To track or to call: comparing methods for estimating population abundance of African lions Panthera leo *in Kafue National Park*

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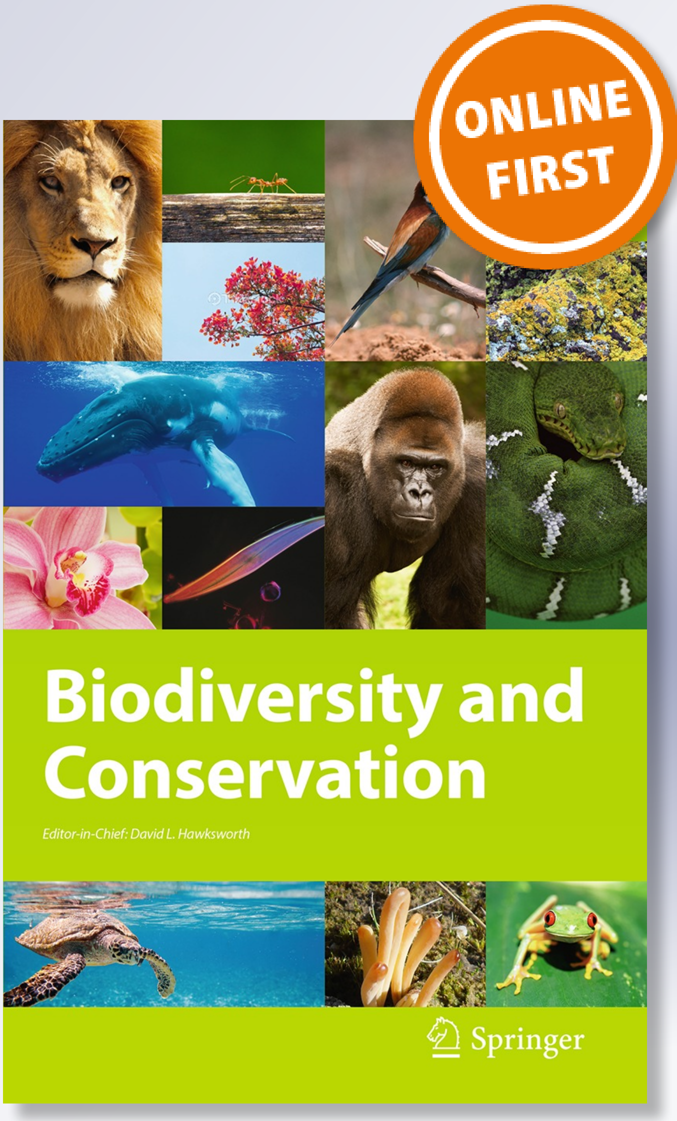

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ORIGINAL PAPER

To track or to call: comparing methods for estimating population abundance of African lions *Panthera leo* in Kafue National Park

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Abstract The wide-ranging behaviour of large carnivores and low densities at which they occur make direct population surveys of these species expensive and time consuming, and consequently indirect methods are widely used. We compared the accuracy, precision and cost of two methods commonly used to survey African lions, namely call-up surveys and track-count surveys. Surveys were performed in the 11,000 km^2 northern sector of Zambia's Kafue National Park (Kafue), an area for which no previous empirical lion population data are available. We estimate lion abundance of 200 individuals over 1 year of age in northern Kafue, at a density of 1.83 lions 100 km^{-2}. We used GPS collars and regular observations of lions to establish a reference population in an Intensive Study Site for comparison with survey results. Both survey methods produced accurate results, though precision was higher for call-up surveys, despite lower costs. Stratification of the study area did not improve the survey estimates. We recommend call-up surveys as the most appropriate method for surveying lions in Kafue and similar large protected areas, and suggest standardisation of survey equipment and protocols.

Keywords Lion · *Panthera leo* · Density · Survey methods · Abundance · Spoor · Call-up

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Introduction

Global biodiversity is declining at an accelerating rate (Ceballos et al. 2005; O'Brien et al. 2010) with 21–36 % of 5,282 extant terrestrial mammal species threatened with extinction (Schipper et al. 2008). Large carnivores, such as the African lion (*Panthera leo*), are among the most severely affected (Inskip and Zimmermann 2009; Karanth and Chellam 2009). Lions have lost more than 75 % of their historical distribution and have experienced a precipitous population decline over the last 30 years (Riggio et al. 2013), primarily as a result of anthropogenic impacts (Loveridge et al. 2010). Reliable, cost effective measures of local abundance and density of extant wild lion populations are required to monitor current and future threats, and evaluate the effectiveness of existing and planned management interventions (Funston et al. 2010; Pollock et al. 2012).

However, limited human and financial resources require a trade-off between the effectiveness (accuracy and precision of population estimates) and efficiency (minimising time and monetary cost) of methods used to obtain such data (Field et al. 2007; Sims et al. 2008; Reynolds et al. 2011). Direct counts have been used to estimate abundance in some long-term studies (e.g., lions, Schaller 1972; Packer et al. 2005; cheetah, Durant et al. 2007), but they are usually too expensive and time-consuming to be applied across large areas for low density carnivore populations (Stander 1998; Gese 2001).

Carnivore population trends can be tracked using relative abundance indices (RAIs) from indirect counts, which are cheaper, faster, repeatable and include a measurement of precision (Ogutu and Dublin 1998; Stander 1998; Mills et al. 2001; Funston et al. 2010). Various indirect methods have been applied to estimate demography and density of terrestrial carnivores, including camera trap surveys (Karanth and Nichols 1998; Karanth et al. 2003; Linkie et al. 2006; Jhala et al. 2010; Soisalo and Cavalcanti 2006; Balme et al. 2009; Chapman and Balme 2010), call-up surveys (Ogutu and Dublin 1998; Mills et al. 2001; Robbins and McCreery 2003), track (spoor) counts (Van Dyke et al. 1986; Smallwood and Fitzhugh 1995; Stander 1998; Gusset and Burgener 2005; Balme et al. 2009; Houser et al. 2009; Melville and Bothma 2006; Hayward et al. 2002; Barlow et al. 2009; Jhala et al. 2010) and mark-recapture analyses using DNA samples (Boulanger et al. 2008; Mondol et al. 2009).

For lions, total counts were conducted in the Serengeti by Schaller (1972) and Packer et al. (2005), and in the Maasai Mara by Ogutu and Dublin (2002). Capture, mark and recapture techniques were utilised in Kruger National Park (Kruger, Smuts 1978) and the Kalahari (Funston et al. 2001b; Castley et al. 2002). Tende et al. (2008) used DNA analysis from scat samples in Nigeria's Yankari National Park (NP), but were only able to generate a minimum count. Distance sampling was employed by Durant et al. (2011), though they caution that the method is only applicable to systems where the habitat is open enough to allow regular observation. Capture-recapture analysis was applied to lion observations in Kenya's Mara Game Reserve, but low encounter rates preclude the use of this technique in areas of lower lion density or when regular observations are not possible due to vegetation (Ogutu et al. 2006). To date the two most widely used methods for lion surveys are track counts (Stander 1998; Funston et al. 2001a; Lichtenfield 2005; Funston et al. 2010; Henschel et al. 2010; Burton et al. 2011; Croes et al. 2011) and call-up surveys (Ogutu and Dublin 1998; Maddox 2003; Whitman 2006; Kiffner et al. 2007; Ferreira and Funston 2010; Burton et al. 2011; Brink et al. 2012).

In this paper we explored both track count and call-up surveys as potential methods for estimating lion density and abundance in the northern sector of Zambia's Kafue National Park (Kafue). We also tested the importance of stratifying the study area to improve results. We used GPS collars and individual identification (Pennycuick and Rudnai 1970) to estimate home range sizes and density of known lions as a reference population in a core "Intensive Study Site" (ISS). We subsequently compared the results of the two survey methods in terms of accuracy, precision and cost. Kafue is a vast area with limited access and provides a good representation of the challenges faced in surveying and monitoring wild lion populations in Zambia and elsewhere.

Results from this study are intended to provide the Zambia Wildlife Authority (ZAWA) with guidance on the most appropriate method for surveying lions in the country. We also generate baseline lion population data for the northern sector of Kafue, an area that comprises a significant proportion of Zambia's remaining lion range.

Methods

Study area

Proclaimed a National Park (IUCN Category II) in 1950, Kafue is 22,319 km^2, situated in western Zambia between 14°00′–16°40′S and 25°15′–26°45′E (Fig. 1), and adjoined by

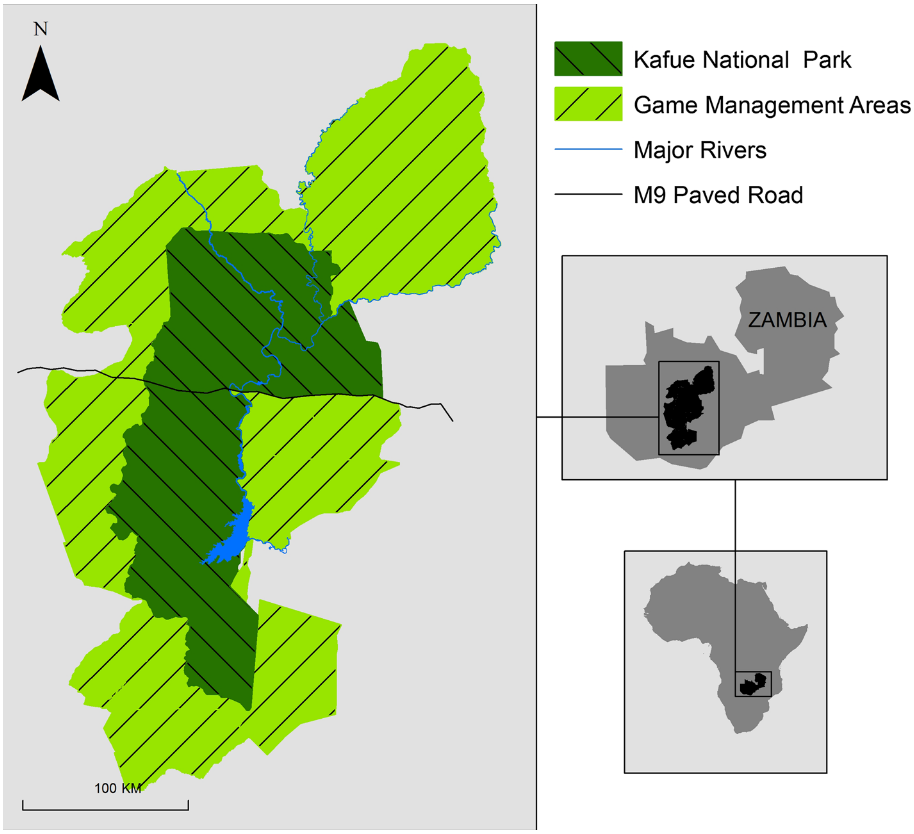

Fig. 1 Kafue National Park and surrounding GMAs

43,692 km^2 of game management areas (GMAs; IUCN Category VI). Three main rivers, the Kafue, Lunga and Lufupa run the length of the park, which is split into northern (10,958 km^2) and southern (11,361 km^2) sectors by the M9, a major regional paved road This road 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 1,020 mm, dropping to 510 mm in the south (Fanshawe 2010). Most rain falls between December and March, and the northern park is largely inaccessible by ground vehicle from December to early May. Using remotely sensed data (FAO 2013) and vegetation descriptions of Fanshawe (2010), we divided Kafue into three major habitat classes, (1) miombo and Kalahari woodland (MIO, 29.0 % of study area) dominated by *Brachystegia spp.* and *Julbernardia spp.*, (2) munga and termitaria woodland (MUN, 32.3 %) dominated by *Acacia spp., Combretum spp.* and *Terminalia spp.,* and (3) munga scrub and grassland (SAG, 38.5 %) comprising open scrubland up to 3 m high and dambo, floodplain and riverine grasslands (see Midlane et al. (2014) for more detail). Within this larger study area we delineated an ISS as a reference population area (Fig. 2).

Reference population

To locate, identify, count and calculate home ranges of lions, we fitted select individuals (one female per pride, one male per coalition) in our study area with VHF/GPS collars. We deployed collars in 2010, 2011 and 2012, set to record locations daily at 18h00, 24h00 and

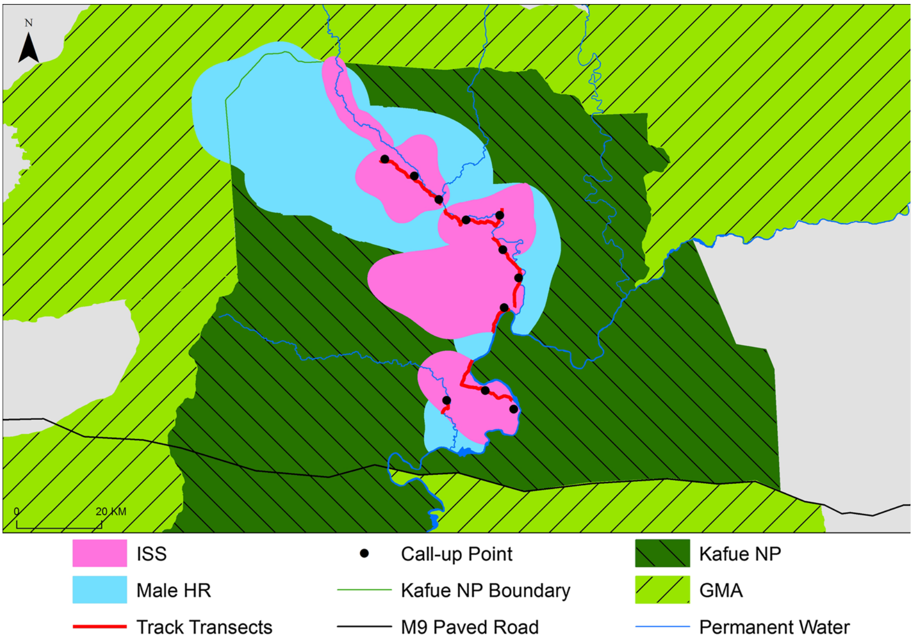

Fig. 2 Intensive Study Site. Location of the Intensive Study Site (ISS), derived from combined home ranges of four collared females, within the northern sector of Kafue National Park (NP). Male home ranges (HR) were derived from the combined home ranges of five male coalitions whose home ranges had some overlap of the ISS

06h00, as lions do most of their moving at night (Schaller 1972). We used photographs of vibrissae patterns and other unique markings (Pennycuick and Rudnai 1970) to identify all lions in the prides and coalitions associated with the collared animals, and regularly located and monitored these groups.

We used daily midnight GPS locations for each collared lion in the HOME RANGES extension of software ARCGIS v9.2 (ESRI, Redlands, California) to calculate dry season home ranges using 90 % fixed kernels (Loveridge et al. 2009). We combined the home ranges of four collared females (representing four prides) whose home ranges included survey points and transects, and used this as our ISS to calculate estimated density of known lions (Fig. 2). The combined home range of four collared male lions (four coalitions) in the system was significantly larger than the ISS, and some of these males spent only a portion of their time within this area (Fig. 2). We calculated the proportion of GPS locations for each collared male that fell within the ISS and multiplied it by the number of males in that coalition to obtain an adjusted male count for the ISS (Stander 1998). We added the sum of all adult females and subadults (>1 year) in prides associated with collared females to the adjusted male count for 2011 and 2012, and divided this by the area of the ISS to obtain a density estimate for our reference lion population. No lions from non-collared groups responded to call-ups in the ISS and, based on our knowledge of collared group size, composition and movements, we were confident that all the tracks detected in the ISS in the 2012 survey could be attributed to known lions. We are confident that the density of the reference lion population can be reasonably compared to the estimates derived from the two surveys in the ISS.

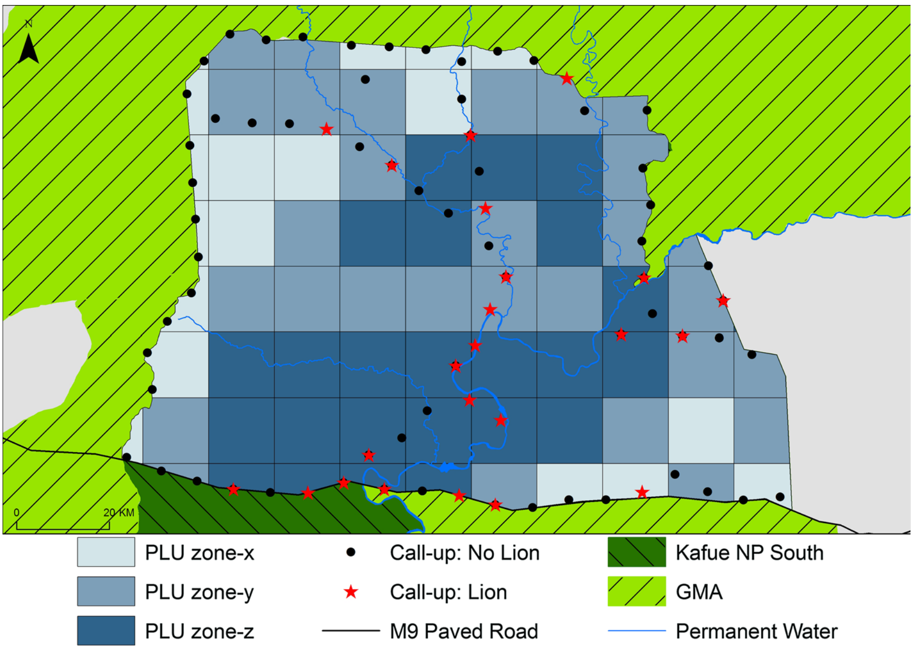

Fig. 3 Call-up survey design. Call-up in northern Kafue NP showing combined lion responses from 2010 to 2011 surveys. *PLU* probability of lion use from occupancy model (Midlane et al. 2014); *NP* national park; *GMA* game management area

Call-up surveys

We conducted call-up surveys from June to September in 2010 and 2011. We located all survey points on roads after a pilot study showed off-road surveys to be unfeasible due to logistical and safety constraints. Using software Google Earth (Google Inc., Mountain View, California), we selected a random point on a road, and thereafter spaced survey points 8 km apart (straight-line distance; Fig. 3) to avoid the double-counting that may arise from attracting the same animals to adjacent sample points (Mills et al. 2001). If vegetation caused limited visibility at a point, we relocated the point a maximum of 500 m in either direction. To avoid habituation of lions, no point was surveyed more than once in a 12-month period.

With the assistance of a ZAWA scout, we completed surveys at three to five points per night, when lions are most active (Schaller 1972; Stander 1992), beginning 45 min after sunset, and ending by 02h00. Limiting our surveys to winter nights eliminated potential effects of seasonal and diurnal changes in lion activity (Ferreira and Funston 2010), and cold nights ensured maximum sound travel (Garstang et al. 1995). We conducted play-backs from the roof of a vehicle, approximately 2.5 m above ground level. At each survey point we recorded luminosity (on a scale of 1–3) and wind speed (on a scale of 0–3). We spent 1 h at each point playing a buffalo *Syncerus caffer* calf distress call at maximum volume through two Foxpro Snow-Crow Pro SP-108SC horn speakers, using a Foxpro Snow-Crow Pro predator caller (Foxpro Inc., Lewistown, Pennsylvania). For consistency, we used the same buffalo call as that used by Ferreira and Funston (2010). We used a

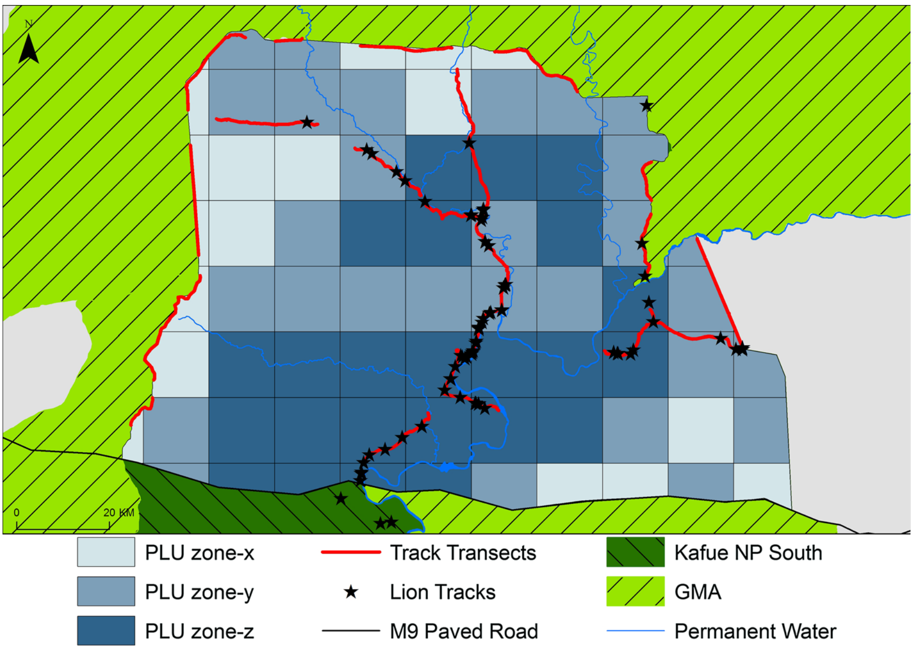

Fig. 4 Track-count survey design. Combined lion track detections from 2011 to 2012 surveys. *PLU* probability of lion use from occupancy model (Midlane et al. 2014); *NP* national park; *GMA* game management area

playback schedule of 20 min on, 10 min off, 10 min on, 10 min off and 10 min on. We faced speakers 180° from each other and rotated them by 90° for every 10 min of audio. We continued the playback in the presence of responding animals in order to avoid bias against other responders that had not yet arrived. We made regular sweeps of the surrounding area using a Lightforce Lance 140 mm Sporting Light (Lightforce Australia Pty. Ltd., Hindmarsh, Australia). Upon sighting an animal, we applied a red filter to the light, and used 10 × 42 binoculars (Swarovski Optik, Absam, Austria) to determine the species, number of animals and age and sex class where possible, and recorded these data for all large carnivores. We also recorded survey days, observer hours and distance driven to complete the 2011 survey for cost comparisons.

Spatial variation in species abundance can influence population estimates and appropriate stratification of the sampling area may be required (Stander 1998; Stephens et al. 2006). We divided our study site into three zones (Figs. 3 and 4) based on an occupancy analysis, which demonstrated that habitat type was the best predictor of Probability of Lion Use (PLU) in northern Kafue (Midlane et al. 2014). We designated these zone-x (PLU = 0.70–0.79), zone-y (0.80–0.89) and zone-z (0.90–1.00), assigned each call-up station to a zone, and calculated zone-specific lion density and abundance estimates for each survey. We summed these to obtain an abundance estimate for our entire study site and divided this by the total area of northern Kafue to estimate local lion density. We excluded lions <1 year old from all analyses due to the high mortality experienced by this age class in Kafue (Midlane 2014).

To estimate lion abundance from our survey data, we selected the calibration of Ferreira and Funston (2010) in Kruger National Park, South Africa (Kruger). We selected this calibration due to (1) the large sample size (170 lions in 37 groups), (2) the largely wooded vegetation of Kruger, which would likely share similar acoustic properties with the wooded vegetation of the majority of Kafue, (3) the survey being done in winter, (4) the use of a buffalo calf distress call audio track and (5) non-baited call-up stations. We calculated 2010 and 2011 estimates independently as some lions were observed in both surveys.

Track count surveys

Two observers, NM and a ZAWA scout, conducted track count surveys during the 2012 dry season. We placed transect start points randomly on the unpaved road network (Fig. 4), and repeated each transect between two and seven times (variation as a result of logistical constraints in reaching remote areas of the study area). We started all surveys within 30 min either side of sunrise when tracks are most visible (Liebenberg 1990) and drove at approximately 10 km h^{-1} to maximise likelihood of track detection. We scanned the road for lion sign, one person sitting on the front left corner of the vehicle and the other in the driver's seat (right hand side). When tracks were detected, we used a ruler and track ID sheets to ensure correct species identification. We identified lion tracks based on their size and shape, and recorded the number of individuals, age and sex classes (where possible), substrate type, substrate quality, vehicle impact, latitude, longitude, distance from the start of the transect, and distance walked on the road (where possible) by the animal(s) for each set of tracks. If we were unable to identify the species with certainty, we ignored the track set. To prevent double counting, we only counted fresh tracks (<24 h old) and avoided surveying the same transect on consecutive days. We discounted multiple tracks of the same species located within 500 m unless it was obvious they were not from the same individual. We recorded substrate quality (ease of detecting tracks; scale of 1–5) and vehicle impact on substrate (impact of other vehicles on likelihood of detecting tracks;

scale of 0–2) for 1 km intervals. In addition, we recorded survey days, observer hours and distance driven to complete the survey.

Where transects covered multiple PLU zones, we split them into appropriate segments where they crossed zone-boundaries and used track count data to calculate track density (number of track sets detected 100 km^{-1} driven) for each segment/transect (Balme et al. 2009; Funston et al. 2010; Stander 1998). We calculated mean track densities (with 95 % CIs) for all segments/transects in each PLU zone. Due to the sandy substrate of Kafue's roads, we used Funston et al.'s (2010) regression for "all carnivores on sandy soil" ($t_i = 3.15\ \chi_i + 0.40$; where t_i is track density and χ_i is lions 100 km^{-2}) to convert track density to lion density.

Comparison of survey methods

We compared measurements for track counts with call-up surveys for effectiveness (accuracy and precision) and efficiency (project cost). To compare accuracy, we calculated the percentage by which the estimate from each survey differed from our reference density of known lions in the ISS. For precision we calculated percentage confidence limits (PCLs) using the formula

$$PCL_j = \frac{UCL_j - \bar{x}_j}{\bar{x}_j}$$

(where UCL is the upper 95 % confidence limit and $\bar{x}$ is the mean for survey j) for the 2011 call-up and the 2012 track count surveys for the entire study area (Ferreira and Funston 2010). To compare cost of the two methods, we used data from fieldwork logbooks and calculated total survey days, observer hours and kilometres driven to complete each survey. We also calculated the cost of any equipment that was not common to both surveys (e.g., predator caller, spotlight).

Results

Reference population

The ISS, derived by combining the home ranges of four female groups, was 1,483 km^2 (Fig. 2). It contained 27.9 known lions in 2011 (23 females and sub-adults; 4.9 "adjusted" males) and 26.9 in 2012 (22 females and sub-adults; 4.9 "adjusted" males), resulting in density estimates of 1.88 and 1.82 lions 100 km^{-2} respectively.

Call-up surveys

We conducted 76 call-ups in 2010 and 73 in 2011, covering an estimated sample area of 4,390 km^2 (40 % coverage) and 4,217 km^2 (38 % coverage) respectively. Twenty-nine per cent of call-ups were in zone x (18 % of study area), 41 % in zone y (43 % of study area) and 30 % in zone z (39 % of study area). Sample effort was 6.9 stations·1,000 km^{-2} in 2010 and 6.7 stations·1,000 km^{-2} in 2011. We attracted 44 lions without cubs (15 groups) in 2010 and 31 (10 groups) in 2011, as well as four lions with one cub (one group) and 11 lions with seven cubs (three groups) in 2010 and 2011 respectively. Number of lion responses did not differ significantly with the time of night of the call-up ($\chi^2 = 2.77$, p = 0.60, df = 4), luminosity ($\chi^2 = 0.66$, p = 0.72, df = 2) or wind speed ($\chi^2 = 10.17$, p = 0.17, df = 3). Applying the calibration of Ferreira and Funston (2010) produced abundance estimates for northern Kafue of 228 lions (95 % CI 179–277) in 2010 and 264 (95 % CI 204–325) in 2011. Estimated population density was 2.08 lions 100 km^{-2} in 2010 (95 % CI 1.63–2.53) and 2.41 100 km^{-2} (95 % CI 1.86–2.96) in 2011 (Table 1).

Track counts

We completed 46 transects, covering a total of 967 km, of which 22 % was in zone-x (18 % of study area), 43 % in zone-y (43 % of study area) and 35 % in zone-z (39 % of study area). Mean transect length was 21.8 km, while mean segment length (i.e. transects split between PLU zones) was 11.2 km. Penetration index (Stander 1998) was 11.3 km^2 per km driven. We located 64 sets of lion tracks, none of which were in zone-x, while zone-y and zone-z produced 31 and 33 sets respectively. Neither vehicle impact on substrate ($\chi^2 = 1.18$, p = 0.55, df = 2) nor substrate quality ($\chi^2 = 4.45$, p = 0.35, df = 4) had a significant effect on observed versus expected numbers of lion tracks detected. Lions walked an average of 0.98 km on the road (n = 61), and in 8 instances crossed the road without walking along it. Using the Funston et al. (2010) regression, we estimated population density for 2012 at 2.21 lions 100 km^{-2} (95 % CI 0.86–3.17), which translated into an abundance estimate for northern Kafue of 243 lions (95 % CI 37–448; Table 1).

Comparison of survey methods

We conducted 11 call-ups within the ISS in 2011 (7.4 stations·1,000 km^{-2}), surveying an estimated 635 km^2 (43 % of the ISS) and attracted nine lions without cubs in two groups. Applying the calibration of Ferreira and Funston (2010), we estimated abundance for the

Table 1 Summary of results of call-up and track count surveys for the overall study area

	Call-ups		Track counts
	2010	2011	2012
Total transect distance (km)	–	–	967
Number of track sets	–	–	64
Number of call-up stations	76	73	–
Number of lion responses (>1 year old)	48	42	–
Study area stratified			
Density (lions 100 km^{-2})	2.08	2.41	2.21
Density 95 % CI	1.63–2.53	1.86–2.96	0.34–4.09
Abundance (no. of lions)	228	264	243
Abundance 95 % CI	179–277	204–325	37–448
Study area not stratified			
Density (lions 100 km^{-2})	1.85	2.06	1.83
Density 95 % CI	1.63–2.07	1.80–2.33	0.86–2.80
Abundance (no. of lions)	202	226	200
Abundance 95 % CI	178–227	197–256	94–307

ISS of 31.7 lions (95 % CI 20.5–42.9) and density as 2.14 lions 100 km^{-2} (95 % CI 1.38–2.89), 13.6 % greater than the reference lion density.

In 2012, we completed 20 track counts in the ISS, surveying a total of 319 km, a penetration index (measure of effort; Stander 1998) of 4.6 km^2 per km driven. We located 28 sets of lion tracks and mean track density was 6.76 tracks 100 km^{-1} (95 % CI 1.97–11.16). Using the Funston et al. (2010) regression, we estimated lion density in the ISS as 1.74 lions 100 km^{-2} (95 % CI 0.23–3.14) and abundance as 25.9 lions (95 % CI 3.3–46.6), underestimating the reference density estimate by 3.9 %.

The 2011 call-up survey of the entire study area produced a percentage confidence limit (PCL) of 22.8 %, compared to 84.5 % for the 2012 track count survey. We stratified the study site after we had conducted our track count survey, which necessitated the splitting of track transects into segments where they straddled multiple PLU zones. The coefficient of variation (CV) for segment length was 54.6 % compared to 13.3 % for transect length and hence splitting track transects negatively influenced the PCL for track counts. Recalculating this metric using complete transects produced a PCL of 42.5 % for the same period.

The cost of equipment required for the call-up survey that was not required for the track count was USD1145 while the track count survey had no special equipment requirements. The 2011 call-up survey required only 41 % of the staff days needed for the 2012 track count survey, and 62 % of the distance travelled, and proportionate savings in survey cost (Table 2).

Discussion

Track counts in the ISS produced a more accurate result than call-ups, but the call-up estimate was more precise. Across the entire study area, the call-up percentage confidence

Table 2 Comparison of survey accuracy, precision and efficiency

	2011 Call-up survey	2012 Track count survey
Intensive Study Site (ISS)		
Reference population estimate (lions 100 km^{-2})	1.88	1.82
Survey density estimate (lions 100 km^{-2})	2.14	1.74
Overestimate	13.6 %	–
Underestimate	–	-3.9 %
Entire Study Area		
PCL	22.8 %	84.5 %
Unstratified PCL[a]	–	42.5 %
Survey days	19	46
Survey hours	133	173
Km driven	1,724	2,802

Comparison of accuracy, precision and efficiency of 2011 call-up survey and 2012 track count survey

PCL Percentage Confidence Limits

[a] PCL calculated under the assumption that transects were not split into segments to accommodate post hoc study site stratification

limit was 3.7 times more precise than the track count. A survey designed after stratification of the study site (to eliminate segmentation of transects) would have reduced this value to 1.9, but the call-up result is still more precise, despite this method requiring less than half the number of survey days, 23 % fewer survey hours and 38 % fewer kilometres driven. The per-survey cost of additional equipment required for the call-up survey decreases with each new survey, and thus the long term costs of call ups will reduce further relative to track counts.

Our call-up survey effort was approximately double the 20 % minimum area coverage recommended by Ogutu and Dublin (1998), but below Ferreira and Funston's (2010) recommendation of >8 stations·1,000 km^{-2}. The risk of double-counting limited the number of stations in our study site, but the accuracy of the result in the ISS suggests that our sampling effort was sufficient.

For track counts, Funston et al. (2010) suggest that 30 track incidences will usually ensure a CV for track frequency of <20 %. However, our CV after 64 incidences (assuming an unstratified study area for comparability) was 220 %. According to Zar (1999), CV is the standard deviation (*s*) divided by the mean, but (Stander 1998) defines CV as the Standard Error (SE) divided by the mean, a definition for which we found no reference in the statistical literature. In this case, as $SE = s/\sqrt{n}$, its use as the numerator in Stander's (1998) equation means that even with constant precision, CV will, by definition, decrease as *n* increases. This equation was used to calculate CV by Funston et al. (2001a), Balme et al. (2009) and Kent and Hill (2013), and, though not explicitly defined, the similarity of the graphical representation of CV decreasing with increasing sample size in Funston et al. (2010: p 61) suggests that Stander's (1998) definition was applied here too. Using our data, the Stander (1998) CV follows a similar trend to these papers, as well as to

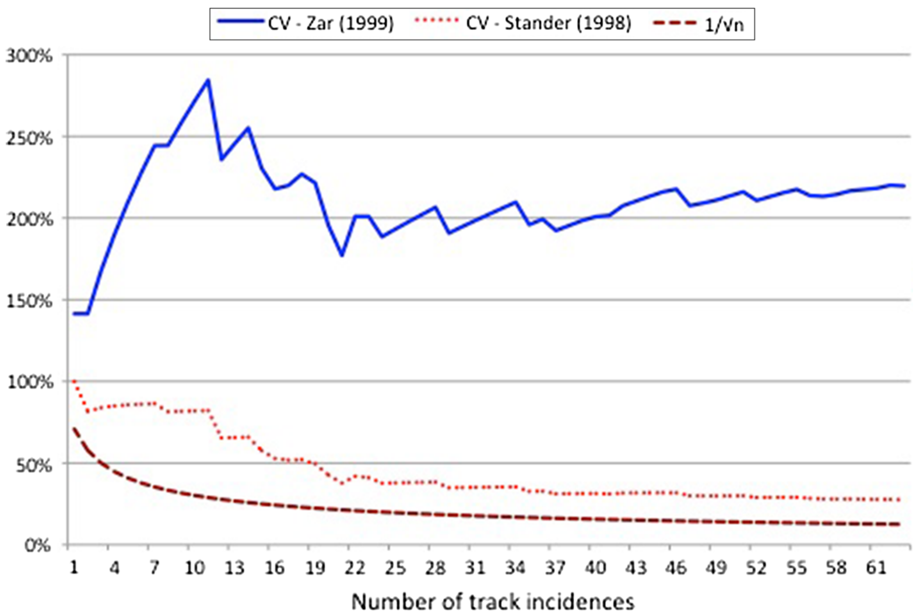

Fig. 5 Coefficient of variation. Comparison of change in coefficient of variation (CV) for track frequency of 2012 survey data, calculated per Zar (1999) and Stander (1998), with increasing sample size. Inclusion of $1/\sqrt{n}$ as an indicator of the effect of the standard error (SE) on the CV as used by Stander (1998)

$1/\sqrt{n}$, while the Zar (1999) CV does not necessarily decrease with increasing n, but does tend to stabilise (Fig. 5; K. Mauff, pers.comm.). This suggests that although track count surveys produce accurate results, there is more variability in the data than previously thought.

In addition to efficiency and effectiveness, both survey methods tested have practical limitations that require consideration. Moderate tracking skills and suitable substrate for track detection are minimum requirements (Stander 1998; Funston et al. 2001a). Balme et al. (2009) found that variable substrate and higher carnivore densities reduced accuracy of density estimates, but Funston et al. (2010) demonstrate a consistent relationship between track density and carnivore density across geographically dispersed sites with varying quality of substrate. Substrate quality did not affect the likelihood of detecting lion tracks in our study site, possibly due to our slow driving speed (10 km h^{-1} cf. 20 km h^{-1} of Stander (1998)) and the fact that, on average, lions walked on the road for almost one kilometer, providing reasonable opportunity to detect tracks. However, track counts may be less useful in areas where carnivores are heavily persecuted by humans, as these animals are less likely to travel on roads (Linkie et al. 2006; Ngoprasert et al. 2007). Conversely, track counts allow for multiple carnivore species to be surveyed simultaneously, including spotted hyaena, and possibly leopard and cheetah (Funston et al. 2010, but see Balme et al. 2009). Call-ups are of limited utility for surveying these species due to changing response rates of spotted hyaena in areas of high lion response rates (Mills et al. 2001; Kiffner et al. 2007) and the wary nature of leopards which increases the risk of non-detection.

Call-up surveys rely on the assumptions that all responders are detected and no animals are double-counted (Mills et al. 2001). The general boldness of approach of lions makes non-detection of responding animals unlikely (Kiffner et al. 2007). Double-counting was also avoided by sufficient spatial separation of call-up stations, and we had no lions respond at more than one station in a survey. However, at least two groups did respond in both years, suggesting that our surveys were sufficiently temporally separated to avoid non-response associated with habituation (Ogutu and Dublin 1998; Ferreira and Funston 2010).

An important limitation of call-up surveys involves calculating the distance at which lions respond from the calling station, and the proportion that respond, in order to convert responses to lion density. Various studies have shown likelihood of response to be affected by (1) location of the call-up within the lion home range, (2) age and sex of lions, (3) presence or absence of cubs, (4) season, (5) duration of calling and (6) whether lions are feeding or not (Kiffner et al. 2007; Ogutu and Dublin 1998; Whitman 2006). Maximum response distance also varies from 1.5 km (Maddox 2003) to 6.1 km (Ferreira and Funston 2010), though the call-ups in the former were only conducted during the day when lions are less active (Schaller 1972). Conversely, response rates were not affected by time of night or moon phase in Katavi NP (Kiffner et al. 2007), and these factors were not significant in our study either. The use of a variety of audio tracks, including carnivore competitors and multiple ungulate distress calls (Whitman 2006; Ogutu and Dublin 1998; Burton et al. 2011) in different studies limits the comparability of results between areas, as lion responses are affected by the type of call used (Cozzi et al. 2013).

These multiple sources of variation in response to audio lures underlie recommendations to calibrate call-up surveys in each new site (Eberhardt and Simmons 1987; Mills et al. 2001; Ogutu and Dublin 1998). However, in PAs such as Kafue, low lion density and limited access mean that attempts at calibration would be costly and time-consuming, produce small sample sizes and risk negative habituation of lions. This led us to select the

Table 3 Sensitivity analysis

Sensitivity of stratified 2011 Kafue lion population estimates to adjustments of parameters in call-up calibration formula of Ferreira and Funston (2010)

	Increase in 2011 population estimate (%)
Decrease in response distance	
10 % (430 m)	23.6
20 % (860 m)	56.4
50 % (2,150 m)	300.4
Decrease in response probability	
10 %	11.4
20 %	25.0
50 %	100.4

calibration of Ferreira and Funston (2010), which produced reasonably accurate results in the ISS for 2011. We note, however, sensitivity of density estimates to variation in the estimated distance, as well as probability, of lion responses (Table 3). The proportion of lion groups with cubs in a population also affects the result, as the probability of a group without cubs responding is 2.4 times higher than for a group with cubs (Ferreira and Funston 2010). In our study, the greater number of lions with cubs responding in 2011 resulted in a higher abundance estimate than in 2010, despite lower total lion responses (0.58 lions per station in 2011 cf. 0.63 in 2010).

Our density estimates for the stratified study area over 3 years (2010–2012) ranged from 2.08 to 2.41 lions 100 km^{-2} (Table 1), >10 % higher than the ISS densities of 1.82–1.88 (Table 2), despite the fact that the ISS only comprised areas of PLU-y and PLU-z, where we expected higher densities. When we reanalysed our data without stratifying the study area, estimates decreased from 2.06 to 1.83 lions 100 km^{-2} (Table 1), which more closely approximate the ISS figures, suggesting that stratification in this case may have led to overestimating density.

Our overall estimate exceeded that of Becker et al. (2012), who used 107 known lions from 2003 to 2005 to estimate density of 1.8 lions 100 km^{-2} for a 4,720 km^2 (arbitrarily defined) section of northern Kafue, but our ISS estimate was similar. However, Becker et al. (2012) excluded lions <2 years old (21 % of their known population, whereas we included all lions >1 year old. Kafue's lion population is at the lower end of density ranges for southern and east African PAs (Bauer and Van Der Merwe 2004), falling between the arid Kgalagadi Transfrontier Park (0.77–1.63; Funston 2011) and Hwange NP (2.7 lions 100 km^{-2}; Loveridge et al. 2007).

In our study, accuracy of results from both methods were comparable, but call-up surveys were more precise and more efficient to complete. We therefore recommend call-up surveys as the preferred method for surveying lions in Kafue and similar PAs. Our results suggest that stratification does not improve the output, and we do not recommend this additional step for future surveys in Kafue.

From a management perspective, we recommend monitoring lion response rates over time as a proxy for population trend, eliminating the complications of stratification and calibration. For this purpose, we recommend standardising survey effort and survey points and repeating standardised surveys on a regular basis (as defined by management objectives). Frequency of repetition must be limited to avoid problems of negative habituation, and we suggest at least 1 year between consecutive surveys. We recommend periodic double-sampling using track counts (Eberhardt and Simmons 1987) to corroborate call-up indices. To ensure comparability between study areas, and reduce behavioural variation in call-up surveys we recommend the use of the buffalo calf distress call (Available online) and standardised equipment, survey design and calling protocol. Application of these survey methods will help provide managers with sufficient data to establish baseline population indices, monitor population trends, identify areas of concern, implement interventions where necessary and assess results of those interventions over time.

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