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Perilous state of critically endangered Northwest African cheetah (*Acinonyx jubatus hecki*) across the Sudano-Sahel

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Acinonyx jubatus hecki; human–wildlife conflict; Pendjari; Zakouma; Siniaka Minia; spatially explicit capture–recapture; transboundary conservation; cheetah.

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Abstract

Northwest African cheetah populations have declined precipitously, with expert opinion estimating that <420 individuals persist across parts of Algeria, Benin, Burkina Faso, Chad, Niger and Mali. However, no reliable density estimates exist in the remaining subspecies strongholds throughout the Sudano-Sahel Zone, including the W-Arly-Pendjari Complex and Greater Zakouma Ecosystem within the Bahr/Salamat landscape. Camera trap surveys were combined with spatially explicit capture–recapture methodologies in both regions to estimate the cheetah density and detectable demographic composition of these populations. Following 15 429 camera trap nights, we detected nine individuals during the dry season and four individuals during the wet season in Pendjari (2021), nine individuals (dry season; 2023) in Zakouma and none in Siniaka Minia. Cheetah densities were thus estimated at 0.17–0.24 and 0.37 cheetah per 100 km^2 in Pendjari and Zakouma, respectively. While marginally higher than predicted, such low-density estimates are concerning in the last remaining habitats harbouring this critically endangered subspecies. Considering the substantial contraction of regional cheetah distribution, we estimate an overall population size of 68 ± 29 individuals across the studied areas. These novel estimates are among the lowest formally determined densities throughout cheetah range in Africa, where a high frequency of people and livestock detected on camera traps highlight the ongoing risks to large carnivores in these protected areas. Subsequent management recommendations include implementation of the established regional conservation strategies that encompass the distributional range of these cheetah, continuous monitoring of populations, genetic analyses to inform management, curbing illegal trade and increasing international awareness around the plight of the subspecies.

Highlights

- Critically endangered Northwest African cheetah populations are understudied.
- Remaining populations of the subspecies survive in only three core areas of the Sudano-Sahelian Zone.
- SECR-based density estimation was applied to the stronghold habitats in Sudano-Sahelian Zone.
- Densities were among the lowest recorded across the global range emphasizing their vulnerability.
- Northwest African cheetah populations are likely smaller than what is generally perceived.

Introduction

Large carnivores are among the most globally threatened species given their sensitivity to anthropogenic impacts, particularly habitat loss and fragmentation (Woodroffe, 2000; Ripple *et al*., 2014). The cheetah (*Acinonyx jubatus*) is especially vulnerable, with the smallest global population among large carnivores, comprising approximately 6500 mature individuals across their African and Asian range (Durant *et al*., 2017, 2022). Despite their vulnerable conservation status (Durant *et al*., 2022), most population estimates are based on expert opinion, rather than systematic population estimation surveys. For instance, no reliable occurance data exist for at least 40% of historical cheetah range (IUCN/SSC, 2012), where, in Africa, <40% of cheetah reside within protected areas (PAs), 87% of which are transboundary, requiring international cooperation and coordination to effectively manage PAs which span across these national borders (Durant *et al*., 2017). Moreover, in many parts of cheetah range, armed conflict and political instability prevent site access for local and international research which often limits the international collaborative support required for repeated transboundary population surveys, particularly across the Sudano-Sahelian Zone (Brito *et al*., 2018; Farhadinia *et al*., 2020). A lack of such reliable large-scale data is an urgent concern for Northwest African cheetah (*A. j. hecki*) which is considered 'Critically Endangered' by the IUCN Red List of Threatened Species with declining populations (Belbachir *et al*., 2015; Sillero-Zubiri *et al*., 2015) that may have severe consequences for the remaining genetic diversity of this species (Charruau *et al*., 2011; Farhadinia *et al*., 2017; Prost *et al*., 2022).

Northwest African cheetah are estimated to comprise <420 mature individuals, persisting within three known or suspected major subpopulations across the Sudano-Sahel and Sahara Zones (Durant *et al*., 2022; Blais *et al*., 2023), located between southern Algeria and Mali, parts of Termit in Niger, and the W-Arly-Pendjari (WAP) Complex linking Benin, Burkina Faso and Niger, as well as in the Greater Zakouma Ecosystem (GZE) in the Bahr/Salamat landscape of southern Chad and northern Central African Republic (Blais *et al*., 2023). This genetically distinct subspecies (Charruau *et al*., 2011; Prost *et al*., 2022) is believed to differ morphologically from other sub-Saharan cheetah, being physically smaller with shorter pale fur (Dragesco-Joffé, 1993). As it is not yet confirmed that the population in the GZE is the Northwest or Northeast (*A. j. soemmerringi*) African cheetah subspecies (Charruau *et al*., 2011; Prost *et al*., 2022), baseline population estimates would have significant implications for strategic conservation management across the region (Meißner *et al*., 2023). The only population surveys conducted for the subspecies were carried out in the Algerian Sahara, a region of extremely low productivity, where correspondingly low densities of one individual per 4000 km^2 were recorded (Belbachir *et al*., 2015; Sillero-Zubiri *et al*., 2015). There is no formal estimate for the subspecies in more productive savannah habitats which comprise a critical proportion of its distributional range (Belbachir *et al*., 2015; Sillero-Zubiri *et al*., 2015). Despite these differences, this subspecies of cheetah is among the least-studied and lacks active international-to-local support for the implementation of established range-wide conservation strategies.

Cheetah are a low-density, wide-ranging species with nomadic movement patterns and cryptic behaviour, which challenges robust population estimation (Belbachir *et al*., 2015; Becker *et al*., 2017; Linden *et al*., 2020). A variety of monitoring methods have been used to estimate cheetah population status with varying success, including long-term observation studies (Caro, 1994; Kelly, 2001; Durant, Kelly, & Caro, 2004; Durant *et al*., 2007), sign and spoor surveys (Funston *et al*., 2010; Boast & Houser, 2012), camera traps (Marnewick, Funston, & Karanth, 2008; Belbachir *et al*., 2015; Brassine & Parker, 2015; Broekhuis & Gopalaswamy, 2016), citizen science (Marnewick *et al*., 2014; Farhadinia *et al*., 2016) and detection-dogs (Becker *et al*., 2017). However, many of these approaches are site-specific, and there is a need for developing and testing a reliable and repeatable approach that can provide robust density estimates for remaining cheetah populations (Strampelli *et al*., 2021), especially in West and Central Africa (IUCN/SSC, 2012). As a result, robust density estimates and the contextual demographic structures of many extant cheetah populations are unknown throughout most of their global range (Table S1; Belbachir *et al*., 2015; Durant *et al*., 2017).

Reliable population estimates are essential for assessing the impact of conservation policy and management interventions aimed at addressing declining populations (Rogan *et al*., 2019). Spatially explicit capture–recapture (SECR) methods (Borchers & Efford, 2008) have enabled accurate and reliable estimates of density for species that are individually identifiable. Currently, SECR models are widely used to estimate the density of many species, including large carnivores (O'Brien & Kinnaird, 2011); Poilecot *et al.*, 2010, by incorporating the spatial locations of animal captures into a unified model (Borchers & Efford, 2008; Royle *et al*., 2009). Integrating such spatial information allows for more accurate and informative estimates of animal density (Borchers & Efford, 2008), which have been successfully applied to other large felids including leopard (*Panthera pardus*; Farhadinia *et al*., 2019; Rogan *et al*., 2022; Briers-Louw *et al.*, 2024), jaguar (*P. onca*; Boron *et al*., 2016; Harmsen, Foster, & Quigley, 2020) and tiger (*P. tigris*; Xiao *et al*., 2016; Ash *et al*., 2020; Phumanee *et al*., 2021).

As SECR-based density estimates require relatively consistent and broad resampling to obtain sufficient recaptures of individuals at multiple sites to determine a robust spatial scale parameter (σ) and meet the assumption of population closure (Sollmann *et al*., 2013; Wilton *et al*., 2014), such analyses are often challenging for small samples sizes, especially when few individuals (Sharma *et al*., 2014; Hearn *et al*., 2019) are infrequently detected (Gerber, Ivan, & Burnham, 2014; Alexander *et al*., 2015; Rostro-García *et al*., 2018). The spatial scale parameter, σ, represents the extent of an individual's movement and is crucial for understanding the decrease in detection probability as the distance from the home-range centre increases. Such limitations are common in the density estimation of large carnivores, such as cheetah, where relatively wide-ranging species with large home-range requirements often occur at low densities and may be subject to edge effects (Obbard, Howe, & Kyle, 2010; Farhadinia et al., 2016; Rovero & Zimmermann, 2016). In these cases, it is essential to design the survey such that it optimizes the probability of repeated detections by considering the study duration, as well as the number and placement of cameras (i.e., detector array, Tobler & Powell, 2013; Wilton et al., 2014), where the extent of the detector array should be similar to or larger than the extent of individual movement (Efford & Fewster, 2013; Wilton et al., 2014) and model accuracy may be improved through a multi-session approach (Efford, 2022).

Given the relatively low population densities observed in cheetah (Table S1), as well as their comparably elusive behaviour (Marnewick et al., 2008), population studies frequently turn to indirect methods, such as spoor surveys and citizen science (Houser, Somers, & Boast, 2009; Boast & Houser, 2012; Groom & Watermeyer, 2017; van der Meer et al., 2021), while SECR models have only been applied to cheetah in a handful of studies (Brassine & Parker, 2015; Broekhuis & Gopalaswamy, 2016; Fabiano et al., 2020). As such, our current knowledge of cheetah distribution, density, and conservation status relies disproportionately on expert opinion or indirect methods rather than direct, individual-based methodologies, which may hamper ongoing conservation policy development and intervention efforts. Here we address this knowledge gap for Northwest African cheetah by using the systematic application of camera traps and multi-session maximum-likelihood SECR modelling to estimate population density and demographic composition within remaining habitat across the Sudano-Sahel Zone of West and Central Africa. These data are considered essential to local conservation authorities and international stakeholders in developing policy and interventions that may arrest the decline of cheetah throughout this region and improve the conservation status of this critically endangered subspecies. By interpreting these baseline findings in the context of broader apex predator declines, this study contributes to global discourse around biodiversity loss, emphasizing the interconnected nature of ecological systems and the necessity for coordinated international conservation efforts to mitigate such concerning trends.

Materials and methods

Study area

This study was conducted across three study areas (Fig. 1) in two remaining strongholds for Northwest African cheetah across the Sudano-Sahel Zone, including the WAP Complex and Bahr/Salamat landscape, with an annual precipitation of 200 to 1000 mm (Karlson, 2016). The first study area, Pendjari National Park (11.2143° N, 01.5218° E) in northern Benin, forms part of the larger WAP Complex (>30 000 km^2) which links a critically important triad of national parks and reserves in the Republics of Benin, Burkina Faso and Niger to form the largest transboundary PA in West Africa (Sinsin et al., 2002). Surveys were conducted within Pendjari National Park and the Konkombri Hunting Zone (hereafter Pendjari; 3042 km^2) in the south-western region of the WAP Complex (Fig. 1a). Falling within the latitudinal tropical Sudanian savanna belt, Pendjari is characterized by a predominantly dry climate with a single wet season, occurring from mid-May to mid-October (Dossou-Yovo, Assogbadjo, & Sinsin, 2016; Vodouhê et al., 2009).

The second and third study areas fell within the in Bahr/-Salamat landscape and southern Chad, including Siniaka Minia Wildlife Reserve (10.4304° N 18.2130° E) and Zakouma National Park (10.8376° N 19.6555° E) which form part of the GZE (>28 000 km^2). These PAs, with important wildlife corridors, ultimately connect Bahr/Salamat landscape to the Central African Republic and Sudan. Surveys were conducted in Siniaka Minia Wildlife Reserve and the Melfi-Roukoum Hunting Zone (hereafter Siniaka Minia; 5260 km^2; Fig. 1b), as well as within Zakouma National Park (hereafter Zakouma; 3041 km^2; Fig. 1c). Falling within the savannah region between the Sahel and the rainforests of the Congo Basin, the GZE protects one of the few remaining intact Sudano-Sahelian ecosystems in Africa (Brottem, 2020). The GZE is characterized by strong seasonal duality, where the wet season spans April to September and its influence is still evident 2 months thereafter, followed by a 4-month dry season (Clark et al., 2023). Where the large flood-plains, particularly in the south of GZE, are inundated during the wet season (Ducros et al., 2023; Poilecot et al., 2010).

Sampling design

Five camera-trap surveys were carried out in the three study areas between April 2021 and May 2023. Surveys were repeated for both wet and dry seasons in Pendjari and Zakouma, while in Siniaka only one wet season survey was conducted following limited captures of large carnivores, especially cheetah and lion (*Panthera leo*) in the first survey. Additionally, there were high capture rates of people and livestock with unsustainable levels of camera trap theft. Remote white flash camera traps, including Panthera® V7 (Panthera, New York, NY 10018, USA), and Spartan® Lumen (Spartan, Georgia, GA, 30096, USA) were deployed within 6.3 × 6.3 km grids with average distances between camera stations ranging from 2 479 m to 4 910 m. Grid cell size was based on reported minimum cheetah home-range size estimates of 40 km^2 (Broomhall, Mills, & Toit, 2003) with grid cell numbers varying between 42 and 65 across sessions, while camera-trap array sizes ranged from 2 435 km^2 to 3 386 km^2 across the five sampling sessions (Table 1). The grid size ensured that multiple camera stations fell within a single cheetah home-range, increasing the likelihood of capturing and recapturing individual cheetah at different stations, which is crucial for accurate SECR analysis (Boast et al., 2013; Green, Chynoweth, & Şekercioğlu, 2020). While female cheetah home-ranges can be as large as 1 000 km^2 (Caro, 1994; Marker et al., 2008), the chosen grid size balances the need for extensive coverage with the logistical feasibility of deploying and maintaining many camera traps, particularly in these highly remote and potentially dangerous landscapes. Smaller grid cells would require

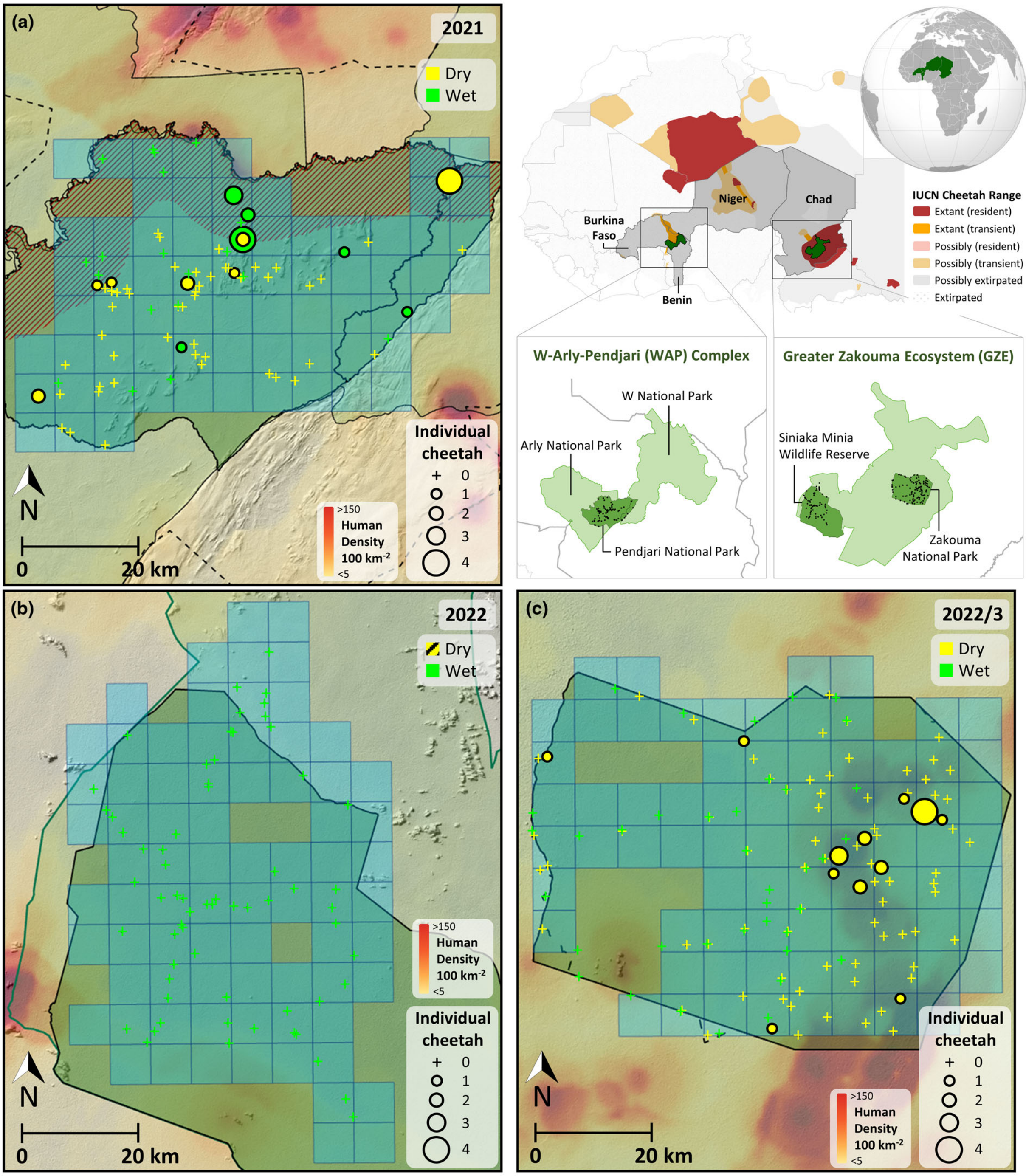

Figure 1 The geographic location of the three study areas within the W-Arly-Pendjari Complex and the Greater Zakouma Ecosystem in the Sudano-Sahel Zone of West and Central Africa. The study area (dark green) falls within larger protected areas (light green), that may include a buffer zone (dashed black lines), militarized zone (red hatching) and varying levels of human density (see insert on maps). Study areas were divided into 6.3 × 6.3 grid cells (indicated in blue) sampled by camera traps (yellow cross = dry season; green cross = wet season), with some cells excluded as inaccessible terrain. Study areas include: (a) Pendjari National Park and the Konkombri Hunting zone (3042 km^2), (b) Siniaka Minia Wildlife Reserve and the Melfi-Roukoum Hunting zone (5260 km^2), and (c) Zakouma National Park (3041 km^2). Independent cheetah detections per season are indicated by filled circles (yellow = dry season; green = wet) with the size of the circle indicating the number of unique individuals detected.

Table 1 Sampling design for estimating the density of Northwest African cheetah in the W-Arly-Pendjari Complex and Greater Zakouma Ecosystem, the last remaining habitat subspecies strongholds in the Sudano-Sahel, using a multi-session spatially explicit capture–recapture (SECR) analyses framework (2021–2023)

Study area	Pendjari		Siniaka Minia	Zakouma	
Season	Dry	Wet	Wet	Wet	Dry
Sampling period (days)	20/04/2021–29/07/2021 (100)	30/07/2021–30/10/2021 (92)	01/05/2022–08/07/2022 (68)	10/05/2022–18/06/2022 (39)	12/01/2023–22/04/2023 (100)
Stations (marking | trail | water)	73 [56|8|9]	28 [22|6|0]	66 [53|7|6]	38 [24|14|0]	92 [28|58|6]
Effort (trap nights)	2995	2324	2804	1332	5974
Mean spacing (m ± SD)	2498 ± 1437	4579 ± 1765	2479 ± 1541	4910 ± 1921	3007 ± 1674
Number of grid cells	51	42	64	47	65
Array size (km^2)	2881	2435	2797	2778	3386

significantly more traps and maintenance, while larger cells might miss finer-scale movements and interactions (Green *et al.*, 2020). This spacing of cameras, with average distances between stations, is thus dense enough to consistently capture individuals at multiple locations within their home-range. This grid spacing was also supported by mean maximum distance moved (MMDM) metrics, which aid in retrospectively estimating effective trap spacing and ensuring comprehensive coverage (Boast *et al.*, 2013), while being comparable to such measures in other studies (Marker *et al.*, 2008; Weise *et al.*, 2015). Additionally, some grid cells did not have cameras, especially during the rainy season due to practical constraints, such as inaccessibility or unsuitable habitat (i.e. densely forested areas) that is not preferred by cheetah. Efforts were made to remove grid cells from the edges of the study areas wherever possible to maintain continuity in sampling and minimize any gaps that could negatively impact the comprehensive coverage of the survey. SECR models can effectively integrate such heterogeneous trap locations to provide robust density estimates despite non-uniform placement (Boast *et al.*, 2013; Green *et al.*, 2020). A quarter of all stations in each survey had paired cameras to simultaneously maximize the number of individuals captured and recapture rates by individual identification. Targeted camera placement was used (Brassine & Parker, 2015), with cheetah scent-marking points being prioritized for placement (Table 1), such as higher elevation, large trees and termite mounds with animal signs, and if these signs are not found in each grid, the next priorities were trails with cheetah spoor, and water access points during dry seasons (Ipavec *et al.*, 2018; Drouilly *et al.*, 2019; 2021; 2023). Sampling periods ranged from 39 to 100 days, and were relatively short given average cheetah lifespan (Durant *et al.*, 2004) in order to avoid violating demographic closure assumptions (Rovero & Zimmerman, 2016).

Data preparation

Individual cheetah were identified from photographs using their unique spot patterns. Two researchers (AS and MSF) independently identified each cheetah, and these identities were then cross validated by a third independent researcher (VNN; Fig. S1). High quality photographs capturing spot patterns on both flanks were used to identify individuals and where only single flanks were captured, other unique characteristics such as tail rings or facial patterning were used as additional characters to aid identification (Chelysheva, 2004; Brassine & Parker, 2015). Sex was determined when external genitalia were visible in the photograph or by the presence of dependent offspring with an adult. While dependent cubs and juveniles were excluded, all independent adolescents and adults were considered in subsequent density analyses. Each 24-h day was designated as a sampling occasion, where a single event was defined as consecutive photographs of the same individual taken no more than 30 minutes apart (Rovero & Zimmerman, 2016). Images of sympatric large carnivores as well as domestic livestock and people (i.e. presence only, without identifiable features) were also recorded.

Statistical analyses

Northwest African cheetah density was estimated using a closed population maximum-likelihood SECR model (Borchers & Efford, 2008) implemented in the *secr* package (v 4.2; Efford, 2022) in R software (v 4.2.1; R Core Development Team, 2022). In Pendjari, multi-seasonal data were combined in a single model framework, treating each season as an independent session without temporal overlap, which allowed for model fitting with pooled parameters that applied across sessions (Efford, 2022). In contrast, a single-session modelling framework was applied to the Zakouma dry season, while the lack of detections excluded the Zakouma wet season and Siniaka Minia from cheetah density estimation. As only one individual was detected in both Pendjari sessions (Fig. S1), the inter-session independence assumption was maintained and the risk of pseudo-replication was minimized (O'Connell, Nichols, & Karanth, 2011; Hamel *et al.*, 2013).

SECR is a form of hierarchical modelling with a state process representing density and an observation process representing the expected probability or rate of capture based on the assumption that the probability of detection decreases as the space between a detector and an animal activity centre increases (Efford, 2004; Efford, Dawson, & Borchers, 2009). In this study, Poisson processes were assumed for both these states. Density was expressed as a point process representing the intensity of activity centres within the state space. We modelled observations using a 'count' detector formulation, such that we recorded the number of independent captures for each individual at each station (Fig. 1; Efford, 2022). The expected number of observations of individual i at trap j was assumed to vary as a function of the distance between trap j and the activity centre of individual i following a hazard half-normal function with two parameters: a baseline detection rate (g_0) and a spatial decay parameter (σ; Efford *et al*., 2009). All models were fitted by maximizing the full likelihood using the Nelder–Mead optimizer (Borchers & Efford, 2008). To ensure that models converged, we used parameter estimates from a model with homogeneous density at starting values for more complex models with inhomogeneous density (Efford & Fewster, 2013).

Multi- and single-session survey phase models considered both trend ($g0\sim T$) and behavioural response ($g0\sim b$) to investigate the influence of time on animal activity and behaviour on detection probability within the SECR framework. The trap-specific behavioural response was considered in the baseline detection model, as we anticipated that cheetah behaviour may change after being detected at a specific trap for the duration of the survey session (bk). This adjustment was made as large terrestrial carnivores, including cheetah, exhibit variations in their home-range sizes, movement patterns, and capture probabilities. Accounting for such behavioural differences is considered important in accurately assessing the observation process in capture–recapture studies (Sollmann *et al*., 2013). To further address heterogeneous capture probabilities, we incorporated a sex-specific covariate in the detection process (Broekhuis *et al*., 2021; Klein *et al*., 2021) as a sex-effect in the encounter rate ($g0$) and spatial scale (σ), as these were observed in previous cheetah studies (Brassine & Parker, 2015; Broekhuis & Gopalaswamy, 2016; Strampelli *et al*., 2021). Session-stratified estimates to capture potential temporal variation were also employed, where likelihood was maximized to obtain session-specific estimates. The integration area, or state-space model, was defined using evenly spaced points in a regular grid with a mesh spacing of 1 km^2 (Fig. 1).

A range of buffer widths around the trap array were tested to define the modelling state space by determining the point at which the density estimate stabilized (Kalle *et al*., 2011) and to account for individuals whose activity centres extended beyond the trapping area (Efford, 2004; Borchers & Efford, 2008). Various buffer sizes were applied incrementally to the trap arrays to identify the optimal buffer width. The process involved running multiple SECR models with different buffer widths and assessing at which buffer size the density estimates stabilized, indicating that the buffer was sufficiently large to encompass the activity centres of the animals being studied (Table S4). A mask with a 50 km buffer was optimum to define the state-space area for Pendjari (Fig. 1a), while a 30 km buffer was optimal for Zakouma (Fig. 1c). These buffers were also consistent with limited GPS-collared home-range estimates of Northwest African cheetah, which anecdotally indicate a diameter of approximately 55 km in Pendjari and 26 km in Zakouma. As cheetah are unlikely to maintain home-range centres in areas of increased negative interactions with people (Klein *et al*., 2021), areas with high levels of anthropogenic impacts, such as large villages and towns were also masked out (Fig. 1).

Several *a priori* models with varying effects on $g0$ and σ were fitted (Tables S2 and S3), following a multi-session framework for Pendjari (n = 14 models) and single-session analyses for Zakouma (n = 10 models). We also examined the two parameters of camera location type (Loc) and sex of identified cheetah (Sex) as covariates in predicting density. Each set of candidate models was evaluated using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2003). Top-performing models were selected on the parsimony principle as the best balance of complexity against goodness of fit and were compared across sets based on overlap in parameter confidence intervals and precision. Goodness of fit for the single-session models was tested using 99 replications of Monte Carlo resampling model deviance divided by the residual degrees of freedom. A model was considered adequate if its goodness-of-fit rank was between 10 and 90.

Results

Sampling effort

After 2 995 dry- and 2 324 wet-season trap nights in Pendjari, a total of 19 and 13 independent cheetah detections were obtained, representing nine (F = 2; M = 7) and four (F = 2; M = 2) unique individuals, respectively (Table 2). All detected adult female cheetah in Pendjari were accompanied by one to four cubs, including two family groups per season of which one family was common between seasons (Fig. 2). However, a cub was lost from this family in the second session, resulting in a cumulative count of three families with eight cubs throughout the study period in 2023.

No cheetah were detected in the wet-season surveys of Siniaka Minia (2 804 trap nights) and Zakouma (1 332 trap nights). However, 5 974 dry-season trap nights in Zakouma yielded a total of 25 independent cheetah detections representing nine (F = 4; M = 4; Unknown = 1) unique individuals, including only one family with two cubs identified.

In addition to cheetah events, a total of two seasons of Pendjari, yielded 211 independent photographic events of other large carnivores, including leopard, lion and spotted hyena (*Crocuta crocuta*), while the 2 804 wet-season trap nights in Siniaka Minia yielded only eight independent large carnivore events of leopard, spotted and striped hyena (*Hyaena hyaena*). A total of 7 306 multi-season trap nights in Zakouma yielded 1 261 events of leopard, lion, spotted and striped hyena (Table 2). A total of 6, 98 and 209 independent photographic events of domestic livestock and/or people were also recorded for these sessions in Pendjari, Siniaka Minia and Zakouma, respectively.

Scent marking sites presented significantly higher cheetah detections than other targeted sites (i.e. trails, or water sources),

Table 2 Detection details of individually recognizable cheetah in Northwest Africa, and sympatric large carnivores and human/domestic animals across multiple study sites in Benin and Chad during 2021–2023. The number within parentheses represent the number of camera trap station with positive independent detections. M = subadult/adult male, F = subadult/adult female and family = mother with dependent cub(s)

Study area	Pendjari		Siniaka Minia	Zakouma	
Season	Dry	Wet	Wet	Wet	Dry
Lion (*Panthera leo*)	18 (6)	23 (8)	–	7 (4)	208 (62)
Leopard (*Panthera pardus*)	24 (11)	11 (5)	3 (3)	9 (5)	139 (45)
Spotted hyena (*Crocuta Crocuta*)	74 (17)	62 (7)	3 (3)	17 (8)	741 (78)
Striped hyena (*Hyaena hyaena*)	–	–	2 (2)	10 (4)	130 (36)
People and domestic animals	4 (3)	2 (2)	98 (28)	66 (13)	143 (41)
Cheetah (*Acinonyx jubatus*)	18 (10)	13 (5)	–	–	25 (12)
# Independent subadult/adult cheetah	9	4	–	–	9
Observed sex ratio (M: F)	1:0.29	1:1	–	–	1:1
# Families	2	2	–	–	1
# Dependent cubs	4	5	–	–	2

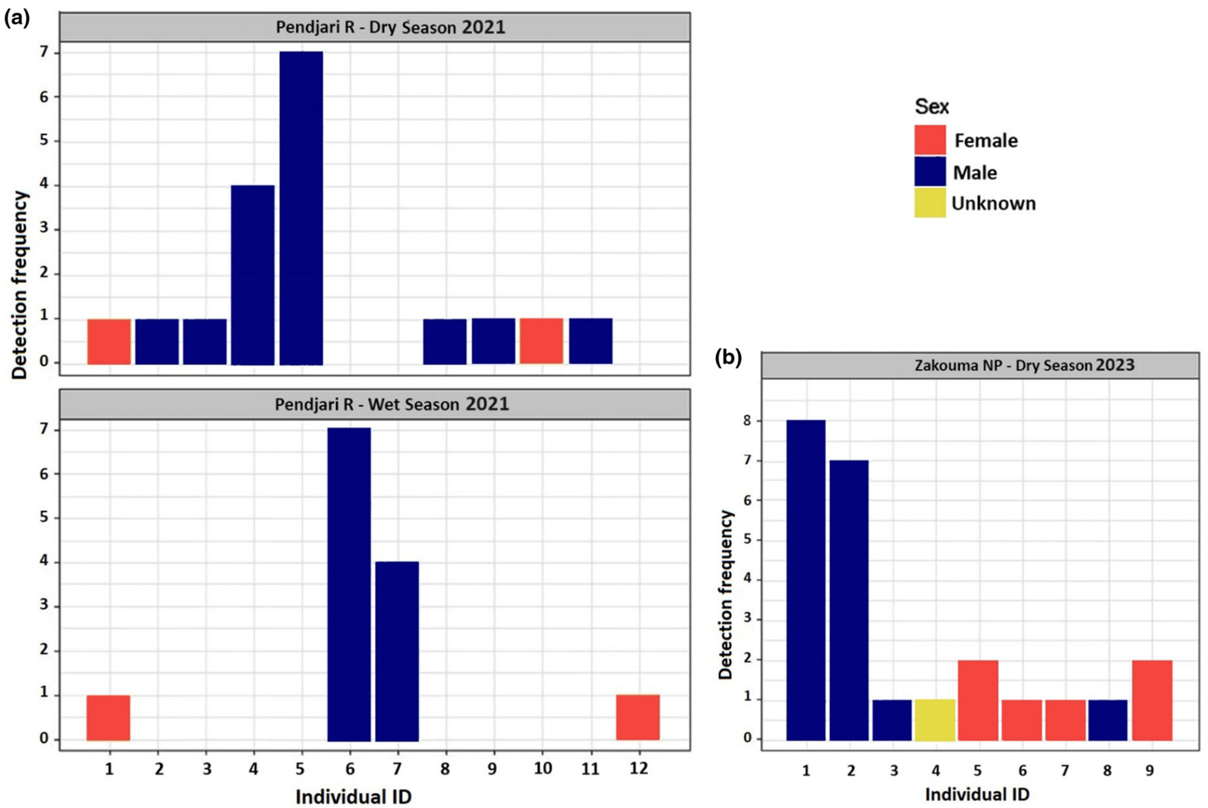

Figure 2 Detection frequency of individual cheetah based on systematic camera trapping across two seasons of (a) Pendjari Reserve of the WAP Complex in Benin and one season (b) in Zakouma National Park in Chad.

accounting for 87% (n = 27) of detections in Pendjari (χ^2 = 4.996, df = 2, P < 0.05) and 67% (n = 16) in Zakouma (χ^2 = 63.93, df = 2, P < 0.05), respectively (Table 1).

Density estimation

In Pendjari, the behavioural response model with specific variability in spatial scale (i.e. D~session g0~bk sigma~1) ranked highest by AICc for multi-session modelling (Table S2), while in Zakouma, two top models were supported (i.e. D~1 g0~bk sigma~1 and D~1 g0~1 sigma~1), requiring model averaging of the behavioural response for cheetah density estimation (Table S3).

Cheetah in Zakouma exhibited less extensive movement than those in Pendjari (Fig. S2), with σ (i.e. the spatial parameter) estimated at 4 711 m in the dry season, compared to 16 232 m in the wet and 16 778 m in the dry season for Pendjari (Table 3). The detection probability ($g0$) was lower during the wet 0.001 ± 0.0007 (SE) compared to the dry season 0.0015 ± 0.0008 in Pendjari, both of which were substantially lower than $g0$ of 0.005 ± 0.0028 in the dry season survey for Zakouma.

Cheetah densities in Pendjari were estimated at 0.17 (95% CI 0.05–0.56) and 0.24 (95% CI 0.08–0.67) independent individuals per 100 km^2 in the wet and dry seasons, respectively, while in Zakouma, dry season density was estimated at a higher 0.37 (95% CI 0.18–0.76) cheetah per 100 km^2 (Table 3). When extrapolated across the study areas, comprising each camera array and surrounding buffer (14 600 km^2 of WAP and 12 100 km^2 of GZE), these densities translate to between 20.9 ± 11.8 (SE) and 26.6 ± 14.2 independent individuals in Pendjari and an estimated 41.9 ± 14.3 cheetah in Zakouma.

Discussion

Sufficient cheetah detections were secured to enable estimation of cheetah density across three survey seasons in two of our three surveyed sites in West and Central African PAs. These density estimates ranged from 0.17 to 0.37 individuals per 100 km^2 for Pendjari and Zakouma National Parks. Despite intensive camera trapping effort, no cheetah were detected in Siniaka Minia, our third site in Chad, indicating the likely perilous state of this cheetah population. Our estimated densities are substantially below the maximum densities of 2.2 and 2.5 per 100 km^2 found in the Kruger National Park of South Africa and Serengeti ecosystem of Tanzania, respectively (Durant *et al.*, 2011; Marnewick *et al.*, 2014), however, these estimates are substantially higher than a density of 1 per 4000 km^2 found for the only other population of *A. j. hecki* in the Saharan Desert (Table S1). Our estimates are more in line with typical densities of 0.18–0.90 individuals per 100 km^2 found across a range of different land use types and ecoregions in southern Africa (Weise *et al.*, 2017). Given that the rainfall, and hence the productivity, of our sites is higher than that in southern Africa, these observed densities are likely lower than expected. Moreover, although only one survey was done outside the core PAs (i.e. Siniaka Minia) which are afforded greater protection, the lack of cheetah detected at that site, despite intensive survey effort, indicates that cheetah may have declined rapidly outside of the immediate survey area. Considering these findings, we recognize the current limitations of these baseline density estimates, where the associated uncertainties around extrapolated population sizes call for an improved understanding of cheetah population dynamics in West and Central African ecosystems.

Table 3 Density estimates of Northwest African cheetah with standard error (SE) and 95% confidence interval (lower and upper) derived from spatially explicit capture–recapture models using camera trap data from Pendjari Reserve and Zakouma National Park. Density (D) is reported as independent cheetahs per 100 km^2. The detection rate at the camera trap location ($g0$) is considered as home-range centre and σ is the scale of an individual's movement distribution (m)

Parameter	Model	Estimate	SE	Lower CI 95%	Upper CI 95%
Pendjari Session 1: Dry season (Apr–July 2021)					
D	g0~bk sigma~1	0.24	0.13	0.08	0.67
g0		0.0015	0.0008	0.0005	0.004
σ		16 778	6126	8386	33 565
Pendjari Session 2: Wet season (July–Oct 2021)					
D	g0~bk sigma~1	0.17	0.11	0.05	0.56
g0		0.001	0.0007	0.0002	0.0042
σ		16 232	4742	8386	33 565
Zakouma Session 1: Dry season (Jan–Apr 2023)					
D	Avg model	0.37	0.14	0.18	0.76
g0		0.0053	0.0028	0.0018	0.0154
σ		4711	899	3252	6826
D	g0~bk sigma~1	0.40	0.16	0.19	0.84
g0		0.0041	0.0019	0.0016	0.0105
σ		5011	946	3472	7233
D	g0~1 sigma~1	0.35	0.13	0.18	0.69
g0		0.0079	0.002	0.0039	0.0159
σ		4292	647	3200	5757

Status of northwest African cheetah

Our total estimate of mature cheetah across Pendjari and surrounding areas (i.e. 44% of WAP) was 20.9 ± 11.8 to 26.6 ± 14.2 in two consecutive seasons which is in line with previous expert estimates of 23 mature individuals in the WAP Complex of Benin, Niger and Burkina Faso (Durant *et al.*, 2022). Our survey area was focused on Pendjari National Park, which is the most well protected part of the WAP ecosystem. Previous surveys using spoor indicate lion numbers are substantially reduced outside the immediate Arly-Pendjari area (Henschel *et al.*, 2016). Moreover, in 2017, intensive camera trap surveys across the Burkina Faso and Niger parts of the WAP ecosystem, including Arly, detected cheetah only once (Harris *et al.*, 2019). Since these surveys, Burkina Faso has faced increasing insecurity, and Arly National Park has been occupied by insurgents (Steiner, 2021). It is therefore extremely unlikely that there are many cheetah outside the core Pendjari National Park survey area, and hence our population estimate is likely to comprise nearly the entire cheetah population occupying the larger WAP protected area complex, supporting recent reports (Ipavec *et al.*, 2018; Drouilly *et al.*, 2019; 2021; 2023).

Our survey in Zakouma and surrounding areas (i.e. 43% of GZE) yielded a total population estimate of 41.9 ± 14.3 mature individuals, however, our survey in the Siniaka Minia did not detect any cheetah. Zakouma comprises the best protected habitat in the Bahr/Salamat landscape, and hence, in the absence of any further information, we are forced to conclude that there are no cheetah, or very low numbers of cheetah, outside of our survey area. This estimate of 42 cheetah is considerably lower than the previous estimate of 218 mature individuals in the Bahr/Salamat landscape (Durant *et al.*, 2017, 2022). The previous estimate was derived from a much older mapping exercise conducted in 2012 which assumed that cheetah were distributed, albeit at low densities, across the entire landscape encompassing 238 234 km^2 (IUCN/SSC, 2012). It is therefore possible that, as was predicted by Durant *et al*. (2017), we are witnessing the extirpation of cheetah outside of core PAs across this landscape.

Overall, our surveys indicate an estimated population of 68 ± 29 mature individuals remaining in the western Sudano-Sahel Zone. This estimate is substantially lower than previous estimations of approximately 241 mature individuals for this region (Durant *et al*., 2017, 2022). The only other known population of *A.j. hecki* is over 1 200 km away, centred around the southern Algerian Sahara, where density estimates from surveys conducted in 2008 and 2010 (Belbachir *et al*., 2015), indicated a remaining population of around 180 mature individuals (Durant *et al*., 2022). Together, these suggest a total population estimate of *c*. 230 Northwest African cheetah, which is substantially lower than the previous estimate of 419 individuals (Durant *et al*., 2022), indicating that this cheetah subspecies is facing an increasingly grave risk of extinction across its remaining range. This situation aligns with predictions by Durant *et al*. (2017), where authors warned of a rapidly increasing threat to cheetah due to ongoing anthropogenic change across the continent, and that biased population estimates focused on core protected areas could be leading to a ‘systematic underestimation’ of these threats.

Almost 80% of the Northwest African cheetah range lies outside of formally designated PAs, implying that there is still habitat available for cheetah outside, as well as inside these areas, but that these landscapes often support large carnivores against substantial anthropogenic pressures (IUCN/SSC, 2012; Schulte to Bühne *et al*., 2017). Our study was conducted within PAs that likely have the highest levels of conservation effort and performance throughout the larger landscapes of the WAP Complex and GZE, and where cheetah were expected to be least affected by external anthropogenic pressures (Brugière, Chardonnet, & Scholte, 2015; Lhoest *et al*., 2022). However, our results show that the cheetah populations within these PAs are relatively small and fragile. In other parts of the Northwest African cheetah range, such as the Algerian Sahara deserts, the cheetah density is even lower, almost one seventh of our estimates in Benin and Chad (Belbachir *et al*., 2015), highlighting that this subspecies has a deeply concerning population status in both its remaining Sahara and Sudano-Sahel Zones.

The underlying reasons for the low densities of Northwest African cheetah populations may be variable throughout its range. In the Algerian Sahara Zone, the low landscape-level productivity and subsequently lower prey availability, exacerbated by high levels of anthropogenic pressure closer to settlements may form the primary bottom-up mechanism regulating cheetah density (Belbachir *et al*., 2015). Such scarcity of food and water typical of deserts suggests that wildlife communities should be primarily governed by such bottom-up processes (i.e. constrained by resource availability; Rocha, Bennett, & Monterroso, 2022). By contrast, in the Sudano-Sahel Zone, additional to these constraints posed by the natural environment and anthropogenic pressure, the relative abundance of other large carnivores such as lion, leopard, and especially spotted hyena in Pendjari and Zakouma, could be further restricting cheetah density in these PAs through inter-specific competition, creating a top-down regulating mechanism (Gigliotti *et al*., 2020; Hayward *et al*., 2019). Taken together, these drivers suggest that cheetah populations may be regulated by both bottom-up (i.e. landscape productivity and prey availability) as well as top-down (i.e. dominant predators and people) ecological functions across their range.

Effects of seasonality and inundation

Cheetah exhibit stable consistent spatial parameter (σ) variability between the two seasons in Pendjari, implying that the wet season does not constrain their movement. In contrast, season has been noted to affect the movement patterns of cheetah in other parts of sub-Saharan Africa (Houser *et al*., 2009; Vanak *et al*., 2013), and while this may ostensibly represent seasonal polarity following optimal habitat, water availability and prey abundance, limited telemetry data from Zakouma and Pendjari (n = 4) suggests that cheetah in this area do not demonstrate a pronounced behavioural response to seasonal changes. Importantly, the spatial parameter σ was substantially lower in Zakouma than in Pendjari, which could be associated with a smaller mean home-range (Efford & Fewster, 2013), as a result, cheetah in Zakouma may be more likely to occur near the centroid of their home-range which is then associated with a higher detection probability ($g0$) as evident in the dry-season comparison of Pendjari and Zakouma (Table 3). Such discrepancies emphasize the importance of more detailed behavioural and movement research on cheetah in these unique landscapes (Fig. S2). The effect of seasonal inundation on habitat suitability, prey densities and predator movement are also likely to have a significant landscape-level effect, however such interpretations would require more extensive monitoring and multi-species response analyses.

Insights into demographic structure

The observed sex ratios varied between the two study sites (Table 2), with an even sex ratio in Zakouma while in Pendjari the population was highly skewed towards males in the dry season (1:0.29). The latter reflects a global pattern of male-skewed sex ratios in cheetah surveyed using camera traps, with such male bias reported in Algeria (Belbachir *et al*., 2015), Iran (Farhadinia *et al*., 2016), and multiple study sites throughout sub-Saharan Africa (Brassine & Parker, 2015; Fabiano *et al*., 2020). There are two common explanations for a male-biased sex ratio in cheetah surveyed using camera traps.

The first is that the placement of cameras at scent-marking sites results in a bias in detection towards adult males who are more likely to frequent such sites (Marker *et al*., 2003; Farhadinia *et al*., 2016; Melzheimer et al., 2018; Fabiano *et al.*, 2020). Adult female cheetah, particularly when accompanied by dependent cubs, may avoid marking sites that are frequented by adult males (Mills & Mills, 2017; Melzheimer *et al.*, 2020), however, this effect may be offset by overlapping female home-ranges (Caro, 1994; Durant *et al.*, 2004). In Pendjari, we recorded a strong male bias where most camera stations were situated at marking sites (77%), whereas in Zakouma we found an even sex ratio, where a smaller proportion (30%) of stations were placed at marking sites (Table 1). Additionally, in Pendjari, every adult female was detected with dependent cubs, while in Zakouma, only one female (25% of all females) had dependent offspring (Table 2). However, the models run by location type covariate obtained lower AICc scores than the trap-specific behavioural response models (Tables S2 & S3).

The second reason is that female cheetah generally have larger home ranges compared to territorial males (Caro, 1994; Marker *et al.*, 2008; Marnewick & Somers, 2015; Welch *et al.*, 2015; Melzheimer *et al.* 2018), which, for a given camera trap spacing would increase the overall likelihood of male detection, but female home ranges also overlap, thus overall detection should remain unchanged (Caro, 1994; Durant *et al.*, 2004). Previous studies have identified high levels of male–male aggression, resulting in a higher male mortality rate and a female biased sex ratio (Caro, 1994; Durant *et al.*, 2004; Marker *et al.*, 2008; Marnewick & Somers, 2015; Welch *et al.*, 2015; Melzheimer *et al.* 2018).

Our relatively small sample size requires us to view these interpretations as suggestive, highlighting the need for further investigation into sex-specific survival of Northwest African cheetah. Skewed demographic parameters generally exacerbate the severity of stochastic events in such relatively small and isolated populations (Fagan & Holmes, 2006), as is currently affecting the persistence of fragile Asiatic cheetah (*A. j. venaticus*) populations (Farhadinia *et al.*, 2016, 2017).

Mortality and growing anthropogenic pressure

Cheetah density confidence intervals overlapped between the two seasons in Pendjari, indicating that this population estimate was relatively similar between seasons (Table 3). However, at least three out of 12 detected cheetah in Pendjari died within 1 year, as confirmed through telemetry-guided observations and the monitoring of cheetah families using repeat photographs from camera traps. Moreover, we had a relatively low recapture rate for individuals (i.e. eight individuals detected only once) and only one independent individual in the two consecutive seasons which were only a month apart in Pendjari (Fig. 2). These lines of evidence suggest that, while cheetah density is relatively stable between the two seasons, this population experiences a high level of turnover which could potentially affect the spatial resident tenure of cheetah in Pendjari.

People and their livestock were frequently detected over large areas in both Siniaka Minia (n = 98) and Zakouma (n = 209) in the GZE (Table 2). While we failed to detect any cheetah in Siniaka Minia, other large carnivores such as leopards and spotted or stripped hyena were also only rarely detected (n = 8). Moreover, in Zakouma National Park, which is regarded as the primary ‘safe zone’ within the GZE, the frequency of detecting anthropogenetic factors on camera traps was 8.3 times more than that of cheetah. This anthropogenic activity within the GZE may reveal a degraded conservation status with adverse consequences for most wildlife including cheetah (Durant *et al.*, 2017; Steiner, 2021). This situation mirrors typical reasons for population declines in other large carnivores such as lions (Bauer *et al.*, 2015), tigers (Goodrich *et al.*, 2015), and wolves (*Canis lupus*; Ripple & Beschta, 2012), emphasizing a broader crisis affecting apex predators globally (Arias *et al.*, 2024). Further research is thus urgently recommended to quantify and contextualize the effect of such nomadic pastoralism on the persistence of large carnivore populations in this landscape.

Management recommendations

Our revised population size estimate is markedly lower than previous projections for the subspecies (Durant *et al.*, 2022), providing an urgently needed assessment of cheetah population size in Northwest Africa that is contemporary and robust, given the difficulties of monitoring in this landscape. Where the critical status of this subspecies is further highlighted through the ever-increasing challenges posed by anthropogenic activities and limited law enforcement capacity across the Sudano-Sahel Zone, which is exacerbated by recent sectarian unrest and ongoing armed conflict (Cusack *et al.*, 2021; Steiner, 2021). Our data urges local management and international stakeholders to focus on improving the conservation status of the Northwest African cheetah, where immediate recommendations include:

1 Stakeholders, particularly range-state governments, should engage with the imminent review and update of the existing range-wide strategy for the conservation of Northwest African cheetah (IUCN/SSC, 2012) currently adopted within the African Carnivores Initiative (ACI), jointly established by the United Nations Environment Program (UNEP) Convention on the Conservation of Migratory Species of Wild Animals (CMS) and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). The updated regional strategy should be prioritized for implementation within the ACI by the establishment of a North-western African Cheetah Working Group to facilitate transboundary coordination to direct resources and efforts towards implementation of the regional strategy. Current priorities include the recovery of suitable habitat and prey populations, as well as a reduction in anthropogenic pressures on the remaining cheetah populations through landscape-level and holistic management of ecosystems that directly accounts for the needs of these cheetah as unique flagships of biodiversity for this system.

2 All three remaining *A. j. hecki* core populations should be subject to regular monitoring by implementing surveys using the methods outlined here and in Belbachir *et al*. (2015) at 2–3-year intervals. Where an in-depth ecological study is needed in at least one site, to better understand the ecological needs of this subspecies and identify the proximal threats to its survival.
3 Genetic analyses are urgently required to understand the phylogeny and genetic diversity of cheetah subspecies across the region. Our data show that the largest population of Northwest African cheetah across the Sudano-Sahel zone persist in GZE in Chad. However, due to the limited availability of genetic samples from these specific regions, it is not yet confirmed that this population in GZE is the Northwest (*A. j. hecki*), as opposed to the Northeast (*A. j. soemmerringi*) African cheetah subspecies (Charruau *et al*., 2011; Prost *et al*., 2022), which would have significant implications for strategic conservation management across the region (Durant *et al*., 2017).
4 Quantify and curb the illegal trade of cheetah skins and parts throughout the Sudano-Sahel Zone.
5 Finally, the Northwest African cheetah requires more international attention to deliver the political will and funding required to reverse its precipitous decline. Currently, these cheetah follow the continued extirpation of multiple key species throughout the Sahara-Sahel (Brito *et al*., 2018; Belbachir *et al.*, 2015). Without urgent action, the iconic biodiversity of this region and the essential ecosystem services it provides may face total collapse.

Overall, our findings provide compelling evidence for the current precarious status of Northwest African cheetah populations and the urgent need to actively implement existing transboundary cooperative strategies towards recovering this subspecies.

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Conflict of interest

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

Author contributions

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Data availability statement

Derived data used in all analyses are available in the Supplementary data, where raw data can be made available upon request.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. An informal review of available peer-reviewed literature regarding cheetah density estimation. SECR, spatially explicit capture-recapture; Non-SECR, non-spatially explicit capture-recapture techniques

Table S2. Model selection results for two sets of 12 fitted multi-session models (totalling 30 models) ranked by Akaike's Information Criterion corrected for small sample sizes (AICc) for two sessions of 2021 Northwest African cheetah density in Penjari Reserve, WAP Complex, Benin. Loc and sex are two parameters whose effects on detection probability were investigated in the models to check the gender of the identification or the type of station influencing the identification (sense mark, trail, or water points)

Table S3. Model selection results for one set of eight fitted multi-session models (totalling 18 models) ranked by Akaike's Information Criterion corrected for small sample sizes (AICc) for dry season of 2023 Northwest African cheetah density in Pendjari NP, Greater Zakouma, Chad. Loc and sex are two parameters whose effects on detection probability were investigated in the models to check the gender of the identification or the type of station influencing the identification (sense mark, trail, or water points)

Table S4. Testing of different buffers with top models in Pendjari and Zakouma

Figure S1. *Pendjari cheetah IDs in 2021*: Photographs of M4, M5, M11 and F10 taken in this survey were compared with previous (2019; 2021) camera trap photographs taken in ZSL-RWCP/Panthera survey. IDs were consolidated using multiple images across multiple stations and collaborative ID kits for the landscape. M8 and M9 were coalition. Only the right flank of M8 was available, which was not matched with any other males right side. *Zakouma cheetah IDs 2023*: F7 had only the left flank. But because it was the only female that had two cubs and it was not matched with any other female or unknown female on the left flank, it was considered a separate female. F9 and F5 got to different flanks. Available flank which was not matched by any other females or unknown. But on the other hand, the pattern of their tails was completely different, and they were considered as 2 separate individuals. U4, with only its left flank identified and an undetermined gender, does not align with any other left sides of cheetahs. It is selected as an independent individual with an unknown sex.

Figure S2. When individuals were detected at different camera traps within a seasonal period, we indicated the straight-line distance between these camera traps with lines Moving paths of individuals between the camera traps in the dry and wet seasons of Pendjari and the dry season of Zakouma.