial from a human-carnivore conflict perspective. 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). It is therefore important to continue monitoring the LMNP spotted hyena population to detect any major fluctuations.

Finally, an assessment of the status of large ungulates and carnivores on the non-protected lands surrounding LMNP should be a key priority. This is motivated by the findings of Rannestad et al. (2006)

who found a higher density of large ungulates in the non-protected lands surrounding LMNP in the wet season.

## 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 used Bayesian spatially explicit capture re-capture modelling of camera trap data, and we present a robust density estimates for both species~~. 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 ca. 11 individuals/100 km$^2$~~ 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. ~~The implementation of a local human-carnivore conflict compensation scheme might have contributed to more tolerance towards conflicts, and a decrease in retaliation against large carnivores in the vicinity of LMNP.~~ Our estimates therefore 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.

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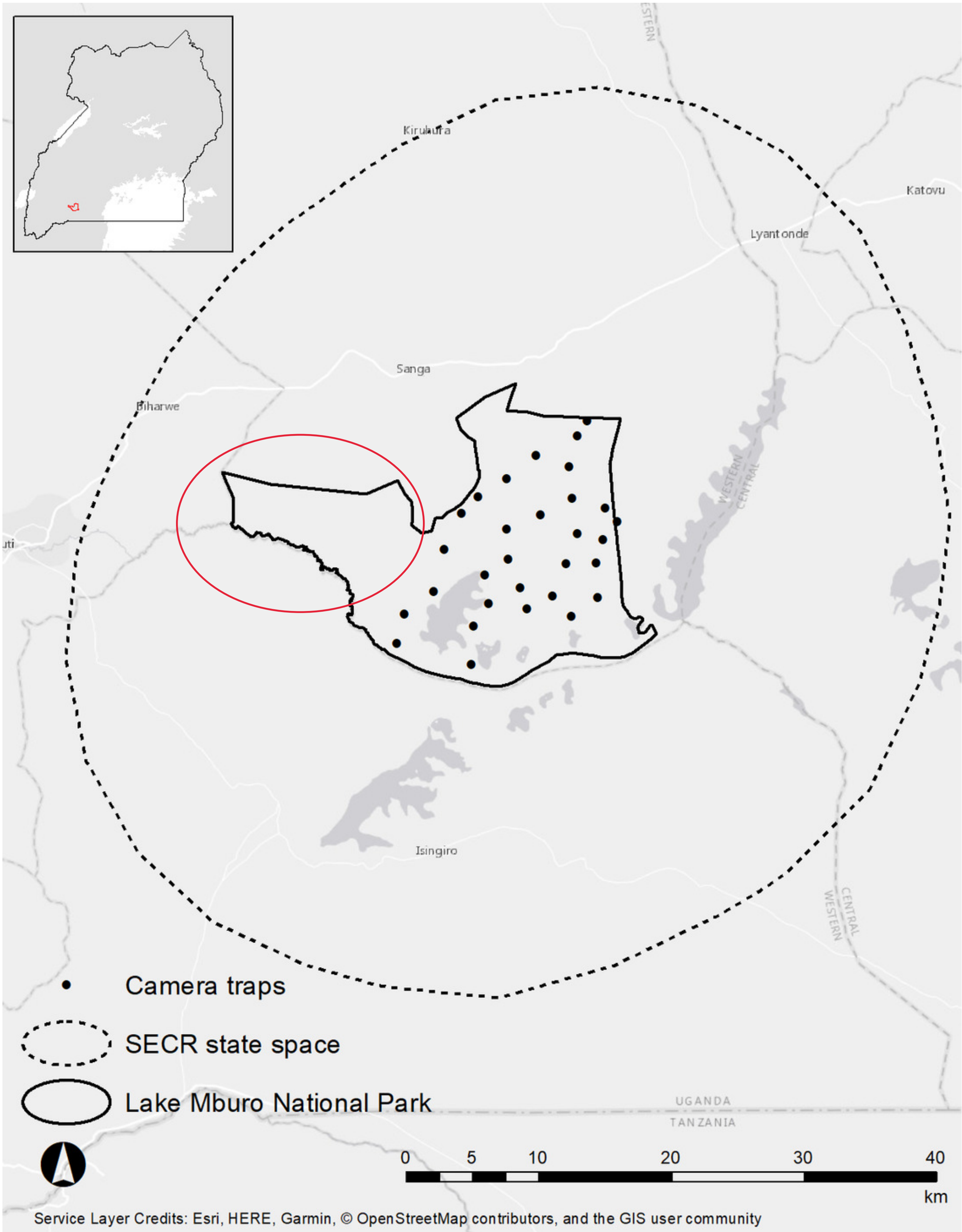
Woodroffe, R. and Ginsberg, J.R. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, *280*(5372), pp.2126-2128.

Yirga, G., Ersino, W., De Iongh, H. H., Leirs, H., Gebrehiwot, K., Deckers, J., & Bauer, H. (2013). Spotted hyena (Crocuta crocuta) coexisting at high density with people in Wukro district, northern Ethiopia. *Mammalian Biology*, *78*(3), 193-197.

# Figure 1

Study area of Lake Mburo

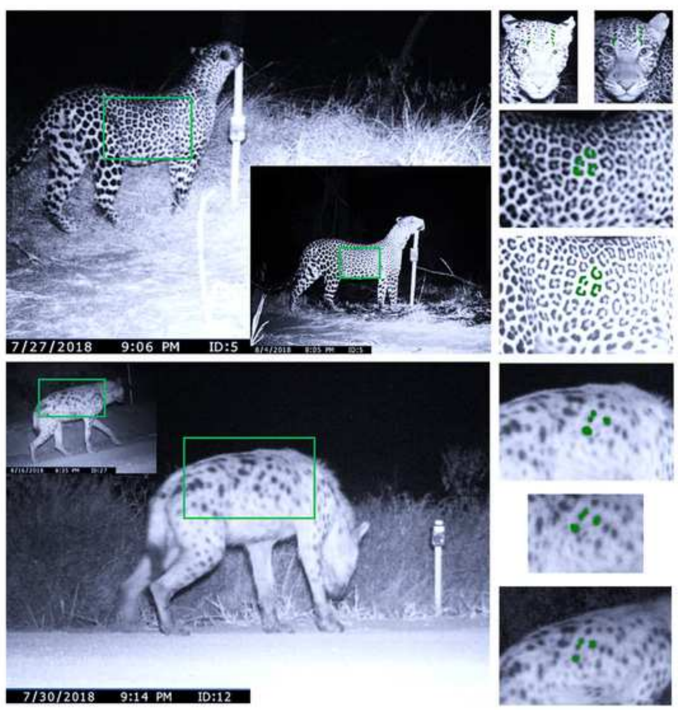
The location of 30 camera traps distributed throughout the 370 km$^2$ LMNP in 26 July 2018 – 16 September 2018. The dashed line represents the 25 km state space buffer around the outermost camera trap locations. Inset shows the location of the park (red outline) in Uganda.


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

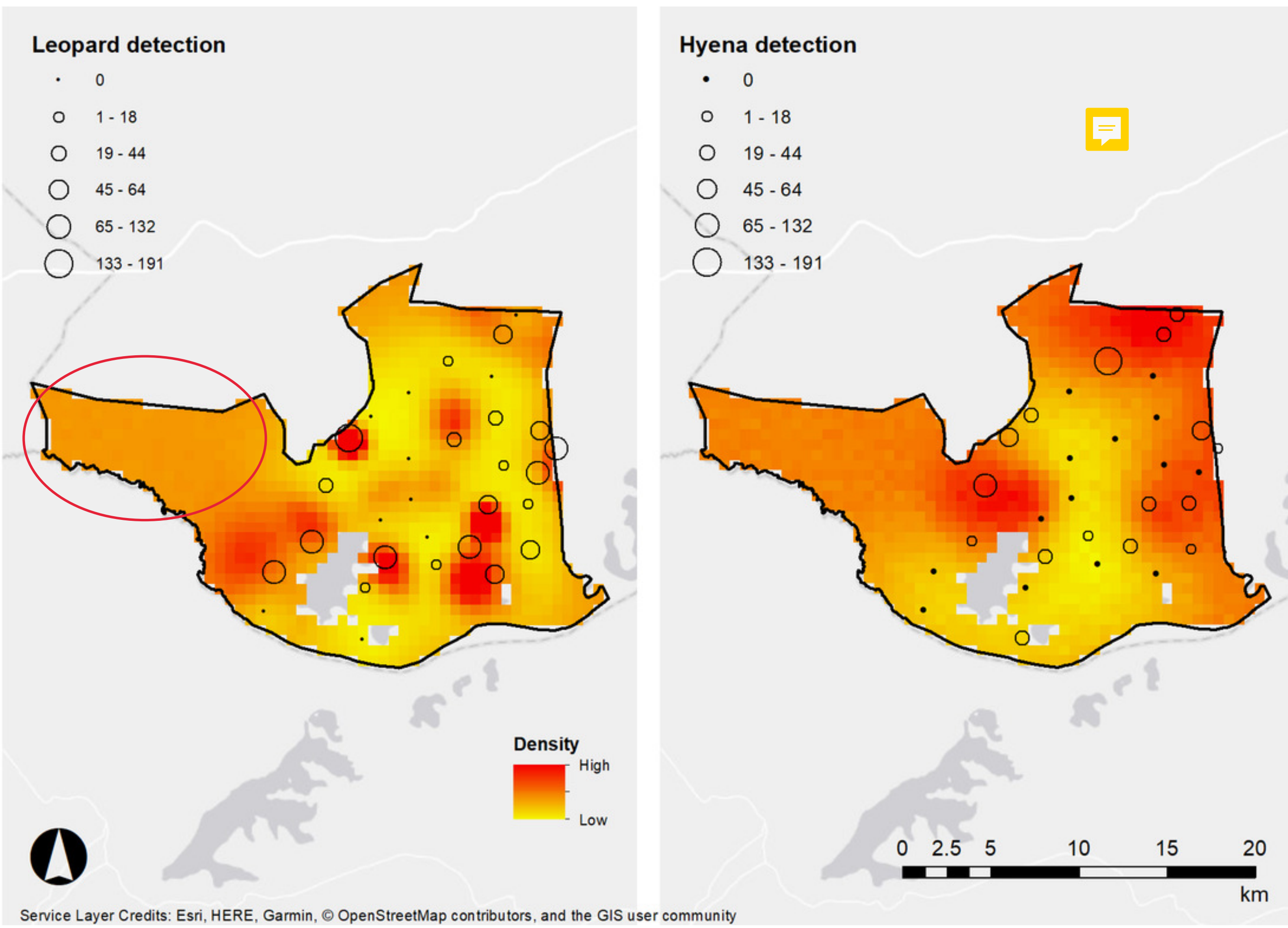
Individual identification information extracted from leopards and spotted hyenas in the LMNP, 2018. Slide 1 (top) denotes a female leopard captured at trap location five on sampling occasion two and ten respectively. Rosette patterns and facial spots were extracted during these two occasions. Slide 2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

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 | 2.6 0 |
| Borah et al. 2014 | Manas National Park, India | Tropical forest and mountains | Borchers and Efford 2008 | 3.40 | 0.8 2 |
| Braczkowski et al. 2016 | Phinda Private Game Reserve, South Africa | Savanna | Royle et al. 2009a | 3.55 | 1.0 4 |
| Braczkowski et al. 2016 | Phinda Private Game Reserve, South Africa | Savanna | Borchers and Efford 2008 | 3.40 | 1.2 0 |
| Devens et al. 2018 | Baviaanskloof mountains, South Africa | Mountain fynbos and thicket (forest in gorges) | Royle et al. 2009a | 0.24 | 0.1 0 |
| Devens et al. 2018 | Langeberg mountains, South Africa | Mountain fynbos and thicket (forest in gorges) | Royle et al. 2009a | 1.89 | 0.3 0 |
| Du Preez et al. 2014 | Bubye Valley Conservancy, Zimbabwe | Mopane woodland (savanna) | Borchers and Efford 2008 | 5.28 | 0.8 9 |
| Du Preez et al. 2014 | Bubye Valley Conservancy, Zimbabwe | Mopane woodland (savanna) | Royle et al. 2009a | 5.46 | 1.1 4 |
| Hedges et al. 2015 | Kenyir Wildlife Corridor, Malaysia | Dipterocarp forest | Borchers and Efford 2008 | 3.30 | 1.2 8 |
| Hedges et al. 2015 | Kenyir Wildlife Corridor, Malaysia | Dipterocarp forest | Royle 2011 | 3.06 | 0.9 1 |
| 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 | 1.2 0 |
| Qi et al. 2015 | Laoye mountains, China | Deciduous forest | Royle et al. 2009a | 0.62 | 0.1 5 |
| Rahman et al. 2018 | Ujong Kulon National Park, Java, Indonesia | Tropical forest | Borchers and Efford 2008 | 12.80 | 1.9 9 |
| Rahman et al. 2018 | Ujong Kulon National Park, Java, Indonesia | Tropical forest | Royle et al. 2009a | 11.54 | 1.2 2 |
| 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 | 0.4 0 |
| Selvan et al. 2014 | Pakke Tiger Reserve, India | Tropical forest | Borchers and Efford 2008 | 2.82 | 1.2 0 |
| Strampelli et al. 2018 | Xonghile Game Reserve, Mozambique | Woodlands and thickets (savanna) | Borchers and Efford 2008 | 2.59 | 0.9 6 |
| Swanepoel et al. 2015 | Farming matrix, Waterberg, South Africa | Livestock and game farms | Borchers and Efford 2008 | 6.59 | 5.2 0 |
| Swanepoel et al. 2015 | Lapalala Game Reserve, South Africa | Mountain bushveld (dystrophic savanna) | Borchers and Efford 2008 | 5.35 | 2.9 3 |
| Swanepoel et al. 2015 | Welgevonden Game Reserve, South Africa | Mountain bushveld (dystrophic savanna) | Borchers and Efford 2008 | 4.56 | 1.3 5 |
| Thapa et al. 2014 | Parsa Wildlife Reserve, Nepal | Dry deciduous forest | Efford et al. 2004 | 3.78 | 0.8 5 |
| Thapa et al. 2014 | Parsa Wildlife Reserve, Nepal | Dry deciduous forest | Royle et al. 2009a | 3.48 | 0.8 3 |
| Williams et | Soutpansberg | Matrix of livestock farms, | Royle et al. | 5.34 | 0.0 |

| | | | | |
|---|---|---|---|---|
| al. 2017 | mountains, South Africa | nature reserves, mountains | 2009a | 2 |

## Table 2 (on next page)

Individual animals recorded during the Lake Mburo Survey

Spotted hyena and African leopard individuals, flanks recorded, and recaptures used for SECR density estimate analysis, LMNP, Uganda, 2018.

| 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)

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 |
| Schenk 2018 - unpublished data | Lake Mburo National Park, Uganda | Semi-wooded savanna | Royle et al. 2009 | 9.20 | 2 |
| 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 |

1

## Table 4(on next page)

Model parameters from our SECR estimates

Model parameters and their definitions used for SECR estimate of African leopard densities, LMNP, Uganda, 2018.

| 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 leopardess 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 |
| βeff | rate of change in the complementary log-log value of detection probability as the (log) effort changes by 1 unit (1 km of drive effort) |
| 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 $Sex\ ratio = \frac{1-\psi}{\psi sex}$ |
| 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 $km^2$ |

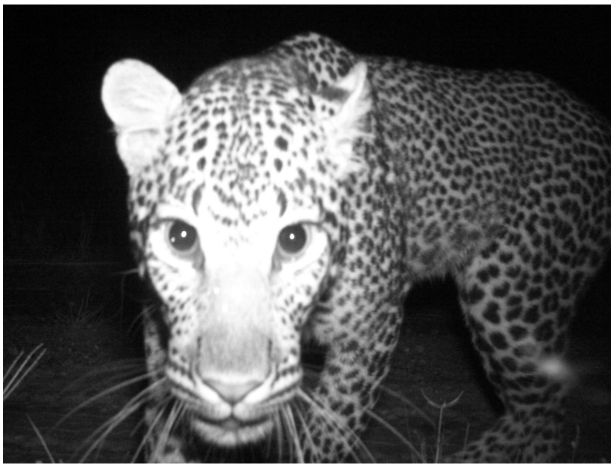
## Table 5(on next page)

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 and location of survey | Model number | Bayes p-value | Marginal likelihood | Total iterations | Burn in required to reach convergence |
|---|---|---|---|---|---|
| Leopards | 1 | 0.74 | -62893.814 | 52000 | 42000 |
| | 2 | 0.75 | -62885.778 | 50000 | 20000 |
| | 3 | 0.79 | -62784.534 | 80000 | 2000 |
| | 4 | 0.73 | -62729.456 | 50000 | 20000 |
| | 5 | 0.71 | -55615.556 | 50000 | 20000 |
| | 6 | 0.76 | -62985.962 | 50000 | 20000 |
| Spotted Hyenas | 1 | 0.59 | -42363.88 | 11000 | 6000 |
| | 2 | 0.57 | -42408.26 | 11000 | 1000 |

**Supporting Information 1 - Final results for leopard density analysis in Lake Mburo National Park with accompanying R code**



**Lake Mburo National Park – south-western Uganda**

We ran six potential secr models to estimate densities of leopards in Lake Mburo Uganda. Each chain initially comprised 50000 iterations and a burn in of 20000 (ideally one would want to run 2000 or 3000 in the burn instage, as it's an unnecessary way of losing chains), but we increased the number of iterations and modified burn in as necessary in order to arrive at a standing distribution. We chose to increase burn in as our initial iterations had very large shrink reduction factors and these did not converge, even with additional burn in. Each of the pasted pieces of code you find below are the commands used for the analyses and are extracted from respective R histories.

**Model selection - using marginal likelihood of Dey et al. (2018):**

**Commented [A1]:** This should come after giving details about the model structure.
Which command led to this result?

1. -62893.814

2. -62885.778

3. -62784.534

4. -62729.456

5. -55615.556

6. -62985.962

**The model structures are as follows:**

**Commented [A2]:** Please make sub-sections easier to identify for the readers.

1) Most parameterized model – in this model theta is estimated by the model
(MSEX=1, MSEXSIGMA=1, XSEX=XSEX, THETA=NA)

Queendata <- SCRi.fn.par1(Queendata1, modelno=modelno, nc=nchains, ni = niter, burn = 5000, skip = 1, nz = 1500,theta=NA,Msigma = 1, Mb = 0, Msex=1, Msexsigma =1, Xsex = Xsex, ss.prob=NULL, coord.scale = 1000, area.per.pixel = 0.336, thinstatespace = 1, maxNN = 40, dumprate = 1000)

2) A model where Msex is not estimated but Msexsigma is – Theta is not specified
(MSEX=0, MSEXSIGMA=1, XSEX=XSEX, XEFF=XEFFORT, THETA=NA)

Queendata <- SCRi.fn.par1(Queendata1, modelno=modelno, nc=nchains, ni = niter, burn = 5000, skip = 1, nz = 1500,theta=NA,Msigma = 1, Mb = 0, Msex=0, Msexsigma = 1, Xsex = Xsex, ss.prob=NULL, coord.scale = 1000, area.per.pixel = 0.336, thinstatespace = 1, maxNN = 40, dumprate = 1000)

3) Model where theta is fixed at 0.75 and Msex is not estimated
(MSEX=0, MSEXSIGMA=1, XSEX=XSEX, XEFF=XEFFORT, THETA=0.75)

Queendata <- SCRi.fn.par1(Queendata1, modelno=modelno, nc=nchains, ni = niter, burn = 5000, skip = 1, nz = 1500,theta=0.75,Msigma = 1, Mb = 0, Msex=0, Msexsigma = 1, Xsex = Xsex, ss.prob=NULL, coord.scale = 1000, area.per.pixel = 0.336, thinstatespace = 1, maxNN = 40, dumprate = 1000)

4) Theta is fixed at 0.75 and Msex is estimated
(MSEX=1, MSEXSIGMA=1, XSEX=XSEX, XEFF=XEFFORT, THETA=0.75)

Queendata <- SCRi.fn.par1(Queendata1, modelno=modelno, nc=nchains, ni = niter, burn = 5000, skip = 1, nz = 1500,theta=0.75,Msigma = 1, Mb = 0, Msex=1, Msexsigma = 1, Xsex = Xsex, ss.prob=NULL, coord.scale = 1000, area.per.pixel = 0.336, thinstatespace = 1, maxNN = 40, dumprate = 1000)

5) Msex is estimated but Msexsigma is not and theta is fixed at 0.75
(MSEX=1, MSEXSIGMA=0, XSEX=XSEX, XEFF=XEFFORT, THETA=0.75)

Queendata <- SCRi.fn.par1(Queendata1, modelno=modelno, nc=nchains, ni = niter, burn = 5000, skip = 1, nz = 1500,theta=0.75,Msigma = 1, Mb = 0, Msex=1, Msexsigma =0, Xsex = Xsex, ss.prob=NULL, coord.scale = 1000, area.per.pixel = 0.336, thinstatespace = 1, maxNN = 40, dumprate = 1000)

**Commented [A3]:** Clearly specify model numbers as it is done in the MS, not simply by using bullet points

**Commented [A4]:** To which parameter does MSEX correspond in the model presented in the MS l.224?

**Commented [A5]:** As in the hyeana file, please give details about these variables.

**Commented [A6]:** As in the hyeana file, please specify the values used for these 2 parameters

**Commented [A7]:** So is it estimated by the model as above, since THETA=NA, as in model 1??

6) Most parameterized model but theta is set to 1 unlike in the very first model where theta is estimated by the model
(MSEX=1, MSEXSIGMA=1, XSEX=XSEX, THETA=NA)

Mburodata <- SCRi.fn.par1(Queendata1, modelno=modelno, nc=nchains, ni = niter, burn = 5000, skip = 1, nz = 1500,theta=1,Msigma = 1, Mb = 0, Msex=1, Msexsigma =1, Xsex = Xsex, ss.prob=NULL, coord.scale = 1000, area.per.pixel = 0.336, thinstatespace = 1, maxNN = 40, dumprate = 1000

**The model results are as follows:**

1) Most parameterized model – in this model theta is estimated by the model
(MSEX=1, MSEXSIGMA=1, XSEX=XSEX, THETA=NA)

52 000 iterations (20 000 burn in) – additional burn in of 22 000 – 10 000 iterations remaining.

**Commented [A8]:** Clearly state that these parameters were refined as done in the MS l.253-254.

```
Log of the estimated Marginal Likelihood using HM method = -62893.814
```

**Commented [A9]:** What command lead to this result?

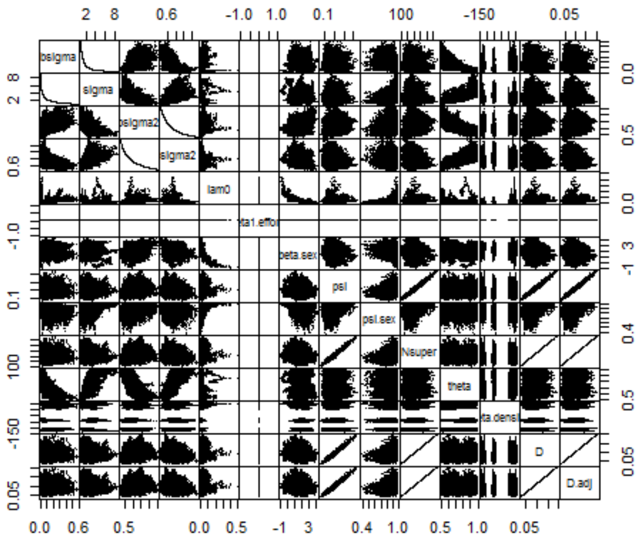
```
gelmandiag
Potential scale reduction factors:

              Point est. Upper C.I.
bsigma              1.02       1.01
sigma               1.04       1.04
bsigma2             1.07       1.05
sigma2              1.07       1.05
lam0                1.08       1.07
beta1.effort.        NaN        NaN
beta.sex            1.01       1.01
psi                 1.01       1.01
psi.sex             1.02       1.02
Nsuper              1.01       1.01
theta               1.06       1.05
beta.density       14.30      13.03
D                   1.01       1.01
D.adj               1.01       1.01
```

**Commented [A10]:** Is that a R command?

**Commented [A11]:** Please format this as a proper table, not tabulated text...
Same for all subsequent bits paste from the R console.

```
gewekediag

Fraction in 1st window = 0.1
Fraction in 2nd window = 0.5

      bsigma        sigma      bsigma2       sigma2         lam0
    -0.04130      0.43835     -0.32767     -0.01615      1.72794
beta1.effort.     beta.sex          psi      psi.sex       Nsuper
         NaN     -2.40560      0.87543      2.51405      0.88848
       theta  beta.density           D        D.adj
     0.24558      3.16782      0.88848      0.88848
```

```
mean.model1
                      est           se
bsigma         0.11931592 0.0061556164
sigma          2.59027417 0.0699781783
bsigma2        1.03596586 0.0232636354
sigma2         0.73208352 0.0082248447
lam0           0.02225034 0.0013208975
beta1.effort.  0.00000000 0.0000000000
beta.sex       2.03807825 0.0408003299
psi            0.19094839 0.0015927432
psi.sex        0.88134357 0.0030731185
Nsuper       289.63241176 2.3825235728
theta          0.74108527 0.0088926359
beta.density   1.94264796 6.5191328060
D              0.08455137 0.0006955217
D.adj          0.08917869 0.0007335862

sd.model1
       bsigma         sigma       bsigma2        sigma2          lam0
   0.09522192    1.08219552    0.38558356    0.13944864    0.02140727
beta1.effort.      beta.sex           psi       psi.sex        Nsuper
   0.00000000    0.67125931    0.04676873    0.07523033   69.55336954
        theta  beta.density             D         D.adj
   0.13762653   91.99495213    0.02030447    0.02141569


HPDinterval(histCH1mcmc)
                     lower        upper
bsigma        8.334468e-03   0.33247766
sigma         9.630237e-01   5.05405255
bsigma2       4.396780e-01   1.70784012
sigma2        5.137420e-01   0.99881515
lam0          3.906975e-03   0.04489434
beta1.effort. 0.000000e+00   0.00000000
beta.sex      3.224792e-01   3.37311047
psi           9.792215e-02   0.26774589
psi.sex       7.129558e-01   0.98829428
Nsuper        1.560000e+02 406.00000000
theta         5.340276e-01   0.98852432
beta.density  8.368026e+01 116.77245611
D             4.554053e-02   0.11852215
D.adj         4.803287e-02   0.12500862
attr(,"Probability")
[1] 0.950005


BayesPval
[1] 0.7093438
```




2) A model where Msex is not estimated but Msexsigma is – Theta is not specified (MSEX=0, MSEXSIGMA=1, XSEX=XSEX, XEFF=XEFFORT, THETA=NA)

No further burn in required

**Commented [A12]:** See comment on the hyaena file about rephrasing this statement.

```
Log of the estimated Marginal Likelihood using HM method = -62885.778


gelmandiag
Potential scale reduction factors:

              Point est. Upper C.I.
X                    NaN        NaN
bsigma              1.07       1.06
sigma               1.04       1.03
bsigma2             1.03       1.02
sigma2              1.03       1.02
lam0                1.01       1.01
beta.behave          NaN        NaN
beta1.effort.        NaN        NaN
beta.sex             NaN        NaN
psi                 1.00       1.00
psi.sex             1.03       1.02
Nsuper              1.00       1.00
theta               1.03       1.03
beta.density        2.65       2.44
D                   1.00       1.00
D.adj               1.00       1.00
```

gewekediag

```
Fraction in 1st window = 0.1
Fraction in 2nd window = 0.5

            X        bsigma         sigma       bsigma2        sigma2 
         -Inf       0.54949      -0.79989      -0.92231       0.78673 
         lam0   beta.behave beta1.effort.      beta.sex           psi 
     -1.80870           NaN           NaN           NaN      -0.08207 
      psi.sex        Nsuper         theta  beta.density             D 
     -3.42523      -0.11703       0.25610       4.79846      -0.11703 
        D.adj 
     -0.11703 
```

mean.model1

```
                       est           se
X             1.500050e+04 4.601555e+02
bsigma        1.814748e-01 5.978526e-03
sigma         2.127976e+00 5.406711e-02
bsigma2       1.194508e+00 1.570325e-02
sigma2        6.722679e-01 5.074421e-03
lam0          1.443385e-01 2.570355e-03
beta.behave   0.000000e+00 0.000000e+00
beta1.effort. 0.000000e+00 0.000000e+00
beta.sex      0.000000e+00 0.000000e+00
psi           1.998249e-01 1.125522e-03
psi.sex       9.418915e-01 1.122372e-03
Nsuper        3.031311e+02 1.686204e+00
theta         6.470703e-01 5.618820e-03
beta.density -6.072033e+01 1.693506e+00
D             8.849201e-02 4.922476e-04
D.adj         9.333499e-02 5.191873e-04
```

Formatted: English (US)

sd.model1

```
            X        bsigma         sigma       bsigma2        sigma2 
 8.660290e+03  1.236648e-01  1.071429e+00  3.625227e-01  1.146170e-01 
         lam0   beta.behave beta1.effort.      beta.sex           psi 
 6.929767e-02  0.000000e+00  0.000000e+00  0.000000e+00  4.958082e-02 
      psi.sex        Nsuper         theta  beta.density             D 
 3.775515e-02  7.388709e+01  1.143335e-01  3.166465e+01  2.156960e-02 
        D.adj 
 2.275006e-02 
```

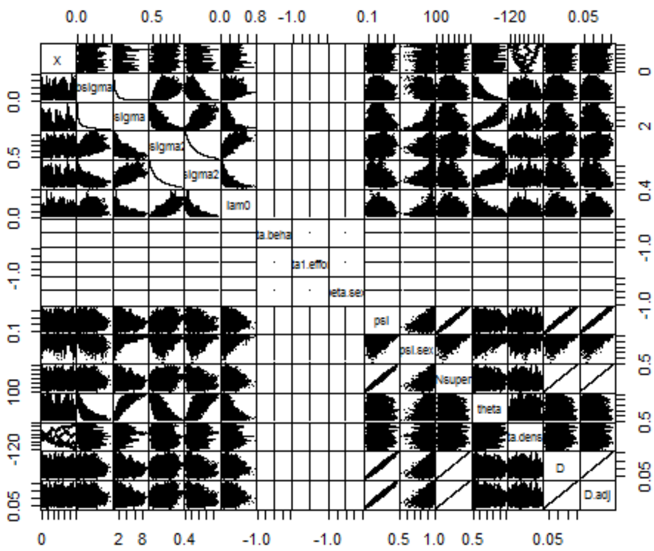
Formatted: English (US)

HPDinterval(histCH1mcmc)

```
                     lower         upper
X               1.00000000 28501.0000000
bsigma          0.01057063     0.3362893
sigma           0.97734865     4.2889316
bsigma2         0.51027424     1.8579438
sigma2          0.49562831     0.9132549
lam0            0.03839662     0.2771246
beta.behave     0.00000000     0.0000000
beta1.effort.   0.00000000     0.0000000
beta.sex        0.00000000     0.0000000
psi             0.10877791     0.2928312
psi.sex         0.88144148     0.9932148
Nsuper        167.00000000   440.0000000
theta           0.50005052     0.8628700
```

```
beta.density  -103.93783638    -59.5050891
D                0.04875172      0.1284477
D.adj            0.05172771      0.1357852
attr(,"Probability")
[1] 0.95
```

```
BayesPval
[1] 0.7061417
```



3) Model where theta is fixed at 0.75 and Msex is not estimated
   (MSEX=0, MSEXSIGMA=1, XSEX=XSEX, XEFF=XEFFORT, THETA=0.75)

   No further burn in needed (50 000 iterations run – burn in of 20 000)

```
Log of the estimated Marginal Likelihood using HM method = -62784.534
```

```
gelmandiag
Potential scale reduction factors:

              Point est. Upper C.I.
X                    NaN        NaN
bsigma              1.01       1.01
sigma               1.01       1.01
bsigma2             1.01       1.00
sigma2              1.00       1.00
lam0                1.01       1.01
```

```
beta.behave          NaN        NaN
beta1.effort.        NaN        NaN
beta.sex             NaN        NaN
psi                 1.00       1.00
psi.sex             1.00       1.00
Nsuper              1.00       1.00
theta                NaN        NaN
beta.density        7.79       6.95
D                   1.00       1.00
D.adj               1.00       1.00
```

gewekediag

```
Fraction in 1st window = 0.1
Fraction in 2nd window = 0.5

            X       bsigma        sigma      bsigma2       sigma2
         -Inf       1.1515      -1.4972      -0.3484       0.6778
         lam0  beta.behave beta1.effort.     beta.sex          psi
      -0.3226          NaN          NaN          NaN       1.2593
      psi.sex       Nsuper        theta beta.density            D
      -1.6471       1.2099          NaN       4.7972       1.2099
        D.adj
       1.2099
```

mean.model1

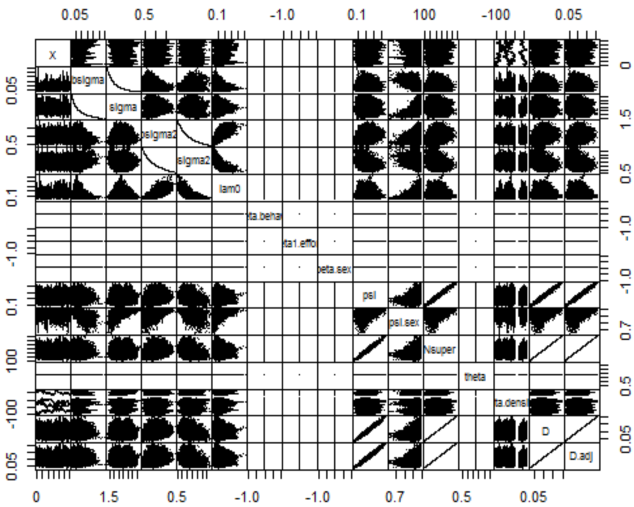
```
                       est           se
X             1.500050e+04 4.601555e+02
bsigma        6.984544e-02 1.137467e-03
sigma         2.807147e+00 2.149278e-02
bsigma2       9.064562e-01 5.128166e-03
sigma2        7.548873e-01 2.168744e-03
lam0          1.126136e-01 1.254204e-03
beta.behave   0.000000e+00 0.000000e+00
beta1.effort. 0.000000e+00 0.000000e+00
beta.sex      0.000000e+00 0.000000e+00
psi           1.993946e-01 1.063958e-03
psi.sex       9.493222e-01 9.343542e-04
Nsuper        3.025269e+02 1.597035e+00
theta         7.500000e-01 0.000000e+00
beta.density -2.320380e+01 2.546469e+00
D             8.831562e-02 4.662168e-04
D.adj         9.314895e-02 4.917318e-04
```

sd.model1

```
            X       bsigma        sigma      bsigma2       sigma2
 8.660290e+03 2.646286e-02 4.963371e-01 1.883472e-01 7.978355e-02
         lam0  beta.behave beta1.effort.     beta.sex          psi
 4.178870e-02 0.000000e+00 0.000000e+00 0.000000e+00 4.893110e-02
      psi.sex       Nsuper        theta beta.density            D
 3.186766e-02 7.282278e+01 0.000000e+00 4.752025e+01 2.125890e-02
        D.adj
 2.242235e-02
```

```
HPDinterval(histCH1mcmc)
                     lower          upper
X               1.00000000 28501.0000000
bsigma          0.02948912     0.1180110
sigma           1.96722680     3.8870321
bsigma2         0.54797057     1.3099951
sigma2          0.59944750     0.9159358
lam0            0.03997435     0.2030636
beta.behave     0.00000000     0.0000000
beta1.effort.   0.00000000     0.0000000
beta.sex        0.00000000     0.0000000
psi             0.11208585     0.3028215
psi.sex         0.89251466     0.9933911
Nsuper        165.00000000   449.0000000
theta           0.75000000     0.7500000
beta.density  -60.50458452   -25.7595830
D               0.04962750     0.1325346
D.adj           0.05234351     0.1397880
attr(,"Probability")
[1] 0.95
```

```
BayesPval
[1] 0.7200083
```



4) Theta is fixed at 0.75 and Msex is estimated
   (MSEX=1, MSEXSIGMA=1, XSEX=XSEX, XEFF=XEFFORT, THETA=0.75)

   No burn in required. 80 000 (2000 burn in) so 78 000 posterior iterations.

```
Log of the estimated Marginal Likelihood using HM method = -62729.456
```

gelmandiag

```
Potential scale reduction factors:

              Point est. Upper C.I.
X                    NaN        NaN
bsigma              1.01       1.01
sigma               1.30       1.31
bsigma2             1.00       1.00
sigma2              1.00       1.00
lam0                1.30       1.30
beta.behave          NaN        NaN
beta1.effort.        NaN        NaN
beta.sex            1.07       1.06
psi                 1.00       1.00
psi.sex             1.01       1.01
Nsuper              1.00       1.00
theta                NaN        NaN
beta.density        2.44       2.26
D                   1.00       1.00
D.adj               1.00       1.00
```

gewekediag

```
Fraction in 1st window = 0.1
Fraction in 2nd window = 0.5

            X       bsigma        sigma      bsigma2
         -Inf     0.003133     0.113139    -0.938720
       sigma2         lam0  beta.behave beta1.effort.
     0.906618     1.676332          NaN          NaN
     beta.sex          psi      psi.sex       Nsuper
    -3.173957    -0.296981     1.187045    -0.298004
        theta beta.density            D        D.adj
          NaN    -2.821574    -0.298004    -0.298004
```

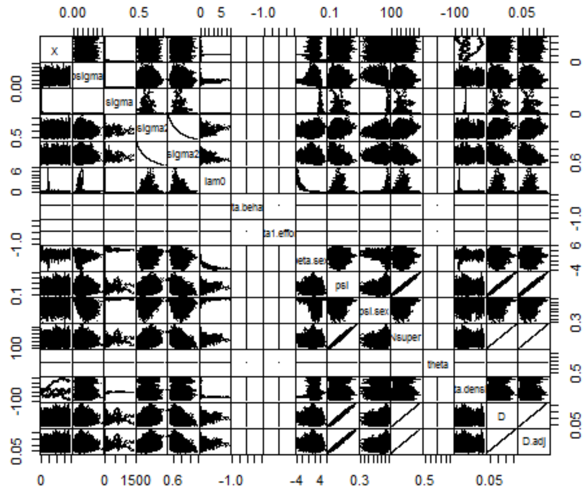
mean.model1

```
                       est           se
X             3.900050e+04 9.462715e+02
bsigma        8.747063e-02 1.136156e-03
sigma         4.967388e+00 1.147671e+00
bsigma2       9.487455e-01 3.157804e-03
sigma2        7.375779e-01 1.224070e-03
lam0          3.522202e-02 6.545535e-03
beta.behave   0.000000e+00 0.000000e+00
beta1.effort. 0.000000e+00 0.000000e+00
beta.sex      1.943516e+00 3.166863e-02
psi           1.889413e-01 6.562943e-04
psi.sex       8.861509e-01 1.655832e-03
Nsuper        2.865815e+02 9.857254e-01
theta         7.500000e-01 0.000000e+00
beta.density  4.648842e+00 2.559284e+00
D             8.366073e-02 2.877594e-04
D.adj         8.823930e-02 3.035078e-04
```

```
sd.model1
           X       bsigma        sigma       bsigma2
 2.251670e+04  3.820380e-02  3.234198e+01  1.955132e-01
       sigma2          lam0   beta.behave beta1.effort.
 7.665150e-02  1.671835e-01  0.000000e+00  0.000000e+00
     beta.sex           psi       psi.sex        Nsuper
 8.825524e-01  4.674361e-02  7.562076e-02  6.954243e+01
        theta  beta.density             D         D.adj
 0.000000e+00  6.056013e+01  2.030128e-02  2.141232e-02
```

```
HPDinterval(histCH1mcmc)
                    lower        upper
X              1.00000000 7.410100e+04
bsigma         0.02231469 1.589850e-01
sigma          1.59900918 3.901050e+00
bsigma2        0.59314822 1.348013e+00
sigma2         0.59087962 8.883068e-01
lam0           0.00183339 1.898533e-01
beta.behave    0.00000000 0.000000e+00
beta1.effort.  0.00000000 0.000000e+00
beta.sex      -1.08989870 3.426458e+00
psi            0.10340935 2.898692e-01
psi.sex        0.75129623 9.920896e-01
Nsuper       156.00000000 4.320000e+02
theta          0.75000000 7.500000e-01
beta.density -62.80295288 2.823272e+01
D              0.04554053 1.261122e-01
D.adj          0.04803287 1.330141e-01
attr(,"Probability")
[1] 0.95
```

```
BayesPval
[1] 0.7147276
```




5) Msex is estimated but Msexsigma is not and theta is fixed at 0.75
   (MSEX=1, MSEXSIGMA=0, XSEX=XSEX, XEFF=XEFFORT, THETA=0.75)

   No further burn in needed!

```
Log of the estimated Marginal Likelihood using HM method = -55615.556

No further burn in needed – 30 000 posterior iterations (20 000 initial bu
rn in).


gelmandiag
Potential scale reduction factors:

              Point est. Upper C.I.
X                    NaN        NaN
bsigma              1.00       1.00
sigma               1.00       1.00
bsigma2             1.00       1.00
sigma2              1.00       1.00
lam0                1.00       1.00
beta.behave          NaN        NaN
beta1.effort.        NaN        NaN
beta.sex            1.00       1.00
psi                 1.00       1.00
psi.sex             1.00       1.00
Nsuper              1.00       1.00
theta                NaN        NaN
beta.density        1.41       1.37
D                   1.00       1.00
D.adj               1.00       1.00
```

gewekediag

```
Fraction in 1st window = 0.1
Fraction in 2nd window = 0.5

           X       bsigma        sigma      bsigma2       sigma2
        -Inf      0.31044     -0.50082      0.31044     -0.50082
        lam0  beta.behave beta1.effort.    beta.sex          psi
     0.77600          NaN          NaN     -0.45022     -0.07818
     psi.sex       Nsuper        theta beta.density            D
     0.02109     -0.08286          NaN     -2.42984     -0.08286
       D.adj
    -0.08286
```

mean.model1

```
                        est            se
X              1.5000500e+04 4.6015553e+02
bsigma         2.8737444e-01 1.0450145e-03
sigma          1.3307613e+00 2.4938442e-03
bsigma2        2.8737444e-01 1.0450145e-03
sigma2         1.3307613e+00 2.4938442e-03
lam0           3.8493553e-02 4.4917314e-04
beta.behave    0.0000000e+00 0.0000000e+00
beta1.effort.  0.0000000e+00 0.0000000e+00
beta.sex       9.0442088e-02 1.3094909e-02
psi            1.3524603e-01 6.4714840e-04
psi.sex        6.8756918e-01 1.5049205e-03
Nsuper         2.0480074e+02 9.6772022e-01
theta          7.5000000e-01 0.0000000e+00
beta.density  -2.1950952e+01 1.0448723e+00
D              5.9786760e-02 2.8250316e-04
D.adj          6.3058764e-02 2.9796397e-04
```

sd.model1

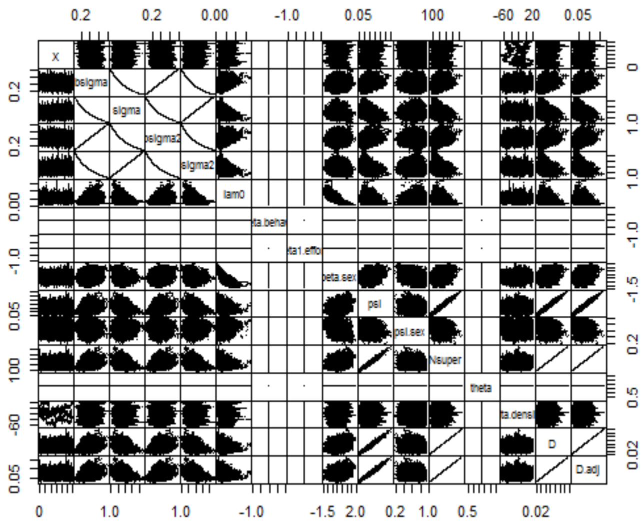
```
            X        bsigma         sigma       bsigma2        sigma2
8.6602901e+03 4.3799485e-02 1.0344306e-01 4.3799485e-02 1.0344306e-01
         lam0   beta.behave beta1.effort.      beta.sex           psi
1.4829029e-02 0.0000000e+00 0.0000000e+00 4.0554139e-01 3.2488845e-02
      psi.sex        Nsuper         theta  beta.density             D
1.1911626e-01 4.7629625e+01 0.0000000e+00 1.9569615e+01 1.3904349e-02
        D.adj
1.4665305e-02
```

HPDinterval(histCH1mcmc)

```
                    lower         upper
X             1.000000000 2.8501000e+04
bsigma        0.205959747 3.7118037e-01
sigma         1.148545575 1.5350022e+00
bsigma2       0.205959747 3.7118037e-01
sigma2        1.148545575 1.5350022e+00
lam0          0.013031503 6.7342268e-02
beta.behave   0.000000000 0.0000000e+00
beta1.effort. 0.000000000 0.0000000e+00
beta.sex     -0.714583147 8.7810789e-01
psi           0.076860370 1.9859342e-01
psi.sex       0.450211970 9.0460898e-01
```

```
Nsuper         121.000000000 2.9800000e+02
theta            0.750000000 7.5000000e-01
beta.density   -32.855094458 1.2482534e+01
D                0.035323104 8.6994091e-02
D.adj            0.037564167 9.2062999e-02
attr(,"Probability")
[1] 0.95
```

```
BayesPval
[1] 0.61125833
```




6) Most parameterized model but theta is set to 1 unlike in the very first model where theta is estimated by the model
(MSEX=1, MSEXSIGMA=1, XSEX=XSEX, THETA=NA)

No further burn in required (50 000 with 20 000 burn in).

```
Log of the estimated Marginal Likelihood using HM method = -62985.962
```

```
gelmandiag
Potential scale reduction factors:

             Point est. Upper C.I.
X                   NaN        NaN
bsigma             1.01       1.01
sigma              1.03       1.03
bsigma2            1.00       1.00
sigma2             1.00       1.00
```

```
lam0                1.04       1.04
beta.behave          NaN        NaN
beta1.effort.        NaN        NaN
beta.sex            1.01       1.01
psi                 1.00       1.00
psi.sex             1.01       1.01
Nsuper              1.00       1.00
theta                NaN        NaN
beta.density        3.27       3.11
D                   1.00       1.00
D.adj               1.00       1.00
```

gewekediag

```
Fraction in 1st window = 0.1
Fraction in 2nd window = 0.5

            X        bsigma         sigma       bsigma2        sigma2
         -Inf        0.4716       -1.0201       -2.6901        2.4169
         lam0   beta.behave beta1.effort.      beta.sex           psi
       0.9645           NaN           NaN       -2.6972       -1.9287
      psi.sex        Nsuper         theta  beta.density             D
      -0.8001       -1.9632           NaN        0.2478       -1.9632
        D.adj
      -1.9632
```

mean.model1

```
                       est            se
X              1.500050e+04 4.601555e+02
bsigma         2.522273e-02 5.562025e-04
sigma          5.087684e+00 7.979924e-02
bsigma2        5.587299e-01 3.459537e-03
sigma2         9.675800e-01 3.054648e-03
lam0           1.533672e-02 5.105321e-04
beta.behave    0.000000e+00 0.000000e+00
beta1.effort.  0.000000e+00 0.000000e+00
beta.sex       1.935267e+00 2.816956e-02
psi            1.890298e-01 1.081556e-03
psi.sex        8.814399e-01 2.520124e-03
Nsuper         2.867093e+02 1.621459e+00
theta          1.000000e+00 0.000000e+00
beta.density  -7.270208e+00 2.441582e+00
D              8.369802e-02 4.733470e-04
D.adj          8.827864e-02 4.992522e-04
```

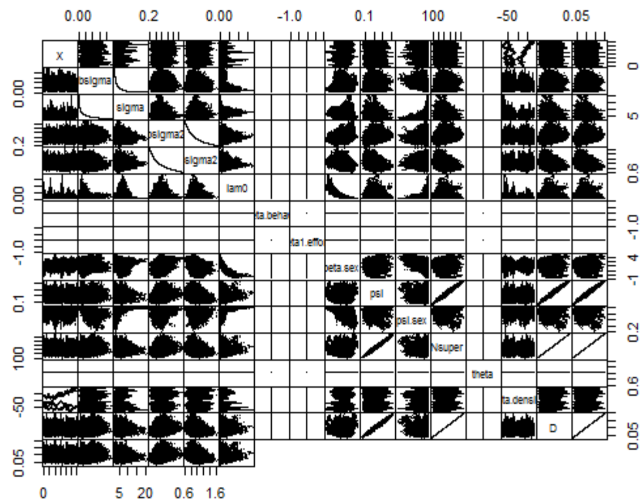
sd.model1

```
            X        bsigma         sigma       bsigma2        sigma2
 8.660290e+03  1.363868e-02  1.758229e+00  1.367008e-01  1.209056e-01
         lam0   beta.behave beta1.effort.      beta.sex           psi
 1.149584e-02  0.000000e+00  0.000000e+00  6.599557e-01  4.602027e-02
      psi.sex        Nsuper         theta  beta.density             D
 7.765814e-02  6.841573e+01  0.000000e+00  4.558027e+01  1.997236e-02
        D.adj
 2.106541e-02
```

HPDinterval(histCH1mcmc)

```
                     lower        upper
X              1.000000000 2.850100e+04
bsigma         0.003795011 4.983595e-02
```

```
sigma            2.643927001  8.158048e+00
bsigma2          0.308080113  8.182125e-01
sigma2           0.744761169  1.201538e+00
lam0             0.003197845  3.259160e-02
beta.behave      0.000000000  0.000000e+00
beta1.effort.    0.000000000  0.000000e+00
beta.sex         0.618352966  3.182224e+00
psi              0.106696586  2.800836e-01
psi.sex          0.737030569  9.867556e-01
Nsuper         162.000000000  4.190000e+02
theta            1.000000000  1.000000e+00
beta.density   -55.922709313 -1.230448e+01
D                0.048751722  1.237768e-01
D.adj            0.049880287  1.290114e-01
attr(,"Probability")
[1] 0.95


BayesPval
[1] 0.7636083
```



**Supporting Information 2 - Final results for spotted hyena density analysis in Lake Mburo National Park**

**Lake Mburo National Park – south-western Uganda**

We ran only two models for the Lake Mburo hyena density estimate as we did not incorporate a measure of sex.

**The model structures is as follows:**

1) Theta set to 1
(MSEX=0, MSEXSIGMA=0, XSEX=NULL, THETA=1)

Mburodata1 <- SCRi.fn.par1(scrMburoData, modelno=modelno, nc=nchains, ni = niter, burn = 1000, skip = 1, nz = 1500,theta=1, Msigma = 1, Mb = 0, Msex=0, Msexsigma = 0, Xsex = NULL, ss.prob=NULL, coord.scale = 1000, area.per.pixel = 0.336, thinstatespace = 1, maxNN = 40, dumprate = 1000)

**Commented [A1]:** Please provide some information about these variables.

**Commented [A2]:** I would suggest precising here nc=4, ni=20000 as specified in the Methods section of the MS l.253-254.

2) A model where Theta is estimated by the model
(MSEX=0, MSEXSIGMA=1, XSEX=XSEX, XEFF=XEFFORT, THETA=NA)

Mburodata2 <- SCRi.fn.par1(scrMburoData, modelno=modelno, nc=nchains, ni = niter, burn = 1000, skip = 1, nz = 1500,theta=NA,Msigma = 1, Mb = 0, Msex=0, Msexsigma = 0, Xsex = NULL, ss.prob=NULL, coord.scale = 1000, area.per.pixel = 0.336, thinstatespace = 1, maxNN = 40, dumprate = 1000)

**The Results are as follows**

Formatted: Font: Bold, Complex Script Font: Bold

1) Theta set to 1
(MSEX=0, MSEXSIGMA=0, XSEX=NULL, THETA=1)

No burn in required!

Commented [A3]: I would rephrase and state "The initial values of iterations and burn in lead to robust model adequacy and MCMC convergence, therefore no adjustment were required."

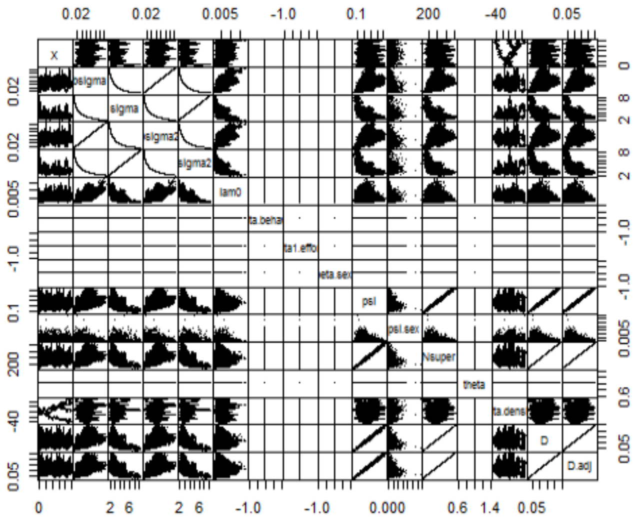
```
Log of the estimated Marginal Likelihood using HM method = -41030.296


gelmandiag
Potential scale reduction factors:

              Point est. Upper C.I.
X                    NaN        NaN
bsigma              1.03       1.03
sigma               1.11       1.11
bsigma2             1.03       1.03
sigma2              1.11       1.11
lam0                1.01       1.01
beta.behave          NaN        NaN
beta1.effort.        NaN        NaN
beta.sex             NaN        NaN
psi                 1.03       1.03
psi.sex             1.00       1.00
Nsuper              1.03       1.03
theta                NaN        NaN
beta.density        2.34       2.16
D                   1.03       1.03
D.adj               1.03       1.03


gewekediag

Fraction in 1st window = 0.1
Fraction in 2nd window = 0.5

           X        bsigma         sigma       bsigma2        sigma2
        -Inf       -2.6268        2.2999       -2.6268        2.2999
        lam0   beta.behave beta1.effort.      beta.sex           psi
     -3.7916           NaN           NaN           NaN       -1.7796
     psi.sex        Nsuper         theta  beta.density             D
      0.8096       -1.8318           NaN      -10.6456       -1.8318
       D.adj
     -1.8318


mean.model1
                        est            se
X             5.0005000e+03 2.0459545e+02
bsigma        5.4326691e-02 1.1936764e-03
sigma         3.2172883e+00 4.7950088e-02
bsigma2       5.4326691e-02 1.1936764e-03
```

```
sigma2         3.2172883e+00 4.7950088e-02
lam0           5.2516902e-03 8.8017559e-05
beta.behave    0.0000000e+00 0.0000000e+00
beta1.effort.  0.0000000e+00 0.0000000e+00
beta.sex       0.0000000e+00 0.0000000e+00
psi            2.3425101e-01 3.7790044e-03
psi.sex        3.0739862e-04 7.3133067e-06
Nsuper         3.5711883e+02 5.7480969e+00
theta          1.0000000e+00 0.0000000e+00
beta.density   3.0627539e+00 1.4749880e+00
D              1.0425244e-01 1.6780217e-03
D.adj          1.0995796e-01 1.7698563e-03
```

```
sd.model1
            X        bsigma         sigma       bsigma2        sigma2
2.8867874e+03 1.9452613e-02 7.3938573e-01 1.9452613e-02 7.3938573e-01
         lam0   beta.behave beta1.effort.      beta.sex           psi
1.8107810e-03 0.0000000e+00 0.0000000e+00 0.0000000e+00 7.1863523e-02
      psi.sex        Nsuper         theta  beta.density             D
1.0244677e-03 1.0872216e+02 0.0000000e+00 2.0857322e+01 3.1738878e-02
        D.adj
3.3475881e-02
```

```
HPDinterval(histCH1mcmc)
                       lower         upper
X              1.0000000e+00 9.5010000e+03
bsigma         2.1634587e-02 8.8409459e-02
sigma          2.3040496e+00 4.5724706e+00
bsigma2        2.1634587e-02 8.8409459e-02
sigma2         2.3040496e+00 4.5724706e+00
lam0           2.2891250e-03 8.9417182e-03
beta.behave    0.0000000e+00 0.0000000e+00
beta1.effort.  0.0000000e+00 0.0000000e+00
beta.sex       0.0000000e+00 0.0000000e+00
psi            1.1511485e-01 3.6804238e-01
psi.sex        4.7773278e-42 1.8241052e-03
Nsuper         1.8100000e+02 5.6200000e+02
theta          1.0000000e+00 1.0000000e+00
beta.density  -8.6857729e+00 3.2985030e+01
D              5.2838693e-02 1.6406268e-01
D.adj          5.6346250e-02 1.7365730e-01
attr(,"Probability")
[1] 0.95
```

```
BayesPval
[1] 0.622225
```




2) A model where Theta is estimated by the model
   (MSEX=0, MSEXSIGMA=1, XSEX=XSEX, XEFF=XEFFORT, THETA=NA)

```
Log of the estimated Marginal Likelihood using HM method = -41045.548
```

No burn in needed!

```
gelmandiag
Potential scale reduction factors:

              Point est. Upper C.I.
X                    NaN        NaN
bsigma              1.04       1.04
sigma               1.08       1.07
bsigma2             1.04       1.04
sigma2              1.08       1.07
lam0                1.03       1.02
beta.behave          NaN        NaN
beta1.effort.        NaN        NaN
beta.sex             NaN        NaN
psi                 1.01       1.01
psi.sex             1.00       1.00
Nsuper              1.01       1.01
theta               1.03       1.03
beta.density        3.16       2.87
D                   1.01       1.01
D.adj               1.01       1.01
```

gewekediag

```
Fraction in 1st window = 0.1
Fraction in 2nd window = 0.5

            X        bsigma         sigma       bsigma2        sigma2 
         -Inf        -1.063         1.068        -1.063         1.068 
         lam0   beta.behave beta1.effort.      beta.sex           psi 
       -1.974           NaN           NaN           NaN         1.142 
      psi.sex        Nsuper         theta  beta.density             D 
       -1.469         1.176         1.433         5.635         1.176 
        D.adj 
        1.176 
```

mean.model1

```
                       est            se
X             5.0005000e+03 2.0459545e+02
bsigma        1.8792591e-01 7.9217956e-03
sigma         1.9018126e+00 4.2981958e-02
bsigma2       1.8792591e-01 7.9217956e-03
sigma2        1.9018126e+00 4.2981958e-02
lam0          7.4979444e-03 1.7827918e-04
beta.behave   0.0000000e+00 0.0000000e+00
beta1.effort. 0.0000000e+00 0.0000000e+00
beta.sex      0.0000000e+00 0.0000000e+00
psi           2.3971171e-01 4.0269724e-03
psi.sex       2.9381761e-04 6.6584628e-06
Nsuper        3.6554175e+02 6.1231782e+00
theta         7.5163962e-01 9.2236022e-03
beta.density  8.4630033e-01 1.4104903e+00
D             1.0671132e-01 1.7875179e-03
D.adj         1.1255140e-01 1.8853450e-03
```

sd.model1

```
            X        bsigma         sigma       bsigma2        sigma2 
2.8867874e+03 1.1872537e-01 6.3744227e-01 1.1872537e-01 6.3744227e-01 
         lam0   beta.behave beta1.effort.      beta.sex           psi 
3.2690645e-03 0.0000000e+00 0.0000000e+00 0.0000000e+00 7.6428051e-02 
      psi.sex        Nsuper         theta  beta.density             D 
9.6976539e-04 1.1562644e+02 1.3869179e-01 1.9952181e+01 3.3754420e-02 
        D.adj 
3.5601729e-02 
```

HPDinterval(histCH1mcmc)

```
                      lower         upper
X              1.0000000e+00  9.5010000e+03
bsigma         5.5065359e-02  3.7503197e-01
sigma          1.0504163e+00  2.6238320e+00
bsigma2        5.5065359e-02  3.7503197e-01
sigma2         1.0504163e+00  2.6238320e+00
lam0           3.0125634e-03  1.3092731e-02
beta.behave    0.0000000e+00  0.0000000e+00
beta1.effort.  0.0000000e+00  0.0000000e+00
beta.sex       0.0000000e+00  0.0000000e+00
psi            1.0126592e-01  3.8838515e-01
psi.sex        2.3455951e-63  1.6990491e-03
Nsuper         1.4900000e+02  5.8300000e+02
```

```
theta           5.3222799e-01  9.5207885e-01
beta.density  -4.5515798e+01 -7.0580125e+00
D              4.3497046e-02  1.7019314e-01
D.adj          4.6493354e-02  1.8012326e-01
attr(,"Probability")
[1] 0.95
```

```
BayesPval
[1] 0.640125
```