Journal of Zoology
Journal of Zoology. Print ISSN 0952-8369

ORIGINAL RESEARCH

Spotted hyaena population density across habitat and land use types in southern Tanzania

C. E. Searle[1,2], P. Strampelli[1,3], J. B. Smit[4,5], L. Mkuburo[4,6], F. Mathews[7], H. Kiwango[8], D. W. Macdonald[1], A. J. Loveridge[1] & A. J. Dickman[1,2]

[1]Wildlife Conservation Research Unit, Department of Biology, University of Oxford, Tubney, UK
[2]Lion Landscapes, Iringa, Tanzania
[3]Panthera, New York, NY, USA
[4]Southern Tanzania Elephant Program, Iringa, Tanzania
[5]Department of Psychology, University of Stirling, Stirling, UK
[6]Tanzanian Elephant Foundation, Kilimanjaro, Tanzania
[7]Department of Evolution, Behaviour and Environment, University of Sussex, Brighton, UK
[8]Tanzania National Parks, Arusha, Tanzania

Keywords
spotted hyaena; *Crocuta crocuta*; spatially explicit capture-recapture; population density; carnivore ecology; camera trap data.

Correspondence
Charlotte E. Searle, Wildlife Conservation Research Unit, Department of Biology, University of Oxford, The Recanati-Kaplan Centre, Tubney, UK.
Email: charlotte.searle@biology.ox.ac.uk

Editor: Matthew Hayward
Associate Editor: Stéphanie Périquet

Received 13 April 2023; revised 24 August 2023; accepted 18 September 2023

doi:10.1111/jzo.13119

Abstract

Although the spotted hyaena (*Crocuta crocuta*) has been widely considered to be resilient to human disturbance, the species is now thought to be undergoing widespread population declines. Nevertheless, only a handful of population density estimates are available for the species, despite the importance of this information for informing conservation management. This is a consequence of both a lack of surveys and logistical challenges associated with processing spotted hyaena data. In this study, we collaborated with a cohort of students to process camera trap data from the Ruaha-Rungwa landscape initially collected to estimate lion (*Panthera leo*) and leopard (*Panthera pardus*) population density. By doing so, we provide the first spatially explicit population density estimates for spotted hyaena in Tanzania, via spatially explicit capture-recapture (SECR) modelling. We also examine the relationship between population densities of spotted hyaena, lion and leopard at each site. Spotted hyaena densities varied from 3.55 ± 0.72 adults and sub-adults per 100 km^2 in a miombo (*Brachystegia-Julbernardia*) woodland area of Ruaha National Park, to 10.80 ± 1.08 per 100 km^2 in a prey-rich open woodland savannah habitat in Ruaha National Park, with intermediate densities recorded in Rungwa Game Reserve and MBOMIPA Wildlife Management Area. Our results suggest that spotted hyaena density is influenced by prey availability and protection, and the species may be less resilient to human pressures than widely thought. Spotted hyaena densities were generally positively correlated with densities of lion and leopard, suggesting that prey availability and anthropogenic disturbance had a greater impact than interspecific effects in shaping large carnivore densities in this system. Overall, our study provides some of the first insights into an under-studied species in an under-researched part of its range, while shedding light into the impact of anthropogenic versus interspecific effects in shaping population status of spotted hyaena in human-impacted African systems.

Introduction

Spotted hyaena (*Crocuta crocuta*) are widespread across Africa, being recorded as present in 39 countries across the continent (Bohm & Höner, 2015). The species is thought to be adaptable to a range of environments and resilient to anthropogenic pressures, and is classified as 'Least Concern' by the IUCN Red List of Threatened Species (Bohm & Höner, 2015). Despite this, spotted hyaena range is believed to have decreased by 24% in the last 40 years (Wolf & Ripple, 2017), primarily as a result of habitat loss, persecution following livestock depredation, direct mortality through snaring, and prey base depletion (Bohm & Höner, 2015).

As a result of this increased conservation concern, there have been calls for more research that can help identify threats and guide conservation management of the species (Davis et al., 2022). In particular, although estimates of population status are crucial for effective wildlife management by allowing the identification of threats, evaluation of conservation interventions and development of conservation priorities (Campbell et al., 2002; Hayward et al., 2015), relatively few spotted hyaena populations have been assessed across the continent (Davis et al., 2022; Strampelli, Campbell, et al., 2022). Population density estimates derived from spatially explicit capture-recapture (SECR) analyses are particularly rare. Although spotted hyaena coat patterns lend themselves to individual identification for use in SECR models, only 11 published studies have generated SECR density estimates for the species (Braczkowski, Gopalaswamy, et al., 2022; Davis et al., 2022; Faure et al., 2022; Tarugara & Clegg, 2022), and only three of these are from East Africa. This is considerably less than for other individually marked large carnivore species in the continent (Strampelli, Campbell, et al., 2022). Furthermore, although most of Tanzania falls within spotted hyaena range (Bohm & Höner, 2015), there are no published spatially explicit spotted hyaena population estimates from the country. As spotted hyaena population density has been shown to vary considerably between habitats and across levels of anthropogenic disturbance (Fouché et al., 2020; Yirga et al., 2017), there is a strong need for increased reporting of population estimates from under-studied regions to inform local conservation management.

One potential source of data suitable for spotted hyaena density estimation is camera trap surveys aimed at estimating population densities of other large carnivores, such as leopard (*Panthera pardus*; Searle, Smit, Strampelli, et al., 2021) or lion (*Panthera leo*; Strampelli, Searle, et al., 2022). Surveys targeting these species are relatively common across Africa (Strampelli, Campbell, et al., 2022), and spotted hyaena data obtained as 'by-catch' from these surveys can be used to obtain insights into the species' population status (Davis et al., 2021; Tarugara & Clegg, 2022). However, such efforts are rare, likely at least in part as a result of the considerable data processing time required to identify individual spotted hyaena, which is a necessary step for SECR analyses. As a result, it is important to explore avenues that may facilitate this process and in doing so incentivize more studies of this kind across Africa.

Finally, there is also uncertainty regarding the effect of sympatric predators on spotted hyaena densities, and how different large carnivore species impact each other at a population level. Both lion and leopard have dietary niches that overlap with that of spotted hyaena, and there is evidence of competitive interference interactions between these species (Périquet et al., 2015; Vanak et al., 2013). Nevertheless, population-level effects between these species remain unclear. In light of this, monitoring efforts should seek to monitor all large carnivores in a system to reduce the risk of management decisions prioritizing focal species at the expense of other species they coexist with.

We conducted four camera trap surveys across different habitat and land management types in the Ruaha-Rungwa landscape in southern Tanzania. We then engaged Bachelor's and Master's level students to carry out individual identification of spotted hyaena from the camera trap photos and, following review and verification of assigned IDs by experienced researchers, used SECR modelling to estimate spotted hyaena population density at these four sites. We compare our findings to density estimates for the species elsewhere in Africa and discuss potential drivers of the observed differences in population density within the study landscape. Finally, we compare population density of spotted hyaena with densities of lion and leopard at our study sites, which were estimated in previous studies from the same dataset, and discuss the implications of our findings for the conservation of large carnivore guilds in modern African conservation systems. Overall, our study provides some of the first insights into spotted hyaena population status in Tanzania, and one of the first explorations of population-level relationships between sympatric large African carnivores.

Materials and methods

Study area

Ruaha-Rungwa is a ~45 000 km^2 multiple-use landscape in southern Tanzania (Fig. 1), recognized as a Key Landscape for Conservation due to its globally important wildlife populations (Directorate-General for International Cooperation and Development (European Commission), 2016). The landscape comprises a number of protected areas which are under a range of management strategies. At its core is Ruaha National Park (NP), which is reserved for photographic tourism, and which is the second largest National Park in East Africa at 20 226 km^2. To the north are three Game Reserves (GRs; Rungwa, Kizigo and Muhesi), which are reserved for trophy hunting. To the east of Ruaha NP are community-managed MBOMIPA and Waga Wildlife Management Areas (WMAs), which act as a buffer between Ruaha NP and the neighbouring village lands. Although both photographic and trophy hunting tourism are permitted in these WMAs, neither were taking place at the time of study. As there are no fences in the landscape, wildlife moves freely between protected areas and between protected and non-protected areas.

The climate is arid to semi-arid, with average annual rainfall of 600 mm (Fick & Hijmans, 2017), the majority of which falls between December and April (Mtahiko et al., 2006). Vegetation cover across the landscape is a mosaic of Southern *Acacia-Commiphora* bushlands and Central Zambezian and eastern miombo (*Brachystegia-Julbernardia*) woodlands, floodplain grasslands and riverine forests. The Great Ruaha, Mzombe and Kizigo rivers are the largest in the system and are key sources of surface water in the dry season, when most smaller tributaries dry up completely.

Camera trap surveys

We carried out camera trap surveys at four sites in Ruaha-Rungwa, each representing a different combination of habitat type and management strategy (Fig. 1):

(1) The well-protected and highly productive core tourist area of Ruaha NP, which is dominated by *Acacia-Commiphora* bushland and open grasslands, is located near the Great

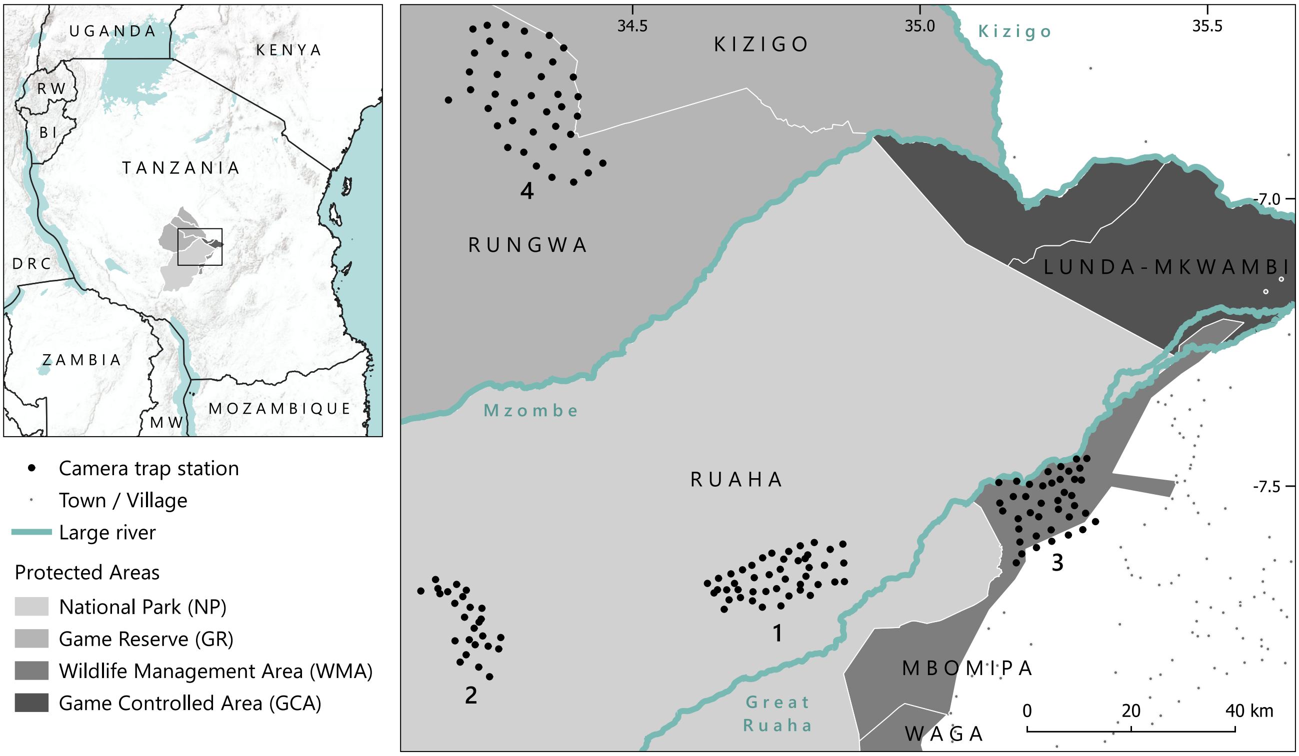

Figure 1 Left: Location of the Ruaha-Rungwa landscape within Tanzania; Right: detail of camera trap grids in (1) the core tourist area of Ruaha NP, (2) Ruaha NP miombo woodlands, (3) MBOMIPA WMA and (4) Rungwa GR.

Ruaha River, and exhibits high dry-season herbivore densities (TAWIRI, 2019);

(2) An area of primarily miombo woodland in Ruaha NP;
(3) MBOMIPA WMA, a more human-impacted area (Strampelli, Henschel, et al., 2022) of *Acacia-Commiphora* habitat, located in a highly productive area near the Great Ruaha River similar to the core tourist area of Ruaha NP, but directly adjacent to unprotected village land; and
(4) The Ikiri hunting block of Rungwa GR, a miombo woodland-dominated area.

Surveys were conducted during the dry seasons of 2018 and 2019; information on the number of stations, mean spacing, area and survey period of each of the four grids is provided in Table 1. Grid size and camera spacing were based on large carnivore home ranges in similar habitats elsewhere (e.g. O'Brien & Kinnaird, 2011), to ensure a non-zero probability of capture for all individuals in the survey area (Noss et al., 2013; Rovero & Zimmermann, 2016). Survey duration was restricted to 2–3 months for each grid, to ensure sufficient captures without violating the assumption of population closure (Tobler & Powell, 2013); as the Rungwa GR survey lasted for 101 days, this dataset was trimmed to 90 days for this study. Although the survey design considerations were initially made with leopard in mind, the design employed is nonetheless appropriate for spotted hyaena (Braczkowski, Gopalaswamy, et al., 2022; Braczkowski, Schenk, et al., 2022; Davis et al., 2021).

Stations were set along roads or trails to maximize captures of large carnivores. Cameras were mounted on trees 3–5 m from the centre of the road or trail at a height of 30–40 cm and set at a perpendicular angle facing the road. Cameras were checked every 2–4 weeks. Although we used various models of motion-activated cameras (Cuddeback Professional Color Model 1347 & X-Change Color Model 1279, Non Typical Inc., De Pere, WI, USA; HC500 HyperFire, Reconyx, Holmen, WI, USA), most cameras used white (xenon) flash, to improve the clarity of markings in photos and assist in the identification of individuals. All but one station had paired cameras to maximize the probability of photographing both flanks of animals. Cameras were mounted in protective cases and secured with binding wire to prevent damage and loss to both humans and wildlife.

Cameras were set to take pictures during both day and night and take one photograph per trigger (the white flash cameras used can take only one photograph per trigger at night). Trigger interval was set on 'Fast as Possible' (<5 s in the day, and ~20 s at night), and image resolution was set to 'high quality' (20 MP).

Individual identification

Individual spotted hyaena were identified from photographs via visual inspection of their unique coat patterns (Davis et al., 2021; see Appendix S1 for examples of individual identification). Photographs where individuals could not be

Table 1 Survey design details and summary results for the four camera trap grids in Ruaha-Rungwa

	Ruaha NP (Core)	Ruaha NP (Woodland)	MBOMIPA WMA	Rungwa GR[a]
Primary habitat type	*Acacia-Commiphora*	Miombo woodland	*Acacia-Commiphora*	Miombo woodland
Survey period	June–September 2018	August–November 2018	September–November 2018	July–October 2019
Survey duration (nights)	83	90	70	90
Stations	45	26	40	40
Trap nights	3601	2187	2689	3191
Mean trap nights per camera	80	84	67	80
Average station spacing	1.96 km	1.88 km	2.08 km	3.46 km
Survey area[b]	223 km^2	152 km^2	270 km^2	555 km^2
Independent spotted hyaena captures[c]	1207	235	325	228
Individuals recorded[c]	112	30	44	70
Spatial recapture rate[d]	82.1%	73.3%	70.5%	64.3%
g0[e]	0.05 ± 0.003	0.04 ± 0.005	0.02 ± 0.002	0.08 ± 0.001
σ[f]	3856 ± 937	4191 ± 270	3872 ± 182	4510 ± 245
Density: Mean ± SE	10.80 ± 1.08	3.55 ± 0.72	5.11 ± 0.81	5.82 ± 0.75
Density: 95% CI	8.89–13.13	2.39–5.25	3.75–6.97	4.52–7.49
HRCIW[g]	20%	40%	32%	26%

[a]Cut down from a survey period of 101 days for this analysis; all information in this table relates to the 90-day dataset.
[b]Area of the minimum convex polygon around all stations (does not include buffer).
[c]Based on right flank captures only. Includes only identifiable captures.
[d]Percentage of identified individuals captured at more than one station during the survey period.
[e]Capture probability at home range centre and associated SE, reported for on-road stations with white flash.
[f]Spatial movement parameter and associated SE.
[g]Half relative confidence interval width.

confidently identified were excluded. Cubs were excluded from analysis (Braczkowski, Gopalaswamy, et al., 2022; Braczkowski, Schenk, et al., 2022; Davis et al., 2021). As photographs of both flanks were not available for all individuals, only photographs depicting the flank with the most captures across all grids were used for identification and analysis, to avoid biases in detection probability resulting from some individuals being identifiable from photographs of either flank and some from only one (Searle, Smit, Strampelli, et al., 2021; Strampelli et al., 2018; Strampelli, Henschel, et al., 2022).

Due to the large number of spotted hyaena images in the dataset, we used a hierarchical approach to manage the task of assigning individual identities. A cohort of Bachelor's and Master's students were each assigned a set number of photographs to analyse, with closely placed cameras being assessed by the same individual. Working as a team with other students analysing data from the same section of the same survey, they then pooled their findings and identified recurrences of the same individual to consolidate duplicate IDs. The data from the entire study area were then combined and checked by a supervising staff member to identify and consolidate any remaining duplicate IDs. Finally, the complete dataset was reviewed by two independent expert observers to confirm individual IDs. See Appendix S2 for the background and identification protocol document provided to the student cohort.

Density estimation

We estimated population density of spotted hyaena – defined here as number of adult and sub-adult individuals per 100 km^2 – at each site via maximum-likelihood SECR (Efford, 2011), using package *secr* 4.5.10 (Efford, 2023) in R 4.2.2 (R Core Team, 2022) and RStudio 2022.12.0 (RStudio Team, 2022).

For each grid, model inputs comprised a capture history detailing the location and sampling occasion of each capture and a trap layout file containing information on the location and activity of each station (all input files are provided in Appendix S3). Each night (24 h, midday to midday) was treated as a sampling occasion, as recommended for nocturnal species (Rovero & Zimmermann, 2016).

Stations were classified as proximity detectors, and we fitted a half-normal detection function to model the distance between home range centre and cameras (Boron et al., 2016; Efford, 2023). A Bernoulli or binomial encounter model was fitted, as this is the most relevant to camera trap studies (Efford, 2023).

As large carnivores often use roads to travel (Mckenzie et al., 2012) and white flash facilitates identification of individuals, station location (on- or off-road) and flash type (white flash or infrared) were modelled as covariates hypothesized to influence capture probability (g0). For each grid, up to four models were therefore fitted to estimate density: secr.0 (null model), secr,road (g0 modelled as a function of station location), secr.flash (g0 modelled as a function of flash type) and secr.road.flash (g0 modelled as a function of station location and flash type). All cameras in Rungwa GR used white flash, so only road was included as a potential covariate for this grid. Models were ranked based on their Akaike information criterion score corrected for small sample size (AICc), and the top-ranked model was used to estimate density. For grids where more than one model had substantial empirical support (ΔAICc

<2), model averaging was used to calculate the final population density and parameter estimates.

In SECR camera trap studies targeting leopard and lion, the standard practice is to sex individuals in order to model the effect of sex on capture probability (g0) and the movement parameter (sigma; e.g. Searle, Smit, Strampelli, et al., 2021; Strampelli, Searle, et al., 2022). Spotted hyaenas have also been shown to exhibit sex-specific ranging patterns (Boydston et al., 2005; Kolowski et al., 2007). However, spotted hyaena are difficult to sex due to their low sexual dimorphism (Davis et al., 2022; Dheer et al., 2022); as a result, we were not able to model the effect of sex on capture probability or movement, which we acknowledge likely results in less precise outputs than for species where this is possible.

In each analysis, we first set the buffer area of the SECR mask (state space) at between four and five times the estimated root pooled spatial variance (RPSV), the overall distance between stations at which an individual was detected (Borchers & Efford, 2008; Efford, 2004). Once the top model was identified, we re-ran analyses while increasing the buffer size by 1 km in each run until we identified the size at which density estimates stabilized (Kalle et al., 2011).

We assessed the precision of our estimates by calculating the half relative confidence interval width (HRCIW) for each site, which provides a measure of the magnitude of population change that an estimate has a reasonable probability of detecting. We calculated HRCIW using the equation: $\text{HRCIW} = ((0.5 \times (\text{UCL} - \text{LCL}))/\text{Density}) \times 100$, where UCL and LCL are the upper and lower 95% confidence limits of the density estimate for that site (Dröge et al., 2020).

Estimates of lion and leopard population density at the four sampling sites were obtained from Strampelli, Searle, et al. (2022) and Searle, Smit, Strampelli, et al. (2021), respectively. Correlation between the population density of each species pair (spotted hyaena-lion; spotted hyaena-leopard; lion-leopard) across the four study sites was measured via Pearson's correlation coefficient. The correlation was considered significant if the magnitude of Pearson's r exceeded the critical value of 0.95 for $P < 0.05$ (for data with 2 d.f.).

Results

Survey effort

Across the four study sites, a total sampling effort of 11 668 camera trap nights across 151 stations yielded 5568 photographs of spotted hyaena. Restricting the dataset to only right flank captures resulted in 2359 photographs. Of the right flank captures, 88% were suitable for individual identification, resulting in a total of 1995 unique capture events from which 256 individuals were identified (Table 1).

Individual identification

Twenty-two students were enlisted to carry out individual identification of 2382 images over a period of 7 days, followed by 2 days of additional sorting and review by two students. Two expert reviewers then took 2 days to review and confirm the identifications.

Out of a total of 2382 spotted hyaena images (with multiple individuals in the same photograph counted as separate 'images'), 78% (n = 1863) were assigned an ID by the students that was confirmed by the expert reviewers, and 8% (n = 194) were classed as unidentifiable by both the students and the expert reviewers. The overall agreement between the students and the expert reviewers was therefore 86% (n = 2057).

Of the remaining images, 10% (n = 245) were classed as unidentifiable by the students but were assigned an ID by the expert reviewers (exclusion error), while 3% (n = 61) were identified as a different individual by the students than the expert reviewers (ID error) and 1% (n = 19) were identified by the students as five unique individuals that were later consolidated into five already identified individuals by the expert reviewers (duplicate individual error). None of the images were identified by the students and not identified by the expert reviewers.

A total of 256 individual spotted hyaena were identified (Table 1). Two individuals with snare injuries were captured in one grid (MBOMIPA WMA); no snared hyaenas were recorded in any of the other grids.

Population density

Buffer width stabilized at between 18 and 22 km for the different grids (Appendix S3). The top-ranked model was secr.road.-flash (capture probability varies with station location and flash type) for the Ruaha NP *Acacia-Commiphora* and miombo grids and secr.road (capture probability varies with station location on- or off-road) for the MBOMIPA and Rungwa grids. The MBOMIPA and Rungwa GR grids both had two models with substantial empirical support (MBOMIPA: secr.road and secr.-road.flash; Rungwa GR: secr.road and secr.0); model averaging was therefore used to determine the density estimate for these grids. Capture probability was higher at stations which were on roads versus those on trails and higher for stations with white flash cameras than those with infrared cameras. Results of model ranking for all sites can be found in Appendix S3.

Population density was highest in the Ruaha NP core tourist area, at 10.80 ± 1.08 (95% confidence interval: 8.89–13.13) adult and sub-adult spotted hyaena per 100 km^2. The next highest density of 5.82 ± 0.75 (4.52–7.49) individuals per 100 km^2 was estimated in the Ikiri block of Rungwa GR, followed by 5.11 ± 0.81 (3.75–6.97) per 100 km^2 in the MBOMIPA WMA grid and 3.55 ± 0.72 (2.39–5.25) per 100 km^2 in the miombo woodland of Ruaha NP. Model outputs for all sites can be found in Appendix S4.

All four density estimates had a HRCIW below 50% (Table 1). This means they were sufficiently precise to have a reasonable probability of detecting a population decline of 50%, which would result in a population being categorized as endangered if that decline takes place within 10 years or three generations (whichever is longer; Dröge et al., 2020; IUCN Standards and Petitions Committee, 2022).

Spotted hyaena population densities at the different sites are shown alongside lion and leopard population densities estimated from the same dataset in Fig. 2. Population densities of spotted hyaena were positively correlated with those of leopard (r(2 d.f.) = 0.95, $P = 0.05$) and lion (r(2 d.f.) = 0.90, $P = 0.10$), although these relationships were not statistically significant. Population densities of lion and leopard were significantly positively correlated across the study sites (r(2 d.f.) = 0.97, $P = 0.03$).

Discussion

Spotted hyaena population densities in Ruaha-Rungwa

This study provides evidence of an important population of spotted hyaena in the Ruaha-Rungwa landscape in southern Tanzania. Although SECR is the recommended density estimation method for spotted hyaena (Davis et al., 2022), it has been underutilized for the species: ours are the first spatially explicit density estimates for spotted hyaena in Tanzania and include one of the first robust estimates in a community-managed conservation area and in a trophy hunting area in Africa. Our estimates form important baselines for future monitoring of this population.

Spotted hyaena population density in the core tourist area of Ruaha NP (10.80 ± 1.08 per 100 km^2) was comparable to some of the highest densities estimated using SECR methods elsewhere in Africa – including in Botswana's Moremi GR (11.80 ± 2.60 per 100 km^2; Rich et al., 2019) and Uganda's Lake Mburo NP (10.99 ± 3.35 per 100 km^2; Braczkowski, Schenk, et al., 2022). However, the estimate was not as high as estimates from Queen Elizabeth NP in Uganda (13.44 ± 2.51 in the north and 14.07 ± 2.79 in the south; Braczkowski, Gopalaswamy, et al., 2022), or from Central Tuli GR in Botswana (14.90 ± 2.23 per 100 km^2; Vissia et al., 2021) and Malilangwe Wildlife Reserve in Zimbabwe (25.1 ± 3.8 per 100 km^2; Tarugara & Clegg, 2022), both sites that are fenced and highly protected. The high density in the core tourist area of Ruaha NP is likely to be driven by both prey availability and protection: spotted hyaena population density generally increases with greater prey densities (Höner et al., 2005; Périquet et al., 2015), and this area exhibits the highest prey availability of the four sampled sites (Searle, Smit, Strampelli, et al., 2021; TAWIRI, 2019). At the same time, protection is likely to have a positive influence on density both indirectly, by supporting a higher density of prey, and directly, by reducing spotted hyaena mortality risk.

Although the area sampled in MBOMIPA WMA comprises similar habitat, is also near the Great Ruaha River, and hosts ungulate densities only slightly lower than in the core tourist area (Searle, Smit, Strampelli, et al., 2021; TAWIRI, 2019), we estimated a population density which, while still relatively high, was approximately half of that in the core tourist area (5.11 ± 0.81 per 100 km^2). This difference is likely due to greater human disturbance in the WMA, which borders unprotected village land and exhibited evidence of relatively high levels of illegal human activity at the time of the study (Strampelli, Henschel, et al., 2022). Indeed, this was the only survey grid where snared hyaenas were recorded: one spotted hyaena with a wire snare around its neck and one with a partially missing limb likely as a result of a snare were photographed at this site (see Appendix S1; we also recorded two striped hyaena, *Hyaena hyaena*, with similar injuries). This suggests

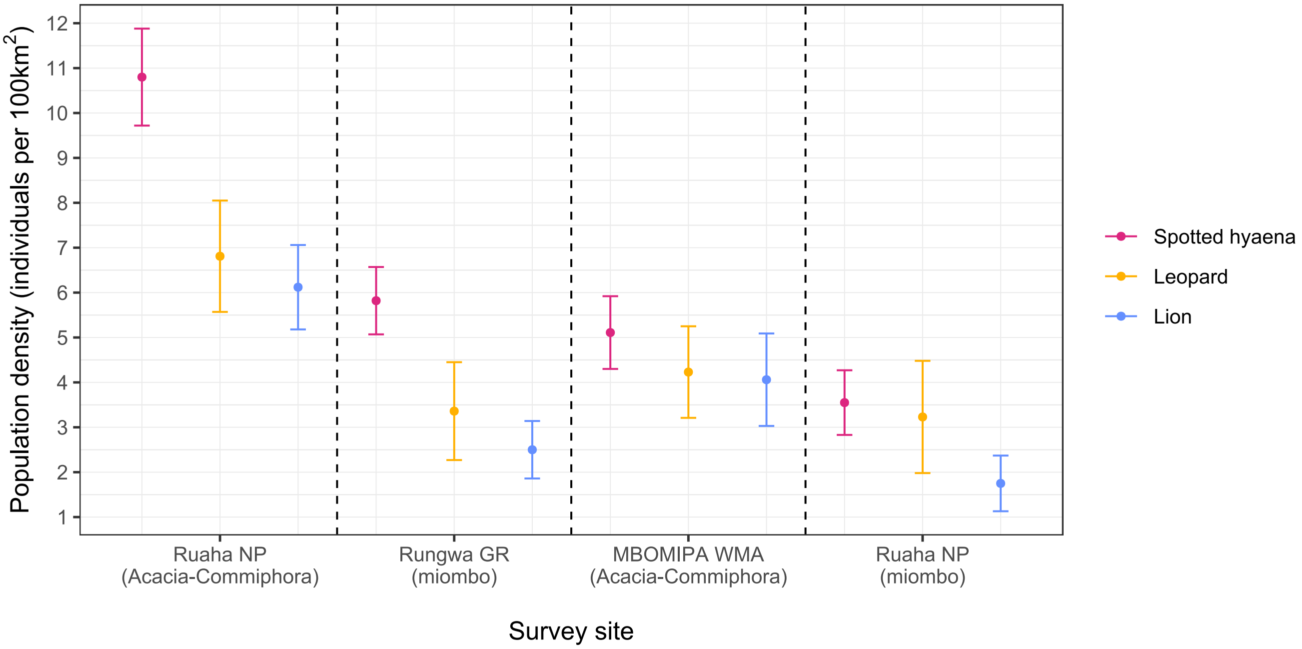

Figure 2 Population density estimates (number of adult and sub-adult individuals per 100 km^2) for spotted hyaena, lion (Strampelli, Henschel, et al., 2022) and leopard (Searle, Smit, Strampelli, et al., 2021) across the four survey sites, with error bars showing the SE for each estimate.

that anthropogenic mortality through by-catch from snaring is likely having a suppressing effect on the population, particularly as animals that manage to escape from snares are likely to be outnumbered by those that succumb to them *in situ* (Loveridge et al., 2020; Mudumba et al., 2021). Further evidence for this is provided by the fact that nine illegal incursions were photographed in MBOMIPA during the survey period, versus three in Rungwa GR, one in the miombo of Ruaha NP, and none in the core tourist area of Ruaha NP. In addition, spotted hyaena are the most common species to attack livestock in the neighbouring village lands and are regularly poisoned, alongside other large carnivores, to prevent or retaliate against livestock depredation (Dickman et al., 2014). These combined edge effects are likely to be exerting top-down limitation on MBOMIPA's spotted hyaena population, and it is probable that the species is experiencing similar impacts in other boundary areas in the landscape. As spotted hyaena often move large distances, these areas may be acting as regional sinks where individuals moving out from core protected areas face increased mortality risk.

Our findings provide some of the first insights into spotted hyaena population ecology in miombo woodland habitat, which represents an important component of the species' range (Davis et al., 2021). Although miombo woodlands cover *c.* 2.7 million km^2 across southern, central, and eastern Africa (Frost, 1996), baseline data on large carnivore densities are lacking for this habitat type (Balme et al., 2007; Davis et al., 2021). Our estimates from miombo woodland in Ruaha NP (3.55 ± 0.72 per 100 km^2) and Rungwa GR (5.82 ± 0.75 individuals per 100 km^2) were considerably higher than spotted hyaena SECR density estimates from miombo habitats elsewhere (Kasungu NP, Malawi: 1.15 ± 0.42 per 100 km^2, Davis et al., 2021; Majete GR, Malawi: 2.62 ± 0.36 per 100 km^2, Briers-Louw, 2017). This is likely a result of the areas sampled in Ruaha-Rungwa being relatively well-protected and exhibiting relatively high prey availability (Strampelli, Henschel, et al., 2022; TAWIRI, 2019), unlike these other sampled miombo habitats, which were either highly disturbed (Kasungu NP; Davis et al., 2021) or recovering (Majete GR; Briers-Louw, 2017). The difference between the two estimates from miombo woodlands in this study is likely due to the area sampled in Rungwa GR exhibiting greater precipitation (Fick & Hijmans, 2017) and consequently higher prey availability (Searle, Smit, Strampelli, et al., 2021; TAWIRI, 2019) than the miombo site in Ruaha NP.

Our sigma model parameter estimates (Table 1) suggest that spotted hyaena are ranging more widely in miombo woodland habitats than in the areas near the Great Ruaha River. This is likely a result of the lower availability of prey in the miombo habitat, resulting in individuals having to range over wider distances to meet their nutritional requirements.

Comparison with sympatric predator densities

Our results reveal that population densities of spotted hyaena, leopard and lion were positively correlated across the four sites sampled (Fig. 2). Although this relationship was only significant for lion and leopard, the comparison was limited by our small sample size ($n = 4$), and we encourage further studies to explore whether a significant relationship would be found for spotted hyaena with data from a larger number of sites.

Relationships between sympatric large carnivores typically comprise a complex mixture of facilitation and competition (Périquet et al., 2015) and are highly site- and situation-specific. Lions can represent a significant source of natural mortality for both spotted hyaena and leopards (Balme, Pitman et al., 2017; Kruuk, 1972) and can suppress populations of both species through food stealing (Balme, Miller et al., 2017; Watts & Holekamp, 2008), while spotted hyaena are similarly known to steal kills from leopards (Vanak et al., 2013). Spotted hyaena can also benefit from lion presence by stealing kills (Périquet et al., 2015), and a study using the same dataset presented here found evidence of spotted hyaena following lion, likely to access scavenging opportunities (Searle, Smit, Cusack, et al., 2021).

In spite of these potential impacts, our findings align with a number of studies that have found lion to have no population-level effect on leopard (Balme, Pitman et al., 2017; Miller et al., 2018) or spotted hyaena (Creel & Creel, 1996; Kissui & Packer, 2004) – although research elsewhere has documented an increase in spotted hyaena after a decline in lion numbers (Green et al., 2018) and lower leopard population densities in areas of high lion abundance (Ramesh et al., 2017), suggesting that there may be a threshold lion density above which suppression of interspecific competitors may occur.

Instead, our results suggest that habitat preferences relating to prey availability and protection from anthropogenic mortality have stronger effects on population density of spotted hyaena, leopard and lion in the landscape than potential interspecific suppression or competition effects, with populations of these species generally increasing or decreasing together. By using behavioural adaptations to offset or minimize the risk of antagonistic encounters, these species are able to maintain access to vital habitat and resources shared by interspecific competitors (Searle, Smit, Cusack, et al., 2021) – adaptations that are likely to be particularly important in anthropogenically impacted areas where resources are more limited, and where humans represent another dominant competitor. We recommend that future studies attempt to assess the relative impact of fluctuations in population density of one species on its competitors, especially as we acknowledge that 'snapshots' from a single point in time are not as effective at disentangling population-level interspecific effects as longer-term assessments (Noss et al., 2013); carnivore reintroductions represent a particularly valuable opportunity for studies of this kind. As it is also possible that such effects are density-dependent (Maputla et al., 2015), we also encourage studies across a range of population densities of the different species to disentangle these relationships.

In our study area, striped hyaena are restricted to a relatively small proportion of the landscape and were captured only in one of the survey grids. As a result, it was not possible to investigate interspecific interactions between spotted and striped hyaena. However, especially as a result of the low levels of research into interspecific interactions between these two species, we recommend that further attention is given to this relationship in Ruaha-Rungwa in the future, particularly as they overlap in boundary areas (e.g. MBOMIPA WMA), where anthropogenic impacts are greatest.

Conservation implications

The variation in spotted hyaena density across Ruaha-Rungwa highlights the importance of surveying different components of a landscape, and of avoiding extrapolation of density estimates from single sites to wider areas (Searle et al., 2020; Suryawanshi et al., 2019). Our findings also further underscore the role of prey availability in driving spotted hyaena population density, indicating that securing healthy prey populations should be a conservation priority for the species across its range (Loveridge et al., 2020).

As a result of their naturally low densities and wide-ranging behaviours, anthropogenic sources of mortality at the edges of protected areas can have strong impacts on large carnivore populations (Woodroffe & Ginsberg, 1998). The fact that we recorded spotted hyaenas with snare injuries in the grid closest to unprotected areas suggests this is a serious threat in boundary areas in the landscape, particularly as the animals photographed only represent individuals that were able to break free from snares. Mortality from snares is likely to occur anywhere that carnivores are present and wire-snare bushmeat poaching is common: research has revealed evidence of this threat in Zimbabwe (Loveridge et al., 2020), Zambia (Becker et al., 2013), Uganda (Mudumba et al., 2021) and Tanzania (Kilewo & Mpanduji, 2012), but the hidden nature of the activity means that its actual prevalence is likely to be widespread. As snaring can impact spotted hyaena populations both directly through mortality and indirectly through prey base depletion, addressing this threat should be seen as a priority for the species.

Our findings suggest that, although spotted hyaena in miombo woodlands are unlikely to reach densities observed in more prey-rich savannah or riverine areas due to naturally low soil productivity (Frost, 1996; Searle, Smit, Strampelli, et al., 2021), miombo habitat can host higher densities of the species than previously shown (Briers-Louw, 2017; Davis et al., 2021), provided they are well-protected.

We also provide the first spatially explicit spotted hyaena density from a trophy hunting area. As sustainable trophy hunting requires regular monitoring of populations to assess impacts and inform quotas (Packer et al., 2009), we encourage similar studies in hunting areas elsewhere across the species' range. Such monitoring may be particularly important for spotted hyaenas as trophy hunters often target larger animals (Shakari Connection, 2022), which in this species are likely to be adult females (McCormick et al., 2022). Removal of adult females often has a particularly detrimental impact on large mammal populations, and this will be especially significant for species like spotted hyaena which have a matrilineal social structure (Holekamp et al., 2012).

Overall, our study provides much-needed insights into the population ecology of a relatively widespread yet under-studied and increasingly threatened species. We echo others in recommending similar studies across the species' range (Davis et al., 2021), especially given the availability of relevant datasets following surveys targeting leopard and/or lion. We also recommend longer-term assessments of studied spotted hyaena populations, to provide a more detailed understanding of the drivers of population density and the effect of changes in sympatric species density on spotted hyaena population status.

The role of students for individual identification of spotted hyaena

Our study illustrates the value of engaging students for individual identification of large carnivores from camera trap images, an approach that has previously been shown to be effective for domestic cats (Aeluro & van Oast, 2022). We found 86% agreement in images identified or discarded by student citizen scientists and expert reviewers. Only 3% represented ID error, whereby an incorrect ID was assigned to an image, and 1% represented duplicate individual error. The most common form of error at 10% was exclusion error, whereby images were classified as unidentifiable and discarded by the student group but were subsequently assigned an ID the expert reviewers. This type of error should be the least problematic in terms of its potential impact (per error) on density estimation, as it will serve to reduce the dataset but will not provide misleading information on animal movement. Nevertheless, including these images increased the number of unique capture events by 9–15% for each grid and increased the resulting density estimates by 2–8% compared to analyses excluding these captures (see Appendix S5). While this is a relatively small difference, this highlights the importance of retaining expert review as part of any camera trap data processing workflow.

Students in a relevant field of study can represent a particularly valuable resource if having to process large amounts of data, as they often have existing knowledge of the subject area and are likely to be more engaged in the activity than a member of the general public (Aeluro & van Oast, 2022). In our case, the student group's supervisor reported one of the highest levels of engagement they had seen among students for a computer-based exercise (F. Mathews, personal observation). While the advent of computer vision-assisted identification through platforms like the African Carnivore Wildbook (https://africancarnivore.wildbook.org) has the potential to reduce the processing time for photographic datasets, these methods still require human validation. We encourage researchers sitting on camera trap data and limited by processing time to consider collaborating with relevant academic institutions to explore the potential for students to facilitate timely data processing, and thus support the dissemination of findings that have value for conservation.

Acknowledgements

Fieldwork for this research was carried out under permits 2018-368-NA-2018-107, 2018-126-NA-97-20, 2019-96-ER-97-20 and 2019-424-NA-2018-184, granted by the Tanzania

Commission for Science and Technology (COSTECH) and Tanzania Wildlife Research Institute (TAWIRI). We would like to thank the Government of Tanzania, TAWIRI, Tanzania National Parks Authority (TANAPA), Tanzania Wildlife Management Authority (TAWA) and Idodi-Pawaga MBOMIPA WMA for their support of this research. We also thank the field staff of the Southern Tanzania Elephant Program (STEP) and Lion Landscapes (then the Ruaha Carnivore Project) for their assistance with data collection and MBOMIPA WMA Village Game Scouts, TANAPA and TAWA Rangers, Essential Destinations, Mdonya Old River Camp, and Tanzania Big Game Safaris for their assistance during fieldwork. We owe special thanks to the students of the University of Sussex Life Sciences Africa Zoology Field Course, who carried out the individual identification of hyaenas for this study when the COVID-19 pandemic prevented them from travelling to Africa. Scholarship funding for CS and PS was provided by the University of Oxford NERC Environmental Research DTP (NE/L002612/1); CS is currently funded by a Dennis Curry Postdoctoral Research Fellowship. AD was funded by a Recanati-Kaplan Fellowship. Additional funding was provided for this research by grants from National Geographic Society Early Career Grants (EC-348C-18), Cleveland Metroparks Zoo Africa Seed Grants, Chicago Zoological Society Chicago Board of Trade (CBOT) Endangered Species Fund, and Pittsburgh Zoo & PPG Aquarium Conservation & Sustainability Fund.

Author contributions

CES and PS conceived the ideas and designed the methodology. CES, PS, JBS and LM collected the data. CES, PS and FM analysed the data. CES and PS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

All input data used for this study are provided in the supplementary material (Appendix S3).

References

Aeluro, S., & van Oast, J. (2022). Photographic identification of individual domestic cats: Comparing the accuracy of life science university students versus cat advocate citizen science volunteers. *Citizen Science: Theory and Practice*, **7**(1). https://doi.org/10.5334/cstp.465

Balme, G., Hunter, L., & Slotow, R. (2007). Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: Prey catchability versus abundance. *Animal Behaviour*, **74**, 589–598. https://doi.org/10.1016/j.anbehav.2006.12.014

Balme, G., Pitman, R., Robinson, H. S., Miller, J. R. B., Funston, P. J., & Hunter, L. T. B. (2017). Leopard distribution and abundance is unaffected by interference competition with lions. *Animal Behaviour*, **28**, 1348–1358. https://doi.org/10.1093/beheco/arx098

Balme, G. A., Miller, J. R., Pitman, R. T., & Hunter, L. T. (2017). Caching reduces kleptoparasitism in a solitary, large felid. *Journal of Animal Ecology*, **86**(3), 634–644.

Becker, M., McRobb, R., Watson, F., Dröge, E., Kanyembo, B., Murdoch, J., & Kakumbi, C. (2013). Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. *Biological Conservation*, **158**, 26–36.

Bohm, T., & Höner, O. (2015). Spotted hyaena (*Crocuta crocuta*). IUCN Red List Threat. Species 8235.

Borchers, D. L., & Efford, M. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, **64**(2), 377–385.

Boron, V., Tzanopoulos, J., Gallo, J., Barragan, J., Jaimes-Rodriguez, L., Schaller, G. B., & Payán, E. (2016). Jaguar densities across human-dominated landscapes in Colombia: The contribution of unprotected areas to long term conservation. *PLoS One*, **11**, e0153973. https://doi.org/10.1371/journal.pone.0153973

Boydston, E. E., Kapheim, K. M., Van Horn, R. C., Smale, L., & Holekamp, K. E. (2005). Sexually dimorphic patterns of space use throughout ontogeny in the spotted hyena (*Crocuta crocuta*). *Journal of Zoology*, **267**(3), 271–281.

Braczkowski, A., Gopalaswamy, A. M., Fattebert, J., Isoke, S., Bezzina, A., & Maron, M. (2022). Spatially explicit population estimates of African leopards and spotted hyenas in the Queen Elizabeth Conservation Area of southwestern Uganda. *Mammalian Biology*, **102**(4), 1199–1213.

Braczkowski, A., Schenk, R., Samarasinghe, D., Biggs, D., Richardson, A., Swanson, N., Swanson, M., Dheer, A., & Fattebert, J. (2022). Leopard and spotted hyena densities in the Lake Mburo National Park, southwestern Uganda. *PeerJ*, **10**, e12307. https://doi.org/10.7717/peerj.12307

Briers-Louw, W. D. (2017). *Ecology of three apex predators in Majete Wildlife Reserve, Malawi*. Stellenbosch University.

Campbell, S. P., Alan Clark, J., Crampton, L. H., Guerry, A. D., Hatch, L. T., Hosseini, P. R., Lawler, J. J., & O'Connor, R. J. (2002). An assessment of monitoring efforts in endangered species recovery plans. *Ecological Applications*, **12**, 674–681. https://doi.org/10.1890/1051-0761(2002)012[0674:AAOMEI]2.0.CO;2

Creel, S., & Creel, N. M. (1996). Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, **10**, 526–538.

Davis, R. S., Gentle, L. K., Stone, E. L., Uzal, A., & Yarnell, R. W. (2022). A review of spotted hyaena population estimates highlights the need for greater utilisation of spatial capture-recapture methods. *Journal of Vertebrate Biology*, **71** (22017), 22017.1–22017.15.

Davis, R. S., Stone, E. L., Gentle, L. K., Mgoola, W. O., Uzal, A., & Yarnell, R. W. (2021). Spatial partial identity model reveals low densities of leopard and spotted hyaena in a miombo woodland. *Journal of Zoology*, **313**, 43–53. https://doi.org/10.1111/jzo.12838

Dheer, A., Samarasinghe, D., Dloniak, S. M., & Braczkowski, A. (2022). Using camera traps to study hyenas: Challenges, opportunities, and outlook. *Mammalian Biology*, **102**(3), 847–854.

Dickman, A., Hazzah, L., Carbone, C., & Durant, S. M. (2014). Carnivores, culture and "contagious conflict": Multiple factors influence perceived problems with carnivores in Tanzania's Ruaha landscape. *Biological Conservation*, **178**, 19–27. https://doi.org/10.1016/j.biocon.2014.07.011

Directorate-General for International Cooperation and Development (European Commission). (2016). *Larger than elephants: Inputs for an EU strategic approach to wildlife conservation in Africa - Regional analysis*. Brussels. https://library.wur.nl and https://doi.org/10.2841/909032

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. *Ecology and Evolution*, **10**(7), 3276–3292.

Efford, M. (2004). Density estimation in live-trapping studies. *Oikos*, **106**, 598–610. https://doi.org/10.1111/j.0030-1299.2004.13043.x

Efford, M. (2011). *secr - Spatially explicit capture-recapture in R*.

Efford, M. (2023). *secr: Spatially explicit capture-recapture models*. R package version 4.5.10.

Faure, J. P. B., Swanepoel, L. H., Cilliers, D., Venter, J. A., & Hill, R. A. (2022). Estimates of carnivore densities in a human-dominated agricultural matrix in South Africa. *Oryx*, **56**(5), 774–781.

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, **4315**, 4302–4315. https://doi.org/10.1002/joc.5086

Fouché, J., Reilly, B. K., de Crom, E. P., Baeumchen, Y. K., & Forberger, S. (2020). Density estimates of spotted hyaenas (*Crocuta crocuta*) on arid farmlands of Namibia. *African Journal of Ecology*, **58**, 563–567. https://doi.org/10.1111/aje.12745

Frost, P. (1996). The ecology of miombo woodlands. In B. Campbell (Ed.), *The miombo in transition: Woodlands and welfare in Africa* (pp. 11–55). Center for International Forestry Research.

Green, D. S., Johnson-Ulrich, L., Couraud, H. E., & Holekamp, K. E. (2018). Anthropogenic disturbance induces opposing population trends in spotted hyenas and African lions. *Biodiversity and Conservation*, **27**, 871–889. https://doi.org/10.1007/s10531-017-1469-7

Hayward, M. W., Boitani, L., Burrows, N. D., Funston, P. J., Karanth, K. U., Mackenzie, D. I., Pollock, K. H., & Yarnell, R. W. (2015). Ecologists need robust survey designs, sampling and analytical methods. *Journal of Applied Ecology*, **52**, 286–290. https://doi.org/10.1111/1365-2664.12408

Holekamp, K. E., Smith, J. E., Strelioff, C. C., van Horn, R. C., & Watts, H. E. (2012). Society, demography and genetic structure in the spotted hyena. *Molecular Ecology*, **21**(3), 613–632. https://doi.org/10.1111/j.1365-294X.2011.05240.x

Höner, O. P., Wachter, B., East, M. L., Runyoro, V. A., & Hofer, H. (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. https://doi.org/10.1111/j.0030-1299.2005.13533.x

IUCN Standards and Petitions Committee. (2022). Guidelines for using the IUCN red list categories and criteria. Version 15.1. Prepared by the Standards and Petitions Committee. https://www.iucnredlist.org/documents/RedListGuidelines.pdf

Kalle, R., Ramesh, T., Qureshi, Q., & Sankar, K. (2011). Density of tiger and leopard in a tropical deciduous forest of Mudumalai Tiger Reserve, southern India, as estimated using photographic capture-recapture sampling. *Acta Theriologica*, **56**, 335–342. https://doi.org/10.1007/s13364-011-0038-9

Kilewo, M. K. N., & Mpanduji, D. G. (2012). A survey of snares causing injuries to wild animals in Serengeti National Park, Northern Tanzania. *Research Opinions in Animal and Veterinary Sciences*, **2**(4), 237–242.

Kissui, B. M., & Packer, C. (2004). Top-down population regulation of a top predator: Lions in the Ngorongoro Crater. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 1867–1874. https://doi.org/10.1098/rspb.2004.2797

Kolowski, J. M., Katan, D., Theis, K. R., & Holekamp, K. E. (2007). Daily patterns of activity in the spotted hyena. *Journal of Mammalogy*, **88**(4), 1017–1028.

Kruuk, H. (1972). *The spotted hyena: A study of predation and social behavior*. The University of Chicago Press.

Loveridge, A., Sousa, L. L., Seymour-smith, J., Hunt, J., Coals, P., Donnell, H. O., Lindsey, P. A., Mandisodza-chikerema, R., & Macdonald, D. W. (2020). Evaluating the spatial intensity and demographic impacts of wire-snare bush-meat poaching on large carnivores. *Biological Conservation*, **244**, 108504. https://doi.org/10.1016/j.biocon.2020.108504

Maputla, N. W., Maruping, N. T., Chimimba, C. T., & Ferreira, S. M. (2015). Spatio-temporal separation between lions and leopards in the Kruger National Park and the Timbavati Private Nature Reserve, South Africa. *Global Ecology and Conservation*, **3**, 693–706. https://doi.org/10.1016/j.gecco.2015.03.001

McCormick, S. K., Holekamp, K. E., Smale, L., Weldele, M. L., Glickman, S. E., & Place, N. J. (2022). Sex differences in spotted hyenas. *Cold Spring Harbor Perspectives in Biology*, **14**(6), a039180.

Mckenzie, H. W., Merrill, E. H., Spiteri, R. J., & Lewis, M. A. (2012). How linear features alter predator movement and the functional response. *Interface Focus*, **2**, 205–216.

Miller, J. R. B., Pitman, R. T., Mann, G. K. H., Fuller, A. K., & Balme, G. A. (2018). Lions and leopards coexist without spatial, temporal or demographic effects of interspecific competition. *The Journal of Animal Ecology*, **87**, 1709–1726. https://doi.org/10.1111/1365-2656.12883

Mtahiko, M. G. G., Gereta, E., Kajuni, A. R., & Chiombola, E. A. T. (2006). Towards an ecohydrology-based restoration of the Usangu wetlands and the Great Ruaha River, Tanzania.

Wetlands Ecology and Management, **14**, 489–503. https://doi.org/10.1007/s11273-006-9002-x
Mudumba, T., Jingo, S., Heit, D., & Montgomery, R. A. (2021). The landscape configuration and lethality of snare poaching of sympatric guilds of large carnivores and ungulates. *African Journal of Ecology*, **59**(1), 51–62.
Noss, A., Polisar, J., Maffei, L., Garcia, R., & Silver, S. (2013). *Evaluating jaguar densities with camera traps*.
O'Brien, T. G., & Kinnaird, M. F. (2011). Density estimation of sympatric carnivores using spatially explicit capture-recapture methods and standard trapping grid. *Ecological Applications*, **21**, 2908–2916. https://doi.org/10.1890/10-2284.1
Packer, C., Kosmala, M., Cooley, H. S., Brink, H., Pintea, L., Garshelis, D., Purchase, G., Strauss, M., Swanson, A., Balme, G., Hunter, L., & Nowell, K. (2009). Sport hunting, predator control and conservation of large carnivores. *PLoS One*, **4**, e5941. https://doi.org/10.1371/journal.pone.0005941
Périquet, S., Fritz, H., & Revilla, E. (2015). The Lion King and the Hyaena Queen: Large carnivore interactions and coexistence. *Biological Reviews*, **90**, 1197–1214. https://doi.org/10.1111/brv.12152
R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/
Ramesh, T., Kalle, R., Rosenlund, H., & Downs, C. T. (2017). Low leopard populations in protected areas of Maputaland: A consequence of poaching, habitat condition, abundance of prey, and a top predator. *Ecology and Evolution*, **7**, 1964–1973. https://doi.org/10.1002/ece3.2771
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. *Biological Conservation*, **233**, 12–20. https://doi.org/10.1016/j.biocon.2019.02.018
Rovero, F., & Zimmermann, F. (2016). *Camera trapping for wildlife research*. Pelagic Publishing.
RStudio Team. (2022). *RStudio: Integrated development for R*. RStudio Inc. http://www.rstudio.com/
Searle, C. E., Bauer, D. T., Kesch, M. K., Hunt, J. E., Mandisodza-Chikerema, R., Flyman, M. V., Macdonald, D. W., Dickman, A. J., & Loveridge, A. J. (2020). Drivers of leopard (*Panthera pardus*) habitat use and relative abundance in Africa's largest transfrontier conservation area. *Biological Conservation*, **248**, 108649. https://doi.org/10.1016/j.biocon.2020.108649
Searle, C. E., Smit, J., Strampelli, P., Mkuburo, L., Ikanda, D., Macdonald, D. W., Loveridge, A. J., & Dickman, A. J. (2021). Leopard population density varies across habitats and management strategies in a mixed-use Tanzanian landscape. *Biological Conservation*, **257**, 109120. https://doi.org/10.1016/j.biocon.2021.109120
Searle, C. E., Smit, J. B., Cusack, J. J., Strampelli, P., Grau, A., Mkuburo, L., Macdonald, D. W., Loveridge, A. J., & Dickman, A. J. (2021). Temporal partitioning and spatiotemporal avoidance among large carnivores in a human-impacted African landscape. *PLoS One*, **16**(9), e0256876.
Shakari Connection. (2022). *Hyena hunting*. Retrieved April 6, 2023, from https://www.shakariconnection.com/hyena-hunting.html
Strampelli, P., Andresen, L., Everatt, K. T., Somers, M. J., & Rowcliffe, J. M. (2018). Leopard *Panthera pardus* density in southern Mozambique: Evidence from spatially explicit capture-recapture in Xonghile Game Reserve. *Oryx*, **54**, 405–411. https://doi.org/10.1017/S0030605318000121
Strampelli, P., Campbell, L. A., Henschel, P., Nicholson, S. K., Macdonald, D. W., & Dickman, A. J. (2022). Trends and biases in African large carnivore population assessments: Identifying priorities and opportunities from a systematic review of two decades of research. *PeerJ*, **10**, e14354.
Strampelli, P., Searle, C. E., Smit, J. B., Henschel, P., Mkuburo, L., Ikanda, D., Macdonald, D. W., & Dickman, A. J. (2022). Camera trapping and spatially explicit capture-recapture for the monitoring and conservation management of lions: Insights from a globally important population in Tanzania. *Ecological Solutions and Evidence*, **3**(1), e12129. https://doi.org/10.1002/2688-8319.12129
Strampelli, P., Henschel, P., Searle, C. E., Macdonald, D. W., & Dickman, A. J. (2022). Habitat use of and threats to African large carnivores in a mixed-use landscape. *Conservation Biology*, **36**(6), e13943. https://doi.org/10.1111/cobi.13943
Suryawanshi, K. R., Khanyari, M., Sharma, K., Lkhagvajav, P., & Mishra, C. (2019). Sampling bias in snow leopard population estimation studies. *Population Ecology*, **61**, 268–276. https://doi.org/10.1002/1438-390X.1027
Tarugara, A., & Clegg, B. W. (2022). Using by-catch camera trapping data for estimating the population size of spotted hyaenas (*Crocuta crocuta*). *African Journal of Ecology*, **60**, 1318–1323.
TAWIRI. (2019). *Aerial survey of large animals and human activities in the Katavi-Rukwa and Ruaha-Rungwa Ecosystems, Tanzania*. Dry Season, 2018. TAWIRI Aerial Survey Report.
Tobler, M. W., & Powell, G. V. N. (2013). Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. *Biological Conservation*, **159**, 109–118.
Vanak, A. T., Fortin, D., Thaker, M., Ogden, M., Owen, C., Greatwood, S., & Slotow, R. (2013). Moving to stay in place: Behavioral mechanisms for coexistence of African large carnivores. *Ecology*, **94**, 2619–2631. https://doi.org/10.1890/13-0217.1
Vissia, S., Wadhwa, R., & VanLangeveld, F. (2021). Co-occurrence of high densities of brown hyena and spotted hyena in central Tuli, Botswana. *Journal of Zoology*, **314**, 143–150. https://doi.org/10.1111/jzo.12873
Watts, H. E., & Holekamp, K. E. (2008). Interspecific competition influences reproduction in spotted hyenas. *Journal of Zoology*, **276**, 402–410. https://doi.org/10.1111/j.1469-7998.2008.00506.x

Wolf, C., & Ripple, W. J. (2017). Range contractions of the world's large carnivores. *Royal Society Open Science*, **4**, 170052. https://doi.org/10.1098/rsos.170052

Woodroffe, R., & Ginsberg, J. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, **280**, 2126–2128. https://doi.org/10.1126/science.280.5372.2126

Yirga, G., Leirs, H., De Iongh, H. H., Asmelash, T., Gebrehiwot, K., Vos, M., & Bauer, H. (2017). Densities of spotted hyaena (*Crocuta crocuta*) and African golden wolf (*Canis anthus*) increase with increasing anthropogenic influence. *Mammalian Biology*, **85**, 60–69. https://doi.org/10.1016/j.mambio.2017.02.004

Supporting Information

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

Appendix S1. Examples of spotted hyaena individual identification.

Appendix S2. Background & identification protocol document prepared for students.

Appendix S3. *secr* input files.

Appendix S4. Outputs of SECR analyses.

Appendix S5. A comparison of the SECR analysis results with and without capture data from images discarded by the student volunteers but identified by the expert reviewers (exclusion errors).