Spatial partial identity model reveals low densities of leopard and spotted hyaena in a miombo woodland

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Abstract

Decline in global carnivore populations has led to increased demand for assessment of carnivore densities in understudied habitats. Spatial capture–recapture (SCR) is used increasingly to estimate species densities, where individuals are often identified from their unique pelage patterns. However, uncertainty in bilateral individual identification can lead to the omission of capture data and reduce the precision of results. The recent development of the two-flank spatial partial identity model (*SPIM*) offers a cost-effective approach, which can reduce uncertainty in individual identity assignment and provide robust density estimates. We conducted camera trap surveys annually between 2016 and 2018 in Kasungu National Park, Malawi, a primary miombo woodland and a habitat lacking baseline data on carnivore densities. We used *SPIM* to estimate density for leopard (*Panthera pardus*) and spotted hyaena (*Crocuta crocuta*) and compared estimates with conventional SCR methods. Density estimates were low across survey years, when compared to estimates from sub-Saharan Africa, for both leopard (1.9 ± 0.19 SD adults/100 km^2) and spotted hyaena (1.15 ± 0.42 SD adults/100 km^2). Estimates from *SPIM* improved precision compared with analytical alternatives. Lion (*Panthera leo*) and wild dog (*Lycaon pictus*) were absent from the 2016 survey, but lone dispersers were recorded in 2017 and 2018, and both species appear limited to transient individuals from within the wider transfrontier conservation area. Low densities may reflect low carrying capacity in miombo woodlands or be a result of reduced prey availability from intensive poaching. We provide the first leopard density estimates from Malawi and a miombo woodland habitat, whilst demonstrating that *SPIM* is beneficial for density estimation in surveys where only one camera trap per location is deployed. The low density of large carnivores requires urgent management to reduce the loss of the carnivore guild in Kasungu National Park and across the wider transfrontier landscape.

Introduction

Density estimation is an important tool for monitoring wildlife populations, which is critical for effective conservation management (Sollmann *et al.*, 2011; Balme *et al.*, 2019). Despite the ecological, economic and social importance of carnivores, basic data on population density and distribution are lacking across large areas of their geographic range (Ripple *et al.*, 2014; Bauer *et al.*, 2015; Jacobson *et al.*, 2016). This is particularly true in Africa, despite well-reported declines across the continent (Ripple *et al.*, 2014; Di Minin *et al.*, 2016; Wolf & Ripple, 2016). With increasing anthropogenic pressures, rising human populations and high rates of poaching, the need for rapid status assessments in understudied areas is critical for

carnivore conservation management and identification of species at high risk of decline (Jacobson *et al.*, 2016; Rosenblatt *et al.*, 2016; Elliot & Gopalaswamy, 2017).

Obtaining robust density estimates for carnivores, which are cryptic, wide-ranging and often solitary, is challenging (Balme *et al.*, 2009a; Sollmann *et al.*, 2011). Various techniques have been employed to estimate carnivore abundance and density, each with their own limitations (Balme *et al.*, 2014; Midlane *et al.*, 2015; Rogan *et al.*, 2019). In recent years, density estimates derived from camera trapping, for example using capture–recapture modelling, have become increasingly important in wildlife ecology and species management (Royle *et al.*, 2014; Rover and Zimmermann, 2016). The development of spatial capture–recapture (SCR) models, incorporating the

spatial location of captures and an explicit model of individual distribution across space, has resolved initial problems with capture–recapture modelling and allows more robust and accurate density estimation (Efford, 2004; Royle *et al*., 2009; Sollmann *et al*., 2011).

Whilst SCR methods are among the most robust methods for density estimation, the fundamental requirement for all captured individuals to be identified with certainty is not always achievable (Link *et al*., 2010; Augustine *et al*., 2018; Augustine *et al*., 2019; Johansson *et al*., 2020). For example, when camera trap arrays are used to survey individually identifiable animals, common practice is to deploy two camera traps at each sampling location, ensuring both sides of the animal are photographed for bilateral identification (Henschel & Ray, 2003). However, in situations where field conditions are limited by circumstances, such as topography, financial resources, malfunctioning equipment or poor image quality, photographs of only one side may be available (Wang & Macdonald, 2009; McClintock *et al*., 2013; Alonso *et al*., 2015; Augustine *et al*., 2018). This leads to partial identification of some, or all, of the study population (Foster & Harmsen, 2012; McClintock *et al*., 2013). In these circumstances, researchers are often forced to omit data from analyses (e.g. Wang & Macdonald, 2009; Alonso *et al*., 2015; Rosenblatt *et al*., 2016; Strampelli *et al*., 2018; Mohamed *et al*., 2019), leading to the loss of valuable recapture data and, potentially, introducing significant bias (Madon *et al*., 2011; Augustine *et al*., 2018).

The recent development of spatial partial identity models (SPIMs; Augustine *et al*., 2018) offers an analytical alternative to conventional SCR for partially identified datasets, allowing the use of a larger proportion of recaptures, whilst reducing the negative bias associated with individual heterogeneity in capture probability (Augustine *et al*., 2018; Augustine *et al*., 2019). SPIMs use a Markov chain Monte Carlo (MCMC) algorithm to reconstruct the true capture histories probabilistically, like previously developed partial identity models (McClintock *et al*., 2013). These partial identity models differ, however, as SPIMs incorporate the spatial location of individual captures to associate latent samples probabilistically, thereby reducing uncertainty in identity assignment (Augustine *et al*., 2018; Augustine *et al*., 2019). As uncertainty regarding partial identity samples is reduced, this allows for better estimation of density and movement parameters that are key to the SCR framework. Like conventional SCR methods, further variables, including age, sex and morphological differences, can be incorporated into SPIMs to resolve partial identities further and improve precision (Augustine *et al*., 2019).

Miombo woodland is the dominant vegetation type across south-central Africa, totalling 2.7 million km^2 (Frost, 1996), yet baseline data on carnivore densities are lacking for this habitat type (Balme *et al*., 2007; Stein *et al*. 2016), and as a result, species management may be ineffective. Malawi is predominantly covered by miombo woodland but is lacking robust assessments of large carnivore density, which, consequently, hampers effective species management that could be used as an exemplar for other countries across south-central Africa. Malawi is experiencing some of the highest rates of environmental degradation, climate change and deforestation in Africa, due to high population density (Stevens & Madani, 2016) and increasing population growth (United Nations, 2019). Therefore, the paucity of carnivore density estimates within miombo woodlands, combined with increasing anthropogenic impacts, makes assessment of large carnivore populations in Malawi a conservation priority for effective species management in the region.

In this study, we estimate large carnivore density in Kasungu National Park (KNP), Malawi, using a spatial partial identity model in a spatial capture–recapture framework. KNP comprises miombo woodland that has been impacted by high rates of anthropogenic pressures, including poaching, which has severely reduced numbers of natural prey (Munthali & Mkanda, 2002; Bhima *et al*., 2003). The study presents the first robust estimate of leopard (*Panthera pardus*) density in a miombo woodland, alongside spotted hyaena (*Crocuta crocuta*, hereafter hyaena) density, and highlights the status of other large carnivore populations in this regionally important protected area. We discuss the implications of our findings for the management of carnivores in KNP, the potential for wider inference across miombo woodlands and the application of SPIMs for camera trap surveys.

Materials and methods

Study area

The study was conducted in KNP, Malawi (central coordinates S12.9092°, E33.1689°; Fig. 1), a 2,316 km^2 legally protected area that encompasses a large part of the Kasungu Plateau. KNP is largely unfenced, with the only erected fencing in the south-east of the park in a state of disrepair and bordered by unprotected land in both Malawi and Zambia. KNP forms part of the 30, 621 km^2 Malawi Zambia Transfrontier Conservation Area (MZTFCA), which is of importance for biodiversity conservation in the Central Zambezian Miombo Woodland Ecoregion. KNP and Lukusuzi National Park, Zambia, form the Kasungu/Lukusuzi Transfrontier Area allowing dispersal of wildlife species between the two parks.

Kasungu National Park is dominated by miombo woodland, comprising *Brachystegia* and *Julbernardia* spp. (Bhima *et al*., 2003). Three main rivers flow through the park (Dwangwa, Lingadzi and Liziwazi) that form an extensive river network and drainage system that intersperses closed-canopy miombo woodland with seasonally wet grassland areas and isolated rocky inselbergs. The altitude ranges between 1,000 and 1,500 m, and mean annual rainfall is 780 mm, with most rainfall occurring during the wet season between November and April (Bhima *et al*., 2003). The area surrounding KNP consists of subsistence farming, charcoal burning and tobacco production, which is beginning to encroach into the protected area along park boundaries (Bhima *et al*., 2003). No human settlements, besides national park authorities (operating from ten ranger camps inside the park), are permanently based in KNP, and trophy hunting is not permitted in the park.

Historically, large carnivores (lion (*Panthera leo*), leopard, hyaena, wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*)) were known to be present in KNP (Nowell & Jackson,
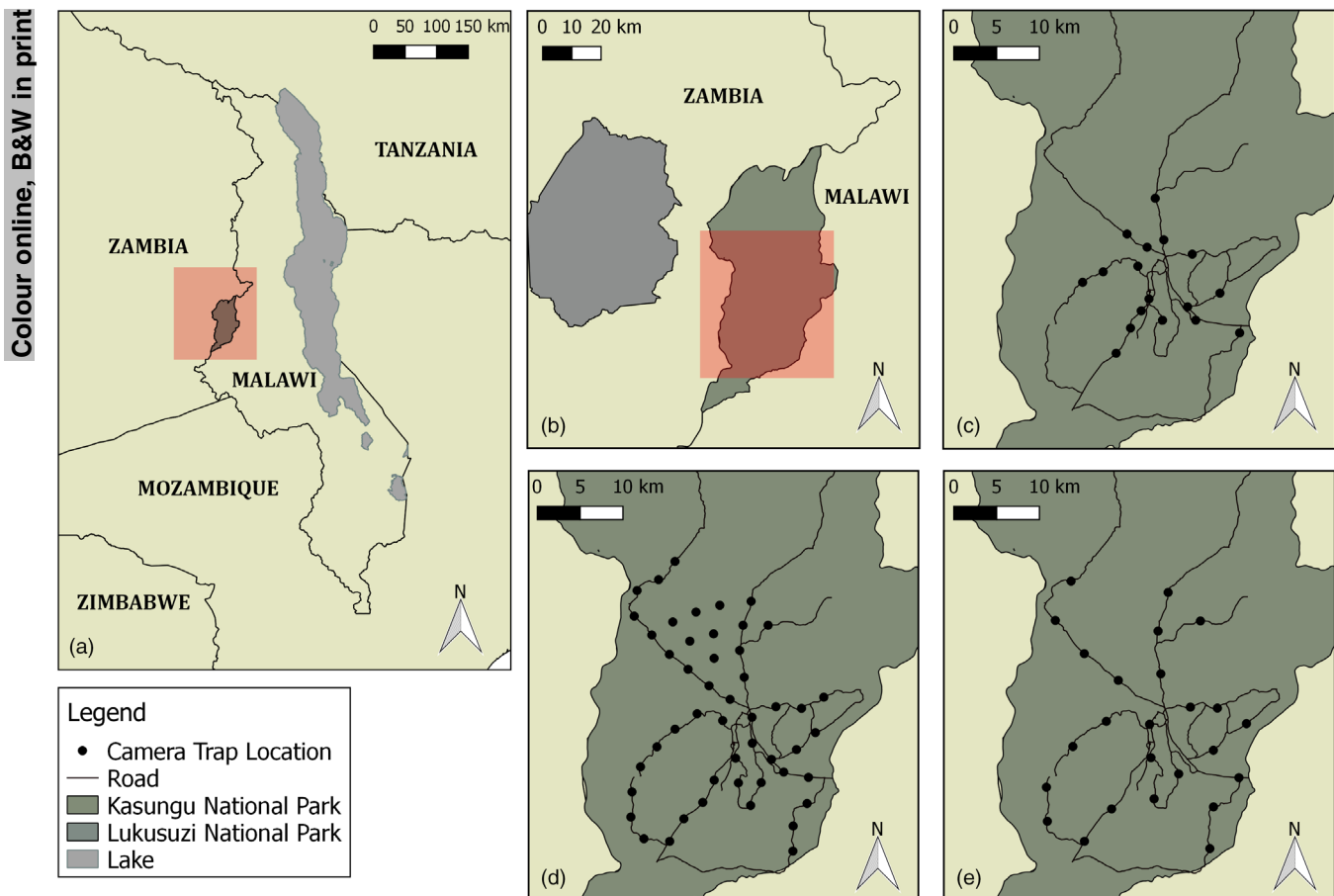
Fig. 1 Map showing (a) the location of Kasungu National Park (KNP) within Malawi and (b) the location of KNP with reference to Lukusuzi National Park, Zambia, and an overview of the area covered for camera trap surveys represented in; (c) camera trap locations for the 2016 survey; (d) camera trap locations for the 2017 survey and (e) camera trap locations for the 2018 survey.

1996; Woodroffe *et al.* 1997; Mills & Hofer, 1998). However, all have experienced declines in the past three decades, with cheetah declared extirpated (Durant *et al.* 2015) and an estimated fourteen wild dogs (Woodroffe & Sillero-Zubiri, 2020) and five lions (Mésochina *et al.* 2010) reported from anecdotal accounts and questionnaire surveys. African elephants (*Loxodonta africana*) declined from approximately 2000 individuals in 1977 to 117 individuals in 2003, due to poaching (Bhima *et al.*, 2003). Black rhinoceros (*Diceros bicornis*) were declared extinct in KNP in 1985 (Bhima & Dudley, 1996), and all other large herbivores present in the park are believed to have suffered population reductions, due to illegal hunting, though data are lacking (Munthali & Mkanda, 2002; Bhima *et al.*, 2003).

Camera trapping

Camera trap surveys were undertaken during the dry season (May to October) in 2016, 2017 and 2018. Surveys were not completed during the wet season due to limited road access and tall grass causing multiple false triggers. A combination of motion-activated white flash camera traps (Cuddeback Models C and F; Cuddeback Inc., Green Bay, WI, USA) and infrared cameras (Bushnell Trophy Cam HD; Bushnell Corporation, Overland Park, KS, USA) was used during all surveys. Infrared cameras were partly used in 2016 and 2017, due to limited numbers of white flash cameras being available. All cameras used in 2018 were white flash. One camera trap was used at each sampling location to maximize the area surveyed with the limited numbers of cameras available, with 17, 50 and 25 trapping locations used per year, respectively (Fig. 1).

Each trapping location was surveyed for 90 days in 2016 and 2018. In 2017, cameras were deployed at locations for 60 days, then redeployed in new locations for a further 60 days, totalling 120 days of survey. These were considered adequate survey lengths for assuming demographic closure and to ensure suitable numbers of photographic captures for large carnivores (Royle *et al.*, 2014; Dupont *et al.*, 2019).

We used a maximum camera spacing of 3–5 km (Devens *et al.*, 2018; Strampelli *et al.*, 2018) to select camera locations prior to deployment, with placement focused on the KNP road network. No home-range estimates are available for large carnivores in KNP, but a maximum spacing of 5 km ensured that there were no gaps in the array large enough to encompass an average adult female leopard home range (30 km^2; Braczkowski *et al.*, 2016). As home ranges of female leopards are smaller than those of male leopards and hyaena, this spacing was considered adequate for both species. We focused placement on roads in KNP, as carnivores are known to utilize road networks (Swanepoel *et al.*, 2015; Braczkowski *et al.*, 2016), and previous pilot data showed capture success was greater on roads than random placement. Final camera positions were selected as close to the predetermined points as possible and chosen based on evidence of carnivore presence or in suitable habitat to maximize the probability of photographic captures (Henschel & Ray, 2003). Although the trap array size and camera locations differed each year, due to logistical reasons, SCR models are generally considered more robust to these changes than conventional capture–recapture models (Sollmann *et al.*, 2011; Braczkowski *et al.*, 2016). Cameras were mounted on trees approximately 40–60 cm above the ground and two metres from the road or game trail and operated continuously, with one image taken per trigger and the minimum delay possible for each model. Each camera trap was visited every 10–14 days to download images, check batteries and ensure all cameras remained operational, in accordance with standard camera trap survey procedures (Henschel & Ray, 2003).

Density estimation and statistical analyses

Individual leopard and hyaena were identified from photographs using their unique pelage patterns (Henschel & Ray, 2003). A database was maintained of identified individuals, with partial (single-flank) or complete (two-flank) identities, to build capture histories for SCR analysis. We initially identified individuals from left-flank captures for both species, due to higher numbers of identified left-flank individuals recorded during preliminary surveys. Complete identities were added where flanks were certain to come from the same individual (from baited stations outside of survey time, live captures, dual-camera trap stations and multiple passes of a single-camera trap). Leopards were sexed by visual determination of external genitalia, presence of the dewlap, frontal bossing and overall body size (Henschel & Ray, 2003; Devens *et al.*, 2018). Any dependent cubs (determined by body size and/or simultaneous capture with an adult female) were excluded from analyses, due to their inclusion leading to inflated density estimates and violating independent capture probabilities (Balme *et al.*, 2019). Sexing was not possible for hyaena due to difficulties in determining sex from external genitalia and body size. Capture histories were developed for spatial captures and trap effort, with each day (24 h) treated as a separate sampling occasion (Goldberg *et al.*, 2015). Trap effort was measured through a binary matrix of active–inactive days, to improve estimates of detection probability, and included the spatial location of each camera station.

Density was modelled using the package *SPIM* (Augustine, 2018) in R v.3.5.2 (R Core Development Team, 2018), to resolve the complete identity of individuals from single-flank samples probabilistically (see Augustine *et al.*, 2018 for complete description of spatial partial identity model). A Bernoulli observation model was fitted, and, for MCMC simulations, a single chain of 50, 000 iterations per single-session analysis was undertaken, with a burn-in of 1,000 iterations and data augmentation of 100–130 individuals for leopard and 125–250 for spotted hyaena. Analyses were conducted with an increasing buffer width from 10 000 to 25 000 m (leopard) and 10 000 to 40 000 m (hyaena), using 5,000 m increments, until density estimates stabilized (Chase-Grey *et al.*, 2013; Devens *et al.*, 2018). Point estimates were calculated using the posterior mode and 95% intervals estimated using the highest posterior density interval. Model convergence of MCMC samples was assessed by examining trace plots and histograms for each parameter. Simulations were undertaken separately for each species and survey year, instead of incorporating a multi-session model, as this process is not currently implemented in the *SPIM* package.

For comparison with *SPIM*, density estimates were modelled using the Bayesian package *SPACECAP* v1.1.0 (Gopalaswamy *et al.*, 2012) in R v.3.5.2. Common practice with partial identities is to use the flank with the greater number of captures for density estimates (e.g. Rosenblatt *et al.*, 2016; Strampelli *et al.*, 2018); therefore, we developed single-flank capture histories for each year and species using the flank with the higher number of identifiable photographs. In addition, we modelled the capture histories where both flanks were known with certainty for each species and included, separately, the partial left- and right-flank images, for which we did not have complete identities. We then averaged the two, both-side plus partial sample models to attain mean density estimates for each species and year. We then compared the single-side and averaged both-side density estimates against the *SPIM* output and measured the 95% credible interval width to assess any gain in precision from using *SPIM*. Wherever possible, we kept MCMC settings as close to simulations in *SPIM* as possible, to aid comparison, and fitted a half-normal detection function, the trap response function and Bernoulli's encounter model. We used a 1-km^2 pixel area to represent potential home-range centres. Chain convergence was assessed using the Geweke diagnostic test, where z-scores between −1.6 and 1.6 imply convergence was achieved. Model fit was also determined from Bayesian p-values provided in the *SPACECAP* output, with p-values close to 0.05 and 1 suggesting inadequate fit.

Results

Camera trap surveys

A total of 17, 50 and 25 cameras were deployed in KNP during 2016, 2017 and 2018, respectively, at 92 locations across the three years (Table 1). Total sampling effort was 5,990 trap nights with an average camera trap spacing of 3.35 km (±0.94 SD) across all survey periods.

Table 1 Summary of camera trap sampling effort between 2016 and 2018 in Kasungu National Park, Malawi. Survey duration is the time period of the survey, with date showing the months surveyed in each year

Sample year	Survey duration (days)	Date	Camera trap stations	Total trap nights	Mean trap nights per camera (± SD)	Average camera spacing (± SD)
2016	90	May–August	17	1283	73 ± 16.85	2.83 ± 1.08
2017	120	June–October	50	2630	52.6 ± 11.99	2.78 ± 0.31
2018	90	June–September	25	2077	83.1 ± 15.41	4.43 ± 0.59

The number of camera trap stations, total trap nights (calculated as the total number of nights camera traps were effectively working during the survey), mean and standard deviation of trap nights per camera and average camera trap spacing (km) are also given per survey year.

Camera trap surveys yielded 274 leopard captures with an average of 91 (±37.54 SD) per year, ranging from 48 in 2016 to 114 in 2018. Using unique pelage patterns, 40 individual leopards (29 females, 8 males and 3 unsexed) were identified in KNP over the three survey years from left-flank spot patterns (Table 2), of which 17 were complete identities (where both left and right flank were certified from the same individual). A further 14 leopards (all female), for which right-side flank information could not be linked to a left-side flank, were included in the analyses to be resolved by the two-flank *SPIM* model. In addition, five dependent cubs, from four different females, were captured across survey years and were excluded from the analyses.

Surveys yielded a total of 346 hyaena captures, with an average of 115 (±44.56 SD) per year, ranging from 64 in 2016 to 144 in 2017. Thirty-three individual hyaena were identified during the survey period from their left-flank spot patterns, of which 19 were complete identities where both flanks were known. Seventeen unresolved right-flank identities were also included in the analyses to be resolved by the two-flank *SPIM* model.

Density estimation

Using *SPIM*, the highest leopard density estimate for KNP was 2.11 adults/100 km^2 in 2016 (Table 3), with an overall mean density estimate (derived from individual estimates from each survey year) of 1.9 (±0.19 SD) adults/100 km^2 (95% CI = 1.48–2.92/100 km^2). Density estimates from *SPIM* increased credible interval precision by 48, 40 and 68%, respectively, compared with the single-flank analyses. Credible intervals from *SPIM* also outperformed the averaged two-flank density estimates by 9% in 2018 and 35% in both 2017 and 2016, respectively. The average value of σ (the spatial scale parameter that determines the rate at which detection probability decreases with distance between an activity centre and a trap) was 3,447 (±684 SD) metres. Buffer width stabilized at 15 000 m for each survey year, and the average state space was 2,361 km^2 (±571 SD). Diagnostic statistics and trace plots suggested model fit and convergence was achieved in all models run in *SPIM* and *SPACECAP* (Table S1).

The highest density estimate for spotted hyaena in KNP was 1.62 adults/100 km^2 in 2018 (Table 4), with an overall mean density estimate of 1.15 (±0.42 SD) adults/100 km^2 (95% CI = 0.72–1.82/100 km^2). The single-flank and both-flank plus partial identity models for 2016 did not converge in *SPACE-CAP* and were excluded from the model list. Density estimates obtained in *SPIM* increased credible interval precision by 27 and 25%, respectively, in comparison with the single-flank models. Estimates from *SPIM* and the averaged two-flank models produced similar results and levels of precision in 2018 and 2017. The spatial scale parameter, σ, was larger for hyaena than leopard, with an average value of 5,768 (±586 SD) metres. Buffer width stabilized at 20 000 m in 2017 and 2018 and 40 000 m in 2016. Average state space size was 4,952 km^2 (±2134 SD). Diagnostic statistics and trace plots suggested model fit and convergence was sufficient for all other models run in *SPIM* and *SPACECAP* (Table S1).

Capture rates for other large carnivores

Other large carnivores were rarely encountered during surveys. Cheetah were not recorded in any survey year. In 2017, one male lion and one male wild dog were recorded. The lion (likely the same individual from diagnostic features) was recorded on 11 sampling occasions at 8 camera locations, whilst the wild dog was captured at 7 camera locations on 9 sampling occasions. Through unique pelage patterns, it was confirmed that all images were of the same individual wild dog. In 2018, the same individual wild dog was recorded on 9 sampling occasions at 6 camera locations. Lion presence was not recorded during the 2018 survey.

Discussion

Leopard density

The spatial partial identity model produced the first successful density estimates for a leopard population in Malawi and for a primary miombo woodland habitat. We estimated a mean density of 1.9 (±0.19 SD) adults/100 km^2 in KNP, with minor variation between the three years suggesting a stable trend in leopard density. Prior to this study, there were no estimates of leopard density from a primary miombo woodland habitat, with the only published estimate from a mosaic of five habitats where a single area of miombo woodland was surrounded by

Table 2 Capture success rates for leopard and spotted hyaena across three years of camera trap surveys in Kasungu National Park, Malawi

Sample Year	Total leopard captures	No. of identified leopards	Leopard capture rate (%)	Total hyaena captures	No. of identified hyaenas	Hyaena capture rate (%)
2016	48	9	3.7	64	13	5
2017	112	18	4.2	144	18	5.4
2018	114	23	5.5	138	25	6.6

Number of identified individuals for each year includes individuals identified in previous years but excludes right-flank individuals that could not be linked to already known individuals. Capture rate is defined as the total number of captures, divided by trap nights and multiplied by 100.

Afromontane forest and Afrotropical rainforest (Havmøller *et al.*, 2019). Our estimates indicate leopard density in KNP is low, in comparison with studies from elsewhere in sub-Saharan Africa, and comparable to leopard densities in human-impacted areas (e.g. 2.49 leopards/100 km^2, Balme *et al.*, 2010; 2.7 leopards/100 km^2, Henschel *et al.*, 2011; 1.18 leopards/ 100 km^2, Devens *et al.*, 2019) and more arid environments (e.g. 1.5 leopards/100 km^2, Stander *et al.*, 1997; 1.0 leopards/ 100 km^2, Stein *et al.*, 2011; 1.2 leopards/100 km^2, Edwards *et al.*, 2016).

The majority of Malawian protected areas (PAs) are under similar environmental pressures to KNP, with bushmeat poaching and habitat loss prevalent (van Velden *et al.*, 2020) and miombo woodland the predominant forest cover (Gondwe *et al.*, 2019). Our leopard density estimate for KNP can therefore, be used as a baseline for PAs in Malawi. However, we encourage further survey efforts to understand the Malawi leopard population status and trends, which has received little conservation attention to date. The Malawi leopard population is thought to be largely restricted to PAs, and reintroduction efforts have already been needed to restore leopard populations in Majete Wildlife Reserve (Briers-Louw *et al.*, 2019). As one of only three PAs in Malawi that is over 1,000 km^2 in size, KNP likely represents one of the few areas where a viable leopard population can persist in Malawi at these low densities. Therefore, the KNP leopard population requires active conservation management to understand and mitigate threats and increase population numbers.

Despite wide habitat tolerance and resilience to anthropogenic threats, habitat specialization is likely to translate to important differences in leopard population density across landscapes (Balme *et al.*, 2007). Miombo woodlands are regarded as relatively poor habitats for large mammals, with low biomass density and nutrient-poor soils, and this may reflect naturally low leopard densities (Frost, 1996; Waltert, Meyer & Kiffner, 2009). The potential for naturally low densities in miombo woodlands is likely further exacerbated in KNP by the decline in prey populations, a factor that has been identified as a key driver of leopard population decline (Henschel *et al.*, 2011; Jacobson *et al.*, 2016). However, as our results are from a single survey area, it is difficult to make inferences about the optimality of KNP and other miombo woodlands for leopard populations. Other regions, such as the miombo woodlands of southern Tanzania, where the size of protected areas is greater and substantial populations of large carnivores are known to be present (Abade *et al.*, 2018; Havmøller *et al.*,

2019), may hold higher densities of leopard, and further surveys in these regions would allow for greater understanding of the importance and potential of miombo woodlands for leopards.

Spotted hyaena density

We estimated a mean hyaena density of 1.15 (±0.42) adults/ 100 km^2 in KNP. Our estimate is comparatively low to other reported densities across sub-Saharan Africa (e.g. 89 hyaena/ 100 km^2, Höner *et al.*, 2005; 94 hyaena/100 km^2, Watts & Holekamp, 2008; 52 hyaena/100 km^2, M'soka *et al.*, 2016) and is over 95% lower than the only previously reported density of 31 hyaena/100 km^2 from a miombo woodland (Creel & Creel, 2002). Hyaena density in KNP is the lowest reported in a woodland habitat to date and is comparable to density estimates from arid environments (0.9 hyaena/100 km^2, Mills, 1990; 2 hyaena/100 km^2, Trinkel & Kastberger, 2005) and those recorded in Majete Wildlife Reserve, Malawi (2.62 hyaena/100 km^2, Briers-Louw, 2017). However, Majete Wildlife Reserve benefits from higher levels of protection compared with KNP and hyaena prey species have been reintroduced over the past decade (Briers-Louw *et al.*, 2019). It is likely that hyaena are found at low densities across Malawi, but whether these low densities are naturally occurring or due to the decline in protected area health over previous decades is difficult to ascertain due to a lack of previous estimates.

The reduction in large mammal numbers (Munthali & Mkanda, 2002; Bhima *et al.*, 2003) and the decline in competing carnivore populations in KNP suggest a period of high anthropogenic disturbance that is likely to have reduced large carnivore densities. The persistence of hyaena and leopard is potentially due to both species displaying higher levels of behavioural plasticity than other large carnivores, with a wide dietary niche and greater tolerance of human-impacted landscapes (Hayward, 2006; Hayward *et al.*, 2006). Despite these high levels of behavioural plasticity, the near extirpation of competing large carnivores and reduction in natural prey is likely to result in increased levels of competition between remaining leopard and hyaena populations (M'soka *et al.*, 2016).

Hyaena are competitively dominant over leopard (Balme *et al.*, 2019), with at least 10% of leopard kills lost to hyaenas and the higher rates of kleptoparasitism suffered by female leopards known to negatively affect reproductive success (Balme *et al.*, 2017). Leopard and hyaena are found at similar

Table 3 Posterior summaries of model parameters for leopards in Kasungu National Park from the spatial partial identity model (SPIM) compared with the single-flank model with the higher number of captures (single) and the mean estimate from the both plus partial left-side (B + L) and both plus partial right-side (B + R) datasets

Year	Model	$D \pm$ SD (95% CI)	(D) CI width	$\sigma \pm$ SD	$\lambda_0 \pm$ SD
2018	SPIM	1.77 ± 0.30 (1.35–2.54)	1.19	3954 ± 343	0.012 ± 0.002
	Mean (B + L, B + R)	2.22 ± 0.36 (1.65–2.86)	1.31	5195 ± 621	0.010 ± 0.003
	Single	2.65 ± 0.63 (1.65–3.94)	2.29	4628 ± 888	0.006 ± 0.003
2017	SPIM	1.81 ± 0.33 (1.21–2.50)	1.29	3718 ± 340	0.010 ± 0.002
	Mean (B + L, B + R)	2.09 ± 0.42 (0.90–2.87)	1.97	4910 ± 729	0.006 ± 0.003
	Single	2.21 ± 0.61 (1.20–3.35)	2.15	3741 ± 708	0.008 ± 0.004
2016	SPIM	2.11 ± 0.79 (1.87–3.71)	1.84	2669 ± 554	0.009 ± 0.003
	Mean (B + L, B + R)	1.80 ± 1.15 (0.72–3.54)	2.82	5115 ± 1806	0.006 ± 0.005
	Single	3.38 ± 1.71 (0.86–6.68)	5.82	4127 ± 2670	0.006 ± 0.004

D is the density per 100 km² with standard deviation (±SD) and 95% credible intervals (95% CI); σ is the detection function spatial scale parameter; and λ_0 is the detection function baseline encounter rate. The width of credible intervals for D is measured to assess any gain in precision from using SPIM.

Table 4 Posterior summaries of model parameters for spotted hyaena in Kasungu National Park from the spatial partial identity model (SPIM) compared with the single-flank model with the higher number of captures (single) and the mean estimate from the both plus partial left-side (B + L) and both plus partial right-side (B + R) datasets

Year	Model	$D \pm$ SD (95% CI)	(D) CI width	$\sigma \pm$ SD	$\lambda_0 \pm$ SD
2018	SPIM	1.62 ± 0.27 (1.17–2.26)	1.09	5192 ± 391	0.011 ± 0.002
	Mean (B + L, B + R)	2.15 ± 0.31 (1.67–2.78)	1.11	5971 ± 546	0.013 ± 0.003
	Single	2.40 ± 0.41 (1.66–3.16)	1.5	5560 ± 791	0.007 ± 0.002
2017	SPIM	1.01 ± 0.24 (0.61–1.47)	0.86	5749 ± 687	0.006 ± 0.001
	Mean (B + L, B + R)	1.29 ± 0.24 (0.93–1.75)	0.82	7989 ± 1441	0.005 ± 0.001
	Single	1.43 ± 0.32 (0.93–2.07)	1.14	6999 ± 1722	0.005 ± 0.002
2016	SPIM	0.81 ± 0.44 (0.38–1.74)	1.36	6364 ± 2653	0.007 ± 0.004

D is the density per 100 km² with standard deviation (±SD) and 95% credible intervals (95% CI); σ is the detection function spatial scale parameter; and λ_0 is the detection function baseline encounter rate. The width of credible intervals for D is measured to assess any gain in precision from using SPIM.

densities in KNP, and with the loss of competing carnivores, most notably lion, and the reduction in natural prey, further research is needed to assess how this affects interspecific competition between the remaining large carnivore guild (Hayward & Slotow, 2009; M'soka *et al.* 2016). This is crucial to future management of large carnivore persistence in KNP and other areas of high anthropogenic disturbance (M'soka *et al.* 2016; Abade *et al.*, 2018).

Prey availability is known to influence hyaena population density (Höner *et al.*, 2005; Périquet *et al.*, 2015). Therefore, securing the remaining prey base and allowing prey populations to recover in KNP should encourage the hyaena population to recover naturally (M'soka *et al.* 2016). High rates of reproductive success for hyaena in the absence of a resident lion population and the benefits of increased clan size for food acquisition (Kruuk, 1972) and cub survival (Watts & Holekamp, 2009) could lead to a rapid increase in the KNP hyaena population. Comparatively, leopard reproductive success is often naturally low (Balme *et al.*, 2013) and further influenced by bottom-up processes in low productivity habitats (Stander *et al.*, 1997) and in populations below carrying capacity (Owen *et al.*, 2010). A growth in the hyaena population could therefore potentially lead to increased competition between the

remaining carnivore guild and a subsequent decline in the KNP leopard population. Consequently, any conservation management interventions (such as increased law enforcement efforts or prey reintroduction/supplementation) in KNP should be closely monitored through annual camera trap surveys (Balme *et al.*, 2009b).

Lion and wild dog presence

Our results suggest that both lion and wild dog are no longer resident in KNP, highlighting the degradation of the protected area. It is likely that lion and wild dog in KNP are dispersing individuals, potentially from nearby populations in Zambia, as connectivity between Malawian PAs is largely restricted by high human population density and loss of forest cover (Gondwe *et al.*, 2019). The presence of dispersing lion and wild dog in 2017 and 2018 demonstrates the ability of carnivores to move through the MZTFCA, a cause for optimism for future conservation management of the region. However, increasing anthropogenic pressure on dispersal corridors and protected area networks in Zambia may jeopardize future dispersal efforts (Watson *et al.*, 2014), highlighting the need for

increased planning and continued international collaboration to protect these corridors and the ecological functionality of the wider region. Furthermore, securing, and increasing, the remaining prey base in KNP is vital to support future dispersers and promote natural recolonization or potential reintroduction efforts.

Application of SPIM and survey considerations

This study provides further evidence that the *SPIM* package can provide robust density estimates, comparable to conventional SCR methods, whilst improving precision for partial identity samples (Augustine *et al.*, 2018; Greenspan *et al.*, 2020). As SCR methods are widely used to inform conservation management, and partial identity is a common problem for researchers, any gain in precision should be of broad interest (Augustine *et al.*, 2018; Johansson *et al.*, 2020). Our results show that in comparison with single-flank estimates, often the preferred and more conservative approach for partial identity samples, *SPIM* improves the precision of density estimates. We therefore recommend the use of *SPIM* for studies deploying single-camera stations or studies where partial identities constitute a large proportion of the data.

Difficulties in sexing hyaena meant that sex could not be included as a covariate, which may have influenced our density estimates. However, the relatively small sample size for each survey year would have resulted in only a minor influence on sex-specific parameters and we are therefore confident in our estimates (Efford & Mowat, 2014; Mohamed *et al.*, 2019). Similarly, for leopard, the small sample size of males to females (one male in 2016, four in 2017) would likely have resulted in minimal difference in sex-specific parameters. Comparative studies with relatively small sample sizes for male and female individuals have found that the null model, whereby sex-specific parameters (detection rate and spatial scale) are not incorporated into model inference, had the highest model support or produced similar estimates to other analytical methods (Chase-Grey *et al.*, 2013; Devens *et al.*, 2018; Strampelli *et al.*, 2018; Balme *et al.*, 2019).

Whilst dual-camera trap survey stations still provide the most accurate and effective way of collecting recapture data for complete identities of large carnivores, the development of *SPIM* (Augustine, 2018) and similar packages for partially identified datasets (McClintock, 2015) allows alternative survey design considerations for conservation management (Augustine *et al.*, 2018; Farhadinia *et al.*, 2019). Robust, and often rapid, density estimates are key for species management (Bauer *et al.*, 2015; Jacobson *et al.*, 2016), and *SPIM* provides a cost-effective and accurate method for analysing camera trap data that deviates from the conventional dual-camera trap survey design (Augustine *et al.*, 2018). The potential to survey a protected area using half the number of camera traps used in conventional designs is highly advantageous for protected area managers, the majority of whom have limited budgets (Mansourian & Dudley, 2008). The use of *SPIM* also allows a wider survey area to be used, when camera numbers are

limited, resulting in a greater proportion of the population being sampled (Foster & Harmsen, 2012; Mohamed *et al.*, 2019; Greenspan *et al.*, 2020).

Populations perceived to be at low densities are often in the most urgent need of assessment and require intensive survey efforts (Balme *et al.*, 2009a; Sollmann *et al.*, 2011). The potential gains in precision from using *SPIM* are greater for populations at low density, where single-flank captures can be linked with increased certainty, and *SPIM* could therefore be beneficial to future survey efforts (Augustine *et al.*, 2018). We recommend that the trade-offs between dual- and single-camera stations are considered on a case-by-case basis, but the use of *SPIM* offers a novel solution to issues with camera trap survey design and analysis (Augustine *et al.*, 2018; Greenspan *et al.*, 2020). We suggest further camera trapping efforts to estimate large carnivore populations in miombo woodlands and other understudied regions, coupled with the use of *SPIM* where necessary, to provide robust estimates for effective conservation management.

Conflicts of interest

The authors declare that they have no conflict of interest.

Ethics approval

Ethical approval was granted by the Nottingham Trent University and Department of National Parks and Wildlife Malawi.

Data availability statement

The datasets in this study are available from the corresponding author on reasonable request.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Geweke diagnostic statistics and Bayes *P*-values generated in SPACECAP for the single-flank and both plus partial sample models for leopard and spotted hyaena in Kasungu National Park, Malawi.