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REVIEW

A review of spotted hyaena population estimates highlights the need for greater utilisation of spatial capture-recapture methods

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Abstract. As apex predators with a regulating effect on interspecific competitors and prey demographics, monitoring of spotted hyaena (*Crocuta crocuta*) population trends can provide a reliable indicator of ecosystem health. However, the ability of current survey techniques to monitor carnivore densities effectively are increasingly questioned. This has led recent studies to advocate increased application of spatial capture-recapture (SCR) methods to estimate population density for large carnivores. We reviewed the literature regarding methods used to estimate population density for spotted hyaena since 2000. Our review found that SCR methods are underutilised for estimating spotted hyaena density, with only eight published studies (13% of articles assessed) using an SCR approach. Call-in surveys were the most frequently used method, featuring in 47% of studies. However, 63% of studies that used call-in surveys could not estimate a site-specific calibration index. The calibration index estimates the distance and rate at which the focal species responds to audio lures and, as response rates are impacted by site-specific ecological and environmental factors, studies that could not calibrate this index are likely inaccurate. Further application of SCR techniques will allow more robust estimation of spotted hyaena density, reducing uncertainty and potential overestimation that limit inference from existing survey methods.

Key words: call-in survey, density, population monitoring, survey methods, track counts

Introduction

Robust population estimates play a pivotal role in the implementation of effective conservation management strategies, reintroduction efforts and monitoring schemes (Hayward et al. 2015). As large carnivore populations continue to experience wide-scale declines (Ripple et al. 2014), robust methods for assessing density and population trends must be at the forefront of evidence-based conservation management (Hayward et al. 2015, Elliot & Gopalaswamy 2017). However, accurate data are often lacking for large carnivores, due to their cryptic behaviour and naturally low densities (Balme et al. 2009, Elliot & Gopalaswamy 2017). In addition, available estimates are often outdated,

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overestimated or subject to a high degree of uncertainty (Braczkowski et al. 2020a). The paucity of reliable data can impact the management of target species and, inadvertently, have a cascading effect on the management of other vulnerable species. For example, intraguild competition can have a detrimental effect on threatened or reintroduced carnivores, such as cheetah (*Acinonyx jubatus*) and African wild dog (*Lycaon pictus*), so reliable density estimates for sympatric large carnivores can provide a valuable metric for reintroduction success (Darnell et al. 2014, Weise et al. 2015).

Spotted hyaena: indicators of ecosystem health

Spotted hyaena (*Crocuta crocuta*) are widespread, social carnivores that occupy a broad range of habitats in sub-Saharan Africa, from sparse deserts to montane woodlands and suburban areas (Holekamp et al. 2012, Yirga et al. 2014). As the most abundant large carnivore in Africa (Watts & Holekamp 2008), spotted hyaena are routinely overlooked as a species of conservation concern. Instead, research has generally focused on spotted hyaena behavioural ecology (Dheer et al. 2022). However, the spotted hyaena is often maligned and subject to high levels of persecution, particularly outside protected areas (Bohm & Höner 2015). In addition, threats such as loss of natural prey, human-wildlife conflict and susceptibility to wire snaring and poisoning, are contributing to declines in spotted hyaena populations across Africa (Frank et al. 2011, Bohm & Höner 2015, Wolf & Ripple 2016, Loveridge et al. 2020). Loveridge et al. (2020) highlighted that wire-snaring is a particular conservation concern, with spotted hyaena representing 92% of large carnivore snaring records in the Zimbabwean region of the Kavango-Zambezi Transfrontier Conservation Area and, as such, the species' conservation status warrants further attention.

Spotted hyaena density varies greatly across their geographic range, from 0.85/100 km^2 in arid environments (Fouché et al. 2020) up to 165/100 km^2 in prey-rich East African savanna ecosystems (Watts & Holekamp 2008). As a dominant member of the large carnivore guild, spotted hyaena play an integral role in ecosystem services by regulating prey numbers, providing carrion for scavengers, and influencing carnivore dynamics through interspecific competition (Périquet et al. 2015, Green et al. 2018). Furthermore, spotted hyaena exhibit high levels of behavioural plasticity that enable them to persist in landscapes where other carnivores cannot compete (Holekamp & Dloniak 2010, Green et al. 2019). High behavioural plasticity makes spotted hyaena good models for assessing environmental change and monitoring wider ecosystem health (Trinkel 2009, Green et al. 2018, 2019). For example, increasing spotted hyaena population density can be an early indicator of competitive release from the regulating effect of competition with lions (*Panthera leo*) and signify declining trends in sympatric carnivores (M'soka et al. 2016, Green et al. 2018).

Current methods limit inference

Uncertainty regarding estimates of population size or density often stems from underlying issues with the survey methodologies employed for large carnivores. The challenges associated with surveying elusive, wide-ranging and often nocturnal large carnivores, combined with the need for rapid and cost-effective survey methods, has led to extensive use of index-calibrated methods to survey large carnivores (Mills et al. 2001, Funston et al. 2010, Winterbach et al. 2016). Index-calibrated methods assume a stable linear relationship between a measurable index (e.g. number of tracks or scats per km searched) and true population density (Funston et al. 2010) and, as these methods tend not to rely on direct observations, they are quicker and cheaper to conduct than more labour-intensive methods such as camera trapping or search-encounter techniques (Balme et al. 2009, Midlane et al. 2015).

In Africa, the use of two index-calibrated methods, track counts and call-in surveys, have frequently been employed to estimate density for spotted hyaena and other large carnivores (Croes et al. 2011, Aebischer et al. 2020, Henschel et al. 2020). However, the capacity of index-calibrated methods to account for variance in detection probability and spatial heterogeneity, whilst overestimating the precision of the putative index to successfully predict true density, has led to concerns that these methods produce spurious estimates and wide error margins (Gopalaswamy et al. 2015, Belant et al. 2019, Dröge et al. 2020). In some cases, confidence intervals do not include the true population size (Belant et al. 2019, Dröge et al. 2020) or are wide enough that inferences on population trends would be meaningless as a basis for conservation management decisions (e.g. Bouché et al. 2016, Bauer et al. 2017). Consequently, numerous authors have cautioned against the widespread application of index-calibrated methods to infer population trends and inform management and policy decisions (e.g. Rosenblatt et al. 2014, Gopalaswamy et al. 2015, Hayward et al. 2015, Dröge et al. 2020).

Call-in surveys, whereby acoustic lures (i.e. prey distress sounds or carnivore social calls) are played from a calling station and a calibration response index applied to estimate population size from the response rate (Mills et al. 2001), are commonly used to survey spotted hyaena and lion populations. Despite the popularity of this method, call-in surveys have several limitations that reduce the precision and inference of results (Elliot & Gopalaswamy 2017, Dröge et al. 2020). The calibration index is a key assumption in call-in surveys that determines the distance at which animals hear and respond to the acoustic lure (see Mills et al. 2001 for a description of the required experiment). Conducting call-in calibration experiments is difficult in dense habitats or areas where animals are not well habituated (Bauer 2007, Cozzi et al. 2013). As a result, researchers are often reliant on previous calibration estimates that may not accurately reflect their study site or population and, consequently, impact the precision of results (Kirsten et al. 2017). Furthermore, attempts to estimate response radius in areas of low density and restricted access can add further time constraints and financial costs, with potentially negative consequences for habituation (Midlane et al. 2015).

Emergence of spatial capture-recapture

In the last two decades, spatial capture-recapture (SCR) modelling has emerged as a reliable and robust technique from which to estimate population density for species that can be individually identified (Efford 2004, Borchers & Efford 2008, Royle et al. 2018). SCR methods utilise the spatial information associated with individual encounter history data to model the movement and distribution of individuals across a defined state space (Royle et al. 2014). The incorporation of a spatially explicit framework distinguishes SCR from conventional capture-recapture (CR) models, thereby addressing the challenges of buffering, heterogeneity in detection probability and trap-level variation that can limit inference from traditional CR studies (Royle et al. 2014). SCR methods are commonly associated with camera trap data, where individuals are often identified through their unique pelage patterns, although these models can also be applied to DNA sampling, acoustic surveys and search-encounter methods, and have been used to estimate density for a wide-range of global taxa (e.g. Sutherland et al. 2016, Sun et al. 2017, López-Bao et al. 2018, Balme et al. 2019). As SCR models have developed to incorporate additional covariates (e.g. age and sex; Sollmann et al. 2011) and supplementary data (e.g. movement data from radio/GPS collars; Royle et al. 2013), the use of SCR has become the standard method for obtaining reliable population estimates for many species with unique identification features (Royle et al. 2018). Despite the growing application and sophistication of SCR models, recent studies have highlighted that SCR approaches have been underutilised for multiple large carnivore species, including lions (Braczkowski et al. 2020a), snow leopards (*Panthera uncia*; Alexander et al. 2015, Sharma & Singh 2020) and wolves (*Canis lupus*; López-Bao et al. 2018).

In this study we review and critically assess the literature on spotted hyaena population estimates and survey methodologies by 1) evaluating the survey methods used to estimate spotted hyaena density and their geographical distribution; 2) discussing the limitations of current spotted hyaena survey methodology; and 3) highlighting the potential for future utilisation of SCR methods, whilst identifying possible survey considerations within the SCR framework for estimating spotted hyaena density.

Material and Methods

We followed the protocol of Braczkowski et al. (2020a) to conduct our literature review and searched for peer-reviewed articles on two comprehensive databases: Web of Science and Google Scholar. We used the following keyword combinations to search for peer-reviewed literature: "spotted hyaena" AND "density" OR "population size" OR "numbers". We then repeated this process, replacing the keyword "spotted hyaena" with "*Crocuta crocuta*" (accounting for the English/US spelling hyaena/hyena) and the same density keyword variations. To remove bias in our search we limited the date range from 2000 to 2020, as SCR models were only developed towards the end of the 20th century (Royle et al. 2014). We checked all search pages for the Web of Science results but limited our Google Scholar results to the first 100 articles. All articles were inspected, and excluded when: 1) there were no population estimates, 2) only when previous or unpublished estimates of

Table 1. Definitions of survey methods used to estimate spotted hyaena density and key literature that details each methodology.

Survey method	Definition	Key literature
Call-in survey	Audio lures (prey distress calls and/or carnivore social calls) are played through loudspeakers to attract large carnivores. The number of responding individuals are recorded and a calibration index applied, whereby the maximum distance a species will respond from is calculated.	Mills et al. 2001, Ferreira & Funston 2016
Track count	Surveys are often road based and consist of driving transects at slow speeds. Tracks encountered are identified to species level, from which track density per 100 km is calculated. Previously estimated models for substrate type and species (see key literature) are then applied to predict true density.	Funston et al. 2010, Winterbach et al. 2016
Spatial capture-recapture (SCR)	SCR models make use of the spatial location of encounter history data to determine an individual's activity centre and uses these data to estimate the density of activity centres across a precisely defined polygon, known as the state space, which contains the trap array. Can be applied to several types of trapping data, e.g. camera trapping, DNA sampling, mist netting, cover boards/ refugia.	Borcher & Efford 2008, Royle et al. 2014
Capture-recapture	Individually unique identifiers (e.g. pelage patterns, ear tags) are used to gather encounter history data. Abundance estimates are calculated based on the number of individuals captured and frequency of recaptures. Density can then be obtained by estimating an effective trapping area and dividing the abundance estimate by the sampled area.	Otis et al. 1978, Karanth & Nichols 1998
Distance sampling	Fixed-width transect surveys are conducted where target animals encountered are recorded, along with distance and angle from transect intercept. Density can then be calculated by modelling a fitted detection function, that can predict detection probability as a function of distance from the transect line.	Buckland et al. 2015
Total count	Population size is estimated by counting all observed individuals over a specified length of time. Counts can use individual identification to limit the effect of double counting.	Gese 2001

density or population size were cited; and/or 3) the survey method used was not explicitly stated. For studies that matched our criteria, we recorded the survey method used to estimate population size or density and calculated the total proportion of articles each method featured in. Table 1 provides definitions of survey methods documented in the literature to estimate spotted hyaena density. For studies that used call-in survey methods we also recorded if the study was able to calibrate a site-specific response rate.

We assessed the spatial coverage of published estimates to determine any geographical preference for individual survey techniques. We recorded the country of each study and calculated the total number of studies per country. We documented the survey method used in each study and, using the geographic regions documented by the African Union (African Union 2020), calculated the total number of times each method was used per region.

Results

We reviewed 153 published studies on spotted hyaena from 19 African countries, in 49 different journals. We identified 60 studies, in 29 journals, that reported population estimates and detailed how these estimates were obtained (Table S1).

Preferred methods for population estimates

Overall, six survey methods were used to estimate spotted hyaena population density. Of the 60 studies assessed, 58 used one survey method

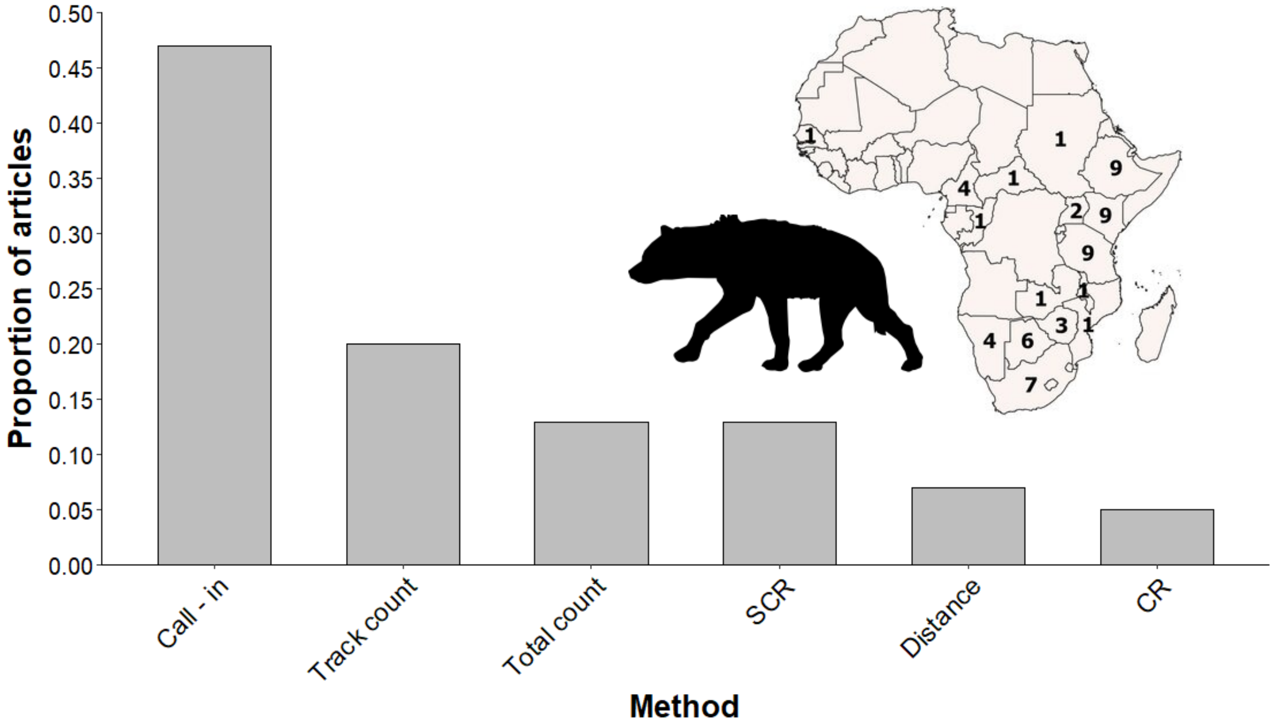

Fig. 1. Survey methods used to obtain estimates of spotted hyaena density or population size and the proportion of reviewed articles that applied each survey method. Insert map shows the location of published studies from sub-Saharan Africa and the number of studies from each country where estimates were available. Hyaena silhouette: PhyloPic 2019.

(97% of studies) and two used multiple methods. Call-in surveys were the most frequently used method, featuring in 46.6% of the articles assessed (n = 28 studies; Fig. 1). Of the 27 studies (one study was removed that used N-mixture models and did not require a calibration index) that used call-in methods, over half (63%) were unable to undertake their own calibration experiments to estimate site-specific response distances of spotted hyaena. Index-calibrated methods (call-in surveys and track counts) were used in 63.3% of studies (n = 38 studies). SCR methods were used in eight studies, 13.3% of articles, with only one study published prior to 2019. Camera traps were used to estimate spotted hyaena density in seven of the eight SCR studies, with a search-encounter method, based on visual identification, used in one study. Of the eight studies that used SCR methods, seven of these studies had a multi-species focus, estimating density for spotted hyaena and at least one other species.

Spatial coverage of survey methods

Density/abundance estimates were available for spotted hyaena populations in 16 African countries, representing 41% of spotted hyaena range states. Studies from East (50% of studies) and Southern (38.3% of studies) Africa accounted for the majority of available estimates (Table 2). There were six studies from the Central African region and one population estimate from West Africa. Call-in surveys or track counts were the most frequently used methods in all four regions. All population estimates using total counts and distance sampling were from East Africa, specifically in Kenya and Tanzania. Six of the eight population estimates derived from SCR methods were conducted in Southern Africa.

Discussion

Here we found that SCR methods are currently underutilised for estimating spotted hyaena density, compared to other available methods. However, with seven of the eight studies using SCR methods published since 2019, this may indicate a growing change in preferred survey methodology. Despite the increase in SCR-derived estimates for spotted hyaena, the number of published studies utilising SCR methods is still relatively low when compared to sympatric carnivores. For example, 57% of published studies (n = 27) estimating leopard (*Panthera pardus*) density in sub-Saharan Africa, since 2000, used SCR methods (see Table S2). Spotted hyaena population estimates are also limited to only 16

Table 2. Number of times individual survey methods were used to estimate spotted hyaena density and/or population size by region and country. Individual survey methods include call-ins, track counts (Track), total counts of individuals (Total), distance sampling (Distance), spatial capture-recapture (SCR) and capture-recapture (CR). Note that the total number of times methods were used here (n = 54) is larger than the number of published studies found in the review (n = 51 studies) as two studies used multiple methods.

	Method					
Region/Country	Call-in	Track	Total	Distance	SCR	CR
East Africa	15	1	8	4	2	-
Ethiopia	8	-	-	1	-	-
Kenya	1	1	5	1	1	-
Sudan	1	-	-	-	-	-
Tanzania	4	-	3	2	-	-
Uganda	1	-	-	-	1	-
Southern Africa	9	8	-	-	6	2
Botswana	2	3	-	-	3	-
Malawi	-	-	-	-	1	-
Mozambique	1	-	-	-	-	-
Namibia	1	1	-	-	1	1
South Africa	5	2	-	-	1	-
Zambia	-	-	-	-	-	1
Zimbabwe	1	2	-	-	-	-
Central Africa	3	3	-	-	-	1
Cameroon	2	2	-	-	-	-
Central African Republic	1	1	-	-	-	-
Republic of Congo	-	-	-	-	-	1
West Africa	1	-	-	-	-	-
Senegal	1	-	-	-	-	-
Total	28	12	8	4	8	3

out of 39 African countries where the species is resident (Bohm & Höner 2015), which evidences that just under two-thirds of range states lack baseline density estimates. Since spotted hyaena density varies considerably between habitats and with levels of anthropogenic disturbance (Yirga et al. 2017, Fouché et al. 2020), there is a need for increased reporting of population estimates from understudied regions to inform local conservation management.

Addressing issues with current methodologies

Our review indicates that call-in surveys are the most frequently used method for estimating spotted hyaena density. However, calculating a site-specific calibration index to estimate response radius remains a significant challenge. This is highlighted here as over half the published studies were unable to conduct site-specific calibration experiments. In addition, some authors acknowledged that their calibration indices were unreliable and subject to wide confidence limits, owing to small sample sizes (e.g. Ogutu et al. 2005). Studies that could not conduct their own calibration experiment often used the calibration estimates provided in Mills et al. (2001). Some studies (e.g. Kirsten et al. 2017, Mohammed et al. 2019) cited Bauer (2007) as the basis for their calibration response, despite this study not conducting independent calibration experiments. A lack of animal habituation and logistical feasibility were often cited as key reasons for not undertaking the calibration experiment. Site-specific differences in habitat structure, competing carnivore densities and anthropogenic disturbance are likely to affect the local response rate of spotted hyaena. Subsequently, it is unlikely these frequently cited calibration indices are widely applicable and corresponding estimates are likely to be inaccurate.

Call-in surveys can also suffer from issues with habituation. For example, Belant et al. (2016) found that lions quickly become habituated to audio lures and habituation levels are not reduced by temporal and spatial variation in calls. As a result, calibration experiments may lower species response rates during survey periods. Habituation from repeated call-in surveys could also impact response rates over multi-season surveys, with a lower response rate potentially leading to incorrect assumptions of population decline over time (Belant et al. 2016). In addition, response rate to acoustic lures can also be reduced in areas where competing carnivore densities are skewed, or human activity is prevalent (Midlane et al. 2015, Kirsten et al. 2017). For example, areas of high lion density can limit the response rate of spotted hyaena (Kiffner et al. 2007, Kirsten et al. 2017), whilst cautious behaviour in areas of increased human disturbance can mean responding individuals are still potentially missed (Bauer 2007). As such, call-in surveys are often of limited value for multi-species surveys and can be inaccurate in low density areas, where population estimates are often most urgently required.

Call-in surveys are an effective tool for confirming the presence of spotted hyaena, and other large carnivores, in understudied regions where conservation efforts have been restricted. For example, the presence of spotted hyaena and lion in Dinder National Park, Sudan, were recently confirmed through call-in surveys (Mohammed et al. 2019). Furthermore, we recognise that call-in surveys are beneficial for obtaining population estimates in areas that are logistically challenging for other survey methods, such as camera trapping. This is highlighted in our review by the extensive use of call-in surveys in Ethiopia, where studies were conducted in peri-urban areas that would make the use of other survey techniques difficult (Yirga et al. 2014, 2017). Where call-in surveys are conducted, we suggest efforts are made to identify responding individuals (Trinkel 2009) and this method has recently been trialled for lions at call-in surveys (Western et al. 2022). However, we appreciate that identifying and documenting individuals at call-in surveys can be difficult with cautious animals and low visibility habitats (Bauer 2007). The collection of individual encounter data at call-in surveys would allow these data to be analysed in an SCR framework (Elliot & Gopalaswamy 2017), if surveys were repeated, thereby improving precision, avoiding double counting, and accounting for imperfect detection. Going forward, we recommend that call-in surveys either adopt an SCR approach to data collection or the survey method is employed as an initial step to confirm species presence.

Track counts were the second most popular method for estimating spotted hyaena density and were represented in a fifth of all published articles. Despite the popularity of track counts, derived population estimates often have wide confidence intervals and overstated precision (Elliot & Gopalaswamy 2017, Belant et al. 2019, Dröge et al. 2020). Low precision stems from unmodelled detection probability and oversimplification of the variance in the relationship between track density and true population density in the initial linear equation (Gopalaswamy et al. 2015, Hayward et al. 2015, Dröge et al. 2020). Dröge et al. (2020) argued that track counts do not comply with IUCN guidelines for population monitoring, as estimates may not be accurate enough to monitor population trends over time. In addition, track counts are reliant on standardised methods and assumptions. A key assumption is that all animals in the surveyed region have the same probability of detection, regardless of environmental (e.g. prey availability, interspecific competition) or anthropogenic (increased human activity) variability (Elliot & Gopalaswamy 2017, Henschel et al. 2020). In the case of spotted hyaena, this assumption is difficult to meet, with spotted hyaena behaviour known to be influenced by human activity (Boydston et al. 2003, Belton et al. 2016), areas of increased prey availability (Davis et al. 2021b) and competition with lions (Périquet et al. 2015). Violating the assumption of equal detection results in underestimation of density (Henschel et al. 2020), with knock on effects for conservation management decisions. It is, therefore, difficult to make a strong case for the future use of track count surveys to monitor spotted hyaena populations.

When analysed in an occupancy framework, track counts are efficient and cost-effective for gathering large carnivore presence/absence data. The limitations of track count data are better incorporated into model inference within occupancy models, as they account for imperfect detection and allow the use of covariates to model heterogeneity in site-use estimates (MacKenzie et al. 2017). Track count data have provided valuable insights into the distribution and drivers of site use for multiple large carnivore species in Africa (e.g. Everatt et al. 2014, Henschel et al. 2016, Petracca et al. 2019) and we encourage further use of occupancy models over index-calibrated density estimates (Dröge et al. 2020). However, efforts to estimate density from occupancy models are cautioned against due to variability in spatial use and home-range utilisation (Link et al. 2018, Rogan et al. 2019).

Distance sampling and total count methods were used in 12 studies to estimate spotted hyaena density or population size, mainly from Kenya and Tanzania, notable for their wide-open grasslands and high visibility (Durant et al. 2011, Farr et al. 2019). Whilst these surveys were able to estimate spotted hyaena density, these models are reliant on open habitats and the study species being reasonably habituated to human presence (Durant et al. 2011). Furthermore, studies that conducted distance sampling in Kenya and Tanzania were able to observe spotted hyaena during daylight hours (Durant et al. 2011). Often spotted hyaena are more nocturnal in areas of anthropogenic disturbance (Kolowski et al. 2007). As such, the wider applicability of distance sampling and total counts appears limited, with low capture success in areas of reduced visibility (e.g. dense woodlands) and/or high levels of anthropogenic disturbance making robust estimates unlikely, or requiring intensive survey effort (e.g. Thorn et al. 2010, Burton et al. 2011). With ≥ 60 observations recommended for robust estimates from distance sampling (Buckland et al. 2015), and reliable data on observed distance and angle necessary, these methods are not applicable across a considerable area of the spotted hyaena's geographical range. Certainly, if the aim of conservation practitioners is to compare population trends between sympatric carnivores, total counts are not a replicable model as the survey method is not viable for more cryptic species.

Total counts were used in long-term studies in Kenya and Tanzania to assess temporal changes in demography and population size (Höner et al. 2005, Green et al. 2018). Whilst direct counts employed for spotted hyaena did incorporate individual identification, allowing for more robust estimates of population size and avoidance of double counting, the time and effort required for direct counts is better combined with long-term behavioural studies (Gese 2001). As these long-term studies often know all individual spotted hyaenas within the study area at any given time (Höner et al. 2005), these sites may provide a unique opportunity to compare the efficacy and accuracy of SCR methods and other survey techniques (as per Rafiq et al. 2019).

Towards robust estimates with SCR

The development of SCR models has overcome several of the issues that limit inference from conventional survey methods for spotted hyaena. Most notably, the incorporation of detection probability and survey effort into SCR models improves the precision of estimates, compared to the wide error margins associated with index-calibrated methods (Broekhuis & Gopalaswamy 2016, Braczkowski et al. 2020a). However, a recent review by Green et al. (2020) found that some SCR density estimates from camera trapping lacked the necessary precision for monitoring population trends over time, with precision increasing when more individuals from the study population were captured. Inference from large carnivore survey methods is often hampered by naturally low densities and small sample sizes, leading to inaccuracies or cautious estimation of population size (Bauer 2007, Winterbach et al. 2016). As small sample sizes are common in spotted hyaena studies (e.g. Mohammed et al. 2019, Fouché et al. 2020, Davis et al. 2021a), by extracting the individual and spatial information from encounter history data, SCR models can be used to make effective use of limited datasets and produce statistically robust estimates (Royle et al. 2014, 2018). Furthermore, by accounting for the spatial location of captures, SCR models allow for estimation of fine-scale variation in density across landscapes (Gopalaswamy et al. 2012). Covariates of interest (e.g. prey density, illegal activity) can also be included in SCR models to investigate potential drivers of spatial distribution, providing a more comprehensive understanding of species density and distribution, thereby informing conservation management (Broekhuis & Gopalaswamy 2016, Ramesh et al. 2017).

Current preferred survey methods for spotted hyaena fail to capitalise on the benefits of individual identification, which can provide additional metrics for assessing population health (Braczkowski et al. 2020a). Information on animal movement, sex ratios and survival rates are embedded within individual encounter history data (Karanth et al. 2006). Key indicators of population decline, or recovery, can be assessed by monitoring parameters derived from individual identification (Harmsen et al. 2017, Braczkowski et al. 2020a). For example, Duangchantrasiri et al. (2016) used survival rates from repeated SCR surveys to determine the efficacy of increased law enforcement efforts for tiger (*Panthera tigris*) population recovery. Using sex-specific movement parameters and calculated sex ratios derived from SCR estimates, Braczkowski et al. (2020b) highlighted increased home range movements and male-biased sex ratios as early indicators of potential collapse in lion population numbers.

In addition, the SCR approach is flexible, lending itself to direct (e.g. search-encounter; Broekhuis & Gopalaswamy 2016) and indirect (e.g. camera trapping; Rich et al. 2019) methods, allowing researchers to select appropriate methodologies for their study site and population. As spotted hyaena occupy a diverse array of habitats and display varying behavioural responses to anthropogenic disturbance (Belton et al. 2016, Yirga et al. 2017), the flexibility of applying SCR models to individual encounter history data provides a standardised framework to monitor the species throughout their range. For example, the open grassland habitats of East Africa would be appropriate for search-encounter methods, as spotted hyaena are regularly encountered in daylight hours and distance sampling techniques are a viable approach. Furthermore, the dense vegetation and high levels of human disturbance documented in countries, such as Cameroon (Croes et al. 2011, Kirsten et al. 2017), would benefit from applying SCR models to frequently used indirect methods, like camera trapping or DNA sampling.

SCR methods have been widely applied to estimate felid densities across Africa, with camera trap surveys routinely used to obtain encounter history data (e.g. Brassine & Parker 2015, Kane et al. 2015, Balme et al. 2019). Spotted hyaena are widely distributed across sub-Saharan Africa and are likely caught as bycatch on camera trap surveys undertaken for sympatric carnivores (e.g. Williams et al. 2020). However, spotted hyaena population estimates are rarely reported from these surveys, despite data occasionally being used as covariates to make inferences about the behaviour or density of the focal species (e.g. Ramesh et al. 2017, Balme et al. 2019). Of the eight studies using SCR methods to estimate spotted hyaena density, seven of these studies had a multi-species focus (e.g. O'Brien & Kinnaird 2011, Rich et al. 2019, Davis et al. 2021a, Vissia et al. 2021). Thereby highlighting that SCR estimates for spotted hyaena can be obtained from camera trap grids with a multi-species focus. A key requirement of SCR is that individuals are captured at multiple detectors, to estimate the spatial scale parameter (σ) reliably (Dupont et al. 2021). This has led to recommendations in trap spacing, whereby trap spacing should be approximately two times σ, thus ensuring multiple traps are placed within an individuals' home range (Sollmann et al. 2012, Sun et al. 2014). As spotted hyaena home ranges are often larger than competing carnivores of interest (e.g. leopard, cheetah), sampling arrays designed for other large carnivores should not violate this assumption for spotted hyaena (Davis et al. 2021a, Braczkowski et al. 2022). Increased reporting of spotted hyaena density, from studies where they may have been previously overlooked, would be beneficial for the conservation management of spotted hyaena and interspecific competitors.

One of the limitations of an SCR approach is the cost of equipment and/or survey effort (Balme et al. 2009, Rafiq et al. 2019, Braczkowski et al. 2020a). We acknowledge that call-in surveys and track counts are often cheaper to conduct (Balme et al. 2009). However, the improvements in precision and benefits of individual identification for long-term population monitoring means that SCR-derived estimates can provide a greater balance of accuracy and cost-effectiveness (Balme et al. 2009, Braczkowski et al. 2020a). In addition, the multi-species SCR approaches of both Rich et al. (2019), using camera traps, and Rafiq et al. (2019), using tourist photographic records, demonstrate the ability of SCR techniques to survey multiple large carnivore species simultaneously, thereby optimising survey costs. In areas where there is high tourism demand, the citizen science approach of Rafiq et al. (2019) has shown that SCR estimates are obtainable at considerably reduced costs. Where a citizen science approach is not possible, a viable option for reducing camera trap survey costs is the utilisation of spatial partial identity models (Augustine et al. 2018) which can produce robust SCR estimates from partial identity samples obtained using single camera trap stations, instead of the conventional dual camera survey design (Davis et al. 2021a).

Sexing spotted hyaena, particularly from camera trap images, could be a potential constraint of SCR methods for estimating spotted hyaena density. Sex-specific variation in space use and movement result in differences in detection probability and, where possible, should be incorporated into candidate models (Sollmann et al. 2011). However, movement patterns between male and female spotted hyaena are known to differ (Boydston et al. 2005, Kolowski et al. 2007) and the species is notoriously difficult to sex (Dheer et al. 2022). Therefore, incorrect classification could result in skewed sex ratios and reduced accountability for heterogeneity in the observation process. Consequently, any attempt to incorporate sex-specific variation should be reliant on agreement between multiple trained observers (see Dheer et al. 2022 for recommendations on sexing) or, in the case of long-term research projects, the incorporation of maintained identification databases to ascertain sex. Alternatively, aging spotted hyaena based on their spot patterns and coat wear is relatively easy (e.g. age groupings in M'soka et al. 2016). As movement patterns also vary between age groups in spotted hyaena (Boydston et al. 2005), the incorporation of age classes into SCR models could improve model inference whilst accounting for variation in detection probability.

A key assumption of SCR models is that individual activity centres are uniformly and independently distributed over the state space (a region that incorporates the study area and a defined buffer which includes all potential activity centres for sampled individuals; Royle et al. 2014). However, this assumption is often violated in social, group-living carnivores (e.g. lions, wolves), potentially influencing precision and affecting the underlying state process model (Bischof et al. 2020). As spotted hyaena are social carnivores, living in clans ranging from 5-90 individuals (Holekamp et al. 2012), these assumptions represent a possible source of bias in SCR-derived estimates. Despite their close-knit social groups, spotted hyaena display fission-fusion dynamics, whereby clan members are often found alone or in smaller subgroups that are subject to compositional change, and, as such, individual encounter history data is often collected. For example, Stratford et al. (2019) found that 62% of recorded camera trap images of spotted hyaena were lone individuals. As individual movements represent a large proportion of encounter history data, the impact on precision and interval coverage will likely be reduced (see Bischof et al. 2020). Indeed, simulations by López-Bao et al. (2018) have shown that SCR models can provide reliable outputs for species violating assumptions of dependence in activity centres. However, further development of SCR models that can incorporate fission-fusion dynamics and group association into the state point process are required (Elliot & Gopalaswamy 2017, Bischof et al. 2020).

Conclusions

Call-in surveys and track counts are currently the preferred methods for estimating spotted hyaena density. However, the efficacy of these methods has recently been questioned for long-term population monitoring (Gopalaswamy et al. 2015, Dröge et al. 2020, Elliot et al. 2020). In comparison, SCR methods have the potential to monitor population change and assess trends in survival (by including individual identification and movement parameters), whilst incorporating environmental attributes (e.g. prey density) and demographic covariates (Karanth et al. 2006, Braczkowski et al. 2020b). Index-calibrated methods account for almost two-thirds of available spotted hyaena estimates but often overestimate density or are subject to wide confidence intervals, creating uncertainty in population size and stability (Braczkowski et al. 2020a, Dröge et al. 2020). We argue that there should be greater concern for the status of spotted hyaena populations across Africa and increased survey efforts for understudied populations. Similar to recent calls for greater utilisation of SCR methods in the conservation management of lion (Braczkowski et al. 2020a) and snow leopard (Sharma & Singh 2020) populations. Here we recommend adoption of an SCR approach to estimate spotted hyaena density, providing a unified framework for population monitoring across the species' geographic range.

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Author Contributions

All authors conceived the study. R. Davis performed the literature review and led the writing of the manuscript with input from all authors.

Data Availability Statement

This manuscript is available online in the Nottingham Trent University repository (http://irep.ntu.ac.uk/id/eprint/44543/).

Literature

Aebischer T., Ibrahim T., Hickisch R. et al. 2020: Apex predators decline after an influx of pastoralists in former Central African Republic hunting zones. *Biol. Conserv. 241: 108326.*

African Union 2020: Member states. *https://au.int/en/member_states/countryprofiles2*

Alexander J.S., Gopalaswamy A.M., Shi K. et al. 2015: Face value: towards robust estimates of snow leopard densities. *PLOS ONE 10: e0134815.*

Augustine B.C., Royle J.A., Kelly M.J. et al. 2018: Spatial capture-recapture with partial identity: an application to camera traps. *Ann. Appl. Stat. 12: 67–95.*

Balme G., Hunter L.T.B. & Slotow R. 2009: Evaluating methods for counting cryptic carnivores. *J. Wildl. Manag. 73: 433–441.*

Balme G., Rogan M., Thomas L. et al. 2019: Big cats at large: density, structure, and spatio-temporal patterns of a leopard population free of anthropogenic mortality. *Popul. Ecol. 61: 256–267.*

Bauer H. 2007: Status of large carnivores in Bouba Ndjida National Park, Cameroon. *Afr. J. Ecol. 45: 448.*

Bauer H., Henschel P., Packer C. et al. 2017. Lion trophy hunting in West Africa: a response to Bouché et al. *PLOS ONE 12: e0173691.*

Belant J.L., Bled F., Mkasanga I.J. et al. 2019: Track surveys do not provide accurate or precise lion density estimates in Serengeti. *Glob. Ecol. Conserv. 19: e00651.*

Belant J.L., Bled F., Wilton C.M. et al. 2016: Estimating lion abundance using N-mixture models for social species. *Sci. Rep. 6: e35920.*

Belton L.E., Cameron E.Z. & Dalerum F. 2016: Spotted hyaena space use in relation to human infrastructure inside a protected area. *PeerJ 4: e2596.*

Bischof R., Dupont P., Milleret C. et al. 2020: Consequences of ignoring group association in spatial capture-recapture analysis. *Wildl. Biol. 2020: wlb.00649.*

Bohm T. & Höner O.R. 2015: *Crocuta crocuta*. The IUCN Red List of Threatened Species 2015. *e.T5674A45194782.*

Borchers D.L. & Efford M.G. 2008: Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics 64: 377–385.*

Bouché P., Crosmary W., Kafando P. et al. 2016: Embargo on lion hunting trophies from West Africa: an effective measure or a threat to lion conservation? *PLOS ONE 11: e0155763.*

Boydston E.E., Kapheim K.M., Van Horn R.C. et al. 2005: Sexually dimorphic patterns of space use throughout ontogeny in the spotted hyena (*Crocuta crocuta*). *J. Zool. 267: 271–281.*

Boydston E.E., Kapheim K.M., Watts H.E. et al. 2003: Altered behaviour in spotted hyenas associated with increased human activity. *Anim. Conserv. 6: 207–219.*

Braczkowski A., Gopalaswamy A.M., Elliot N.B. et al. 2020a: Restoring Africa's lions: start with good counts. *Front. Ecol. Evol. 8: 138.*

Braczkowski A., Gopalaswamy A.M., Nsubuga M. et al. 2020b: Detecting early warnings of pressure on an African lion (*Panthera leo*) population in the Queen Elizabeth Conservation Area, Uganda. *Ecol. Solut. Evid. 1: e12015.*

Braczkowski A., Schenk R., Samarasinghe D. et al. 2022: Leopard and spotted hyena densities in the Lake Mburo National Park, southwestern Uganda. *PeerJ 10: e12307.*

Brassine E. & Parker D. 2015: Trapping elusive cats: using intensive camera trapping to estimate the density of a rare African felid. *PLOS ONE 10: e0142508.*

Broekhuis F. & Gopalaswamy A.M. 2016: Counting cats: spatially explicit population estimates of cheetah (*Acinonyx jubatus*) using unstructured sampling data. *PLOS ONE 11: e0153875.*

Buckland S.T., Rexstad E.A., Marques T.A. et al. 2015: Distance sampling: methods and applications. *Springer Publishing, New York, USA.*

Burton A.C., Sam M.K., Kpelle D.G. et al. 2011: Evaluating persistence and its predictors in a West African carnivore community. *Biol. Conserv. 144: 2344–2353.*

Cozzi G., Broekhuis F., McNutt J.W. et al. 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.*

Croes B.M., Funston P.J., Rasmussen G. et al. 2011: The impact of trophy hunting on lions (*Panthera leo*) and other large carnivores in the Bénoué Complex, northern Cameroon. *Biol. Conserv. 144: 3064–3072.*

Darnell A.M., Graf J.A., Somers M.J. et al. 2014: Space use of African wild dogs in relation to other large carnivores. *PLOS ONE 9: e98846.*

Davis R.S., Stone E.L., Gentle L.K. et al. 2021a: Spatial partial identity model reveals low densities of leopard and spotted hyaena in a miombo woodland. *J. Zool. 313: 43–53.*

Davis R.S., Yarnell R.W., Gentle L.K. et al. 2021b: Prey availability and intraguild competition regulate the spatiotemporal dynamics of a modified large carnivore guild. *Ecol. Evol. 11: 7890–7904.*

Dheer A., Simarasinghe D., Dloniak S.M. et al. 2022: Using camera traps to study hyenas: challenges, opportunities, and outlook. *Mamm. Biol. doi: https://doi.org/10.1007/s42991-021-00188-1.*

Dröge E., Creel S., Becker M.S. et al. 2020: Assessing the performance of index calibration survey methods to monitor populations of wide-ranging low-density carnivores. *Ecol. Evol. 10: 3276–3292.*

Duangchantrasiri S., Umponjan M., Simcharoen S. et al. 2016: Dynamics of a low-density tiger population in Southeast Asia in the context of improved law enforcement. *Conserv. Biol. 30: 639–648.*

Dupont G., Royle J.A., Nawaz M.A. et al. 2021: Optimal sampling design for spatial capture-recapture. *Ecology 102: e03262.*

Durant S.M., Craft M.E., Hilborn R. et al. 2011: Long-term trends in carnivore abundance using distance sampling in Serengeti National Park, Tanzania. *J. Appl. Ecol. 48: 1490–1500.*

Efford M. 2004: Density estimation in live-trapping studies. *Oikos 106: 598–610.*

Elliot N.B., Bett A., Chege M. et al. 2020: The importance of reliable monitoring methods for the management of small, isolated populations. *Conserv. Sci. Pract. 2: e217.*

Elliot N.B. & Gopalaswamy A.M. 2017: Toward accurate and precise estimates of lion density. *Conserv. Biol. 31: 934–943.*

Everatt K.T., Andresen L. & Somers M.J. 2014: Trophic scaling and occupancy analysis reveals a lion population limited by top-down anthropogenic pressure in the Limpopo National Park, Mozambique. *PLOS ONE 9: e99389.*

Farr M.T., Green D.S., Holekamp K.E. et al. 2019: Multispecies hierarchical modeling reveals variable responses of African carnivores to management alternatives. *Ecol. Appl. 29: e01845.*

Ferreira S.M. & Funston P.J. 2016: Population estimates of spotted hyaenas in the Kruger National Park, South Africa. *Afr. J. Wildl. Res. 46: 61–70.*

Fouché J., Reilly B.K., de Crom E.P. et al. 2020: Density estimates of spotted hyaenas (*Crocuta crocuta*) on arid farmlands of Namibia. *Afr. J. Ecol. 58: 563-567.*

Frank L.G., Cotterill A., Dolrenry S. et al. 2011: The role of carbofuran in the decline of lions and other carnivores in Kenya. In: Richards N. (ed.), Carbofuran and wildlife poisoning: global perspectives and forensic approaches. *John Wiley & Sons Ltd., Chichester, UK: 70–74.*

Funston P.J., Frank L., Stephens T. et al. 2010: Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *J. Zool. 281: 56–65.*

Gese E.M. 2001: Monitoring of terrestrial carnivore populations. In: Gittleman J.L., Funk S.M., MacDonald D.W. & Wayne R.K. (eds.), Carnivore conservation. *Cambridge University Press & The Zoological Society of London, Cambridge, UK: 372–396.*

Gopalaswamy A.M., Delampady M., Karanth K.U. et al. 2015: An examination of index-calibration experiments: counting tigers at macroecological scales. *Methods Ecol. Evol. 6: 1055–1066.*

Gopalaswamy A.M., Royle J.A., Hines J.E. et al. 2012: Program SPACECAP: software for estimating animal density using spatially explicit capture-recapture models. *Methods Ecol. Evol. 3: 1067–1072.*

Green A.M., Chynoweth M.W. & Sekercioglu C.H. 2020: Spatially explicit capture-recapture through camera trapping: a review of benchmark analyses for wildlife density estimation. *Front. Ecol. Evol. 8: 473.*

Green D.S., Farr M.T., Holekamp K.E. et al. 2019: Can hyena behaviour provide information on population trends of sympatric carnivores? *Philos. Trans. R. Soc. Lond. B. 374: 20180052.*

Green D.S., Johnson-Ulrich L., Couraud H.E. et al. 2018: Anthropogenic disturbance induces opposing population trends in spotted hyenas and African lions. *Biodivers. Conserv. 27: 871–889.*

Harmsen B.J., Foster R.J., Sanchez E. et al. 2017: Long term monitoring of jaguars in the Cockscomb basin wildlife sanctuary, Belize; Implications for camera trap studies of carnivores. *PLOS ONE 12: e0179505.*

Hayward M.W., Boitani L., Burrows N.D. et al. 2015: Ecologists need robust survey designs, sampling and analytical methods. *J. Appl. Ecol. 52: 286–290.*

Henschel P., Petracca L.S., Ferreira S.M. et al. 2020: Census and distribution of large carnivores in the Tsavo national parks, a critical east African wildlife corridor. *Afr. J. Ecol. 58: 383–398.*

Henschel P., Petracca L.S., Hunter L.T. et al. 2016: Determinants of distribution patterns and management needs in a critically endangered lion *Panthera leo* population. *Front. Ecol. Evol. 4: 110.*

Holekamp K.E. & Dloniak S.M. 2010: Intraspecific variation in the behavioral ecology of a tropical carnivore, the spotted hyena. *Adv. Study Behav. 42: 189–229.*

Holekamp K.E., Smith J.E., Strelioff C.C. et al. 2012: Society, demography and genetic structure in the spotted hyena. *Mol. Ecol. 21: 613–632.*

Höner O.P., Wachter B., East M.L. et al. 2005: The effect of prey abundance and foraging tactics on the population dynamics of a social, territorial carnivore, the spotted hyena. *Oikos 108: 544–554.*

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.*

Karanth K.U. & Nichols J.D. 1998: Estimation of tiger densities in India using photographic captures and recaptures. *Ecology 79: 2852–2862.*

Karanth K.U., Nichols J.D., Kumar N.S. et al. 2006: Assessing tiger population dynamics using photographic capture-recapture sampling. *Ecology 87: 2925–2937.*

Kiffner C., Waltert M., Meyer B. et al. 2007: Response of lions (*Panthera leo* Linnaeus 1758) and spotted hyaenas (*Crocuta crocuta* Erxleben 1777) to sound playbacks. *Afr. J. Ecol. 46: 223–226.*

Kirsten I., Bakker C.E., Trujilo L.L. et al. 2017: Lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*) abundance in Bouba Ndjida National Park, Cameroon; trends between 2005 and 2014. *Afr. J. Ecol. 56: 414–417.*

Kolowski J.M., Katan D., Theis K.R. et al. 2007: Daily patterns of activity in the spotted hyena. *J. Mamm. 88: 1017–1028.*

Link W.A., Schofield M.R., Barker R.J. et al. 2018: On the robustness of N-mixture models. *Ecology 99: 1547–1551.*

Loveridge A.J., Sousa L.L., Seymour-Smith J. et al. 2020: Evaluating the spatial intensity and demographic impacts of wire-snare bush-meat poaching on large carnivores. *Biol. Conserv. 244: 108504.*

López-Bao J.V., Godinho R., Pacheco C. et al. 2018: Toward reliable population estimates of wolves by combining spatial capture-recapture models and non-invasive DNA monitoring. *Sci. Rep. 8: 1–8.*

MacKenzie D.I., Nichols J.D., Royle J.A. et al. 2017: Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. *Elsevier, London, UK.*

Midlane N., O'Riain M.J., Balme G.A. et al. 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.*

Mills M.G.L., Juritz J.M. & Zucchini W. 2001: Estimating the size of spotted hyaena (*Crocuta crocuta*) populations through playback recordings allowing for non-response. *Anim. Conserv. 4: 335–343.*

Mohammed A., Bauer H., El Faki A. et al. 2019: Lion and spotted hyaena abundance in Dinder National Park, Sudan. *Afr. J. Ecol. 58: 316–318.*

M'soka J., Creel S., Becker M.S. et al. 2016: Spotted hyaena survival and density in a lion depleted ecosystem: the effects of prey availability, humans and competition between large carnivores in African savannahs. *Biol. Conserv. 201: 348–355.*

O'Brien T.G. & Kinnaird M.F. 2011: Density estimation of sympatric carnivores using spatially explicit capture-recapture methods and standard trapping grid. *Ecol. Appl. 21: 2908–2916.*

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.*

Otis D.L., Burnham K.P., White G.C. et al. 1978: Statistical inference from capture data on closed animal populations. *Wildl. Monogr. 62: 3–135.*

Petracca L.S., Funston P.J., Henschel P. et al. 2019: Modeling community occupancy from line transect data: a case study with large mammals in post-war Angola. *Anim. Conserv. 23: 420–433.*

Périquet S., Fritz H. & Revilla E. 2015: The lion king and the hyaena queen: large carnivore interactions and coexistence. *Biol. Rev. 90: 1197–1214.*

Rafiq K., Bryce C.M., Rich L.N. et al. 2019: Tourist photographs as a scalable framework for wildlife monitoring in protected areas. *Curr. Biol. 29: R681–R682.*

Ramesh T., Kalle R., Rosenlund H. et al. 2017: Low leopard populations in protected areas of Maputaland: a consequence of poaching, habitat condition, abundance of prey, and a top predator. *Ecol. Evol. 7: 1964–1973.*

Rich L.N., Miller D.A., Muñoz D.J. et al. 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.*

Ripple W.J., Estes J.A., Beschta R.L. et al. 2014: Status and ecological effects of the world's largest carnivores. *Science 343: 1241484.*

Rogan M.S., Balme G.A., Distiller G. et al. 2019: The influence of movement on the occupancy–density relationship at small spatial scales. *Ecosphere 10: e02807.*

Rosenblatt E., Becker M.S., Creel S. et al. 2014: Detecting declines of apex carnivores and evaluating their causes: an example with Zambian lions. *Biol. Conserv.* 180: 176–186.

Royle J.A., Chandler R.B., Sollmann R. et al. 2014: Spatial capture-recapture. *Academic Press, Waltham, USA.*

Royle J.A., Chandler R.B., Sun C.C. et al. 2013: Integrating resource selection information with spatial capture-recapture. *Methods Ecol. Evol. 4: 520–530.*

Royle J.A., Fuller A.K. & Sutherland C. 2018: Unifying population and landscape ecology with spatial capture-recapture. *Ecography 41: 444–456.*

Sharma R.K. & Singh R. 2020: Over 100 years of snow leopard research: a spatially explicit review of the state of knowledge in the snow leopard range. *WWF, Gland, Switzerland.*

Sollmann R., Furtado M.M., Gardner B. et al. 2011: Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture-recapture models for jaguars in central Brazil. *Biol. Conserv. 144: 1017–1024.*

Sollmann R., Gardner B. & Belant J.L. 2012: How does spatial study design influence density estimates from spatial capture-recapture models? *PLOS ONE 7: e34575.*

Stratford K., Stratford S. & Périquet S. 2019: Dyadic associations reveal clan size and social network structure in fission-fusion society of spotted hyaenas. *Afr. J. Ecol. 58: 182–192.*

Sun C.C., Fuller A.K., Hare M.P. et al. 2017: Evaluating population expansion of black bears using spatial capture-recapture. *J. Wildl. Manag. 81: 814–823.*

Sun C.C., Fuller A.K. & Royle J.A. 2014: Trap configuration and spacing influences parameter estimates in spatial capture-recapture models. *PLOS ONE 9: e88025.*

Sutherland C., Muñoz D.J., Miller D.A. et al. 2016: Spatial capture-recapture: a promising method for analyzing data collected using artificial cover objects. *Herpetologica 72: 6–12.*

Thorn M., Green M., Bateman P.W. et al. 2010: Comparative efficacy of sign surveys, spotlighting and audio playbacks in a landscape-scale carnivore survey. *Afr. J. Wildl. Res. 40: 77–86.*

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.*

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.*

Watts H.E. & Holekamp K.E. 2008: Interspecific competition influences reproduction in spotted hyenas. *J. Zool. 276: 402–410.*

Weise F.J., Lemeris J.R.,Jr., Munro S.J. et al. 2015: Cheetahs (*Acinonyx jubatus*) running the gauntlet: an evaluation of translocations into free-range environments in Namibia. *PeerJ 3: e1346.*

Western G., Elliot N.B., Sompeta S.L. et al. 2022: Lions in a coexistence landscape: repurposing a traditional field technique to monitor an elusive carnivore. *Ecol. Evol. 12: e8662.*

Williams K.S., Pitman R.T., Mann G.K.H. et al. 2020: Utilizing bycatch camera-trap data for broad-scale occupancy and conservation: a case study of the brown hyaena *Parahyaena brunnea*. *Oryx 55: 216–226.*

Winterbach C.W., Ferreira S.M., Funston P.J. et al. 2016: Simplified large African carnivore density estimators from track indices. *PeerJ 4: e2662.*

Wolf C. & Ripple W.J. 2016: Prey depletion as a threat to the world's large carnivores. *R. Soc. Open Sci. 3: 160252.*

Yirga G., Imam E., De Iongh H.H. et al. 2014: Local spotted hyena abundance and community tolerance of depredation in human-dominated landscapes in Northern Ethiopia. *Mamm. Biol. 79: 325–330.*

Yirga G., Leirs H., De Iongh H.H. et al. 2017: Densities of spotted hyaena (*Crocuta crocuta*) and African golden wolf (*Canis anthus*) increase with increasing anthropogenic influence. *Mamm. Biol. 85: 60–69.*

Supplementary online material

Table S1. Summary of the 60 publications found in the literature search that reported spotted hyaena (*Crocuta crocuta*) population estimates and the survey methods used. The survey method used is denoted as: call in (CI), track count (TC), total count (TO), spatial capture-recapture (SCR), capture-recapture (CR), distance sampling (DS). The country and region of Africa where the study was conducted is also presented.

Table S2. Literature reviewed on leopard (*Panthera pardus*) population estimates and methods used to estimate density in sub-Saharan Africa between 2000 and 2022.

(https://www.ivb.cz/wp-content/uploads/JVB-vol.-71-2022-Davis-et-al.-Table-S1-S2.pdf)