# Estimated baseline density of a spotted hyaena population in a post-war landscape

Willem D. Briers-Louw *[1,2] ⓘ, Tamar A. Kendon [2] ⓘ, Matthew S. Rogan [3] ⓘ
Alison J. Leslie [1] ⓘ, Drew Bantlin [4] ⓘ, Emma Evers [4] ⓘ, David Gaynor [5] ⓘ
Peter Lindsey [6] ⓘ, João Almeida [7] and Vincent N. Naude [1] ⓘ

**Abstract** The spotted hyaena *Crocuta crocuta* is relatively understudied across its range despite evidence of widespread declines. It is therefore essential that robust baseline population density assessments are conducted to inform current management and future conservation policy. In Mozambique this is urgent as decades of armed conflict followed by unchecked poaching have resulted in large-scale wildlife declines and extirpations. We conducted the first robust population density estimate for a spotted hyaena population in Mozambique using spatially explicit capture–recapture methodologies. We recorded a relatively low population density of 0.8–2.1 hyaenas/100 km² in the wildlife management area Coutada 11 in the Zambezi Delta of central Mozambique in 2021. These densities are well below the estimated carrying capacity for the landscape and are comparable to published densities in high human-impact, miombo woodland-dominated and arid environments. The combination of historical armed conflict, marginal trophy hunting and bushmeat poaching using wire snares and gin traps (with physical injuries evident in 9% of identified individuals) presents persistent anthropogenic pressure, limiting the post-war recovery of this resident hyaena population. We provide insights into the dynamics of hyaena population status and recovery in such post-war landscapes, adding to mounting evidence that the species is less resilient to severe anthropogenic disturbances than previously believed. We recommend long-term monitoring of this and other carnivore populations in post-war landscapes to ascertain demographic trends and implement effective conservation interventions for population recovery.

**Keywords** Armed conflict, bushmeat poaching, camera trapping, *Crocuta crocuta*, Mozambique, population density, spatially explicit capture–recapture, trophy hunting

The supplementary material for this article is available at doi.org/10.1017/S0030605324000966

## Introduction

Anthropogenic threats imperil global biodiversity (Johnson et al., 2017), yet amongst the most widespread and insidious of these is armed conflict, having occurred in > 90% of high-biodiversity regions and up to 70% of protected areas in Africa since the 1940s (Daskin & Pringle, 2018). During war and political instability, environmental concerns often wane, with conservation activities being suspended by both the state and private sectors in the face of more immediate military or humanitarian concerns (Hart et al., 1997; Hanson et al., 2009). Subsequent reduction in management and law enforcement within protected areas may facilitate overexploitation of wildlife and natural resources for subsistence or commercial use (Hatton et al., 2001). Although environmental policies may be re-established post-conflict, this is rarely prioritized immediately, and displaced people may settle within or near protected areas (Hatton et al., 2001; Gaynor et al., 2016; Daskin & Pringle, 2018). When wildlife population declines have been driven by localized exploitation (Johnson et al., 2017), regardless of whether armed conflict safeguards wildlife through anthropogenic exclusion (Dudley et al., 2002), post-war recovery of wildlife populations is possible where intervention strategies are proactive and have consistent support and evaluation, as evidenced by the local recovery of ungulate and large carnivore populations in parts of Africa (Pringle, 2017; Bouley et al., 2018; Braga-Pereira et al., 2020).

Large carnivores are ecologically important (Estes et al., 2011) and have socio-economic benefits (Ripple et al., 2014). Yet these species are amongst the most globally threatened, as their relatively slow generational turnover, low densities and large spatial and energetic requirements make them prone to extinction (Ripple et al., 2014). The global decline of large carnivores is driven by anthropogenic pressures, such as bushmeat poaching and loss of suitable habitats and prey, leading to the fragmentation of rangelands and resulting in a conservation crisis for most of these species (Ripple et al., 2014). This is of concern, and the majority of protected areas in Africa have populations of large

carnivores that are below estimated carrying capacities (Strampelli et al., 2022). Consequently, robust population density assessments, which are a fundamental precursor for effective wildlife management (e.g. population viability assessment and offtake quota evaluation) and conservation policy development (e.g. conservation status evaluation and regional-level strategic planning), are imperative for the identification and management of threatened populations (Balme et al., 2009; Sollmann et al., 2011; Jacobson et al., 2016). Yet such baseline estimates are lacking for most large carnivore species.

The spotted hyaena *Crocuta crocuta* (hereafter hyaena) is widely distributed in Africa, with an estimated global population of 27,000–47,000 (Bohm & Höner, 2015). Although the species is categorized as Least Concern on the IUCN Red List (Bohm & Höner, 2015), there is a paucity of baseline data on ranging behaviour and population densities throughout its range (Dheer et al., 2022b), despite purported declines across the continent (Ripple et al., 2014; Wolf & Ripple, 2016). Estimating population densities, particularly in understudied landscapes, is thus critical for improved regional conservation management and international policy development. Historically, hyaenas were considered widespread and abundant throughout Mozambique (Smithers & Tello, 1976), but following decades of war, both independence (1964–1975) and civil (1977–1992), wildlife management became compromised by poverty, food insecurity, insufficient legislation and poor law enforcement. In addition to combatant groups allegedly using bushmeat to feed soldiers, many people who had settled within protected areas have not been resettled. The subsequent widespread use of snares and gin traps has affected carnivores, with evidence suggesting that large carnivores are more widely depleted in Mozambique than in many other countries (Hatton et al., 2001; Beilfuss et al., 2010). Since the 1992 ceasefire, there has been an improved national policy and framework for conservation, and better wildlife management and law enforcement (Hatton et al., 2001).

Despite these advances, anthropogenic pressures, largely through widespread bushmeat poaching, continue to drive extirpations of large carnivore populations in many protected (Bouley et al., 2018; Everatt et al., 2019b) and wildlife management areas (Lindsey & Bento, 2012; Briers-Louw et al., 2024). Hyaenas are legally hunted in several wildlife management areas across Mozambique, and although sustainable trophy hunting could fund anti-poaching efforts and foster conservation (Lindsey et al., 2007), offtake quotas rarely consider the additive pressures of illegal poaching, which could result in unsustainable harvest (Jorge et al., 2013; Briers-Louw et al., 2024). Reliable baseline ecological data are crucial for developing such quotas, and recent studies indicate that robust estimates of leopard *Panthera pardus* densities are well below the outdated estimates used to derive hunting quotas (Strampelli et al., 2020;

Briers-Louw et al., 2024). Despite this, there is currently no robust, spatially explicit capture–recapture estimate of hyaena densities in Mozambique that could be used to set sustainable hunting quotas.

We used remote camera trapping within a spatial capture–recapture framework to determine the baseline population density of a hyaena population in the post-war wildlife management area Coutada 11, within the large, unfenced Zambezi Delta landscape of central Mozambique. We contextualize this estimate relative to range-wide hyaena density estimates to provide a better understanding of the status of this population globally and to suggest regional management recommendations for improved species conservation.

## Study area

The 9,754 km² Marromeu–Coutada Complex in the southern Zambezi Delta (hereafter, the Delta) of central Mozambique (Fig. 1), is partitioned into the Marromeu National Reserve and four wildlife management areas (Coutadas 10, 11, 12 and 14). The climate is tropical, with distinct dry (May–October) and wet (November–April) seasons and a mean annual rainfall of 1,200 mm (Beilfuss, 2001). The Delta comprises several threatened ecoregions (IUCN Red List of Ecosystems; Lötter et al., 2023) supporting a range of vegetation types, including grasslands, papyrus swamps, miombo woodland and sand forest (Beilfuss, 2001). This diverse landscape supports abundant large ungulate populations that continue to recover post-war (Beilfuss et al., 2010; Macandza et al., 2022) and a large carnivore community, including resident hyaenas, leopards, African wild dogs *Lycaon pictus* and reintroduced lions *Panthera leo* and cheetahs *Acinonyx jubatus* (Briers-Louw et al., 2023).

## Methods

### Sampling design

We conducted camera-trapping surveys in Coutada 11 in 2019 (60 days, 48 stations) and 2020 (64 days, 48 stations). These pilot surveys provided insights for appropriate camera-trap placement for the hyaena population; however, hyaena detections were too low to estimate density accurately. Subsequently, we conducted a more comprehensive survey (140 days, 76 stations) in 2021 (Fig. 1; Briers-Louw et al., 2024), in which we optimized site coverage through adjacent block sampling (Karanth & Nichols, 2002). We considered camera coverage sufficiently expansive to encompass the hyaena home range and sufficiently intensive to ensure multiple recaptures of individuals (Darnell et al., 2014), thus meeting spatial capture–recapture
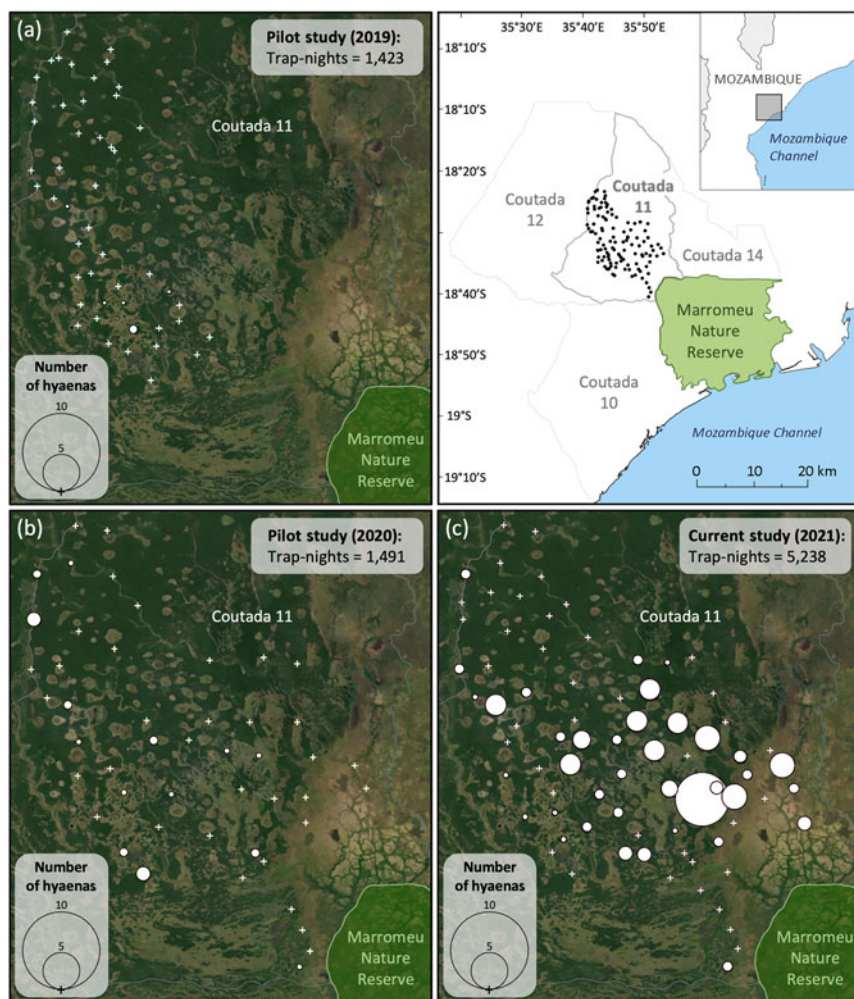
FIG. 1 Camera-trap locations and detection frequencies of spotted hyaenas *Crocuta crocuta* across the two pilot surveys in (a) 2019 and (b) 2020 and (c) in the comprehensive survey in 2021, in wildlife management area Coutada 11 in the Zambezi Delta, central Mozambique. Camera-trap sites are indicated by crosses (no hyaena captures) and circles (hyaena captures), with the number of individual hyaenas photographed indicated by circle size.

assumptions (Efford, 2004). The 140-day sampling window accepted marginal violation of the population closure assumption for increased precision for a species with a slow life history (Dupont et al., 2019; Briers-Louw et al., 2024). The mean inter-trap distance was 2.09 km (0.99–3.60 km), which facilitated comprehensive sampling of hyaenas, based on minimum clan home ranges of 30–52 km² in comparable landscapes (M'soka et al., 2016; Braczkowski et al., 2022). Stations comprised paired infrared cameras (Cuddeback model 1453, Cuddeback, USA) across roads or trails at a distance of c. 2 m from the path, mounted on trees or wooden poles 40–60 cm above the ground.

## Data preparation

We classified camera-trap images to species and processed them using the *camtrapR* (Niedballa et al., 2016) package in *R 4.2.1* (R Core Team, 2022). We identified individual hyaenas from photographic captures by their unique, asymmetrical pelage patterns (O'Brien & Kinnaird, 2011), using *Hotspotter* (Crall et al., 2013) pattern recognition software.

Four observers independently assigned individual identities to hyaena photographs (i.e. authors WDB-L, TAK, DB, EE and VNN) and we only included those for which we reached a consensus in subsequent density analyses. We excluded images from further analyses in which individuals were unidentifiable or for which there was no consensus amongst observers (Braczkowski et al., 2022). We maintained a record of all identified individuals with complete (i.e. both flanks) and partial (i.e. right or left flank only) evidence. For partially identified individuals we selected the flank with the greatest number of captures to avoid mismatching flanks and mistakenly double-counting individuals (Henschel et al., 2014). Although we acknowledge this introduces individual heterogeneity into capture probabilities and thus negative bias, resulting in underestimation of abundance (Augustine et al., 2018), precautionary undercounting is less of a risk to conservation management than overestimating abundance (Palmero et al., 2023). The presence of pseudo-scrotums in female hyaenas makes sex identification notoriously unreliable (Muller & Wrangham, 2002) and thus we did not consider this useful for identification purposes. We selected sampling

occasions of 24 h (00.00–23.59) to ensure independence of unique hyaena photographic capture events (Vissia et al., 2021). We also recorded any signs of poaching injuries (e.g. scars, or wounds around the neck).

Density estimation

We estimated hyaena density using a closed-population maximum-likelihood spatial capture–recapture model (Borchers & Efford, 2008) implemented in the *R* package *secr 4.5.5* (Efford, 2022; Supplementary Material 1). We modelled density as an inhomogeneous Poisson point process representing the intensity of activity centres within the state space, a standard approach in spatial capture–recapture analyses to facilitate computation as the process intensity varies over space and time (Efford & Fewster, 2013). We modelled the expected number of independent observations of individual $i$ at trap $j$ over $k$ occasions as a binomial process with $k$ trials and a detection probability $p$ estimated according to a half-normal function of the distance between trap $j$ and the latent activity centre of individual $i$ with a spatial decay parameter $\sigma$ and a baseline detection probability $go$ (Efford, 2022).

A 1 km grid extending 25 km around the trap array defined the modelling state-space area and accounted for individuals whose activity centres extended beyond the trapping area (Borchers & Efford, 2008; Efford, 2022). We identified a starting buffer width of 25 km using the *suggest.buffer* function in *secr*. We tested larger buffer widths but density estimates remained stable and the estimated relative bias was tolerable at < 0.05 per 100 km², and thus we used the smaller buffer width for computational efficiency (Efford, 2022). We fitted all models by maximizing the full likelihood using the Nelder–Mead optimizer (Borchers & Efford, 2008). To ensure model convergence, we implemented parameter estimates from a model with homogeneous density as starting values for more complex models with inhomogeneous density (Efford & Fewster, 2013).

Based on past research we postulated that hyaena density would be influenced by the relative availability of suitable habitat and the intensity of anthropogenic activity (Supplementary Table 1). We used the ESPACCI 20 m resolution land-cover dataset for Africa (ESA, 2017) to define habitat as grassland, shrubland, tree cover or community/cropland. We extracted the mean proportion of each land-cover type from a 7 km buffer (i.e. approximate core use area) around each point in the habitat mask (Pitman et al., 2017). However, after testing the proportion of each land-cover type for multicollinearity, we used proportion of tree cover to categorize landscape-level habitat (Briers-Louw et al., 2024). We log-transformed distance to the nearest community and used this to measure relative human activity. We scaled these continuous predictor variables to a mean of 0 and a standard deviation of 1 before including them as predictor variables in the density process.

A finite-mixture model approach (Efford & Fewster, 2013) accounted for variation in detection probability as individuals could not be reliably grouped into sex or age classes. We also included site-level habitat (i.e. cover of trees or open vegetation around each camera trap), a human activity index (i.e. number of independent human captures per trap effort) and a prey relative abundance index (i.e. number of independent suitable prey captures per trap effort) as predictors for $go$ (Supplementary Table 1). We fitted an initial set of candidate models as single-session spatial capture–recapture models with a two-class latent mixture as a covariate for $\sigma$ and $go$ (Supplementary Table 2). This revealed a rare class (i.e. c. 5%, equivalent to a single individual in the observed sample) with 14-fold greater detectability than the more common class according to the area under the detection curve. This model did not adequately fit the data (goodness of fit P = 0.99), which suggested that the individual outlier could be masking other sources of detection heterogeneity within the population (Supplementary Table 3). To investigate this, we fitted a second set of models to a capture history that excluded the outlier, which estimated substantial variation in the remaining c. 95% of the population (Supplementary Tables 4 & 5). We therefore fitted models to the complete dataset (i.e. including the outlier) with a three-class latent mixture as covariates for $\sigma$ and $go$. The robustness of three-class mixtures has not yet been established, but they are known to converge at local maxima (Efford, 2022). Thus, we are confident this represents an appropriate specification of the detection process for this population as the parameter estimates for the three classes were equivalent to those suggested by the two classes in the models both with and without the outlier using the robust two-class mixtures. We evaluated the subsequent candidate models using the Akaike information criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2003). We selected top-performing models on the parsimony principle to prevent overfitting.

To contextualize this density estimate, in December 2023 we conducted an informal review of academic and peer-reviewed literature on hyaena densities, using the keywords 'spotted hyaena' OR 'spotted hyena' OR '*Crocuta crocuta*' AND 'density' in Google Scholar (Google, 2023), with searches limited to 25 standard pages. Where meta-analyses were available, we used the snowball approach to capture all relevant studies represented therein. We calculated ecological carrying capacity estimates for hyaenas based on the Hayward et al. (2007) model, which incorporates preferred prey species and preferred prey weight ranges of hyaenas. The prey abundance data required for these

calculations were derived from regular aerial surveys (Macandza et al. 2022). Given the lack of hyaena dietary information in the Delta we derived prey preferences from a nearby protected area with relatively similar prey composition and vegetation (Briers-Louw & Leslie, 2020; Briers-Louw et al., 2024). We also compiled hyaena trophy hunting quotas and offtake data for the Delta for 2017–2021.

## Results

### Sampling effort

Overall effort comprised 5,238 trap-nights across 76 stations covering an area of 619 km² during the single-session dry-season annual survey (12 July–16 December 2021), resulting in 517 hyaena images. A total of 435 (84%) of these were suitable for individual identification, from which we derived 294 independent capture events and identified 23 individuals (Fig. 2). We recorded hyaenas at 54 camera-trap stations (naïve occupancy 71%), with at least one recapture for every individual (146 recaptures in total) and a mean of $6.3 \pm SE \ 1.0$ recaptures per individual.

### Density estimation

The single-session spatial capture–recapture model, $D \sim 1$, $go \sim (h3 + HumanIndex)$, $\sigma \sim h3$, was the highest-ranking model and had significantly more support ($\Delta AICc < 2$) than alternative models (Table 1). The hyaena density estimate following this best-fit model was $1.3 \pm SE \ 0.3$ hyaenas/100 km² (95% CI 0.8–2.1), which indicates a population of 23–37 individuals in Coutada 11 (Table 2). Based on this

model, hyaena detection was positively correlated with human activity.

During the 2021 camera-trap survey, two (9%) individuals were photographed with visible signs of injuries caused by snaring (Plate 1). One individual (no. 5) had a snare wound around the neck and the other (no. 11) was missing a back foot, presumably sustained from a steel gin trap. The only visible evidence of snaring in the 2019 and 2020 pilot surveys was an individual (no. 4) with a deep snare wound to the neck in 2020; this individual was legally hunted in 2021.

This baseline density assessment for the hyaena population in the Delta falls within the lowest 10% of all 101 available range-wide density estimates and in the bottom 22% of all 18 spatial capture–recapture estimates (Fig. 3, Supplementary Table 6). Prey-based carrying capacity estimates indicate that hyaena density should be almost an order of magnitude higher (9.3–12.4 hyaenas/100 km²; Supplementary Table 7). During the survey periods (2019–2021), four adult hyaenas were trophy hunted in Coutada 11, and no more than four hyaenas per year were legally hunted throughout the Delta since 2017 (Supplementary Table 8).

## Discussion

Reliable density estimates are fundamental for assessing the status of large carnivore populations and facilitating their recovery (Ripple et al., 2014). This is especially important in the context of carnivore conservation in Africa, where anthropogenic threats often affect these ecologically and economically significant species (Harris et al., 2023). Yet hyaena populations remain comparatively understudied amongst large
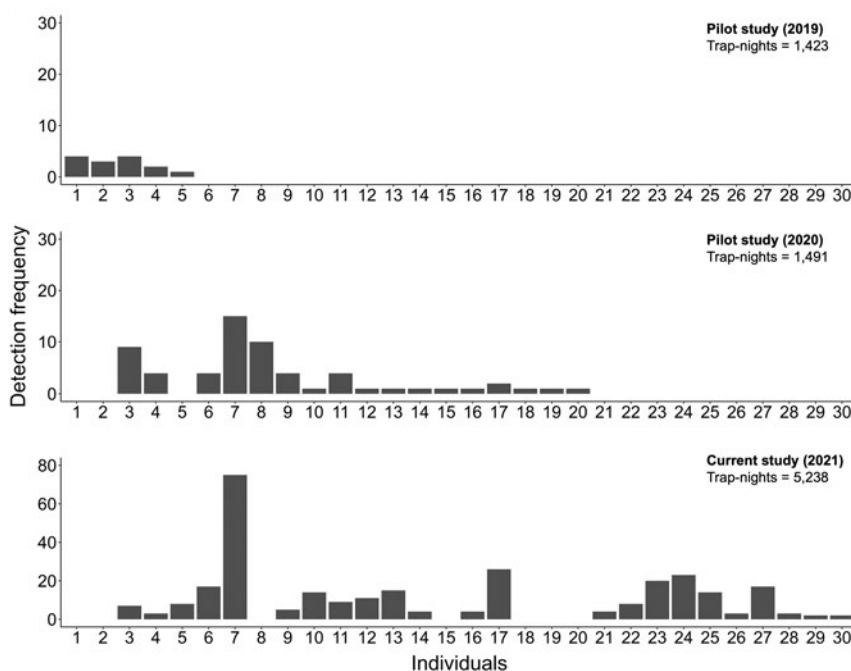


FIG. 2 Detection frequencies of individually identified spotted hyaenas across the two pilot surveys (2019 and 2020) and comprehensive camera-trapping survey (2021) in Coutada 11 (Fig. 1). Twenty-three individuals were identified in 2021 and a total of 30 individuals in the three surveys.

TABLE 1 Latent three-class spatial capture–recapture models for estimating density of the spotted hyaena *Crocuta crocuta* in the wildlife management area Coutada 11 in the Zambezi Delta, central Mozambique (Fig. 1), in 2021, ranked according to Akaike information criterion corrected for small sample sizes (AICc, with ΔAICc denoting the difference to the best-performing model). We included potential covariates for density (D) and probability of detection ($g0$) in the models, and a spatial scale parameter ($\sigma$) in the detection function. Covariates are detailed in Supplementary Table 1.

| Model[1] | df | AICc | ΔAICc | Weight |
|---|---|---|---|---|
| D $\sim$ 1, $g0 \sim$ (h3 + HumanIndex), $\sigma \sim$ h3 | 10 | 1,174.54 | 0.00 | 0.94 |
| D $\sim$ 1, $g0 \sim$ (h3 + Habitat + HumanIndex), $\sigma \sim$ h3 | 11 | 1,180.20 | 5.66 | 0.06 |
| D $\sim$ 1, $g0 \sim$ h3, $\sigma \sim$ h3 | 9 | 1,219.21 | 44.67 | 0.00 |
| D $\sim$ 1, $g0 \sim$ (h3 + Habitat), $\sigma \sim$ h3 | 10 | 1,220.57 | 46.04 | 0.00 |
| D $\sim$ 1, $g0 \sim$ (h3 + PreyIndex), $\sigma \sim$ h3 | 10 | 1,224.28 | 49.75 | 0.00 |
| D $\sim$ Comm_log, $g0 \sim$ h3, $\sigma \sim$ h3 | 10 | 1,225.90 | 51.36 | 0.00 |
| D $\sim$ TreeCover, $g0 \sim$ h3, $\sigma \sim$ h3 | 10 | 1,227.10 | 52.57 | 0.00 |
| D $\sim$ TreeCover + Comm_log, $g0 \sim$ h3, $\sigma \sim$ h3 | 11 | 1,233.77 | 59.24 | 0.00 |
| D $\sim$ TreeCover $\times$ Comm_log, $g0 \sim$ h3, $\sigma \sim$ h3 | 12 | 1,244.21 | 69.67 | 0.00 |

[1]HumanIndex, relative abundance index; Habitat type, tree cover or open vegetation; PreyIndex, prey relative abundance index; Comm_log, distance to the nearest community; TreeCover, proportion of tree cover.

carnivore species (Davis et al., 2022; Wilkinson et al., 2023). Our baseline estimate of 0.8–2.1 hyaenas/100 km² in Coutada 11 in central Mozambique is the first robust spatial capture–recapture density estimate for the species in the country.

The hyaena density we recorded in this study is relatively low compared to elsewhere, in the lower 25% of 18 range-wide spatial capture–recapture density estimates for the species (Supplementary Table 5). Our estimate is also substantially lower than recent spatial capture–recapture-based estimates for wildlife management areas in Tanzania (5.1–5.8 hyaenas/100 km²; Searle et al., 2023), and, similar to leopard

TABLE 2 Specifications of the highest-ranking three-class spatial capture–recapture model used to estimate spotted hyaena density (D) in Coutada 11 in 2021. Model parameters are covariate coefficient ($\beta$), probability of detection ($g0$), spatial scale parameter ($\sigma$) and mixing proportion parameter (pmix) for each of the three latent classes (h3). We also calculated hyaena abundance (N) based on suitable habitat (Briers-Louw et al., 2024).

| Model parameters | |
|---|---|
| N | 24 (23–37) |
| D $\pm$ SE (95% CI) | 1.33 $\pm$ 0.31 (0.85–2.08) |
| **Coefficient (HumanIndex)** | |
| $\beta \pm$ SE (95% CI) | 0.27 $\pm$ 0.04 (0.19–0.34) |
| **h3 = 1** | |
| $g0 \pm$ SE | 0.01 $\pm$ 0.00 |
| $\sigma \pm$ SE | 4,854 $\pm$ 334 |
| pmix | 0.46 |
| **h3 = 2** | |
| $g0 \pm$ SE | 0.10 $\pm$ 0.04 |
| $\sigma \pm$ SE | 7,185 $\pm$ 1,057 |
| pmix | 0.04 |
| **h3 = 3** | |
| $g0 \pm$ SE | $< 0.01 \pm 0.01$ |
| $\sigma \pm$ SE | 5,695 $\pm$ 779 |
| pmix | 0.50 |

estimates in our study area (Briers-Louw et al., 2024), hyaena density appears to be well below the expected carrying capacity of 9.3–12.4 hyaenas/100 km². Our hyaena density estimate was comparable to estimates for Limpopo National Park in southern Mozambique (1.49 hyaenas/100 km²; Everatt et al., 2019a), human-impacted miombo woodland-dominated protected areas in Malawi (1.15 hyaenas/100 km², Davis et al., 2021; 2.62 hyaenas/100 km², Briers-Louw, 2017) and arid savannah environments (0.85 hyaenas/100 km², Fouché et al., 2020; 2.1 hyaenas/100 km², Trinkel, 2009), despite the Delta being a largely mesic landscape with relatively high prey availability (Macandza et al., 2022). Our estimate was also similar to estimates from environmentally comparable post-war southern Angola and adjacent protected areas in northern Namibia (0.9–1.4 hyaenas/100 km²; Funston et al., 2017; Hanssen et al., 2017).

Large carnivore density is influenced by ecological factors such as intraguild competition, habitat type and prey density (Carbone & Gittleman, 2002; Caro & Stoner, 2003). Competition generally has a negligible influence on hyaena populations (Jones et al., 2021), and other large carnivore densities in the Delta are relatively low (Briers-Louw et al., 2024), suggesting that intraguild competition plays a minor role in hyaena density. Habitat suitability and availability are also improbable explanations for the low density as hyaena density in a similar floodplain–woodland habitat is almost an order of magnitude higher than in the Delta (e.g. 10.1 hyaenas/100 km² in the Okavango Delta, Botswana; Rich et al., 2019). Furthermore, although the Delta was subject to decades of armed conflict and sustained bushmeat poaching, improved protection of the landscape has resulted in substantial recovery and growth of prey populations (Beilfuss et al., 2010; Macandza et al., 2022).

Anthropogenic disturbance may be a strong determinant of hyaena density, distribution and behaviour (Croes et al., 2011; Schuette et al., 2013; Green & Holekamp, 2019).

PLATE 1 Photographic evidence of spotted hyaenas *Crocuta crocuta* affected by snaring in the wildlife management area Coutada 11 (Fig. 1). A1 and A2 are adult hyaena no. 11 with a missing foot presumably from a gin trap; B1 and B2 are adult hyaena no. 5 with a snare wound around the neck.

However, the relationship between carnivorous scavengers and human density can be highly variable and is generally poorly understood as it is often scale-dependent and linked to the relative opportunity costs and risks associated with navigating transformed anthropogenic landscapes. For example, detectability of scavenging predators may increase with relatively small-scale human impacts (Green et al., 2018), whereas large-scale human impacts often decrease detectability as a result of depleted prey and increased levels of human activity (Mwampeta et al., 2021). In Kruger National Park, South Africa, human infrastructure and activity offered favourable hunting opportunities for hyaenas at night and were linked to smaller home range sizes (Belton et al., 2016). The positive influence of human activity on hyaena detectability in the Delta could thus be explained by hyaenas being almost exclusively nocturnal and having little conflict with local communities because of low livestock densities.

Bushmeat poaching is widespread throughout Africa and is a significant threat to large carnivore populations (Lindsey et al., 2013; Everatt et al., 2019b; Naude et al., 2020; Rogan et al., 2022). In central Mozambique, wire snares and gin traps are the most frequently used poaching tools, and
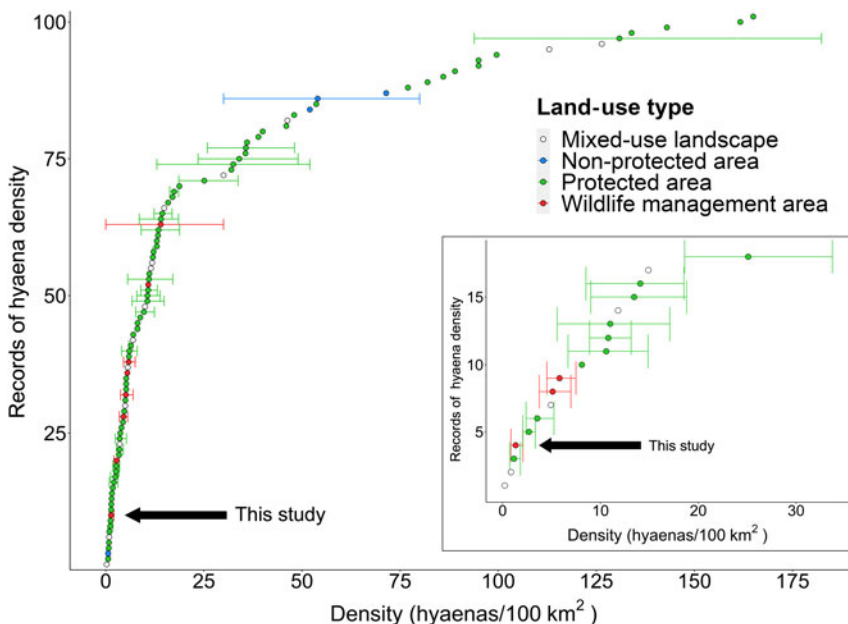


FIG. 3 Spotted hyaena population density estimates (n = 101) across the species' range (Supplementary Table 6). Inset indicates density estimates derived from a spatially explicit capture–recapture framework (n = 18). Dots indicate mean density estimates and bars indicate confidence intervals. Colours of dots and bars indicate land-use type, and black arrows indicate density estimates from this study. (Readers of the printed journal are referred to the online article for a colour version of this figure.)

their use is highly unsustainable because of their indiscriminate nature (Lindsey et al., 2013). Although we recorded only two hyaenas (9% of the individuals identified) visibly affected by poaching, this is probably an undercount of the true impact as these are the individuals that escaped the traps (Lindsey et al., 2013; Loveridge et al., 2020; Kendon et al., 2022; Searle et al., 2023; Briers-Louw et al., 2024). In the Ruaha-Rungwa landscape in Tanzania only two of 256 individuals (< 1%) had snare injuries (Searle et al., 2023), and in the Zimbabwean section of the Kavango–Zambezi Transfrontier Conservation Area 85 of 2,037 individuals (4%) had snare injuries (Loveridge et al., 2020). However, our findings are comparable to the Serengeti National Park in Tanzania where 8% of breeding females died annually as a result of bushmeat snares (Hofer et al., 1993). As high-ranking females play a significant role in maintaining clan persistence and accelerating population recovery, the loss of such individuals or their reduced fitness from snare-related injuries can have detrimental demographic effects (Benhaiem et al., 2018, 2023; Dheer et al., 2022a). Snaring survival rates of hyaenas (0.25–0.62; Loveridge et al., 2020) suggest that 1–6 hyaenas could have died undetected in snares during our study. It is thus plausible that bushmeat poaching has limited the post-war recovery of hyaenas, as with other large carnivores across Mozambique (Lindsey & Bento, 2012; Lindsey et al., 2013; Bouley et al., 2018; Everatt et al., 2019b). We recommend that future studies include information on snared individuals, to help assess snaring trends and highlight hotspots where it may be a significant threat to sustaining viable large carnivore populations (Becker et al., 2024). Our findings suggest hyaenas may be less resilient to anthropogenic pressures than previously thought and emphasizes the need for population assessments and improved protection across the range of this species.

Hyaenas can display behavioural plasticity in response to disturbance. For example, in the Serengeti and Ngorongoro Crater hyaena populations increased rapidly following increases in prey (Hofer & East, 2003; Höner et al., 2005). However, hyaenas are generally slow to recover post-war, especially with sustained pressure from surrounding communities, such as that experienced in southwest Africa, where transboundary animal movement and variable conservation practices and policies further complicate management (Braga-Pereira et al., 2020). Even following moderate disturbance hyaena populations may require > 15 years to recover (Benhaiem et al., 2018) as the relatively low fecundity rates and high levels of parental investment in their young confound population recovery (Becker et al., 2024). In Majete Wildlife Reserve and Kasungu National Park in Malawi, where there was intensive poaching followed by improved protection, hyaena densities have remained low (Briers-Louw, 2017; Davis et al., 2021). Hyaena density is largely dependent on prey availability

and protection (Searle et al., 2023). Thus, there is scope for population recovery given recovering prey populations and provided that improvements in protection are prioritized. Regionally, hyaenas are absent or occur in low numbers outside the Delta (Lindsey & Bento, 2012), although reintroduction of hyaenas into neighbouring Gorongosa National Park following their post-war extirpation (Pringle, 2017; Bouley et al., 2018) increases the likelihood of population connectivity and recovery in central Mozambique.

Monitoring is essential for informing sustainable trophy hunting quotas. This is especially important for hyaenas as they are difficult to sex (Dheer et al., 2022b) and adult females tend to be slightly larger than males (McCormick et al., 2022). Trophy hunters, who generally target larger individuals, could primarily be harvesting females, thereby reducing reproductive output and suppressing population growth. However, the regular protection activities supported by hunting operators can also be key determinants of large carnivore persistence (Strampelli et al., 2022). In the Ruaha-Rungwa landscape of Tanzania large carnivore occurrence was influenced more by management and law enforcement levels than by whether an area was used for photographic or trophy hunting tourism (Strampelli et al., 2022). The comparatively well-managed, low-volume and consistent trophy hunting in the Zambezi Delta could be justified as a mixed land-use system, primarily financed and secured by hunting, maximizes conservation value compared to alternative and currently infeasible or unsustainable protection models for the region. Encroachment of human activity within and around these wildlife management areas is regulated, and bushmeat poaching has only recently been reduced to a manageable level (an 87% reduction in bushmeat snares and traps during 2017–2021) through effective anti-poaching efforts (Briers-Louw et al., 2024). Nevertheless, to facilitate population recovery, a more conservative quota should be considered as cryptic bushmeat poaching also contributes to offtake. Future quotas and the possibility of hunting offtake should be dependent on continued monitoring of the population using consecutive and comparable surveys and analytical frameworks, such as those used in our survey, to identify and account for discrepancies between modelled quota effects and reality (Strampelli et al., 2020; Briers-Louw et al., 2024).

Although law enforcement efforts have dramatically reduced bushmeat poaching post-war (Briers-Louw et al., 2024), the comparatively low hyaena density and evidence of snares suggest that poaching is probably suppressing the inherently slow population recovery of hyaenas in the Delta. To ensure the long-term viability and growth of this hyaena population, we recommend management prioritizes anti-poaching efforts and considers demographic augmentation to promote population growth and genetic diversity.

**Conflicts of interest** None.

**Ethical standards** This study abided by the *Oryx* guidelines on ethical standards, and was conducted under a research permit (ANAC RP# 06/10/23) from the Administração Nacional das Áreas de Conservação in Mozambique. Permission was obtained from the concessionaire to conduct camera trapping in Coutada 11. In accordance with the ethical criteria of Stellenbosch University, this non-invasive research did not require ethical approval. Where people were incidentally and unintentionally photographed by camera traps, these photographs were securely stored in an access-controlled database, and any metadata collected were anonymized, in compliance with standard ethical practices for the collection of personal images and information without consent in camera-trap research.

**Data availability** Open-access supporting data is available at github.com/WillemBriersLouw/ZD_SpottedHyaenaDensity.

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