On tracks: A spoor-based occupancy survey of lion *Panthera leo* distribution in Kafue National Park, Zambia

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ABSTRACT

The African lion has lost more than 75% of its historic range and numbers of wild lions continue to decline. Protected areas are critical to the species' future, yet its conservation status in many of these presumed sanctuaries remains unknown. Zambia is one of nine countries estimated to hold over 1000 wild lions, and Kafue, its largest National Park, is a key stronghold for the species. Understanding lion distribution and threats facing the species in the park are of particular relevance given the recent ban on lion hunting in Zambia and the uncertainty over this industry's future in the country. We used a single-season occupancy model based on detection of lion tracks to estimate proportion of area used and derive spatially explicit probability of lion use for northern Kafue, an area for which no previous empirical lion data exist. Our top-ranking model predicted that lions use 72.1% of the study area, 23.3% greater than the naïve estimate. Contrary to our expectations, and possibly due to apparent ubiquity of illegal bushmeat hunting in the park, neither prey biomass nor anthropogenic edge effects emerged as important drivers of lion distribution, with habitat class instead the best predictor. Our findings provide the management authority with survey methodology as well as focal areas for further lion research in the Kafue system. More broadly, we demonstrate the utility of track-based occupancy models in establishing the distribution of large carnivores within previously unsurveyed African protected areas.

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1. Introduction

The continuing exponential growth of the earth's human population and the ensuing transformation of natural landscapes are recognised as the primary drivers of species extinctions on a global scale (May et al., 1995; Pimm and Raven, 2000). In this context, protected areas (PAs) play a key role in the continued existence of a multitude of threatened fauna and flora (Gaston et al., 2008). However, human population growth rates in many developing countries are significantly higher on the borders of PAs than elsewhere (Wittemyer et al., 2008; but see Joppa et al., 2009). Illegal resource extraction from PAs (Brashares et al., 2004) and human-wildlife conflict along the borders with densely populated areas (Graham et al., 2005) have led to the decline and even extirpation of many species within the nominally secure boundaries of PAs (Caro and Scholte, 2007). Large carnivores, such as the African lion (*Panthera leo*), are particularly vulnerable to such edge effects due to their wide-ranging behaviour, and the real and perceived threats they pose to human lives and livelihoods (Woodroffe and Ginsberg, 1998; Woodroffe, 2000). However, these species fulfil key economic (Caro and O'Doherty, 1999) and ecological (Creel and Christianson, 2008) roles in PAs, and are thus a conservation priority for wildlife managers (Sergio et al., 2006).

As one of only nine countries estimated to have more than 1000 wild lions remaining, Zambia is a critical stronghold for the species, which has lost more than 80% of its historic range (Riggio et al., 2013) and is classified as vulnerable by the IUCN (Bauer et al., 2013). The majority of the country's lions occur in PAs in three ecosystems, the Kafue, the Luangwa Valley and the Lower Zambezi, but limited management and conservation-relevant data exist for these populations (but see Becker et al., 2012). Legally protected within PAs, lions are nevertheless regularly killed as by-catch in wire snares set by illegal bushmeat hunters (Becker et al., 2013), whose activities simultaneously impose indirect pressure on the species by reducing available prey biomass (Lindsey et al., 2013a). These twin threats persist in the Game Management Areas (GMAs; IUCN Category VI buffer zones adjacent to Zambian PAs), where local communities have rights to the land but ownership of the wildlife vests with the Zambia Wildlife Authority (ZAWA) and limited consumptive utilisation is permitted (Lewis and Alpert, 1997). Until recently, trophy hunting of lions was an additional

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source of anthropogenic mortalities in GMAs, but in January 2013, citing declining numbers, the Zambian government banned all trophy hunting of lion (and leopard Panthera pardus; http://www.bbc.co.uk/news/world-africa-20969868, accessed March 15 2013). The current paucity of data on the country's lion population has left the issue of whether or not to reopen trophy hunting of the species unresolved and led to calls for additional research. This paper will provide an understanding of lion distribution within northern Kafue, a key lion stronghold in Zambia, and thus contribute to an informed decision on the future of the country's lion hunting industry.

To determine the distribution of a species of interest, surveys are traditionally conducted in predetermined landscape units (natural e.g. ponds or abstract e.g. grids) within the study area wherein the presence or absence of the species is recorded (Mackenzie, 2005a). However, these results may be biased by false absences (i.e. species present but not detected). This limitation can be overcome through the use of occupancy models, which use a detection history (a dataset generated by multiple spatial and/or temporal survey replicates in each survey unit), to first calculate the probability of detecting the species given that it was present in the unit during the survey (the detection probability, p). Thereafter, p is used to adjust the naïve presence estimate to a probability of occupancy (ψ) by accounting for the effects of false absences in survey units with no detections (Hines et al., 2010; Mackenzie, 2005a; Mackenzie et al., 2002). The occupancy probability can be manipulated to represent the spatially explicit probability of an individual site being occupied, and can also be interpreted as the proportion of the study site that is likely occupied (the Probable Area Occupied, or PAO, Mackenzie et al., 2006).

Various methods have been used to compile detection histories in carnivore occupancy surveys. For example, detection of spoor has been used to indicate tiger (Panthera tigris) presence in India (Harihar and Pandav, 2012; Hines et al., 2010; Karanth et al., 2011) and Sumatra (Guillera-Arroita et al., 2011; Linkie et al., 2006; Wibisono et al., 2011), river otters (Lontra canadensis) in the United States (Aing et al., 2011) and wolverines (Gulo gulo) in Canada (Magoun et al., 2007). Zeller et al. (2011) used interviews with local communities to determine jaguar (Panthera onca) presence in Nicaragua, while hair traps and rub trees indicated the passage of grizzly bears (Ursos arctos) in the US (Graves et al., 2011). Motion-sensitive camera traps have been widely utilised for detecting presence, including for American martens (Martes americana) in the US (Baldwin and Bender, 2008), sun bears (Helarctos malayanus) in Sumatra (Wong et al., 2012), brown hyaenas (Hyaena brunnea; Thorn et al., 2009) in South Africa and complete carnivore guilds in Ghana's Mole NP (Burton et al., 2011) and Kenya's Rift Valley (Schuette et al., 2013a). In this study we use spoor surveys as our detection method in order to investigate the occupancy of lions in Zambia's Kafue National Park (Kafue), a Type I Lion Conservation Unit (IUCN SSC Cat Specialist Group, 2006) and one of Africa's largest PAs. Spoor surveys on roads have been successfully utilised to estimate large carnivore density in Africa (Funston et al., 2010) and are thus a valid method of detecting lion presence.

Distribution of dominant carnivore species is largely governed by the availability and biomass of suitable prey (Carbone and Gittleman, 2002; Karanth et al., 2004; Spong, 2002), whilst subordinate species are affected by the presence of these dominant competitors (Creel and Creel, 1996). However, all large members of the taxa can be strongly influenced by anthropogenic persecution, such as trophy hunting (Loveridge et al., 2007; Packer et al., 2009) and snaring (Lindsey et al., 2011), which typically manifest as edge effects within PAs (Woodroffe and Ginsberg, 1998). These human disturbances can have similar impacts on dispersion of ungulate (i.e. prey) biomass (Kiffner et al., 2012; Metzger et al., 2010), which may also be affected by availability of resources such

as water (Valeix et al., 2010). We thus predicted that lion occupancy in Kafue would be higher (1) in areas with greater prey biomass and (2) with increasing distance from negative human disturbances. We considered potential natural drivers (e.g. prey biomass, habitat type, proximity to water) of lion occupancy as well as proxies for negative (e.g. distance to boundary) and positive (e.g. anti-poaching patrol effort) human influences. Lions are territorial with female home ranges primarily configured around resources such as food and denning sites, while males establish ranges based on the need to access and defend female prides (Schaller, 1972). Lion ranging behaviour varies seasonally in Kafue (Midlane et al., in preparation), and our results should thus be interpreted as representing dry season occupancy only. We analysed the effects of all the identified factors by including them as covariates in a set of candidate univariate and multivariate occupancy models, used the top-ranked model to determine the primary drivers of lion distribution in the study area and finally produced a map of spatially explicit probability of lion occupancy for northern Kafue.

2. Materials and methods

2.1. Study area

Proclaimed a National Park (IUCN Category II) in 1950, Kafue is 22.319 km², situated in western Zambia between 14°00′–16°40′S and 25°15′–26°45′E (Fig. 1), and adjoined by 43.692 km² of GMAs. Three main rivers, the Kafue, Lunga and Lufupa run the length of the park, which is split into northern (10,958 km²) and southern (11,361 km²) sectors by the M9, a major regional paved road, which also formed the southern boundary of the study area. The region experiences two distinct seasons, a wet season from December to May, and a dry season from June to November. Mean annual rainfall in the north is 1020 mm, dropping to 510 mm in the south (Fanshawe, 2010). The majority of this rain falls between December and March, and the park is largely inaccessible by vehicle from December to early May. Using remotely sensed data (http://www.fao.org/geonetworks/srv/en/main/home, accessed February 4, 2013) and vegetation descriptions of Fanshawe (2010), we divided Kafue into three major habitat classes, (i) miombo and Kalahari woodland (MIO, 29.0% of study area) dominated by *Brachystegia* spp. and
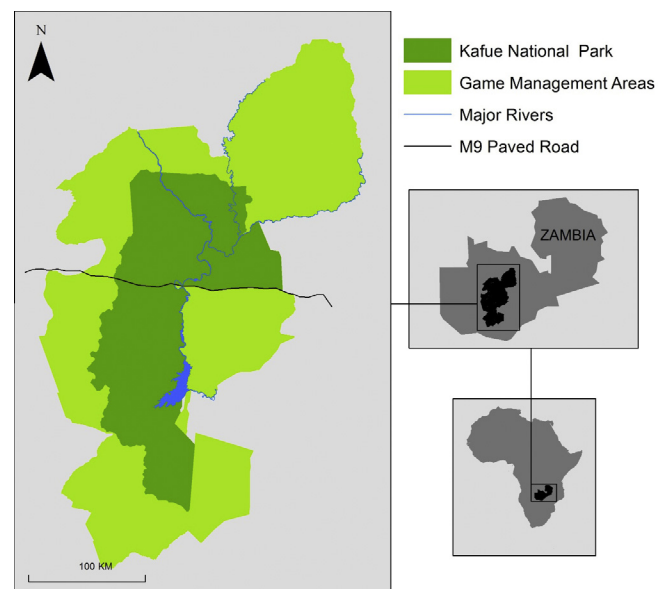

Fig. 1. Kafue National Park and surrounding GMAs.

Julbernardia spp., (ii) munga and termitaria woodland (MUN, 32.3%) dominated by *Acacia* spp., *Combretum* spp. and *Terminalia* spp., and (iii) munga scrub and grassland (SAG, 38.5%) comprising open scrubland up to 3 m high and dambo, floodplain and riverine grasslands.

2.2. Field data collection

We used a grid of square cells to define survey sites for the occupancy model, and the objectives of our study were to estimate Probable Area Occupied (PAO) by lions and spatially explicit Probability of Lion Occupancy (PLO), rather than finer scale habitat selection. Mackenzie et al. (2006) recommend a balance between sites being large enough for a reasonable likelihood of the species being present, and small enough for occupancy measures to be meaningful, while for estimating PLO, cells greater than the largest home range of the species in the study area are suggested by Karanth et al. (2011). In this study, 90% kernel density estimates based on GPS collar (Vectronic Aerospace GmbH, Berlin, Germany) data from nine Kafue lions (five male, four female) for the 2010 and 2011 dry seasons produced home range estimates from 62.1 to 589.3 km^2 (Online Appendix A, Table A1). Due to this significant variation ($\bar{x} = 257.8$ km^2, CV = 80.6%), and the coarse resolution that would result from cells >590 km^2 (Karanth et al., 2011), we calculated the median home range (188.7 km^2) and accordingly selected a grid cell size of 200 km^2. Using ArcGIS v10.1 (ESRI, Redlands, California), we randomly overlaid our grid on the northern half of Kafue. The grid comprised 73 cells covering 14,600 km^2, of which 11,480 km^2 was National Park and the remainder a combination of GMAs and a privately managed Open Area (OA).

Using Google earth (Google Inc., Mountain View, California), we identified grid cells ($n = 41$) that contained unpaved roads (for track detection), and selected segments of these roads for survey transects. Unlike work conducted in Asia on tigers (e.g. Hines et al., 2010), off-road animal trails were predominantly on hard clay soils unsuitable for track detection. We were thus constrained in our selection of transects by the limited network of roads with suitable substrate, a situation likely to be encountered in most large African PAs.

Valid inference from occupancy models usually requires detections to be independent of each other (Mackenzie et al., 2006, 2002). However, Hines et al. (2010) developed a model which accounts for the spatial correlation of animal sign detections along sequential segments of a road or trail, thus allowing logistically feasible survey designs that follow the biologically likely reality of animals traveling along these routes (Karanth et al., 2011). The model adds three parameters, θ_0, denoting probability of detection on a segment given absence on the previous segment, θ_1, denoting probability of detection on a segment given presence on the previous segment (Hines et al., 2010) and $\theta_0\pi$, for the situation where a transect does not begin at a natural boundary (e.g. a major river that cannot be crossed by the species of interest), and thus the preceding segment could have a presence or an absence of sign (introduced in PRESENCE, Hines, 2013).

We identified 17 transects between 17 and 30 km in length, each traversing more than one grid cell, ensuring coverage of as many cells as possible (Fig. 2). We drove each transect 2–4 times between 1 July and 15 October 2012, with at least a week separating temporal replicates, and split transects into one-km segments (Hines et al., 2010; Karanth et al., 2011), resulting in a detection history comprising temporal and spatial replicates numbering 4–60 per surveyed cell. We started all surveys within 30 min either side of sunrise when tracks are most visible (Liebenberg, 1990) and drove at a speed of approximately 10 km h^{-1} to maximise the likelihood of track detection. Two observers, including the lead author, scanned the road for signs of lion, the first observer sitting on the front left corner of the vehicle and the second driving. Both team members were competent at detecting and identifying tracks. Observers recorded substrate quality (ease of detecting tracks; scale of 1–5) and vehicle impact on substrate (impact of other vehicles on likelihood of detecting fresh tracks; scale of 0–2) for each segment (Online Appendix A, Table A2). We identified lion tracks based on their size and shape and recorded the detection (1) or non-detection (0) of lions on each one-km segment. If we were uncertain of the species responsible for a track we discounted it to ensure that we did not violate the model requirement of no false detections (Mackenzie et al., 2002).

2.3. Model building and selection and data analysis

A further assumption of occupancy models is that the species of interest does not become extinct from, nor colonise, any sites during the survey period (Mackenzie, 2006; Mackenzie et al., 2002). The short duration (3.5 months) of our study should ensure population closure, but wide-ranging species such as lions may have home ranges that overlap multiple sites, thus jeopardising the assumption of geographic closure. However, the random occupation of sites by lions during the survey period (i.e. on any given day an animal could be present in any of the sites within its home range) renders occupancy and detection parameters unbiased, although their interpretation changes (Kendall and White, 2009; Mackenzie et al., 2006). We thus interpret ψ_i as the probability that a lion(s) used site i, and p_i as the probability that the lion(s) was/(were) detected given use of the site i during the survey. We thus calculate proportion of area used (PAU) rather than PAO, and our spatial model predicts probability of lion use (PLU) rather than PLO.

Occupancy models also assume that both detection and occupancy probabilities remain constant across survey sites (Mackenzie et al., 2002). Spatial variation in abundance may induce heterogeneity in both parameters, but this violation can be overcome by modelling relevant covariates in the occupancy analysis (Mackenzie, 2005b; Royle and Nichols, 2003). We therefore used ArcGIS to derive spatially explicit values, allocated to individual cells in our grid, for a suite of factors hypothesised to potentially influence lion occupancy in Kafue. Site specific factors considered are prey biomass (PB), habitat class (MUN, MIO, SAG), fire (FI) and law-enforcement effort (LE) (Table 1), and proximity (measured from the centre of the cell) to: water (PW), park boundary (PE), external human activities (PP), photographic tourism camps (PT), safari hunting camps (PH) and permanently manned Zambia Wildlife Authority posts (PZ). Although in all cases we used the best available data sets to derive layers for these factors (Online Appendix A, Table A2), we caution that some of these may have inferential limitations. Additionally, we considered the effect of the number of replicates (NR) per cell on occupancy to determine whether our sampling regime affected the model outcome. We did not consider elevation, slope or aspect due to the relatively homogeneous elevation of northern Kafue. We also modelled vehicle impact on roads (VI) and substrate quality (SU) as survey-specific factors (i.e. affecting p_i), giving an initial total of 15 covariates.

We used software PRESENCE (Hines, 2013) for occupancy analyses, and AIC$_c$ values (Akaike Information Criterion adjusted for small sample sizes) to rank candidate models (Burnham and Anderson, 2002). We compared the top-ranked model with others in the set using evidence ratios (ER) (Mazerolle, 2006), based on the formula ER = w_j/w_i where w_j is the AIC$_c$ weight of the top-ranked model and w_i the AIC$_c$ weight of the model being compared. The lowest AIC$_c$ ranking indicated the top-ranked model, and we considered resulting models with ΔAIC$_c$ < 2 to be competing with the top model, while models with ΔAIC$_c$ from 2 to 7 had some support (Burnham and Anderson, 2002: 70). We analysed β (i.e.

Fig. 2. Occupancy survey design.

Table 1
Site-specific covariate values entered into PRESENCE.

Covariate	Description
Prey biomass (PB)	Estimated mass of ungulate prey per cell based on aerial survey data, smoothed using a kernel density estimator. The aerial survey was conducted in 2011 (Frederick, 2011), but found no significant decreases in ungulate populations from a previous 2008 survey. We were thus confident that prey biomass had not decreased significantly by the time of our survey
Habitat MUN (MUN)	Proportion of cell comprised of munga and termitaria woodland based on satellite imagery
Habitat MIO (MIO)	Proportion of cell comprised of miombo and Kalahari woodland based on satellite imagery
Habitat SAG (SAG)	Proportion of cell comprised of munga scrub and grassland based on satellite imagery
Proportion of cell burnt (FI)	Mean proportion of cell burnt from 2010 to 2012
Law enforcement effort (LE)	Number of GPS points recorded by law enforcement patrols from January 2009 to October 2012

For more detail on derivation of covariate layers refer to Online Appendix A, Table A2.

regression coefficient) of individual covariates within the top ranking models for significance of effect (i.e. 95% confidence intervals (CI) exclude zero; Zeller et al., 2011)) and calculated ERs comparing the top model with all models with $\Delta AIC_c < 7$ (Mazerolle, 2006).

Processing our detection history in PRESENCE with no covariates, we obtained AIC_c scores of 794.22 and 683.48 for the "Custom" ($\psi(\cdot)p(\cdot)$) and "Custom with Spatial Correlation" ($\psi(\cdot)p(\cdot)\theta_0(\cdot)\theta_1(\cdot)\theta_0 \pi(\cdot)$) models respectively. We therefore used the latter for all subsequent analyses in PRESENCE. We allowed the software to estimate θ_0, θ_1 and $\theta_0\pi$ for all candidate models, and denote the inclusion of these parameters as $sc(\cdot)$ in our model building process.

To build candidate models, we first considered covariates affecting p_i (i.e. survey-specific) through univariate analysis of each factor, as well as multivariate combinations thereof, in PRESENCE, holding $\psi(\cdot)$ constant (Karanth et al., 2011). We carried the model with the lowest resulting AIC_c score forward for the selection of site-specific covariates, and used it to conduct univariate analyses in PRESENCE. Thereafter we used a Spearman's correlation matrix in program STATISTICA (Statsoft, Tulsa, Oklahoma) to test for pair-wise correlation between these covariates (Graham, 2003). For each pair with a strong correlation ($r \geqslant 0.80$) we eliminated the covariate with the lower AIC_c score from subsequent analyses (See Online Appendix A Table A5 for correlation matrix). Following Zeller et al. (2011), we also eliminated covariates that had a

non-significant effect (95% CI included zero) in univariate form from the final model set. Next we compared AIC_c scores for covariates in the same category (e.g. habitat class) and retained only the highest ranked factor in each category. Using our a priori hypotheses and predictions based on lion biology and the Kafue system, we created a final set of candidate models and entered these in PRESENCE. We used PRESENCE to apply the resulting predictive model to both surveyed and unsurveyed sites and ArcGIS to derive a map of spatially explicit PLU for the study area. Finally, we calculated the coefficient of variation of PLU for each cell as a measure of the variability in our data (Sunarto et al., 2012).

3. Results

We drove six transects four times and 11 transects twice for a total of 46 individual surveys and 1010 1 km segments. We graded substrate quality on 6.6% of segments as very good, 27.9% good, 49.9% moderate, 14.6% poor and 1.0% very poor. There was no vehicle impact on 94.3% of segments, light impact on 5.3% and heavy impact on 0.4%. We detected lion tracks on 147 segments (14.6%), and in 24 of 41 surveyed cells, producing a naïve occupancy estimate of 0.585. The null model $\psi(\cdot)p(\cdot)sc(\cdot)$ estimated PAU, after adjusting for detection probability, as 0.721 (95% CI: 0.529–0.913).

Table 2
Survey-specific model selection results.

Model	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight	Evidence ratio	Number of parameters
$\psi(\cdot)p(\cdot)sc(\cdot)$	683.48	0.00	0.5806	1.0	5
$\psi(\cdot)p(SU)sc(\cdot)$	685.43	1.95	0.2194	2.6	6
$\psi(\cdot)p(VI)sc(\cdot)$	686.24	2.76	0.1463	4.0	6
$\psi(\cdot)p(SU+VI)sc(\cdot)$	688.24	4.76	0.0537	10.8	7

Role of survey-specific covariates in determining probability of detecting lion sign on 1 km long segments using the model of Hines et al. (2010). Number of sites = 41. Covariates are substrate quality (SU) and vehicle impact on substrate (VI).

The null model $\psi(\cdot)p(\cdot)sc(\cdot)$ had the highest AIC$_c$ ranking in analysis of survey-specific factors affecting p_i. Based on ERs, this model fit the data 2.6 times better than the closest competing model, $\psi(\cdot)p(SU)sc(\cdot)$ (SU = substrate quality; Table 2). Both SU and vehicle impact (VI) had 95% confidence intervals for β that included zero, indicating non-significant effects (Zeller et al., 2011). We therefore held the $p(\cdot)$ term constant with no covariates for subsequent analyses.

Only four site-specific covariates had significant effects on PLU in the univariate analysis, namely habitat MUN (positive), habitat MIO (negative), mean proportion of cell burnt (FI; positive) and proximity to water (PW; positive). These were thus the only covariates considered for the final model set in univariate form, although we nevertheless retained those covariates required to build our hypothesised multivariate models. Univariate analysis ranked $\psi(MUN)p(\cdot)sc(\cdot)$ as the top model, with an AIC$_c$ weight of 0.69 (Online Appendix A Table A6). The next best fitting model was $\psi(MIO)p(\cdot)sc(\cdot)$ with AIC$_c$ weight of 0.23, but this model had ΔAIC$_c$ = 2.24 and was 3.1 times less likely than the top-ranked model. In addition, correlation testing detected a very strong negative correlation ($r = -0.91$) between MUN and MIO. We therefore eliminated MIO from subsequent analyses. Although there was a weak negative correlation between habitats MUN and SAG ($r = -0.21$), the model $\psi(SAG)p(\cdot)sc(\cdot)$ was 761.3 times less likely than $\psi(MUN)p(\cdot)sc(\cdot)$. We therefore eliminated habitat SAG from multivariate combinations and MUN was the only habitat class considered in further analyses.

Due to the relative strength of the model $\psi(MUN)p(\cdot)sc(\cdot)$, it was unlikely that a multivariate combination excluding habitat MUN would generate a competitive AIC$_c$ score, and most of our high-ranking candidate model combinations therefore include this factor. We nevertheless excluded it from some models in order to test our original hypotheses. Our final set of candidate models tested in PRESENCE comprised the null model $\psi(\cdot)p(\cdot)sc(\cdot)$, 3 univariate and 25 multivariate models. We present the top ten results in Table 3 ranked by AIC$_c$, which selected $\psi(MUN+PW)p(\cdot)sc(\cdot)$ (PW = proximity to water) as the top model, ahead of $\psi(MUN)p(\cdot)sc(\cdot)$ and $\psi(MUN+PW-PH)p(\cdot)sc(\cdot)$ (PH = proximity to safari hunting camp),

although the latter had a ΔAIC$_c$ > 2 and is thus not a competing model. A further 18 models had ΔAIC$_c$ < 7 and thus received some support, but were at least 3.5 times less likely than the best model. The highest ranked model excluding MUN, $\psi(FI+PW)p(\cdot)sc(\cdot)$ was ranked 10th with ΔAIC$_c$ = 3.14. However, FI was correlated with MUN ($r = 0.73$), below our cut-off of 0.80 and we suspect this is the reason for the positive relationship between PLU and area burnt, as other studies have found that lions do not preferentially use burnt areas (e.g. Eby et al., 2013). AIC$_c$ scores of high ranking models did not improve with the addition of number of replicates (NR) as a covariate.

Due to the low ER between them (1.3) and ΔAIC$_c$ of 0.57 for the second model, we considered the top two models as having equivalent support. However, in the top ranked model, the influence of PW was not significant ($\beta = -10.3$, 95% CI: -21.6 to 1.0; Zeller et al., 2011). Due to the lack of competing models, and the equivocal utility of the method (Richards et al., 2011), we did not conduct model-averaging and instead followed the principle of parsimony sensu Wibisono et al. (2011). We thus selected $\psi(MUN)p(\cdot)sc(\cdot)$ as our final occupancy model, indicating a significant positive relationship between habitat class MUN ($\beta = 2.3$, 95% CI: 1.1–3.5) and probability of lion use (PLU). Site-specific PLU's for the survey area based on the final model ranged from 0.760 to 0.952. Of the 73 grid cells, PLU was below 0.800 for 19 cells (26.0%), 29 cells (39.7%) were between 0.800 and 0.899 and 25 (34.3%) were greater than 0.900. We applied these values to our survey grid in ArcGIS to produce a map of spatially explicit PLU for northern Kafue (Fig. 3).

4. Discussion

Our study is the first to survey lions using track-based occupancy techniques, and allowed effective analysis of data sampled from a very large area with limited access and resources. Ignoring the issue of false absences, our survey would have predicted that lions used approximately 8541 km^2 of our study grid (i.e. the naïve estimate). This estimate grew to 10,527 km^2 (95% CI: 7723–13,330 km^2) – an increase of 23.3% – when we accounted for imperfect detection

Table 3
Multivariate model results.

Model	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight	Evidence ratio	Number of parameters
$\psi(MUN+PW)p(\cdot)sc(\cdot)$	672.28	0.00	0.1967	1.0	7
$\psi(MUN)p(\cdot)sc(\cdot)$	672.85	0.57	0.1482	1.3	6
$\psi(MUN+PW-PH)p(\cdot)sc(\cdot)$	674.66	2.38	0.0600	3.3	8
$\psi(MUN+PW+FI)p(\cdot)sc(\cdot)$	674.79	2.51	0.0562	3.5	8
$\psi(MUN+PW+PB)p(\cdot)sc(\cdot)$	674.82	2.54	0.0553	3.6	8
$\psi(MUN+PH)p(\cdot)sc(\cdot)$	675.03	2.75	0.0497	4.0	7
$\psi(MUN+PW+LE)p(\cdot)sc(\cdot)$	675.22	2.94	0.0453	4.3	8
$\psi(MUN+FI)p(\cdot)sc(\cdot)$	675.36	3.08	0.0422	4.7	7
$\psi(MUN+PW+PT)p(\cdot)sc(\cdot)$	675.38	3.10	0.0418	4.7	8
$\psi(FI+PW)p(\cdot)sc(\cdot)$	675.42	3.14	0.0409	4.8	7

Top ten multivariate models in determining probability of use of cells by lions in Kafue using the model of Hines et al. (2010). Number of sites = 41. Covariates considered are munga and termitaria woodland (MUN), proximity to water (PW), proximity to safari hunting camp (PH), mean proportion of cell burnt 2009–2012 (FI), prey biomass (PB), law enforcement patrol effort (LE) and proximity to tourist camp (PT).
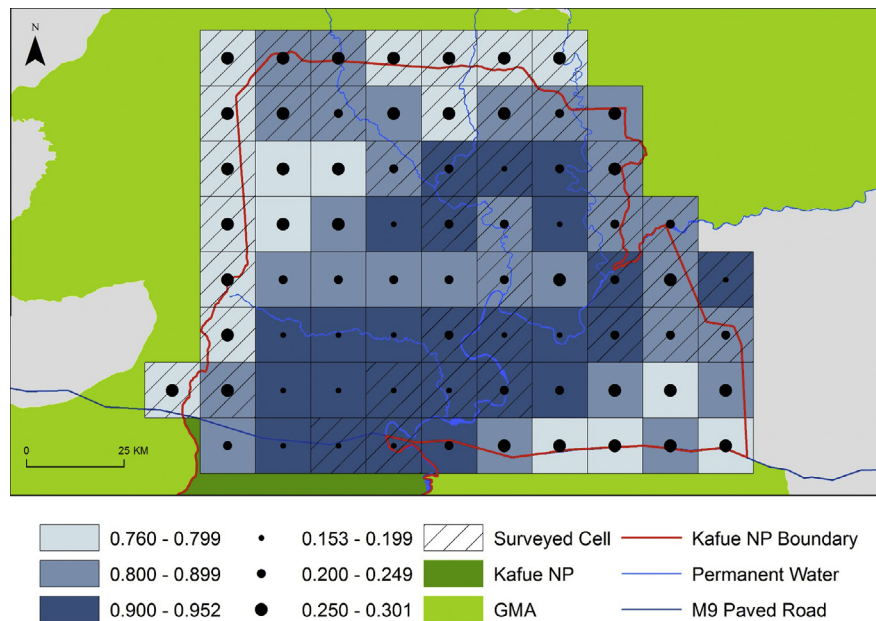
Fig. 3. Occupancy survey results. Probability of lion use (PLU) of individual grid cells, represented by color of cells, resulting from the final selected occupancy model $\psi(MUN)p(\cdot)sc(\cdot)$. Black dots represent cell-specific coefficient of variation of the estimate.

probability through the use of occupancy modeling, and clearly demonstrates the benefit of this approach.

By incorporating individual covariates in our models, we refined this estimate into a unique probability of lion use (PLU) for each grid cell, whether surveyed or not (Fig. 3). Our first prediction was that cells with the greatest prey biomass would have the highest PLU, but this model had little support and ranked 13th out of 14 candidates in the univariate set. We note some caution around this result, as our prey biomass layer was based on a single aerial survey conducted in the 2011 dry season. We initially trialled distance-sampling techniques on road transects (sensu Buckland et al., 2004) to calculate prey biomass, but low encounter rates made this method unfeasible. Although aerial surveys can underestimate the abundance of smaller ungulates (Ferreira and Van Aarde, 2009), these species are out of the preferred prey range of lions (Hayward and Kerly, 2005), and the effect is likely limited. We used a kernel density estimator (Online Appendix A, Table A2) to smooth the aerial survey data spatially, thus allowing for some intra- and inter-seasonal movements of ungulates. We thus believe that our prey biomass distribution layer is reasonable, but note the possibility that this factor may have ranked more highly in our model set if it had been measured concurrently with our occupancy survey.

Loveridge et al. (2007) demonstrated the effects of sport hunting outside Hwange NP in Zimbabwe on lion populations inside the PA, while in the Save Valley Conservancy, snaring, more prevalent near the boundaries, accounted for seven known lion mortalities (Lindsey et al., 2011). Accordingly, presence of three lion-hunting concessions adjacent to northern Kafue (where at least one of our collared animals, collared within the park, was shot by safari hunters), and observations of seven and six snared lions in our 2011 and 2012 field seasons respectively (Midlane, unpublished data), led to our prediction of anthropogenic edge effects (Woodroffe and Ginsberg, 1998) influencing lion distribution in Kafue. However, none of the models including covariates used as proxies for these edge effects (i.e. distance to nearest park boundary, human settlement or safari hunting camp) fit our detection history well and all were ranked lower than the null model. Our expectation that PLU would increase as a result of the deterrent effect on illegal hunters of increasing ZAWA patrol effort or

proximity to ZAWA scout posts and photographic tourist camps also received little support among our set of candidate models.

Our a priori predictions were thus poorly supported by the occupancy model framework. Instead, habitat class MUN (munga and termitaria woodland) emerged as the best supported of the univariate models and the second-ranking model in the final set. The top-ranking model in the set (Table 3) was the additive combination of MUN habitat and proximity to water. However, as in the findings of Schuette et al. (2013b) in Kenya, proximity to water was a non-significant factor. We thus selected the second-ranked MUN model as the basis for our spatially explicit prediction of PLU (Fig. 3). Habitat type emerged as an important occupancy driver for tigers (Harihar and Pandav, 2012; Karanth et al., 2011; Sunarto et al., 2012; Wibisono et al., 2011) and jaguars (Zeller et al., 2011), and our results suggest it is also the most significant factor driving lion spatial use in northern Kafue. We postulate that increased PLU in munga and termitaria woodland is due to the patchy, heterogeneous nature of this habitat being more suited to the stalk-and-pounce hunting technique of the species (Hopcraft et al., 2005) than heavily wooded miombo woodland (MIO) or the sparse cover of scrub and grassland (SAG).

Our final model produced PLU for individual grid cells ranging from 0.760 to 0.952, meaning that lions were 25.3% more likely to use the most suitable cell than the least. Although the underlying driver of PLU differed from our primary hypothesis, the resulting spatial distribution of cells in our three classes (PLU <0.800, from 0.800 to 0.899 and >0.900; Fig. 3) was a reasonable match to our a priori expectations of lion distribution in Kafue, engendering confidence in the model.

We were surprised that anthropogenic disturbance was not an important factor in predicting probability of lion use (Kiffner et al., 2009; Woodroffe and Ginsberg, 1998) or dispersion of prey biomass (Laurance, 2008), which was only weakly correlated with increasing distance from boundaries ($r = 0.13$) and human settlements ($r = 0.23$). This does not, however, preclude the possibility that these factors may influence lion abundance in Kafue. Snaring is often more extensive closer to human settlements (Muchaal and Ngandjui, 1999, Wato et al. 2006) and Van der Westhuizen, (2007) found a greater frequency of illegal activities in GMAs and near the boundary of the North Luangwa NP than deeper within the PA.

Illegal hunting of wildlife is highly prevalent in some Zambian wildlife areas. For example, in their study area straddling South Luangwa NP and adjacent GMAs, Becker et al. (2013) found that 11.5% of lions over one year old and 20% of adult males (>4 years) were snared. However, in Kenya's Maasai Mara National Reserve (MMNR), Ogutu et al. (2011) found that despite major decreases (driven primarily by illegal human activities) in wildlife populations over a 30-year period, declines at the edges of the reserve were no more dramatic than those in the interior. Similarly, Katavi NP in Tanzania faced significant pressure from illegal hunting, but proximity to the park edge or human villages had no significant effect on herbivore distribution, leading Kiffner et al. (2012) to hypothesise that the problem was simply too widespread to manifest as an edge effect. We believe that a similar situation exists in Kafue, where Lindsey et al. (2013b), using biomass estimation methods of Coe et al. (1976), found that Kafue's ungulate biomass was significantly below carrying capacity. Our results imply that the interiors of even the largest of Africa's PAs are not immune to this threat, and highlight the urgent need for more effective law enforcement in this park.

As the first application of the Hines et al. (2010) spatial correlation occupancy model in the context of an African felid, our study demonstrates the utility of the method in obtaining an understanding of the distribution of lions in a vast, previously unsurveyed African PA. Primary limiting factors for managers to consider prior to employing track surveys as a detection method are road networks with suitable substrate for tracking and staff with requisite tracking skills. We caution that the approach may not be as effective in multiple use landscapes outside of PAs, as carnivores in these areas are more wary of humans and less likely to use roads to move through their ranges (e.g. in fragmented landscapes in India, tiger occupancy was negatively associated with proximity to public roads; Linkie et al., 2006). In these landscapes, alternative means of detection such as audio lures (Ferreira and Funston, 2010) or camera traps (Schuette et al., 2013b) may be more appropriate.

We chose to analyse our data in a single-season single-species framework, but further options are available to practitioners, including multi-species (Burton et al., 2012; Schuette et al., 2013b) and multi-season models (Mackenzie et al., 2006). The former enable analysis of intraguild effects on occupancy, while the latter can provide a valuable proxy for population trends in areas where data on species abundance are not readily available. The explicit inclusion of relevant covariates in occupancy analysis can present management with further insight into the key threats faced by species in their reserves and thus assist in the effective deployment of scarce human and financial resources. Our study delivers this initial insight for northern Kafue, and provides a basis for further research, better understanding and more effective management of one of southern Africa's key lion populations.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.02.006.

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