Global Ecology and Conservation 51 (2024) e02908

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Review article

# Towards effective and harmonized lion survey methodologies: A systematic review of practice across Africa

Samantha K. Nicholson [a,b,*], David R. Mills [a,b,c], Erin C. Adams [a], David G. Marneweck [d,e], Hans Bauer [f], Lizanne Roxburgh [a], Rob Slotow [g,h]

[a] *The Endangered Wildlife Trust, Johannesburg, South Africa*
[b] *School of Life Sciences, University of KwaZulu-Natal, Pvt Bag X01, Scottsville, Pietermaritzburg, South Africa*
[c] *Panthera – 8 West 40th St, New York, NY 10018, USA*
[d] *Conservation Alpha, Southern Africa*
[e] *Department of Conservation Management, Faculty of Science, Nelson Mandela University, George, South Africa*
[f] *University of Oxford, Biology, Wildlife Conservation Research Unit Tubney House, OX13 5QL, UK*
[g] *Oppenheimer Fellow in Functional Biodiversity, Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal , , Pietermaritzburg, Pvt Bag X01, Scottsville, Pietermaritzburg, South Africa*
[h] *Department of Genetics, Evolution, and Ecology, University College London, United Kingdom*

ARTICLE INFO

*Keywords:*
Carnivore
Conservation
Populations
Population estimates
*Panthera leo*

ABSTRACT

Understanding the population status of a species is vital for their conservation. Over the last two decades, multiple methods for surveying lion (*Panthera leo*) populations have been designed and tested. Each have strengths and weaknesses, with different applications, and varying levels of reliability, accuracy and precision. We conducted a PRISMA systematic review to identify and assess survey methods for estimating lion population abundance. We searched the Web of Science and Google Scholar for peer reviewed papers between January 1991 and December 2022. Sixty-five papers were included, with some using multiple methods or multiple study sites; when these were separated, 93 studies were identified. Seven broad population survey methods for lions were identified: call ups (34.8% of studies), spoor counts (32.5%), direct observations (15.7%), direct observations with capture recapture elements (12.4%), camera trap-based capture-recapture analysis (4.5%), genetic surveys (3%) and distance-based surveys (1.1%). Our literature review suggests that the most reliable methods for determining lion density or abundance are direct observations and camera trap-based capture recapture surveys. Genetic surveys combined with spatially-explicit capture recapture analysis also hold significant potential. Due to their lack of reliability and tendency to over-estimate populations, call ups and spoor counts are not recommended for determining population abundance. We further recommend that harmonized methods be developed that can produce comparable and reliable estimates, which can be used to inform conservation decisions across the species range.

* Corresponding author at: The Endangered Wildlife Trust, Johannesburg, South Africa.
*E-mail address:* samknicholson90@gmail.com (S.K. Nicholson).

https://doi.org/10.1016/j.gecco.2024.e02908
Received 29 September 2023; Received in revised form 18 March 2024; Accepted 18 March 2024
Available online 24 March 2024

## 1. Introduction

To effectively monitor and conserve wild species, an accurate understanding of their population sizes, demographics, and temporal dynamics are required (Braczkowski et al., 2020a; Maximillion et al., 2020; Stander, 1998; Young-Overton et al., 2014). In this context, accurate measures of population abundance and density can help with understanding how best to conserve a given population (Braczkowski et al., 2020a; Jędrzejewski et al., 2018). Tracking population density or abundance over time allows us to detect declines or improvements, and to deploy timely, effective, and targeted conservation interventions. Similarly, to be effective, conservation interventions, strategies, and national and international policy and action plans must be guided by reliable population estimates that are comparable among and within populations over time (Braczkowski et al., 2020a; Maximillion et al., 2020).

The lion (*Panthera leo*) population in Africa, like those of many other large carnivores, is declining rapidly across much of its range and is currently listed as Vulnerable (Bauer et al., 2015; Nicholson et al., 2023; Wolf and Ripple, 2017). These declines are mainly driven by prey loss, habitat loss, and direct persecution (Bauer et al., 2020). As human populations and global resource needs continue to grow, the pressure on lion populations will inevitably increase, with remote and fragmented populations across the continent being particularly at risk (Bauer et al., 2020; Wolf and Ripple, 2017). It is, therefore, essential to ensure effective monitoring of remaining populations to help identify those populations that require urgent conservation intervention. This requires rigorous monitoring and reliably determining abundance and density of lion populations, especially to allow for the interpretation of trends in lion populations (Young-Overton et al., 2014).

Globally, a range of methods have been used to survey large carnivores (Barea-Azcón et al., 2007; Wilson and Delahay, 2001). The most common are those that use field signs (e.g., scat, spoor, hair) to determine presence and estimate their relative or absolute abundance (Barea-Azcón et al., 2007). Initial studies indicated a close fit between sign frequency and population density for several carnivore species (Barea-Azcón et al., 2007; Stander, 1998), although concerns regarding the accuracy of these estimates have been long-standing (Barea-Azcón et al., 2007). Spoor counts, or track counts, are often done following roads or set transects and have been used in terrain where substrate allows the clear identification of tracks (Midlane et al., 2014; Stander, 1998). Snow counts involve using snow during winter seasons to cover existing tracks and then subsequently counting tracks in subsequent days to determine abundance (Kojola et al., 2014). This method has been used widely for surveying wolves, *Canis lupus*, in Finland (Kojola et al., 2014) and the interior of Alaska (Becker et al., 1998), wild boars, *Sus scrofa,* in the Czech Republic (Plhal et al., 2011) and Eurasian lynx, *Lynx lynx,* in Norway (Linnell et al., 2007). In Africa, spoor counts have been used extensively to survey African wild dogs, *Lycaon pictus,* (Stander, 1998), leopards, *Panthera pardus* (Balme et al., 2009) and lions (Stander, 1998). Another spoor-based method is total counts based on identification of individual pug marks (Sharma et al., 2005), which has been used with Amur tigers, *Panthera tigris altaica*, in Northeast China (Alibhai et al., 2023), leopards in Malaysia (Sanei et al., 2011) and mountain lions, *Puma concolor,* in California (Fitzhugh and Gorenzel, 1985). Other forms of indirect methods include genetic surveys, which often use scent detection dogs to increase sample size, have been used to count snow leopards, *Panthera uncia*, in Nepal (Karmacharya et al., 2011) and in Kyrgyzstan and China (Long et al., 2011; McCarthy et al., 2008; Thompson et al., 2012). Audio based counts have also been used extensively to survey carnivores (Wilson and Delahay, 2001). Howling response counts are used to estimate wolf pack size, composition and home range size, and are based on the replies to mimicked howling (Ausband et al., 2014; Fuller and Sampson, 1988; Harrington and Mech, 1982). Similarly, roar counts, which record the number of roars produced in a given period, have also been used to survey lions (Rodgers, 1973). Call up surveys, sometimes referred to as call-in or playback surveys, differ from audio counts because they use calls of conspecifics, prey in distress, or competitors to draw individuals to a specific site so they can be visually counted. They have also been used to estimate abundance of spotted hyena, *Crocuta crocuta,* (northern Botswana (Cozzi et al., 2013), Etosha National Park in Namibia (Trinkel, 2009) and in Ethiopia's National Parks (Yirga et al., 2021, 2014), and lions in the Masai Mara in Kenya (Ogutu and Dublin, 1998), Kafue National Park in Zambia (Midlane et al., 2015) and northern Botswana (Cozzi et al., 2013). Direct observation-based studies typically require some form of individual identification and have been used and adapted widely (Beukes et al., 2017; Bouley et al., 2018; Brink et al., 2012). Although they are challenging to implement over large spatial scales (Brink et al., 2012), they have been used to survey cheetahs, *Acinonyx jubatus*, and wild dogs in Kruger National Park in South Africa where citizen science was used to gather photographs of individuals to determine an overall population estimate (Marnewick et al., 2014). Total counts of known individuals have been used for African wild dogs (Nicholson et al., 2020) and lion (Beukes et al., 2017). For species that are individually recognizable from photographs, surveys using camera traps deployed in a pre-determined grid or along a transect can be implemented to obtain a population estimate by using a capture-recapture approach (Wilson and Delahay, 2001). This technique was pioneered with tigers using their unique pelage (Karanth, 1995; Karanth and Nichols, 2010), and has also been done for cheetahs (Brassine and Parker, 2015; Marnewick et al., 2008), spotted and brown hyenas, *Hyaena brunnea*, (Vissia et al., 2021), jaguars, *Panthera onca*, in the Brazilian Pantanal (Soisalo and Cavalcanti, 2006) and more recently, lions (Cusack et al., 2015; Kane et al., 2015) and leopards (Balme et al., 2019; Pin et al., 2022). Other methods tested to estimate abundance, but not widely used, include using predator to prey ratios, (tested on snow leopards in Kyrgystan and China (McCarthy et al., 2008)), thermal imagery (tested on mountain lions in Florida (Havens and Sharp, 1998; Wilson and Delahay, 2001)) and distance-based survey methods (Durant et al., 2011; Wilson and Delahay, 2001).

To survey lions, various methods are used to determine population abundance, including direct observations that use individual identification with capture-recapture (Beukes et al., 2017; Rosenblatt et al., 2014) or without capture-recapture (Bouley et al., 2018; Kissui and Packer, 2004), genetic based surveys (Tende et al., 2010), spoor counts (also called spoor transects or track counts (Bauer et al., 2014; Henschel et al., 2010; Stander, 1998), call up surveys (also referred to as call in surveys) (Mohammed et al., 2020; Ogutu and Dublin, 2002) and camera trap studies with capture-recapture analysis (Elliot and Gopalaswamy, 2017; Kane et al., 2015;

Strampelli et al., 2022b; Western et al., 2022). As species continue to decline, it is imperative that trends are reliably monitored to prioritize populations that require conservation action. However, there is still a lack of consensus regarding the suitability of each method and when it can be applied effectively (Belant et al., 2019; Dröge et al., 2020; Henschel et al., 2020). Despite the widespread use of many of these methods, there has historically been some disagreement among practitioners regarding the appropriate choice, implementation, and interpretation of these survey methods (Braczkowski et al., 2020a, 2020b; Dröge et al., 2020; Elliot et al., 2020). This lack of consensus can hamper the ability to compare abundance estimates across sites and over time, even when the same methods are used. Some of the most significant disparities that exist include the reliability of spoor surveys for determining population abundance (Belant et al., 2019; Dröge et al., 2020; Funston et al., 2010a; Midlane et al., 2014; Stander, 1998; Winterbach et al., 2016) and whether call up surveys can be used in areas where lions are hunted or persecuted (Kiffner et al., 2009; Mwampeta et al., 2021).

For a global conservation strategy to be developed and for Range States to adopt national strategies and prioritize conservation action, there needs to be an understanding of the number and density of lions within each population. It is also critically important to obtain robust confidence intervals for those figures to detect changes in population trends over time. However, there is no universally accepted standard or norm in terms of lion survey methodology. Consequently, there is an urgent range-wide need to review methods of population estimation for lions in Africa and to recommend scientifically supported, harmonized survey methods that can be widely adopted. While doing this, we need to look beyond current practice to identify areas for opportunity and potential knowledge gaps, while considering methods under development, updated analytical techniques, and improved data collection methods for existing methodologies. Through a systematic literature review, we described and assessed the current state of knowledge regarding lion survey methodology. We addressed four questions: (1) What survey methods are being used to survey lions and for what purpose? (2) What are the strengths and weaknesses of methods used to survey lions? (3) What are some of the potential knowledge gaps that exist relating to lion survey methodology? Lastly, (4) based on the literature we reviewed, what methods are recommended to estimate lion abundance? In addition to these research questions, we aimed to provide a comprehensive comparison of existing methods for estimating lion abundance in Africa.

## 2. Materials and methods

In July 2023, we systematically searched for peer-reviewed, accredited scientific journal papers focussing on lion surveys in two comprehensive databases of scientific publications: the Web of Science (WoS) and Google Scholar. We excluded grey literature items, as conclusions may not be scientifically sound or may be inaccurate because of a lack of a peer-review process. In addition, there is no

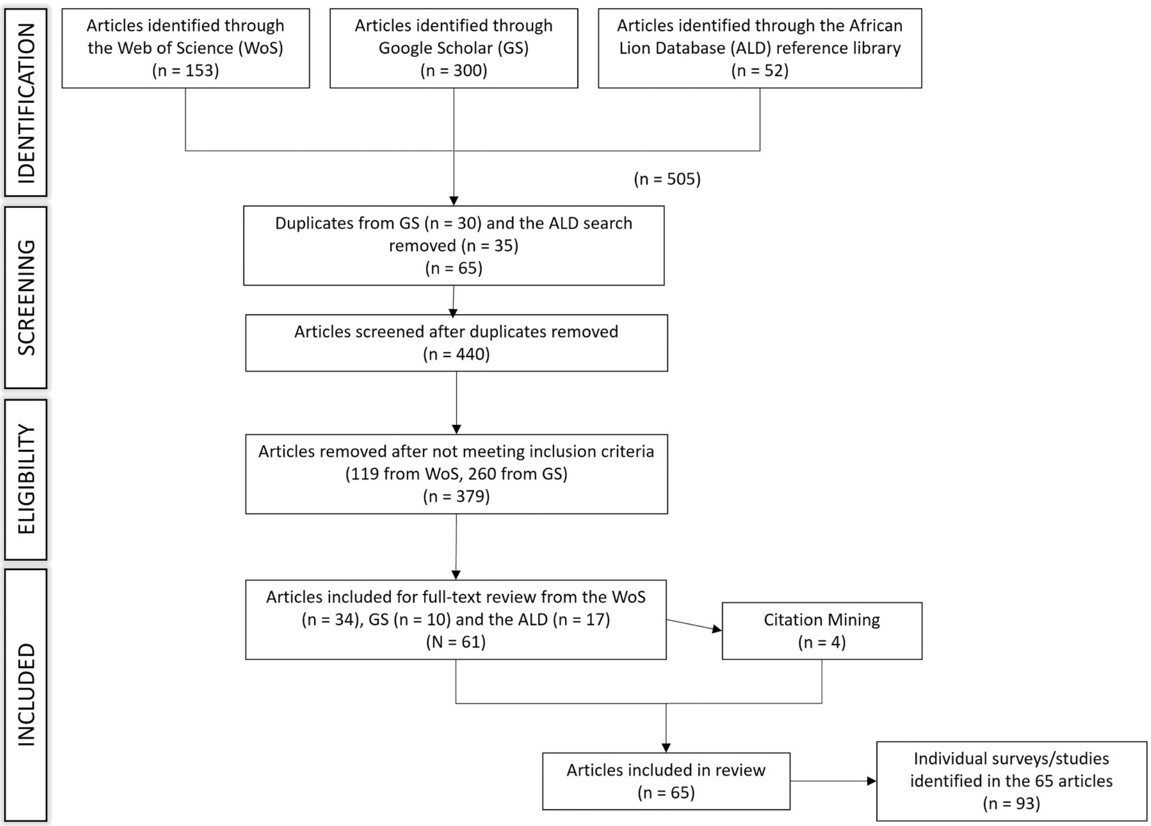


**Fig. 1.** Flow chart of the article selection process for the systematic review of lion population survey methods.

consistent means by which to assess the scientific rigor of these publications in grey literature, nor a systematic method for retrieving research items (Holland et al., 2018). We followed the PRISMA method for conducting systematic literature reviews (Page et al., 2021).

A preliminary search was conducted on the WoS to identify potential methods used to survey large carnivores (particularly lions) and the common wording for those methods. From there a full search was done of papers on the WoS and Google Scholar, for which we used the following search phrase:

ALL=("Panthera leo") AND (ALL=("camera trap") OR ALL=("call*") OR ALL=("track") OR ALL=("individual identification") OR ALL=("spoor"))

We limited our search to papers published in the last three decades (between 1991 and the end of 2022) to capture the latest findings and methodologies used to survey lions. These parameters were strategically selected after conducting a preliminary scan of the literature. Results obtained from the WoS were included in our review, as well as the first 300 results from Google Scholar. We focused on the first 300 results, as the criteria (see below) for inclusion were no longer met past this point. In addition, we considered papers housed in the African Lion Database (ALD) that met our inclusion criteria (African Lion Database, Unpublished Data. 2022). Based on approaches followed by similar review papers (Holland et al., 2018), we only included publications that were in English.

For inclusion in this review, the article must have met the following criteria:

- One of the study species was the lion
- The study was carried out on wild lions in Africa
- A measure of abundance or density of lions was stated. An exception was made in the cases where authors were testing and developing methods to survey lions. For example, one study tested and developed indices for spoor counts at 18 sites (Funston et al., 2010a). Also, the case with Winterbach et al., 2016.
- Only studies where the intention was to provide some abundance metric (e.g., population number, density, spoor density) were used

**Table 1**
Summary of the information extracted by reviewers of each paper (n = 65 papers), linked to the four research questions: (1) What survey methods are being used to survey lions and for what purpose?; (2) What are the strengths and weaknesses of methods used to survey lions?; (3) What are some of the potential knowledge gaps that exist relating to lion survey methodology? and, (4) Based on the literature we reviewed, what methods are recommended to estimate lion abundance? Other relevant data were extracted from each paper to enable descriptive comparisons between studies.

| Information Extracted | Description | Research question |
|---|---|---|
| **Publication year** | Year the article was published. | 1 |
| **Paper title and authors** | Full title and list of authors. | |
| **Study objectives** | Objectives of the stated as stated by the authors. | 1 |
| **Study category** | "**Implementing**" - Studies that were purely carrying out study methods to determine a population number.<br>**"Testing"-** studies that were determining the reliability or accuracy of a method.<br>**"Testing and developing"** – studies that were a testing method as well as making changes in the methodologies in an effort to develop them further. | 1 |
| **Method comparison** | Making a note on whether lion survey methods were compared. | |
| **Survey period** | Start and end date of the field work. | |
| **Study site details** | Country, survey area, name, survey size ($km^2$), habitat type, substrate (if spoor surveys were done). | |
| **Survey method** | Call up, spoor survey, camera trap, distance-based surveys, faecal DNA, direct observations. Direct observations were split into those that used some element of capture recapture and those that did not. | 1 |
| **Data collection method** | Camera trapping, satellite collars, systematic surveys, intensive searches, etc. | |
| **Data captured** | Photos, individual IDs, spoor occurrence, faeces, sightings data, number of responses (for call up surveys), satellite tracking data, detections. | |
| **Analysis framework implemented** | Summarizing the analysis approach taken. | |
| **If detection was accounted for** | How detection was accounted for. | |
| **Population estimate** | The reported population abundance estimated by the study and any confidence intervals or standard error provided. | |
| **Lion density** | The reported population density estimated by the study and any confidence intervals or standard error provided. | |
| **Population trends** | Reporting whether trends were assessed in the study or whether the authors of the studies indicated the method was suitable for detecting trends. | |
| **Strengths of the method** | Listing all strengths or advantages provided by the authors in the paper for the method. | 2, 4 |
| **Weaknesses of the method** | Listing all weaknesses or disadvantages provided by the authors in the paper for the method. | 2, 4 |
| **Limitations in the methods implemented** | Noting any limitations of the implemented survey methods for each survey as indicated by the authors. | |
| **Notes on accuracy/precision** | Any notes made on the accuracy or precision of the methods. | 4 |
| **Suggestions on methodological improvement** | Noting any statements made by the authors on potential ways to improve the method. | 3 |
| **Future research needed** | Noting any statements made by the authors on future research needed relevant to the methods. | 3 |
| **Survey costs** | Any costs related to implementing the method. | |

Our searches returned a total of 505 papers (153 from WoS, 300 from Google Scholar, 52 from the ALD; Fig. 1). We removed 30 duplicate papers from the Google Scholar results and 35 from the ALD library, resulting in 440 papers. We then systematically went through the title, abstract and methods of the remaining papers. In total, 379 (75%) of the papers were removed as they did not meet our criteria for inclusion or were of tangential topics, as a result 61 records were included in our review. Citation mining was then done on those 61 papers by manually reading the references and reviewing papers with titles indicating potential relevance to our review. An additional four papers that met our inclusion criteria were found. We reviewed the full manuscript to confirm an appropriate focus on survey methodologies to determine population or density estimations for lions in each study area. In total, 65 peer-reviewed publications dating from 1991 to December 2022 were included in this systematic review (Fig. 1).

To provide a summary of selected papers, we determined if there were multiple surveys carried out within each of the 65 papers (i. e., a multiple study). We defined a multiple study when separate surveys were completed in different areas (for example; we regarded one paper as three independent surveys as call up surveys were carried out in three different areas, namely, Queen Elizabeth National Park, Murchison Falls Conservation Area, and Kidepo Valley National Park in Uganda (Omoya et al., 2014)); or surveys that focused on one study area but carried out multiple methods (for example; one study in Zambia was regarded as two surveys as both call up and spoor surveys were carried out in Kafue National Park (Midlane et al., 2015). Each survey method–survey area combination was included as a unique entry. While reviewing the papers, considerable notes were taken regarding the strengths and weaknesses of each method that were detailed by the relevant paper authors, as well as potential opportunities to improve the method.

Each article was reviewed in full by two of the authors (SN, EA or DM) and the necessary information extracted to enable us to address our four research questions (Table 1). For example, to determine what survey methods were used to survey lions and for what purpose, we looked at the objectives of the article as well as the general method used. To provide a summary of what purpose the methods were used for, we indicated whether a study was purely implementing the method, testing it, developing it, or testing and improving it (Table 1). We also utilized other information within the paper (e.g., data captured and analysis framework) to determine the survey method. If responses of the two reviewers differed, a third reviewer assessed the work, engaged in discussions and a consensus was reached. Information was extracted to allow a descriptive review and comparison of lion survey methods, rather than specifically testing methods against one another. This information was used to address our research questions and provide a comparison of methods.

We used all information extracted from the papers to develop a comparison summary of lion survey methods. Studies which compared methods were used to rank methods according to their reliability, intensiveness and resource requirements. We detailed which research questions each method could address, whether they produced a reliable measure of abundance, the land use and habitat type they were best suited to, equipment required, ability to detect population trends and notes on their precision and bias. We ranked methods based on their invasiveness, ease and cost of implementation and the overall requirements. Finally, we also developed a generic flow diagram to help guide implementors in choosing the appropriate method based on their questions, area and funding.

## 3. Results

In total, 93 surveys from 65 peer-reviewed papers were included in this systematic literature review of lion survey studies. We classified each within one of seven broad methodological categories (Fig. 2): Call up surveys (34.8%, n = 31), spoor counts (32.6%, n =

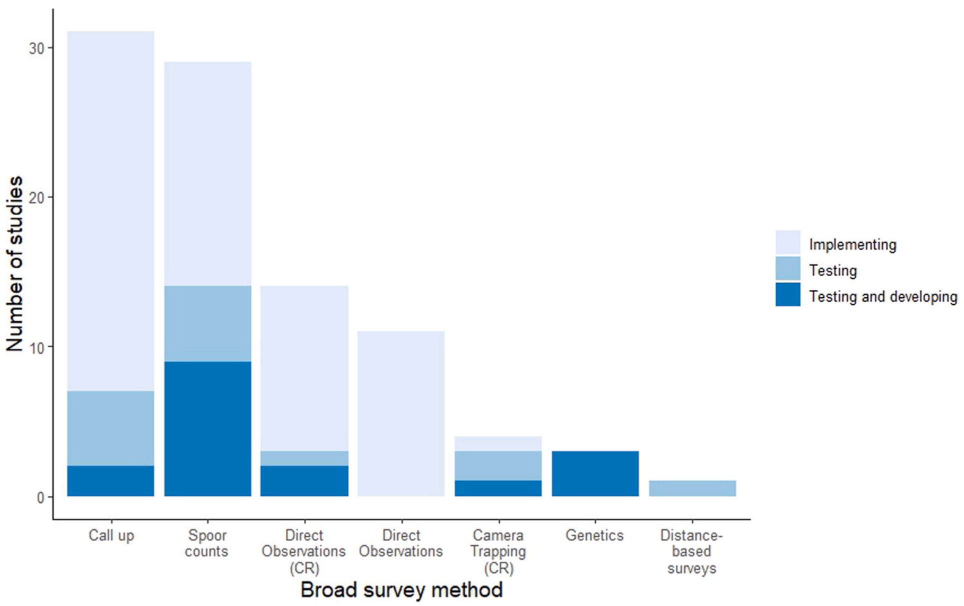


**Fig. 2.** The lion survey methods carried out in the 65 peer-reviewed publications, and the study category of each of those studies (n = 93).

29), direct observation surveys with capture-recapture modelling (15.7%, n = 14), direct observation surveys without a capture-recapture type framework (12.4%, n = 11), camera trapping combined with capture-recapture modelling (4.5%, n = 4), genetic surveys with capture-recapture modelling (3.4%, n = 3) and distance based surveys (1.1%, n = 1). Overall, two thirds of the studies used index-based methodologies (call up or spoor counts; 62.5%; n = 60).

Most studies were conducted in Tanzania (17.2% of studies; n = 17; Fig. 3) and Kenya (11%; n = 11). No published peer-reviewed studies were found from Angola, Chad, Democratic Republic of Congo, Gabon, Malawi, Rwanda, Somalia and South Sudan – all of which are lion range states. Most studies (67%; n = 62) were considered implementation studies (Table 1, Figs. 2,3). Seventeen studies (18.5%) tested and developed ways to improve existing methods for surveying lions. Fourteen studies (15%) tested survey methods. There were more papers published in the last decade than previously (72%, n = 47, Figs. 4, 5). The field work required for observation-based studies were carried out over longer time periods than index-based methods (Fig. 5). Publication of survey results often only occurred several years after the completion of the survey (Fig. 5).

Several knowledge gaps were identified while conducting this review (Table 3). Most related to call up surveys, particularly around detection, survey design, or calibration. Inadequate overall study design and a lack of robust model design and validation were the biggest data gaps regarding camera trap surveys. Fewer gaps were identified for spoor counts (Table 3). We identified three knowledge gaps (Table 3) that span the lion survey topic in general – particularly the need to develop a "unified framework to assess lion densities" (Dröge et al., 2020; Elliot and Gopalaswamy, 2017).

Based on the literature we searched, we summarize below the key advantages, disadvantages, knowledge gaps, reliability, and applicability of each of the methods to survey lions.

### 3.1. Call up surveys

The most published survey method is the call up survey (34.8%, n = 31), which gained increased research interest in 2014 (Figs. 4,5). This method of surveying lions (and hyenas) involves the structured and routine playback of a particular sound (e.g. prey distress calls) across a given area in an attempt to lure lions closer to the call up station (Midlane et al., 2015), generally at night when lions are most active. The number of lion responses is used to determine their density in area. Key strengths of call up surveys include their comparatively high detection frequency (Midlane et al., 2015), efficiency (Ogutu et al., 2005), ease of execution, relatively low cost (Henschel et al., 2014; Midlane et al., 2015), and low effort (Table 2) (Bauer, 2007; Brink et al., 2012; Henschel et al., 2014; Mwampeta et al., 2022; Ogutu et al., 2005; Young-Overton et al., 2014). In addition, call up surveys can be conducted in a range of landscapes independent of substrate and habitat (Cozzi et al., 2013). Midlane et al., (2015) estimated that additional cost of equipment required to add a call up component to an existing spoor survey was USD$ 1145.

Several factors may reduce the reliability of estimates generated by call ups. If spotlights are used, the bright light can cause

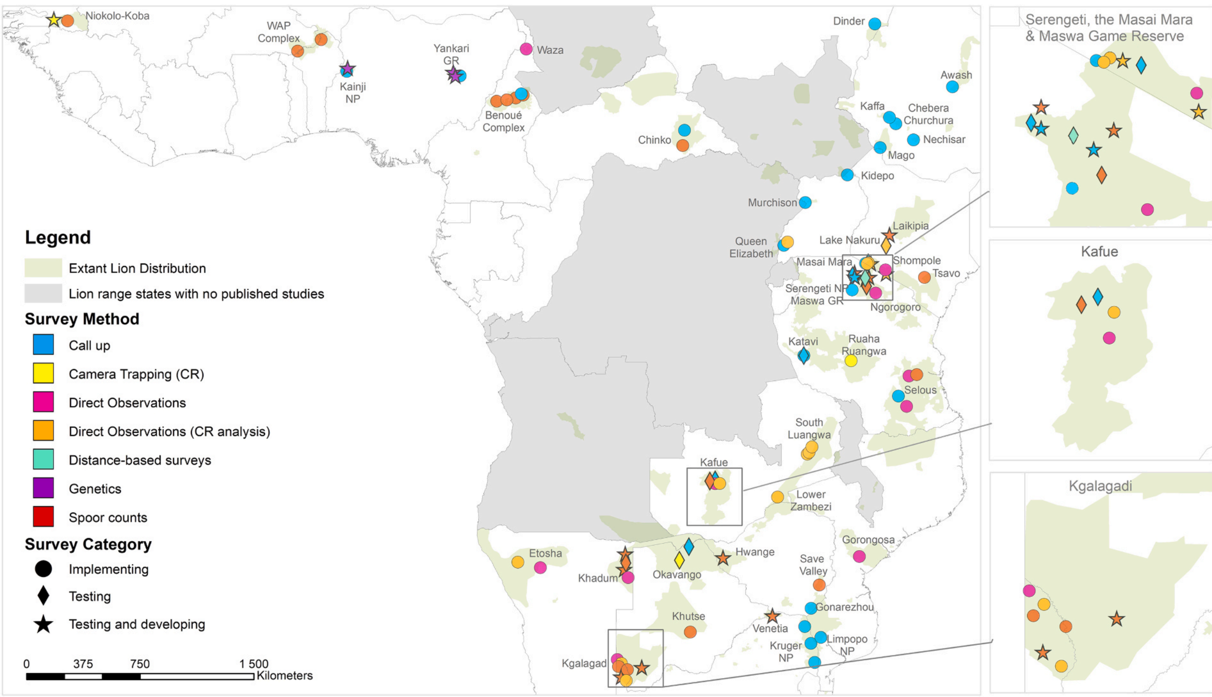


**Fig. 3.** Study sites where methods to survey lions have been carried out. This literature review identified seven broad methods to survey lions and categorized them into studies that implemented them to determine a population estimate, or those that tested the methods (generally to determine their reliability or accuracy) or those that both tested and developed them (Source for lion range: Nicholson et al., 2023).

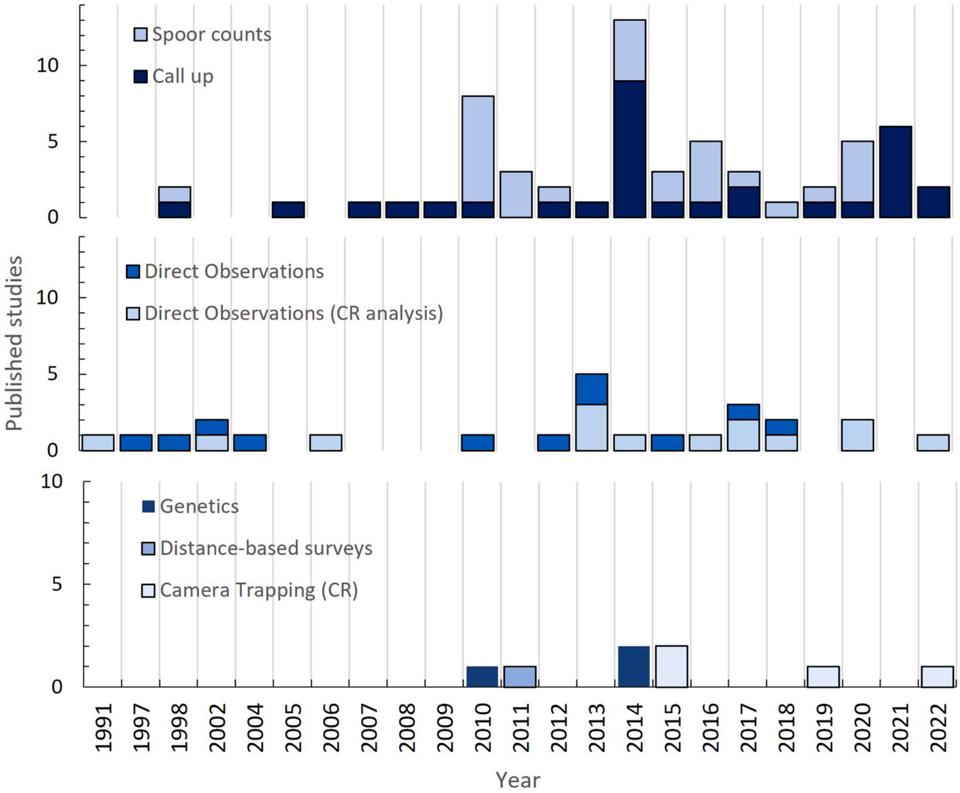


**Fig. 4.** Lion survey method studies (n = 93) published between 1991 and 2022.

disturbance (Mwampeta et al., 2022), discouraging individuals from emerging into the field of view. This risk can be partially mitigated by the use of red filters on spotlights, which have increased lion detection during surveys in the Serengeti National Park. In areas with moderate or high human activity, which may result in avoidance of humans, forward looking infrared (FLIR) thermal monocular spotlights may be more effective.

When call up surveys are carried out too frequently, lions may become habituated to the fact that, for example, there is no distressed prey animal present (Belant et al., 2017; Mwampeta et al., 2022; Ogutu et al., 2005), resulting in decreased response rates and, therefore, a lower estimate (Belant et al., 2017). Call ups may not be suitable for low-density populations, or in areas where persecution levels are high, as response rates may be too low to calculate robust estimates (Ogutu and Dublin, 1998). Although there is debate in the literature on whether they are best suited here or not. In addition, the bright light can cause disturbance (Mwampeta et al., 2022), and habituation may result in decreased response rates and, therefore, a lower estimate (Belant et al., 2017). Notwithstanding this, various types of spotlights can have different levels of efficacy depending on the species, the population, and the area management regime, and researchers are encouraged to select the options that are most suitable for their environment and species (Mwampeta et al., 2022). For example, spotlights with red filters are more effective in detecting and counting lions in Serengeti National Park (a non-hunted area) than forward looking infrared (FLIR) thermal monocular spotlights (Mwampeta et al., 2022).

Our literature review indicated knowledge gaps or potential research needs (Table 3) for call up surveys including: calibration in West Africa (Bauer, 2007; Henschel et al., 2014; Ogutu et al., 2005), factors influencing detection across sites (Belant et al., 2017; Kirsten et al., 2018), determining optimal length between call ups (Belant et al., 2017), and solutions to reducing habituation (Belant et al., 2017).

This method is most suitable when resources (e.g., man-power, financial and equipment) are limited (Belant et al., 2016; Brink et al., 2012; Midlane et al., 2015; Ogutu et al., 2005). Call up surveys are also preferred in Central Africa were there are lower carnivore densities and poorer infrastructure (Bauer, 2007), and are also preferred in mesic savannahs (Young-Overton et al., 2014). However, multiple studies demonstrate that this method is not accurate for determining population abundance (Belant et al., 2019; Dröge et al., 2020).

### 3.2. Spoor counts

Spoor counts, or track surveys, were used by almost a third of the published studies (32.6%, n = 29). These surveys involve using track frequency as an index of a species' density (Funston et al., 2010b; Winterbach et al., 2016) based on a linear correlation between the true density of a species and the density of their tracks in some habitats (Winterbach et al., 2016).

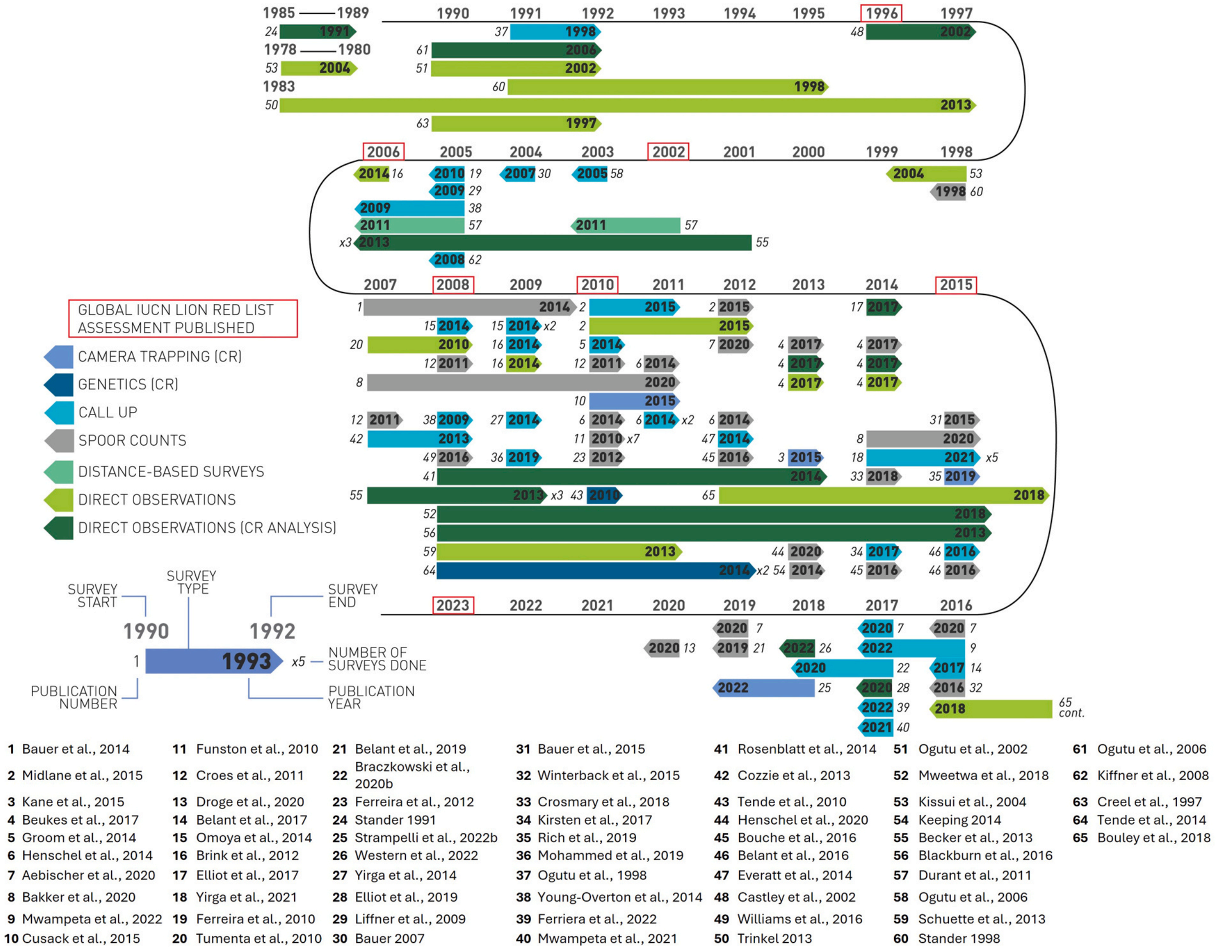


**Fig. 5.** Field study period of the lion survey method studies (n = 93) published between January 1991 and December 2022 in 65 papers in this systematic review.

Spoor count strengths include that it is cost effective (Bakker et al., 2020; Henschel et al., 2020; Midlane et al., 2015), easily repeated (Ferreira and Funston, 2010; Midlane et al., 2015), can cover large spatial extents (Winterbach et al., 2016), can be used to survey multiple carnivore species at once (Midlane et al., 2015), and can be used where individuals are shy or heavily persecuted (Brink et al., 2012). Density estimates resulting from populations that are less than 0.27 animals per 100 $km^2$ (<0.88 tracks/100 $km^2$) are not reliable (Winterbach et al., 2016). Spoor count weaknesses are that they are not reliable for estimating abundance (Belant et al., 2019; Dröge et al., 2020). Regarding their reliability and accuracy, recent studies have argued that this method of surveying lions is not reliable as it overstates precision with wide confidence intervals (Belant et al., 2019; Beukes et al., 2017; Dröge et al., 2020).

A key weakness of spoor counts is that it requires an experienced tracker and an extensive road network (Kirsten et al., 2018; Stander, 1998). This method is not suitable for all areas as it depends on the substrate (Beukes et al., 2017; Winterbach et al., 2016), and is not suitable in areas where there is high traffic where evidence of tracks is destroyed (Beukes et al., 2017).

Recent studies have argued that this method of surveying lions is not reliable as it overstates precision and has wide confidence intervals (Belant et al., 2019; Beukes et al., 2017; Dröge et al., 2020). Based on the literature, it is evident that this method is not reliable for estimating abundance (Belant et al., 2019; Dröge et al., 2020), and is only suitable for verifying the presence of lions within an area and to collect data to model lion distribution within an occupancy framework (Henschel et al., 2016; Midlane et al., 2014; Petracca et al., 2020).

### 3.3. Direct Observations (with and without capture recapture analysis)

Direct observation type surveys are also frequently used to survey lions (26.9%, n = 25). These surveys can either be implemented with capture recapture modelling (15.7%, n = 14) or without (12.4%, n = 11). These forms of surveys involve identifying individual lions through opportunistic sightings (Beukes et al., 2017; Braczkowski et al., 2020b) or intensive monitoring (Blackburn et al., 2016; Bouley et al., 2018; Ogutu and Dublin, 2002), and rely on either the natural individual marking of individuals (e.g., whisker spot patterns or scars (Elliot and Gopalaswamy, 2017; Strampelli et al., 2022b) or through the direct marking of individuals (e.g., branding;

**Table 2**
Reported weaknesses and strengths of survey methods taken from published studies found in this literature review (93 studies in 65 peer reviewed publications).

| Method | Disadvantage/weakness of the method | Advantage/strength of the method |
|---|---|---|
| Call up surveys | o Cannot provide reliable estimates of population density[1].<br>o Wide confidence intervals.<br>o If used, "bright light emitted can disturb, cause avoidance and reduce animal detection"[2].<br>o Habituation of target species after multiple sessions results in poor estimates of precision or prevents any responses[3, 4].<br>o Not useful in areas where lions are hunted/persecuted as individuals may be too cautious to approach stations with human-activity[5,6]. | o Comparatively high detection efficiency[7].<br>o Possible to simultaneously estimate lion and hyena density from a single survey[8,9].<br>o Conducted in a shorter time than some other methods (dependent on survey size)[10].<br>o Used across various landscapes independent of substrate and habitat and across large areas[1].<br>o Limited equipment, skills/training requirements[1,9].<br>o Easy to execute[7, 9].<br>o Low cost[7,11]. |
| Spoor counts | o Cannot provide reliable estimates of population density[12,13,14].<br>o Requires experienced trackers[15,16].<br>o Track detection is more challenging when there is a high frequency of road use as tracks are destroyed[13].<br>o Large confidence intervals in population estimates[16].<br>o Imprecision precludes detecting trends over time[16].<br>o Estimates either overstate precision or are too imprecise to be meaningful[12].<br>o Track detection varies across substrates[13].<br>o Require much greater sampling effort to compensate for the lack of precision[13].<br>o Not suitable for low density populations. The validity of density estimates below 0.27 carnivores/100 $km^2$ (<0.88 tracks/100 km) is questionable[17]. | o Multiple carnivore species can be surveyed simultaneously (e.g., spotted hyena, and possibly leopard, wild dogs, and cheetah)[18,19].<br>o Comparatively high detection efficiency, and low effort and cost[7].<br>o Relatively inexpensive method[7].<br>o Easy to implement, multi-scale and effective tool for carnivore population monitoring[7,19].<br>o Cover large spatial areas[19].<br>o Robust and repeatable technique for assessing large carnivore densities[7,16], distribution and population size. |
| Direct observation surveys (with and without capture recapture modelling) | o Registering individuals, particularly at low population densities, takes large amounts of resources and time[13,15].<br>o Conducting mark-recapture through individual identification may not be feasible in environments where low encounter rates or poor visibility restrict observations[13,15].<br>o Some difficulties in finding and monitoring low density, wide-ranging species[13,17]. | o Most robust method for defining population characteristics[13].<br>o It can be used under a citizen-science approach. This could make the costs of such surveys considerably lower than traditional methods[20].<br>o Suitable for small sample sizes[21].<br>o They provide an appropriate standardized framework to monitor species that occur in diverse habitats, at varying densities and with changeable behaviour[21].<br>o Provide repeatable and inexpensive measures of some population parameters[22].<br>o If SECR models are applied, has been shown to provide reliable estimates of population density[21,23].<br>o Produce statistically rigorous and precise estimates of population[23]. |
| Camera trapping surveys with CR analysis | o Initial financial layout is costly[24].<br>o Current drawback of the Random Encounter Models (REM) is its reliance on independent estimates of animal speed of movement and camera detection zone dimensions[25].<br>o Scaling the method to larger areas is likely to be costly and/or challenging[25].<br>o Deploying and checking cameras requires considerable time, as does the identification of individuals captured[24]. | o Shown to provide reliable estimates of population density[25,24].<br>o Determine occupancy or density of multiple small- to wide-ranging species concurrently[27,28].<br>o REM may offer a promising and more cost-effective alternative to estimating animal density[25].<br>o Provides accurate and precise estimates of abundance[24,25]. |
| Genetic surveys | o DNA can degrade resulting in low quantity and / or poor-quality DNA available for use[27].<br>o Amplification failures during PCR and false alleles can also affect population size estimates[27]. | o Non-invasive sampling technique[27,28].<br>o Works well for secretive species and / or in dense habitats[27,28].<br>o Allows for genetic studies of wild animals without trapping them or observing them[27,28].<br>o Provides data on the health status of a population, e.g., inbreeding, which cannot be obtained easily using observation in the field[27,28].<br>o Has potential for application of SECR models. |
| Distance-based surveys | o Wide confidence intervals[29].<br>o Only suitable in habitats similar to the Serengeti (flat and little vegetative cover).<br>o Some issues with detection confidence[29]. | o Relatively quick to implement[29].<br>o Cost effective[29].<br>o Applicable to most habitats with good visibility, such as short grass plains, grassland or desert[29].<br>o Can be used to effectively detect long-term trends[29]. |

[1]Cozzi et al. (2013); [2] Mwampeta et al. (2022); [3] Belant et al. (2017); [4] Ogutu et al. (1998); [5] Kiffner et al. (2009); [6] Creel & Creel (1997); [7] Henschel et al. (2014); [8] Bauer (2007); [9] Ogutu and Dublin (1998); [10] Belant et al. (2016); [11] Brink et al. (2012); [12] Dröge et al. (2020); [13] Beukes et al. (2017); [14] Belant et al. (2019); [15] Midlane et al. (2015); [16] Henschel et al. (2020); [17] Winterbach et al. (2016); [18] Midlane et al. (2015); [19] Bakker et al. (2020), [20] Braczkowski et al. (2020b); [21] Elliot et al. (2020); [22] Stander (1998); [23] Elliot and Gopalaswamy (2017); [24] Strampelli et al. (2022); [25] Cusack et al. (2015); [26] Rich et al. (2019); [27] Tende et al. (2010); [28] Tende et al. (2014); [29] Durant et al. (2011).

**Table 3**
Knowledge gaps identified in published studies found in this literature review for the recommended methods.

| Method | Knowledge gap and identified research needs | References |
|---|---|---|
| Camera trap surveys combined with capture-recapture modelling | Further develop Spatial Mark Resight (SMR) models (especially to "allow for the inclusion of finite-mixture covariates such as sex), for cases where identification rates are lower". | (Strampelli et al., 2022) |
| | "Test the suitability of other models of xenon-flash camera traps for the individual identification of lions, as this may not be equal across models" | (Strampelli et al., 2022) |
| | Further advance survey design advancements to improve precision of density estimates produced. | (Strampelli et al., 2022) |
| | "Explore the scalability of this method to larger areas". | (Strampelli et al., 2022) |
| | Explore how the dispersion of recaptures affects accuracy of estimates (this may provide additional insights into how to optimally space traps when movement patterns differ among species). | (Rich et al., 2019, Strampelli et al., 2022) |
| Observational studies | Continually develop SECR methods as they are a reliable method for surveying African carnivores. | (Elliot and Gopalaswamy, 2017) |
| Genetic surveys | Evaluate and test the potential of SECR modelling. | (Strampelli et al., 2022; Gopalaswamy et al., 2012) |
| All | Develop a "handbook of best practices in monitoring populations of apex carnivores". | (Droge et al., 2020) |
| | Develop "a "unified framework" to assess lion densities in key sites across their range to allow for accurate population assessments and trend analyses". | (Elliot and Gopalaswamy, 2017) |
| | Conduct a cost benefit analysis of each method. | This review |

(Stander, 1991)).

Direct observation surveys are generally the most robust and reliable method for defining population characteristics such as demographic composition (Beukes et al., 2017; Rosenblatt et al., 2014), can include citizen scientists (Braczkowski et al., 2020b), and can be used for small populations (Elliot et al., 2020). While this method is reliable for determining abundance (Beukes et al., 2017), it tends to be fairly expensive because of the cost of equipment involved and can be relatively resource intensive (Beukes et al., 2017; Braczkowski et al., 2020b). Survey methods that utilize satellite tracking or radiotelemetry are also adapted to determine population sizes (Becker et al., 2013; Mweetwa et al., 2018). There are, however, techniques to combine statistical modelling with direct observation to obtain density estimates with moderate effort and cost. For example, a recent lion survey in Uganda's Queen Elizabeth National Park cost ~USD$ 3690 for a 93-day long survey analysed using a spatial explicit capture re-capture analysis (SECR) based analytical framework (Braczkowski et al., 2020b).

This method has probably evolved the most relative to other lion survey methods, especially with regards to statistical analysis (Braczkowski et al., 2020a, 2020b; Elliot et al., 2020; Elliot and Gopalaswamy, 2017; Western et al., 2022). Combining direct observations with SECR is more reliable than analytical methods previously used and generate highly robust animal densities (Braczkowski et al., 2020a, 2020b). This type of analysis has only been applied to lions in the last decade (Braczkowski et al., 2020a; Kane et al., 2015). Intensive monitoring is often deployed by conservation management to identify individuals within the population to achieve a population estimate (Bouley et al., 2018). These types of surveys provide additional information on the population, including demographic break-down, life histories, survival rates, and, if tracking collars are used, spatial use and home-ranges (Bouley et al., 2018).

This method is best suited as part of long-term or intensive monitoring studies. It can be adapted to accommodate the resources available for the survey. In addition, these studies can be designed and implemented rapidly (Elliot et al., 2020; Elliot and Gopalaswamy, 2017) or over longer time periods (Beukes et al., 2017; Bouley et al., 2018; Western et al., 2022).

### 3.4. Camera trap-based capture-recapture surveys

Camera trap surveys combined with capture-recapture (CR) modelling is a new survey technique for lions, conducted in only four published studies (4.5%), with the first published studies in 2015 (Figs. 4, 5; (Cusack et al., 2015; Kane et al., 2015)). The first study of this type was conducted in Niokolo-Koba National Park in Senegal and combined with mark-resight analysis (Kane et al., 2015). Camera trap surveys were previously thought to be inefficient in estimating population density and abundance because individual lions can be difficult to distinguish in camera trap images (Beukes et al., 2017). However, recent studies have found that this is not the case, as a result of advances in camera trap technologies including the increased quality and resolution of images and the use of a white flash (Cusack et al., 2015; Strampelli et al., 2022b).

The strengths of using camera trap surveys for lion density estimation is that the method is reliable, repeatable, relatively simple to implement, and does not require large teams (Cusack et al., 2015; Kane et al., 2015; Strampelli et al., 2022b). The weakness of camera trapping is that it requires considerable time to deploy and check traps, capture large amounts of data in databases, and process photos (Strampelli et al., 2022b) and can be costly. Individual identification, though possible, is still difficult, and requires experienced personnel. Finally, there is a risk that cameras get stolen, resulting in lost data, potential gaps in the survey, and lower sample sizes.

Camera trap surveys have not yet been carried out over large survey areas (Cusack et al., 2015; Kane et al., 2015; Rich et al., 2019; Strampelli et al., 2022b). Further studies are required to determine the feasibility of implementing this method at larger scales than have currently been implemented at (Strampelli et al., 2022b). Larger survey areas will potentially require wider spacing of trapping

**Table 4**
Comparative summary of the preliminary lion survey methods according to the literature included in this systematic literature review. A descriptive narrative of how we compared methods, including their ranking, can be found in the supplementary materials.

| | Call Ups | Spoor Surveys | Direct Observations (with or without capture recapture analysis) | Camera trap-based capture recapture surveys | Genetic surveys with capture-recapture modelling | Distance-based Surveys |
|---|---|---|---|---|---|---|
| **Key methodological papers** | (Ferreira and Funston, 2010; Midlane et al., 2015; Mwampeta et al., 2022) | (Funston et al., 2010; Keeping, 2014; Midlane et al., 2015; Winterbach et al., 2016; Henschel et al., 2020) | (Pennycuick and Rudnai, 1970; Becker et al., 2013; Rosenblatt et al., 2014; Bouley et al., 2018) | (Cusack et al, 2015; Strampelli et al. 2022) | (Tende et al. 2014) | (Durant et al., 2011) |
| **Research questions** | Lion presence | Lion presence | Lion presence<br>Lion density<br>Population estimate<br>Population trend<br>Population structure | Lion presence<br>Lion density<br>Population estimate<br>Population trend | Lion presence<br>Genetic health<br>Population estimate<br>Genetic relatedness | Lion presence<br>Population trend |
| **Direct or indirect method** | Direct | Indirect | Direct | Indirect | Indirect | Direct |
| **Reliable measure of abundance** | × | × | ✓ | ✓ | ✓ | ✓ |
| **Reliability in estimating abundance** | 4 | 5 (least reliable) | 2 | 1 (most reliable) | *3* | *No information available* |
| **Detect trends** | × | × | ✓ | ✓ | ✓ | ✓ |
| **Precision and bias** | High precision | Precision is overstated | Precise when used with capture-recapture | *No information available* | *No information available* | *No information available* |
| **Confidence intervals** | Poor assessment of variation around count (dependent on calibration effort) | Wide confidence intervals. Poor assessment of variation around count | *No information available* | *No information available* | *No information available* | Wide confidence intervals |
| **Invasiveness** | 5 | 1 (least invasive) | 6 (most invasive) | 4 | 1 (least invasive) | 3 |
| **Land use type** | All land use types but less suitable in areas where lions are shy (e.g. hunting or remote areas) | All - especially suitable in areas where lions are particularly shy | Across all land use types | Across all land use types (camera theft needs to be considered in some areas) | Across all land use types | Across all land use types |
| **Habitat type** | Appropriate across all habitats | Ideally soft-substrate | Appropriate across all habitats | Appropriate across all habitats | Appropriate across all habitats | Habitats that allow good visibility |
| **Ease of implementation** | 1 (easiest) | 2 | 4 | 6 (hardest) | 5 | 3 |
| **Cost of implementation** | 2 Cost of equipment required for the call-up survey was USD$ 1145. The per-survey cost of additional equipment required for the call-up survey decreases with each new survey (Midlane et al. 2015) | 1 (cheapest) | 6<br>(most expensive if satellite collars are required and extensive fieldwork)<br>USD$ 3690 on their 93-day SECR lion survey in Queen Elizabeth National Park (USD$ 900 for vehicle and petrol costs, and USD$ 2790 on food and lodging).<br>Braczkowski et al. (2020b) | 5<br>Surveying an area of 5000 km$^2$, with cameras placed at regular 5-km intervals (wider than in our study, but likely still suitable for lion), would require ~200 stations (400 cameras, if paired). At ~150 USD per camera (https://www.cuddeback.com/shop), this would amount to ~ USD$ 60,000 of camera trap costs, in addition to significant accessory costs (for import fees, batteries, memory cards, and protective cases).<br>Stampelli et al. 2022 | 4 | 3 |
| **Time requirement** | 2 | 1 (shortest study period) | 6 | 6 (longest study period) | 4 | 3 |

(*continued on next page*)

**Table 4** (*continued*)

| | Call Ups | Spoor Surveys | Direct Observations (with or without capture recapture analysis) | Camera trap-based capture recapture surveys | Genetic surveys with capture-recapture modelling | Distance-based Surveys |
|---|---|---|---|---|---|---|
| **Equipment** | Vehicle, speakers, spotlight | Vehicle | Vehicle, photobook, Satellite/VHF collars (optional) | Vehicle, cameras, batteries, camera mounts, SD cards | Genetic sample kits, genetic laboratory, potentially sniffer dogs (not always required) to locate faecal matter | Vehicle, distance range finder |
| **Minimum number of people required** | 2 | 2 (tracker and driver) | 1 | 1 | 2 | 2 |
| **Key skills or expertise required** | None | Experienced tracker | Potentially statistical analysis if incorporating capture recapture analysis | Experience in camera trap surveys and analysis | Genetic analysis or link to a genetic lab | Distance surveys and analysis |
| **Key comparisons with other studies done** | "Call ups are more precise than spoor counts, despite this method requiring less than half the number of survey days, 23% fewer survey hours and 38% fewer kilometres driven" (Midlane et al. 2015) | | "Intensive monitoring produced estimates with 3X to 7X greater precision than rapid indices of abundance". (Rosenblatt et al. 2014) | "Estimates achieved through Random Encounter Modelling with camera traps were more precise (i.e., narrower confidence intervals) than those obtained for Serengeti lions using distance sampling, which also required a higher level of sampling effort." (Cusack et al. 2015) | *No comparisons to other studies done* | "Distance-based transects provided estimates of density of carnivores with greater accuracy (density was underestimated by up to 65% in fixed-width transects) and precision (lower CVs were achieved in distance-based transects) than fixed-width transect" (Durant et al. 2010) |

stations, designing models aimed at accurately identifying single-sided individuals and potentially rotating grids to allow greater area coverage (Strampelli et al., 2022b), while still considering the statistical assumptions for SECR analysis. In addition to assessing the scalability of this method, aspects around model validation and survey design should also be assessed (Table 3; Rich et al., 2019; Strampelli et al., 2022b).

Strampelli et al. (2022b) estimated that surveying an area of 5000 km$^2$ with cameras would cost ~ USD$ 60,000 (including camera trap costs and accessory costs). This cost is estimated based on camera trap stations placed at 5 km intervals, requiring ~200 stations (400 cameras, if paired) at ~USD$ 150 per camera (https://www.cuddeback.com/shop) (Strampelli et al., 2022b).

Artificial Intelligence software is now widely used to identify species within images, saving thousands of work hours (Green et al., 2020; Mandisodza-Chikerema et al., 2022), although the capability to identify to an individual level has yet to be developed. While the initial financial investment in camera trap surveys is high (e.g., purchasing cameras, camera mounts, batteries, SD cards), they can be used over multiple years to conduct repeat surveys or survey new areas, which reduces their overall cost per survey. In addition, they can be utilized to survey other species simultaneously, which, overall, increases their cost effectiveness.

This method is suited across all landscapes and where sufficient resources are available (particularly to cover the costs of equipment). As this method is indirect, it can be used effectively where lions are elusive.

### 3.5. Genetics with capture-recapture modelling

Genetic studies were carried out in three studies (3.4%), although by the same author and restricted to two populations in Nigeria (Yankari Game Reserve and Kainji Lake National Park) (Tende et al., 2014, 2010). This method involved analysing the Mitochondrial DNA of individuals using PCR methods gathered from lion faecal matter to determine a minimum population size (Tende et al., 2014, 2010). The strengths of this method include that it is non-invasive and works well for secretive species, potentially those that are in highly persecuted environments (Tende et al., 2010)(Table 2). An added benefit of this survey technique is that it offers insight into the health status of a population (e.g., inbreeding), which cannot be determined through conventional survey methods (Tende et al., 2010). Weaknesses of this method include that it can be intensive to obtain sufficient samples, can be costly and requires specialists to analyse and interpret the results (Table 2). There is significant potential for applying SECR modelling with genetic survey data (Gopalaswamy et al., 2012; Strampelli et al., 2022b).

While the current literature does not provide much information regarding where this method is best suited, it likely to be applicable across a wide range of landscapes. This method is particularly applicable when various aspects relating to population health are required (Tende et al., 2014, 2010) or when determining the minimum number of individuals in a population is required for management decisions.

### 3.6. Distance-based surveys

One paper (1.12%) implemented distance-based surveys for counting lions (Durant et al., 2011). Distance-based surveys involve recording all species and their numbers within a certain distance from a transect line (Durant et al., 2011). Distance sampling can be used as a tool for rapid counts and monitoring of several species. The strengths of this method are that it is relatively cost effective and can be completed in a short study period (Durant et al., 2011). The weaknesses are that there are several issues relating to detection (e.g., detection probability, imperfect detection, group size estimation) (Durant et al., 2011) and wide confidence intervals that raises some concern over their precision (Durant et al., 2011). These surveys are possibly only practical in habitats like the Serengeti where the area is flat, and it is relatively easy to see animals (such as desert or grasslands; Durant et al., 2011). This method is thus best suited where resources are limited and where the habitats allow animals to be visually detected over long ranges, generally where vegetation is sparse.

### 3.7. Method comparison and summary

We summarized and compared the seven methods for surveying lions (Table 4) based on the 65 papers (93 studies) reviewed. A full descriptive narrative is available in the Supplementary Material 1.

Seven papers (10.8%) compared lion survey methods (Belant et al., 2019, 2016; Beukes et al., 2017; Bouley et al., 2018; Groom et al., 2014; Midlane et al., 2015; Ogutu and Dublin, 1998). A comparison paper of call up and spoor surveys in northern Kafue National Park (Zambia) determined that spoor surveys were less resource intensive (Midlane et al., 2015), with spoor surveys estimated to require less than half the number of survey days, 23% less survey hours and 38% less km's driven when compared to call up surveys (Midlane et al., 2015). However, call up surveys were far more precise, and therefore this study recommended call up surveys over spoor counts (Midlane et al., 2015). Another paper compared spoor counts, direct observations with capture recapture and total counts (direct observations) in the Kgalagadi Transfrontier Park (Beukes et al., 2017). Spoor counts produced a population estimate of 242 individuals (95% CI: 176 – 307), direct observations with capture recapture estimated 246 individuals (95% CI: 237 – 256) and a total count of known animals identified 261 individuals (Beukes et al., 2017). Minimum Known Alive calculations were found to significantly under-estimate the population (n = 145). Although spoor counts gave a similar estimate to direct observations with capture recapture, they were imprecise as indicated by wide confidence intervals (Beukes et al., 2017). A comparison of total counts (through direct observations) and call up surveys in the Masai Mara National Reserve (Kenya) found that the estimates from both methods for lions was almost equal (Ogutu and Dublin, 1998). The total count identified 447 lions and the call ups estimated 450 (95% CI: 436 – 464) (Ogutu and Dublin, 1998); the narrow confidence intervals imply reliability in the method as results were shown to have high precision and low bias (Ogutu and Dublin, 1998). In Gorongosa National Park (Mozambique), call up surveys proved to be ineffective because when implemented in areas where lions were known to be, none responded to any of the calling stations (Bouley et al., 2018). However, direct observation through intensive monitoring determined a population of 104 individual lions (Bouley et al., 2018).

In general, we found that all methods could answer research questions relating to lion presence within an area, but direct observations and camera trapping were the most suitable for estimating abundance (Beukes et al., 2017; Bouley et al., 2018; Kane et al., 2015; Strampelli et al., 2022b). It is possible that call up surveys can estimate population abundance, but results should be interpreted with caution as there is uncertainty regarding the reliability as confidence intervals vary from wide (Beukes et al., 2017) to narrow (Ogutu and Dublin, 1998). Indirect survey methods, spoor, camera trapping and genetic surveys, are the least invasive and potentially more effective in areas where lions are less approachable. When it comes to ease of implementation, call up and spoor surveys ranked the least resource intensive (Bauer et al., 2014; Henschel et al., 2020; Midlane et al., 2015, 2014) and camera trapping and genetic surveys the most resource intensive (Kane et al., 2015; Strampelli et al., 2022b; Tende et al., 2014). Similarly, call up and spoor surveys are the least expensive (Midlane et al., 2015), while direct observation and camera trapping surveys are the most expensive (Braczkowski et al., 2020b). The most suitable methods to detect trends are direct observation studies (Bouley et al., 2018; Mweetwa et al., 2018; Rosenblatt et al., 2014), distance-sampling (Durant et al., 2011) and potentially camera trap studies (Kane et al., 2015).

## 4. Discussion

Over the past several decades, many studies have developed and evaluated methods for estimating density of lions in a variety of ecosystems (Braczkowski et al., 2020a, 2020b; Elliot et al., 2020; Funston et al., 2010a; Stander, 1998). Broadly, methods to survey lions for abundance have included index-based methods, such as spoor counts (Funston et al., 2010a; Stander, 1998) and call-ups (Brink et al., 2012; Midlane et al., 2015), and capture-recapture frameworks that use camera traps (Braczkowski et al., 2020b; Elliot and Gopalaswamy, 2017), direct observations (Elliot et al., 2020; Elliot and Gopalaswamy, 2017), or genetic data (Tende et al., 2010). Long-term direct monitoring of individuals (Elliot et al., 2020; Mweetwa et al., 2018) has also been employed by some longitudinal studies to monitor populations (Blackburn et al., 2016; Brink et al., 2012; Mweetwa et al., 2018). These methods have evolved through time, making use of technological advances (e.g. improved camera traps) and more robust analytical approaches (e.g., SECR analyses).

The most robust, accurate, and precise methods for counting lions, and indeed most large carnivores, involve individual identification (Beukes et al., 2017; Braczkowski et al., 2020b; Dröge et al., 2020; Strampelli et al., 2022b; Tende et al., 2014). These include direct and intensive monitoring, camera trapping, and genetic surveys. Identification of lions, which are not clearly marked with spots or stripes, can be challenging. Individual identification of lions began in the mid-1960's by George Schaller and Brian Bertram in the Serengeti, Tanzania (Rees, 2017). Whisker spot patterns were then also used to identify and count individual lions between 1968 and 1970 in Nairobi National Park, Kenya (Pennycuick and Rudnai, 1970; Rudnai, 1973). Although this method was only used in small, relatively habituated populations where identifying lions was less challenging than in many wild populations (Smuts, 1976). Some studies have used artificial marks to identify individuals. For example, branding was used in Kruger National Park, South Africa, in the mid-1970 s (Bryden, 1976; Smuts, 1976; Smuts et al., 1977) and in the Kalahari Gemsbok National Park, South Africa (Mills et al., 1978). The earliest published method in our review (1991) assessed the demography of lions in Etosha National Park (Namibia) using direct observations analysed in a capture-recapture framework between 1985 and 1989 (Stander, 1991). More recently, advances in the resolution and clarity of camera trap images have allowed scientists to identify individuals using whisker spots, scars, ear notches, and other marks (Braczkowski et al., 2020b). Though many of these change over time, they are unlikely to change dramatically within a single survey period. Camera trap surveys have been used to estimate lion densities in Tanzania, Uganda and Zimbabwe (Cusack et al., 2015; Kane et al., 2015; Strampelli et al., 2022b). The first published studies for camera trap surveys combined with SECR modelling for surveying lions were published in 2015, with the added benefit that this is an effective way to survey multiple species simultaneously (Kane et al., 2015; Rich et al., 2019; Strampelli et al., 2022b). Individual identification is further enhanced using Artificial Intelligence (AI). Machine learning algorithms, such as those designed by WildBook, Tech4Conservation, and the African Carnivore Book can now distinguish individuals with increasing accuracy (Verschueren et al., 2023). Determining population size through genetic analysis has been utilized to determine population size by identifying the minimum number of individuals in an area (Tende et al., 2010; Becker et al., 2017; Rossettie et al., 2022). Genetic samples can be obtained through faecal matter (Tende et al., 2014, 2010) or hair samples (Rossettie et al., 2022). Between 2008 and 2014, the use of DNA in lion faecal matter to identify individual lions was used to determine the minimum number of lions in a population (Tende et al., 2014, 2010). While this method has not been used widely for lions, it has been used with detection dogs to determine population numbers of cheetahs in Western Zambia (Becker et al., 2017), where 27 scat samples were found to provide a population estimate of 8–14 individuals (Becker et al., 2017). Hair samples were successfully collected using modified foothold traps from mountain lions in New Mexico to determine a minimum population size (Rossettie et al., 2022). This method holds potential to be used more widely for lions (either through hair or faecal samples), especially within an SECR framework, and has been used for other carnivores (Karmacharya et al., 2011; Long et al., 2011; McCarthy et al., 2008; Thompson et al., 2012; Rossettie et al., 2022).

Due to the intensive input of time and resources required to calculate reliable population estimates using many of the individual identification methods, especially over large systems, spoor counts and call up surveys were developed (Ogutu and Dublin, 1998; Stander, 1998). Due to their broad applicability and relatively low cost, spoor counts have been a popular method used to survey lions in many areas across the species' range (Funston et al., 2010a; Stander, 1998). Initially, spoor counts were frequently used and implemented in southern Africa (Funston et al., 2010a; Stander, 1998; Winterbach et al., 2016), while call up surveys were used in East

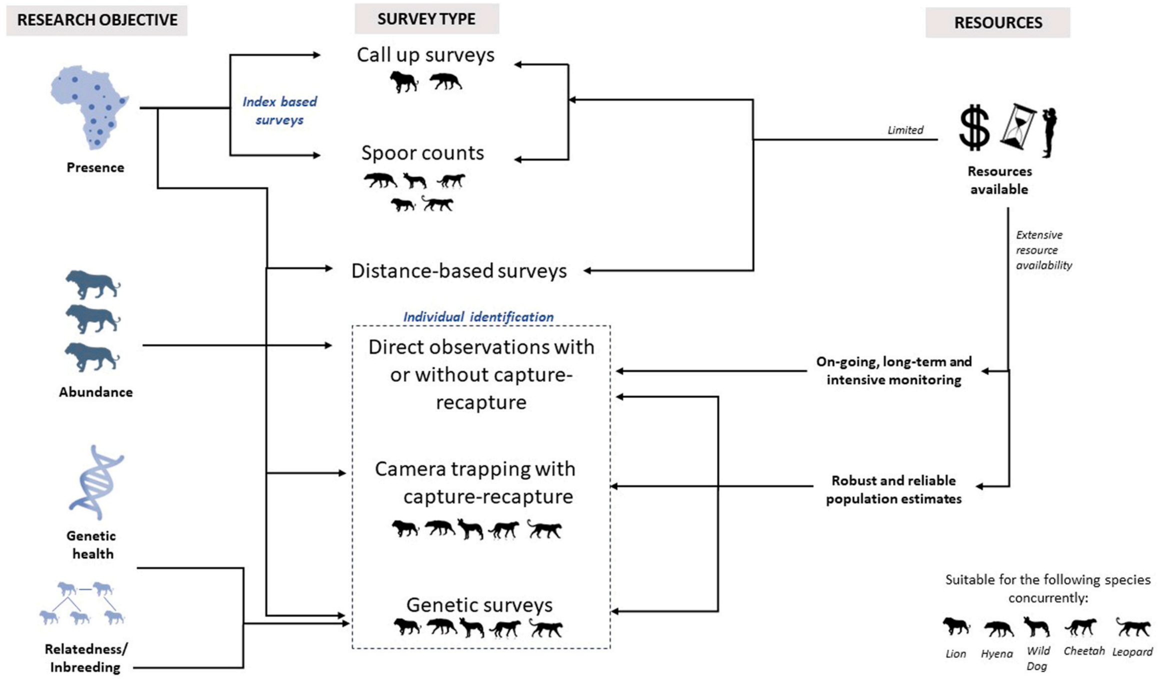


**Fig. 6.** High-level overview of the methods used to survey lions relative to research primary research objective.

Africa (Kiffner et al., 2009, 2008; Ogutu et al., 2005; Ogutu and Dublin, 1998). However, recent research suggests that this method produces high variation in abundance estimates with wide confidence intervals, making it difficult to detect even large changes in population size (Dröge et al., 2020). Call up surveys have also been used for decades across a variety of habitats, but also carry serious biases relating to individual responsiveness, and the possibility of undercounting shy individuals in areas with lions that are wary because of human persecution (Midlane et al., 2015).

As technology and analytical techniques have evolved and these index-based methods have been repeatedly tested, it has become apparent that they are not reliable for estimating density and abundance (Belant et al., 2019; Dröge et al., 2020). For example, a simulation study published in 2020 found that spoor surveys generate estimates that either overstate precision or are too imprecise to be of any value (Dröge et al., 2020). As a result, these methods are no longer recommended for counting lions (Dröge et al., 2020). Nevertheless, they remain valuable tools for confirming lion presence in study areas, to understand space use and human impacts in an occupancy framework, and to map lion distributions (Henschel et al., 2016; Petracca et al., 2020). We caution the utility of estimating lion population size from methods that are shown to be unreliable for estimating abundance, especially to inform conservation and management decisions. Doing so would particularly apply to estimates derived from questionnaire or interview type surveys (Dröge et al., 2020; Mesochina et al., 2010a, 2010b; Riggio et al., 2013). The latter method requires collecting information on lion observations to determine frequency of occurrence and applying it to an equation that accounts for variables to estimate a population size of lions (Jacobson et al., 2013; Mesochina et al., 2010b, 2010a; Riggio et al., 2013). This method has a strong likelihood of overestimating numbers and is scientifically questionable (Riggio et al., 2013). Additionally, spoor surveys have also been shown to produce questionable estimates that are not reliable (Belant et al., 2019; Dröge et al., 2020; Midlane et al., 2015).

Other methods have been implemented to survey lions, but not extensively tested for robustness. Roar counts were tested in the Selous Game Reserve in 1974, but no further studies utilized this method (Rodgers, 1973). While lions do reply to playbacks of conspecifics, this is not as predictable as seen with wolves and not all pride members vocalise in response to calls. In 2011, in the Serengeti National Park (Tanzania), distance-based surveys successfully demonstrated that trends in lion abundance could be understood (Durant et al., 2011). However, this approach can only be implemented in systems such as the Serengeti where the landscape and sparse vegetative cover allow animals to be seen easily over relatively large distances.

We identified several key knowledge gaps that exist across the seven survey methods. Broadly, these gaps included the need to account for detection probability and understand its impact on lions in different contexts, clarifying the efficacy and reliability of equipment used (Mwampeta et al., 2022), the need to develop a robust a-priori survey design for each survey and to investigate opportunities for improvement, and implementing and refining analytical model design and validation techniques (Belant et al., 2016; Strampelli et al., 2022b). Additionally, there is limited information regarding the cost of these methods. A cost analysis comparing the different suitable methods would be beneficial, as this kind of information is limited in the literature (Midlane et al., 2015), and would reveal the true financial cost of each survey method which would give practitioners with limited resources important information (Midlane et al., 2015).

It appears that lion populations in East and southern Africa are surveyed more than those in Central or West Africa, supporting the findings of other studies that found biases towards large carnivore surveys in the same regions (Strampelli et al., 2022a). Published lion population/abundance surveys are not available for Angola, Chad, Democratic Republic of the Congo (DRC), Malawi, Rwanda, Somalia and South Sudan. As most of the small populations in Malawi and Rwanda are recent reintroductions into fully fenced and intensively monitored reserves, urgent surveys may not be a priority. However, large expanses of potential lion range in Chad, DRC, and South Sudan have never been formally surveyed, and considerable uncertainty exists regarding lion status there. This lack of data is potentially because of long periods of political unrest and insecurity in these countries (Angelo and Mcguinness, 2012; Ploch, 2010; Van Damme and De Cordier, 2017). Surveys in these areas should be prioritised (African Lion Database, Unpublished Data. 2022). Similar data gaps have been found for other carnivores where there is a strong negative bias for carnivore research (Strampelli et al., 2022a). Notably, survey results (population numbers) are often only published years after survey work has been completed (Fig. 5). This delay in publication is potentially problematic as decisions made with available (published) information, which are likely to be outdated by the time they are published, could result in conservation action or management decisions being made based on information that might no longer be correct.

Due to the globalisation of conservation and science and the need to understand and compare lion population status across their range, there is a growing consensus that standardised survey methodologies for the counting of lions is urgently needed. Standardized survey methodologies will greatly enhance our capacity to assess the need for conservation intervention, to measure the impacts of ongoing conservation efforts across their range, and to direct conservation funding and other resources to the most critical locations.

One of the challenges in implementing survey methods is that the most appropriate methodology is not always selected, and guidelines for standardized implementation are not available. While some studies use the same method, they may not always follow the exact same methodological implementation, and this renders the results incomparable across both space and time. For example, not taking sampling or observer bias into account during study design and during implementation could result in limited replication of the study in subsequent years, thus preventing temporal comparison of results. This, combined with the range of survey methods available and the sometimes-contradicting information, highlights the need for standardized guidelines on surveying lions (Dröge et al., 2020; Elliot and Gopalaswamy, 2017). To better track population trends over time, standardized methodology should be repeated at set intervals. This has been valuable for monitoring local populations, instrumental in identifying declines (Bauer et al., 2015) and has led to policy change at the local and national level (Becker et al., 2013). Directly coordinated and comparable estimates obtained over space and time using standardised and rigorous methodology will allow for easier identification of range-wide population trends. Additionally, such coordinated estimates will also provide a reliable source for deciding where to direct limited resources to lion populations that are most at risk, and to compare the effectiveness of conservation interventions.

A decision tool, or framework, should be developed that will guide researchers and protected area managers on how best to select the most appropriate method based on their research objectives and the resources available to them (e.g., funding, human capital, and time availability). Based on the literature within our review, we provide a preliminary guidance tool to demonstrate how a decision tool could assist in selecting the most suitable methodology (Fig. 6). For example, if population abundance needs to be determined, call up and spoor surveys should probably not be used, but direct observation-based surveys, distance-based surveys, camera trapping with capture-recapture, and genetic studies would be more suitable lion survey methods. Whether there are sufficient resources available will also factor into decision making (Fig. 6). There is an urgent need for greater consensus on methods and to develop a unified framework for deciding when to employ which methods. While we have attempted to do that based on the information in this review, a more robust tool with input from survey experts would be beneficial. In addition, including elements on the cost of conducting surveys or monitoring per $km^2$ would be immensely valuable.

The methods discussed within this review, as well as their strengths, weaknesses, and reliability are broadly applicable to other large carnivores globally (Balme et al., 2009; Becker et al., 2017; Gompper et al., 1973; Gopalaswamy et al., 2012; Karanth, 1995; Karanth and Nichols, 2010; Marnewick et al., 2008; Wilson and Delahay, 2001). Just as various methods were employed and refined for surveying lions, researchers studying other species should adapt and develop survey methods that are tailored to the specific ecological and behavioural characteristics of the target species. Many of these methods were originally developed and refined to count elusive species like tigers and jaguars (Gopalaswamy et al., 2012; Karanth and Nichols, 2010). Few large carnivores, other than lions, can be monitored through direct or intensive survey methods. Attempts to monitor some species, such as leopards (Balme et al., 2019), through such methods have been made. While these have provided insights into population demography, survivorship, reproductive success, and other valuable information, they are only applicable over a relatively small area. Camera traps and genetic sampling hold the most promise for surveying large carnivores, and some small carnivores with distinguishable markings (Bahaa-el-din et al., 2016). These non-invasive techniques allow us to count even the most elusive carnivores (Bahaa-el-din et al., 2016). However, when surveying for multiple species, particularly using camera traps, it is critical to understand how one species impacts the presence of others. For example, African wild dogs avoid areas of high lion activity. If the area surveyed is too small or biased towards areas of known lion activity, this could lead to misleading results indicating low African wild dog density (Dröge et al., 2017). Carnivores also operate at different spatial scales. Surveys intended for wide ranging species like lions or wild dogs may create data gaps for species with smaller home ranges that ultimately preclude density analysis for the smaller species because of a lack of recaptures, a key requirement for capture-recapture frameworks. Nevertheless, camera trap and genetic surveys are powerful tools for gathering data on multiple species at once, thereby maximizing the impact of conservation resources.

## 5. Conclusions

Our findings highlight the need for minimum standards for harmonised survey methods, including consensus on the prohibitive limitations of some older methods. This would ensure that population estimates are reliable and comparable. We also encourage that surveys be carried out where data gaps exist across lion range in Africa to provide a clearer understanding of the status of lions throughout Africa. Based on the literature, we determine that reliable estimates of lions can only be estimated through direct observation (both with and without capture recapture frameworks) surveys and camera trap-based capture-recapture surveys.

## Ethics approval

This article does not contain any studies with human participants or animals performed by any of the authors.

## Author contributions

SN, RS, conceptualised the study. SN, EA, DM collected and analysed the data. SN wrote the draft manuscript. The other authors provided editorial input.

## Consent to participate

Not applicable.

## Consent for publication

All authors gave consent.

## CRediT authorship contribution statement

**Erin Adams:** Writing – review & editing, Project administration, Methodology, Investigation, Formal analysis, Data curation. **David Marneweck:** Writing – review & editing, Investigation, Conceptualization. **Hans Bauer:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Conceptualization. **Lizanne Roxburgh:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Rob Slotow:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Conceptualization. **Samantha Karin Nicholson:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **David Mills:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data Availability

Data will be made available on request.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02908.

## References

Alibhai, S.K., Gu, J., Jewell, Z.C., Morgan, J., Liu, D., Jiang, G., 2023. 'I know the tiger by his paw': A non-invasive footprint identification technique for monitoring individual Amur tigers (Panthera tigris altaica) in snow. Ecol. Inf. 73. https://doi.org/10.1016/j.ecoinf.2022.101947.

Angelo, V., Mcguinness, K., 2012. Security and Stability: Reflections on the Impact of South Sudan on Regional Political Dynamics.

Ausband, D.E., Rich, L.N., Glenn, E.M., Mitchell, M.S., Zager, P., Miller, D.A.W., Waits, L.P., Ackerman, B.B., MacK, C.M., 2014. Monitoring gray wolf populations using multiple survey methods. J. Wildl. Manag. 78, 335–346. https://doi.org/10.1002/jwmg.654.

Bahaa-el-din, L., Sollmann, R., Hunter, L.T.B., Slotow, R., Macdonald, D.W., Henschel, P., 2016. Effects of human land-use on Africa's only forest-dependent felid: The African golden cat Caracal aurata. Biol. Conserv 199, 1–9. https://doi.org/10.1016/j.biocon.2016.04.013.

Bakker, C.E., Kirsten, I.E., Bauer, H., Croes, B.M., Tamis, W.L.M., Tumenta, P.N., Adam, S., Kamgang, A.S., De Iongh, H.H., Bauer, H., Croes, B.M., Tumenta, P.N., Adam, S., Fr, S., 2020. Divergent trends of large carnivore populations within the Bénoué Complex, North Cameroon, shown by long-term fine-scale monitoring. Eur. J. Wildl. Res 66, 82. https://doi.org/10.1007/s10344-020-01420-y/Published.

Balme, G., Rogan, M., Thomas, L., Pitman, R., Mann, G., Whittington-Jones, G., Midlane, N., Broodryk, M., Broodryk, K., Campbell, M., Alkema, M., Wright, D., Hunter, L., 2019. Big cats at large: Density, structure, and spatio-temporal patterns of a leopard population free of anthropogenic mortality. Popul Ecol. 61, 256–267. https://doi.org/10.1002/1438-390X.1023.

Balme, G.A., Hunter, L.T.B., Slotow, R., 2009. Evaluating Methods for Counting Cryptic Carnivores. J. Wildl. Manag. 73, 433–441. https://doi.org/10.2193/2007-368.

Barea-Azcón, J.M., Virgós, E., Ballesteros-Duperón, E., Moleón, M., Chirosa, M., 2007. Surveying carnivores at large spatial scales: A comparison of four broad-applied methods. Biodivers. Conserv 16, 1213–1230. https://doi.org/10.1007/s10531-006-9114-x.
Bauer, D., Schiess-Meier, M., Mills, D.R., Gusset, M., 2014. Using spoor and prey counts to determine temporal and spatial variation in lion (Panthera leo) density. Can. J. Zool. 92, 97–104. https://doi.org/10.1139/cjz-2013-0176.
Bauer, H., 2007. Status of large carnivores in Bouba Ndjida National Park, Cameroon. Afr. J. Ecol. 45, 448–450. https://doi.org/10.1111/j.1365-2028.2006.00751.x.
Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T.B., Macdonald, D.W., Packer, C., 2015. Lion (Panthera leo) populations are declining rapidly across Africa, except in intensively managed areas. Proc. Natl. Acad. Sci. 112, 14894–14899. https://doi.org/10.1073/pnas.1500664112.
Bauer, H., DIckman, A., Chapron, G., Oriol-Cotterill, A., Nicholson, S.K., Sillero-Zubiri, C., Hunter, L., Lindsey, P., MacDonald, D.W., 2020. Threat analysis for more effective lion conservation. ORYX 56, 108–115. https://doi.org/10.1017/S0030605320000253.
Becker, E.F., Spindler, M.A., Osborne, T.O., 1998. A Population Estimator Based on Network Sampling of Tracks in the Snow. J. Wildl. Manag. 62, 968–977.
Becker, M.S., Watson, F.G.R., Droge, E., Leigh, K., Carlson, R.S., Carlson, A.A., 2013. Estimating past and future male loss in three Zambian lion populations. J. Wildl. Manag. 77, 128–142. https://doi.org/10.1002/jwmg.446.
Becker, M.S., Durant, S.M., Watson, F.G.R., Parker, M., Gottelli, D., M'soka, J., Droge, E., Nyirenda, M., Schuette, P., Dunkley, S., Brummer, R., 2017. Using dogs to find cats: detection dogs as a survey method for wide-ranging cheetah. J. Zool. 302, 184–192. https://doi.org/10.1111/jzo.12445.
Belant, J.L., Bled, F., Wilton, C.M., Fyumagwa, R., Mwampeta, S.B., Beyer, D.E., 2016. Estimating Lion Abundance using N-mixture Models for Social Species. Sci. Rep. 6 https://doi.org/10.1038/srep35920.
Belant, J.L., Bled, F., Mwampeta, S.B., Mkasanga, I.J., Wilton, C.M., Fyumagwa, R., 2017. Temporal and spatial variation of broadcasted vocalizations does not reduce lion Panthera leo habituation. Wildl. Biol. 2017. https://doi.org/10.2981/wlb.00287.
Belant, J.L., Bled, F., Mkasanga, I.J., Wilton, C.M., Mwampeta, S.B., Beyer, D.E., Mwakilema, W., Fyumagwa, R., 2019. Track surveys do not provide accurate or precise lion density estimates in serengeti. Glob. Ecol. Conserv 19. https://doi.org/10.1016/j.gecco.2019.e00651.
Beukes, B.O., Radloff, F.G.T., Ferreira, S.M., 2017. Estimating african lion abundance in the Southwestern Kgalagadi Transfrontier Park. Afr. J. Wildl. Res 47, 10–23. https://doi.org/10.3957/056.047.0010.
Blackburn, S., Hopcraft, J.G.C., Ogutu, J.O., Matthiopoulos, J., Frank, L., 2016. Human–wildlife conflict, benefit sharing and the survival of lions in pastoralist community-based conservancies. J. Appl. Ecol. 53, 1195–1205. https://doi.org/10.1111/1365-2664.12632.
Bouley, P., Poulos, M., Branco, R., Carter, N.H., 2018. Post-war recovery of the African lion in response to large-scale ecosystem restoration. Biol. Conserv 227, 233–242. https://doi.org/10.1016/j.biocon.2018.08.024.
Braczkowski, A., Gopalaswamy, A.M., Elliot, N.B., Possingham, H.P., Bezzina, A., Maron, M., Biggs, D., Allan, J.R., 2020a. Restoring Africa's Lions: Start With Good Counts. Front Ecol. Evol. 8 https://doi.org/10.3389/fevo.2020.00138.
Braczkowski, A., Gopalaswamy, A.M., Nsubuga, M., Allan, J., Biggs, D., Maron, M., 2020b. Detecting early warnings of pressure on an African lion (Panthera leo) population in the Queen Elizabeth Conservation Area, Uganda. Ecol. Solut. Evid. 1 https://doi.org/10.1002/2688-8319.12015.
Brassine, E., Parker, D., 2015. Trapping elusive cats: Using intensive camera trapping to estimate the density of a rare african felid. PLoS One 10. https://doi.org/10.1371/journal.pone.0142508.
Brink, H., Smith, R.J., Skinner, K., 2012. Methods for lion monitoring: a comparison from the Selous Game Reserve, Tanzania. Afr. J. Ecol. 51, 366–375.
Bryden, B.R., 1976. The biology of the African Lion. University of Pretoria, Pretoria.
Cozzi, G., Broekhuis, F., McNutt, J.W., Schmid, B., 2013. Density and habitat use of lions and spotted hyenas in northern Botswana and the influence of survey and ecological variables on call-in survey estimation. Biodivers. Conserv 22, 2937–2956. https://doi.org/10.1007/s10531-013-0564-7.
Cusack, J.J., Swanson, A., Coulson, T., Packer, C., Carbone, C., Dickman, A.J., Kosmala, M., Lintott, C., Rowcliffe, J.M., 2015. Applying a random encounter model to estimate lion density from camera traps in Serengeti National Park, Tanzania. J. Wildl. Manag. 79, 1014–1021. https://doi.org/10.1002/jwmg.902.
Dröge, E., Creel, S., Becker, M.S., M'soka, J., 2017. Spatial and temporal avoidance of risk within a large carnivore guild. Ecol. Evol. 7, 189–199. https://doi.org/10.1002/ece3.2616.
Dröge, E., Creel, S., Becker, M.S., Loveridge, A.J., Sousa, L.L., Macdonald, D.W., 2020. Assessing the performance of index calibration survey methods to monitor populations of wide-ranging low-density carnivores. Ecol. Evol. 10, 3276–3292. https://doi.org/10.1002/ece3.6065.
Durant, S.M., Craft, M.E., Hilborn, R., Bashir, S., Hando, J., Thomas, L., 2011. Long-term trends in carnivore abundance using distance sampling in Serengeti National Park, Tanzania. J. Appl. Ecol. 48, 1490–1500. https://doi.org/10.1111/j.1365-2664.2011.02042.x.
Elliot, N.B., Gopalaswamy, A.M., 2017. Toward accurate and precise estimates of lion density. Conserv. Biol. 31, 934–943. https://doi.org/10.1111/cobi.12878.
Elliot, N.B., Bett, A., Chege, M., Sankan, K., de Souza, N., Kariuki, L., Broekhuis, F., Omondi, P., Ngene, S., Gopalaswamy, A.M., 2020. The importance of reliable monitoring methods for the management of small, isolated populations. Conserv Sci. Pr. 2 https://doi.org/10.1111/csp2.217.
Ferreira, S.M., Funston, P.J., 2010. Estimating lion population variables: Prey and disease effects in Kruger National Park, South Africa. Wildl. Res. 37, 194–206. https://doi.org/10.1071/WR09030.
Fitzhugh, E.L., Gorenzel, W.P., 1985. Design and analysis of Mountain Lion track surveys. Cal-Neva wildlife transactions. West. Sect. 78–85.
Fuller, T.K., Sampson, B.A., 1988. Evaluation of a Simulated Howling Survey for Wolves, Source: The Journal of Wildlife Management.
Funston, P.J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D.M., Durant, S., Packer, C., Mosser, A., Ferreira, S.M., 2010b. Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. J. Zool. 281, 56–65. https://doi.org/10.1111/j.1469-7998.2009.00682.x.
Funston, P.J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D.M., Durant, S., Packer, C., Mosser, A., Ferreira, S.M., 2010a. Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. J. Zool. 281, 56–65. https://doi.org/10.1111/j.1469-7998.2009.00682.x.
Gompper, M.E., Kays, R.W., Ray, J.C., Lapoint, S.D., Bogan, D.A., Cryan, J.R., 1973. A Comparison of Noninvasive Techniques to Survey Carnivore Communities in Northeastern North America. Wildl. Soc. Bull. 34, 1142–1151.
Gopalaswamy, A.M., Royle, J.A., Delampady, M., Nichols, J.D., Ullas Karanth, K., Macdonald, D.W., 2012. Density estimation in tiger populations: combining information for strong inference. Ecology.
Green, S.E., Rees, J.P., Stephens, P.A., Hill, R.A., Giordano, A.J., 2020. Innovations in camera trapping technology and approaches: The integration of citizen science and artificial intelligence. Animals. https://doi.org/10.3390/ani10010132.
Groom, R.J., Funston, P.J., Mandisodza, R., 2014. Surveys of lions Panthera leo in protected areas in Zimbabwe yield disturbing results: What is driving the population collapse? ORYX. https://doi.org/10.1017/S0030605312001457.
Harrington, F.H., Mech, L.D., 1982. An analysis of howling response parameters useful for wolf pack censusing. USGS North. Prairie Wildl. Res. Cent. 7, 686–693.
Havens, K.J., Sharp, E.J., 1998. Using Thermal Imagery in the Aerial Survey of Animals, Source: Wildlife Society Bulletin.
Henschel, P., Azani, D., Burton, C., Malanda, G., Saidu, Y., Sam, M., Hunter, L., 2010. Lion status updates from five range countries in West and Central Africa, CATnews.
Henschel, P., Coad, L., Burton, C., Chataigner, B., Dunn, A., MacDonald, D., Saidu, Y., Hunter, L.T.B., 2014. The lion in West Africa is critically endangered. PLoS One 9. https://doi.org/10.1371/journal.pone.0083500.
Henschel, P., Petracca, L.S., Hunter, L.T.B., Kiki, M., Sewadé, C., Tehou, A., Robinson, H.S., 2016. Determinants of distribution patterns and management needs in a Critically Endangered lion Panthera leo population. Front Ecol. Evol. 4 https://doi.org/10.3389/fevo.2016.00110.
Henschel, P., Petracca, L.S., Ferreira, S.M., Ekwanga, S., Ryan, S.D., Frank, L.G., 2020. Census and distribution of large carnivores in the Tsavo national parks, a critical east African wildlife corridor. Afr. J. Ecol. 58, 383–398. https://doi.org/10.1111/aje.12730.
Holland, K.K., Larson, L.R., Powell, R.B., 2018. Characterizing conflict between humans and big cats Panthera spp: A systematic review of research trends and management opportunities. PLoS One 13. https://doi.org/10.1371/journal.pone.0203877.
Jacobson, A.P., Cattau, M.E., Riggio, J.S., Petracca, L.S., Fedak, D.A., 2013. Distribution and abundance of lions in northwest Tete Province. Available online: 〈www.tropicalconservationscience.org〉 Mongabay.com Open Access Journal-Tropical Conservation Science 6, 87–107.

Jędrzejewski, W., Robinson, H.S., Abarca, M., Zeller, K.A., Velasquez, G., Paemelaere, E.A.D., Goldberg, J.F., Payan, E., Hoogesteijn, R., Boede, E.O., Schmidt, K., Lampo, M., Viloria, Á.L., Carreño, R., Robinson, N., Lukacs, P.M., Nowak, J.J., Salom-Pérez, R., Castañeda, F., Boron, V., Quigley, H., 2018. Estimating large carnivore populations at global scale based on spatial predictions of density and distribution - Application to the jaguar (Panthera onca). PLoS One 13. https://doi.org/10.1371/journal.pone.0194719.

Kane, M.D., Morin, D.J., Kelly, M.J., 2015. Potential for camera-traps and spatial mark-resight models to improve monitoring of the critically endangered West African lion (Panthera leo). Biodivers. Conserv 24, 3527–3541. https://doi.org/10.1007/s10531-015-1012-7.

Karanth, K.U., 1995. Estimating Tiger Panthera tigris populations from camera-trap data using capture recapture models. Biol. Conserv.

Karanth, K.U., Nichols, J.D., 2010. Non-invasive Survey Methods for Assessing Tiger Populations. In: Tigers of the World: The Science, Politics and Conservation of Panthera tigris. Elsevier, pp. 241–261. https://doi.org/10.1016/B978-0-8155-1570-8.00018-9.

Karmacharya, D.B., Thapa, K., Shrestha, R., Dhakal, M., Janecka, J.E., 2011. Noninvasive genetic population survey of snow leopards (Panthera uncia) in Kangchenjunga conservation area, Shey Phoksundo National Park and surrounding buffer zones of Nepal. BMC Res Notes 4. https://doi.org/10.1186/1756-0500-4-516.

Kiffner, C., Waltert, M., Meyer, B., Mühlenberg, M., 2008. Response of lions (Panthera leo LINNAEUS 1758) and spotted hyaenas (Crocuta crocuta ERXLEBEN 1777) to sound playbacks. Afr. J. Ecol. 46, 223–226. https://doi.org/10.1111/j.1365-2028.2007.00813.x.

Kiffner, C., Meyer, B., Mühlenberg, M., Waltert, M., 2009. Plenty of prey, few predators: What limits lions Panthera leo in katavi national park, western Tanzania? ORYX 43, 52–59. https://doi.org/10.1017/S0030605307002335.

Kirsten, I., Bakker, E., Lucas Trujillo, L., Bour, P., Nhiomog, N., Bauer, H., de Iongh, H., 2018. Lion (Panthera leo) and spotted hyaena (Crocuta crocuta) abundance in Bouba Ndjida National Park, Cameroon, trends between 2005 and 2014. Afr. J. Ecol. 56, 414–417. https://doi.org/10.1111/aje.12453.

Kissui, B.M., Packer, C., 2004. Top-down Population Regulation of a Top Predator: Lions in the Ngorongoro Crater. Proc. Biol. Sci. 271, 1867–1874.

Kojola, I., Helle, P., Heikkinen, S., Lindén, H., Paasivaara, A., Wikman, M., 2014. Tracks in snow and population size estimation: The wolf Canis lupus in Finland. Wildl. Biol. 20, 279–284. https://doi.org/10.2981/wlb.00042.

Linnell, J.D.C., Fiske, P., Herfindal, I., Odden, J., Brøseth, H., Andersen, R., 2007. An evaluation of structured snow-track surveys to monitor Eurasian Lynx lynx lynx populations. Wildl. Biol. 13, 456–466. https://doi.org/10.2981/0909-6396(2007)13[456:AEOSSS]2.0.CO;2.

Long, R.A., Donovan, T.M., MacKay, P., Zielinski, W.J., Buzas, J.S., 2011. Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. Land. Ecol. 26, 327–340. https://doi.org/10.1007/s10980-010-9547-1.

Mandisodza-Chikerema, A., Chakuya, R., Malunga, J., Munkuli, A., Seymour-Smith, N., Sibanda, J., Sousa, A., Wijers, L., 2022. Interim report on camera trap surveys in the Zambezi Valley, Zimbabwe. England.

Marnewick, K., Funston, P.J., Karanth, U.K., 2008. Evaluating camera trapping as a method for estimating cheetah abundance in ranching areas. South Afr. J. Wildl. Res. 38, 59–65.

Marnewick, K., Ferreira, S.M., Grange, S., Watermeyer, J., Maputla, N., Davies-Mostert, H.T., 2014. Evaluating the status of and African wild dogs Lycaon pictus and cheetahs Acinonyx jubatus through tourist-based photographic surveys in the Kruger National Park. PLoS One 9. https://doi.org/10.1371/journal.pone.0086265.

Maximillion, A., Wang, S., Olson, L., Li, Q., Krofel, M., 2020. Counting cats for conservation: seasonal estimates of leoparddensity and drivers of distribution in the Serengeti. Biodivers. Conserv 29, 3591–3608.

McCarthy, K.P., Fuller, T.K., Ming, M., McCarthy, T.M., Waits, L., Jumabaev, K., 2008. Assessing Estimators of Snow Leopard Abundance. J. Wildl. Manag. 72, 1826–1833. https://doi.org/10.2193/2008-040.

Mesochina, P., Mbanwa, O., Chardonnet, P., Mosha, R., Mtui, B., Drouet, N., Crosmary, W., Kissui, B., 2010a. Conservation status if the lion (Panthera leo Linnaeus, 1758) in Tanzania.

Mesochina, P., Sefu, L., Sichali, E., Chardonnet, P., Ngalande, J., Lipita, W., 2010b. Conservation status of the lion (Panthera leo Linnaeus, 1758) in Malawi.

Midlane, N., O'Riain, M.J., Balme, G.A., Robinson, H.S., Hunter, L.T.B., 2014. On tracks: A spoor-based occupancy survey of lion Panthera leo distribution in Kafue National Park, Zambia. Biol. Conserv 172, 101–108. https://doi.org/10.1016/j.biocon.2014.02.006.

Midlane, N., Justin O'Riain, M., Balme, G.A., Hunter, L.T.B., 2015. To track or to call: comparing methods for estimating population abundance of African lions Panthera leo in Kafue National Park. Biodivers. Conserv 24, 1311–1327. https://doi.org/10.1007/s10531-015-0858-z.

Mills, M.G.L., Wolff, P., Le Riche, E.A.N., Meyer, I.J., 1978. Some population characteristics of the lion Panthera leo in the Kalahari Gemsbok National Park. Koedoe 21, 163–171.

Mohammed, A.A., Bauer, H., El Faki, A., Sillero-Zubiri, C., 2020. Lion and spotted hyaena abundance in Dinder National Park, Sudan. Afr. J. Ecol. 58, 316–318. https://doi.org/10.1111/aje.12683.

Mwampeta, S.B., Wilton, C.M., Mkasanga, I.J., Masinde, L.M., Ranke, P.S., Røskaft, E., Fyumagwa, R., Belant, J.L., 2021. Lion and spotted hyena distributions within a buffer area of the Serengeti-Mara ecosystem. Sci. Rep. 11 https://doi.org/10.1038/s41598-021-01518-6.

Mwampeta, S.B., Wilton, C.M., Mkasanga, I.J., Bled, F., Masinde, L.M., Røskaft, E., Ranke, P.S., Fyumagwa, R., Belant, J.L., 2022. Efficacy of spotlights and thermal cameras to detect lions Panthera leo and spotted hyenas Crocuta crocuta depends on species and management regime. Wildl. Biol. https://doi.org/10.1002/wlb3.01030.

Mweetwa, T., Christianson, D., Becker, M., Creel, S., Rosenblatt, E., Merkle, J., Dröge, E., Mwape, H., Masonde, J., Simpamba, T., 2018. Quantifying lion (Panthera leo) demographic response following a three-year moratorium on trophy hunting. PLoS One 13. https://doi.org/10.1371/journal.pone.0197030.

Nicholson, S., Bauer, B., Strampelli, S., Sogbohossou, E., Ikanda, D., Tumenta, P., Venkataraman, M., Chapron, G., Loveridge, A., 2023. Global Lion (*Panthera leo*) Red List Assessment.

Nicholson, S.K., Marneweck, D.G., Lindsey, P.A., Marnewick, K., Davies-Mostert, H.T., 2020. A 20-Year Review of the Status and Distribution of African Wild Dogs (Lycaon pictus) in South Africa. Afr. J. Wildl. Res 50, 8–19. https://doi.org/10.3957/056.050.0008.

Ogutu, J.O., Dublin, H.T., 1998. The response of lions and spotted hyaenas to sound playbacks as a technique for estimating population size. Afr. J. Ecol. 36, 83–95. https://doi.org/10.1046/j.1365-2028.1998.113-89113.x.

Ogutu, J.O., Dublin, H.T., 2002. Demography of lions in relation to prey and habitat in the Maasai Mara National Reserve. Kenya Afr. J. Ecolgy 40, 120–129.

Ogutu, J.O., Bhola, N., Reid, R., 2005. The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya. J. Zool. 265, 281–293. https://doi.org/10.1017/S0952836904006302.

Omoya, E.O., Mudumba, T., Buckland, S.T., Mulondo, P., Plumptre, A.J., 2014. Estimating population sizes of lions Panthera leo and spotted hyaenas Crocuta crocuta in Uganda's savannah parks, using lure count methods. ORYX 48, 394–401. https://doi.org/10.1017/S0030605313000112.

Page, M.J., Moher, D., Bossuyt, P.M., Boutron, I., Hoffmann, T.C., Mulrow, C.D., Shamseer, L., Tetzlaff, J.M., Akl, E.A., Brennan, S.E., Chou, R., Glanville, J., Grimshaw, J.M., Hróbjartsson, A., Lalu, M.M., Li, T., Loder, E.W., Mayo-Wilson, E., Mcdonald, S., Mcguinness, L.A., Stewart, L.A., Thomas, J., Tricco, A.C., Welch, V.A., Whiting, P., Mckenzie, J.E., 2021. PRISMA 2020 explanation and elaboration: Updated guidance and exemplars for reporting systematic reviews. BMJ. https://doi.org/10.1136/bmj.n160.

Pennycuick, C.J., Rudnai, D.J., 1970. A method of identifying individual lions Panthera leo with an analysis of the reliability of identification. J. Zool. 160, 497–508.

Petracca, L.S., Funston, P.J., Henschel, P., Cohen, J.B., Maclennan, S., Frair, J.L., 2020. Modeling community occupancy from line transect data: a case study with large mammals in post-war Angola. Anim. Conserv 23, 420–433. https://doi.org/10.1111/acv.12555.

Pin, C., Phan, C., Kamler, J.F., Rostro-García, S., Penjor, U., In, V., Crouthers, R., Macdonald, E.A., Chou, S., Macdonald, D.W., 2022. Density and occupancy of leopard cats across different forest types in Cambodia. Mamm. Res 67, 287–298. https://doi.org/10.1007/s13364-022-00634-6.

Plhal, R., Kamler, J., Homolka, M., Adamec, Z., 2011. An assessment of the applicability of photo trapping to estimate wild boar population density in a forest environment. Folia Zool. Brno 60, 237–246. https://doi.org/10.25225/fozo.v60.i3.a8.2011.

Ploch, L., 2010. Instability in Chad. CRS Report for Congress Prepared for Members and Committees of Congress.

Rees, A., 2017. Wildlife agencies: practice, intentionality and history in twentieth-century animal field studies. BJHS Themes 2, 127–149. https://doi.org/10.1017/bjt.2017.10.

Rich, L.N., Miller, D.A.W., Muñoz, D.J., Robinson, H.S., McNutt, J.W., Kelly, M.J., 2019. Sampling design and analytical advances allow for simultaneous density estimation of seven sympatric carnivore species from camera trap data. Biol. Conserv 233, 12–20. https://doi.org/10.1016/j.biocon.2019.02.018.

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., de Iongh, H., Lichtenfeld, L., Pimm, S., 2013. The size of savannah Africa: A lion's (Panthera leo) view. Biodivers. Conserv 22, 17–35. https://doi.org/10.1007/s10531-012-0381-4.

Rodgers, W.A., 1973. The lion (Panthera leo, Linn.) population of the eastern Selous Game Reserve. East Afr. Wildl. J. 12, 313–317.

Rosenblatt, E., Becker, M.S., Creel, S., Droge, E., Mweetwa, T., Schuette, P.A., Watson, F., Merkle, J., Mwape, H., 2014. Detecting declines of apex carnivores and evaluating their causes: An example with Zambian lions. Biol. Conserv 180, 176–186. https://doi.org/10.1016/j.biocon.2014.10.006.

Rudnai, J., 1973. Reproductive biology of lions (Panthera leo massaica Neumann) in Nairobi National Park. East Afr. Wildl. J. 11, 241–253.

Sanei, A., Zakaria, M., Yusof, E., Roslan, M., 2011. Estimation of leopard population size in a secondary forest within Malaysia's capital agglomeration using unsupervised classification of pugmarks. Trop. Ecol. 52, 209–217.

Sharma, S., Jhala, Y., Sawarkar, V.B., 2005. Identification of individual tigers (Panthera tigris) from their pugmarks. J. Zool. 267, 9–18. https://doi.org/10.1017/S0952836905007119.

Smuts, G.L., 1976. Population characteristics and recent history of lions in two parts of the Kruger National Park. Koedoe 19, 153–164.

Smuts, G.L., Whyte, I.J., Dearlove, T.W., 1977. A mass capture technique for lions. East Afr. Wildl. J. 15, 81–87.

Soisalo, M.K., Cavalcanti, S.M.C., 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture-recapture sampling in combination with GPS radio-telemetry. Biol. Conserv 129, 487–496. https://doi.org/10.1016/j.biocon.2005.11.023.

Stander, E., 1998. Spoor counts as indices of large carnivore populations: the relationship between spoor frequency sampling effort and true density. J. Appl. Ecol. 35, 378–385.

Stander, R.E., 1991. Demography of lions in the Etosha National Park, Namibia. Madoqua 18, 1–9.

Strampelli, P., Campbell, L.A.D., Henschel, P., Nicholson, S.K., Macdonald, D.W., Dickman, A.J., 2022a. Trends and biases in African large carnivore population assessments: identifying priorities and opportunities from a systematic review of two decades of research. PeerJ 10. https://doi.org/10.7717/PEERJ.14354.

Strampelli, P., Searle, C.E., Smit, J.B., Henschel, P., Mkuburo, L., Ikanda, D., Macdonald, D.W., Dickman, A.J., 2022b. Camera trapping and spatially explicit capture–recapture for the monitoring and conservation management of lions: Insights from a globally important population in Tanzania. Ecol. Solut. Evid. 3 https://doi.org/10.1002/2688-8319.12129.

Tende, T., Ottosson, U., Hansson, B., Kesson, M.A., Bensch, S., 2010. Population size of lions in Yankari Game Reserve as revealed by faecal DNA sampling. Afr. J. Ecol. 48, 949–952.

Tende, T., Hansson, B., Ottosson, U., Åkesson, M., Bensch, S., 2014. Individual identification and genetic variation of lions (Panthera leo) from two protected areas in Nigeria. PLoS One 9. https://doi.org/10.1371/journal.pone.0084288.

Thompson, C.M., Royle, J.A., Garner, J.D., 2012. A framework for inference about carnivore density from unstructured spatial sampling of scat using detector dogs. J. Wildl. Manag. 76, 863–871. https://doi.org/10.1002/jwmg.317.

Trinkel, M., 2009. A keystone predator at risk? Density and distribution of the spotted hyena (Crocuta crocuta) in the Etosha National Park, Namibia. Can. J. Zool. 87, 941–947. https://doi.org/10.1139/Z09-082.

Van Damme, P., De Cordier, B., 2017. From Lake Chad to Somalia: wither the aid order? Afr. Focus.

Verschueren, S., Fabiano, E.C., Kakove, M., Cristescu, B., Marker, L., 2023. Reducing identification errors of African carnivores from photographs through computer-assisted workflow. Mamm. Res 68, 121–125. https://doi.org/10.1007/s13364-022-00657-z.

Vissia, S., Wadhwa, R., van Langevelde, F., 2021. Co-occurrence of high densities of brown hyena and spotted hyena in central Tuli, Botswana. J. Zool. 314, 143–150. https://doi.org/10.1111/jzo.12873.

Western, G., Elliot, N.B., Sompeta, S.L., Broekhuis, F., Ngene, S., Gopalaswamy, A.M., 2022. Lions in a coexistence landscape: Repurposing a traditional field technique to monitor an elusive carnivore. Ecol. Evol. 12 https://doi.org/10.1002/ece3.8662.

Wilson, G., Delahay, R., 2001. A review of methods to estimate the abundance of terrestrial carnivores using field signs and observations. Wildl. Res. 28, 151–164.

Winterbach, C.W., Ferreira, S.M., Funston, P.J., Somers, M.J., 2016. Simplified large African carnivore density estimators from track indices. PeerJ 2016. https://doi.org/10.7717/peerj.2662.

Wolf, C., Ripple, W.J., 2017. Range contractions of the world's large carnivores. R. Soc. Open Sci. 4 https://doi.org/10.1098/rsos.170052.

Yirga, G., Gebresenbet, F., Deckers, J., Bauer, H., 2014. Status of Lion (Panthera leo) and Spotted Hyena (Crocuta crocuta) in Nechisar National Park, Ethiopia. Momona Ethiop. J. Sci. (MEJS).

Yirga, G., Amare, S., Gebresenbet, F., De Iongh, H.H., Vos, M., Sillero-Zubiri, C., Bauer, H., 2021. Lion (Panthera leo) ecology and survival in protected areas of Ethiopia. Mamm. Biol. 101, 791–801. https://doi.org/10.1007/s42991-021-00137-y.

Young-Overton, K.D., Funston, P.J., Ferreira, S.M., 2014. Rainfall driven changes in behavioural responses confound measuring trends in lion population size. Wildl. Biol. 20, 344–355. https://doi.org/10.2981/wlb.00015.