






## RESEARCH ARTICLE

# Population status of leopard in one of Africa's largest wilderness areas and the challenge of monitoring at scale

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**Handling Editor:** Jim Vafidis**Abstract**

1. Remarkably little is still understood about how the leopard (*Panthera pardus*) is faring in much of its remaining African range, despite the species' importance for ecosystem function and generating funding for conservation via tourism. In this study, we address this knowledge gap in southern Tanzania's Selous–Nyerere ecosystem, one of the largest intact wilderness areas on the continent, by estimating leopard population density via spatially explicit capture–recapture (SECR) modelling of data from seven camera trap surveys.
2. Population density was highest in Nyerere National Park's Matambwe sector ( $8.08 \pm \text{SE } 1.54$  adult and subadult leopards per  $100 \text{ km}^2$ ), followed by Selous Game Reserve's Miguruwe sector ( $7.38 \pm 1.26$  per  $100 \text{ km}^2$ ); Nyerere NP's Msolwa sector ( $6.05 \pm 0.78$  per  $100 \text{ km}^2$ ); Selous GR's Liwale sector ( $5.93 \pm 0.88$  per  $100 \text{ km}^2$ ), western Kingupira sector ( $5.58 \pm 0.87$  per  $100 \text{ km}^2$ ) and eastern Kingupira sector ( $5.22 \pm 0.71$  per  $100 \text{ km}^2$ ); and Nyerere NP's Kalulu sector ( $3.80 \pm 0.64$  per  $100 \text{ km}^2$ ).
3. Together, our surveys covered an important component of extant leopard range in Tanzania, and our findings highlight the importance of the Selous–Nyerere ecosystem as a leopard stronghold. The estimates include the highest leopard densities yet documented in miombo woodland, which represents nearly one fifth of the species' remaining African range.
4. Unlike lion, leopard population density was highly correlated with relative abundance of preferred prey. Although limited by a small number of data points, this suggests that the two species may not be uniformly affected by anthropogenic threats. Threats to leopard in Selous–Nyerere include accelerating habitat

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conversion in boundary areas and bushmeat poaching, which impacts leopard indirectly by suppressing prey populations and directly via accidental snaring.

5. *Practical implication.* Placed in the context of range-wide leopard monitoring, this study highlights the need to address persistent knowledge gaps on the species' continental status and prioritise sites for monitoring based on their potential to inform evidence-based conservation management.

#### KEYWORDS

camera traps, leopard, *Panthera pardus*, population density, SECR, Selous–Nyerere, spatially explicit capture–recapture, Tanzania

## 1 | INTRODUCTION

The world is facing a biodiversity crisis, with monitored wildlife populations having declined by more than two thirds on average between 1970 and 2018 (69%; WWF, 2022). However, the true scale of the crisis is likely to be greater than the evidence suggests: against a backdrop of limited capacity and funding for conservation research (Buxton et al., 2021; Lindsey et al., 2018), very few wildlife populations have been the subject of population status assessments, let alone any form of long-term monitoring (Kindsvater et al., 2018).

Such population information is lacking even for species that attract a disproportionate amount of research attention and conservation funding (Prokop et al., 2022). For instance, significant knowledge gaps remain around the status of large carnivore populations in Africa (Strampelli, Campbell, et al., 2022), partly as a result of the difficulty of monitoring such species due to their naturally low densities and secretive nature. Nevertheless, the tools to monitor such populations are increasingly well-established (although noteworthy gaps remain for certain species; Strampelli, Campbell, et al., 2022). As such, there are increasing calls to expand efforts to understand and monitor large carnivore populations (Ripple et al., 2014), particularly as trends in large carnivore communities can be useful indicators of overall biodiversity and ecosystem health (Dalerum et al., 2008).

Among the African large carnivores, the leopard is still popularly thought of as relatively thriving – at least in comparison with leopard populations in Asia and some populations of other large carnivores in Africa, a number of which have collapsed in recent decades (Brugière et al., 2015; Searle et al., 2023; Stein et al., 2024). However, this assertion is based on a relatively limited evidence base, with little to nothing known about how the species is faring across the majority of its continental range (Stein et al., 2024; Strampelli, Campbell, et al., 2022). The species is also facing multiple threats in Africa that have driven local extinctions of leopard elsewhere in their global range (Rostro-García et al., 2023). These include widespread losses of habitat (21% loss in sub-Saharan Africa over 25 years) and prey (59% decline in African protected areas; Stein et al., 2024), which together with direct threats like snaring, retaliatory killing and unsustainable trophy hunting are thought to have caused the African

subspecies (*Panthera pardus pardus*) to decline by more than 30% over the last three generations (Stein et al., 2024). As a result, the IUCN's recent updated Red List assessment of the species called for detailed status assessments of leopard in different parts of Africa, to address regional needs and requirements (Stein et al., 2024).

Of the 38 countries in Africa with extant leopard populations, only a third have at least one published population density estimate (34%; see Appendix S1), and even within countries where studies have been carried out, there remain huge swathes of extant or possible range for which we have no information on the species' status (Stein et al., 2024). Without assessments and monitoring, there can be no alert system for when populations suffer declines, which precludes any efforts to slow or reverse such trends. As such, without effective monitoring in place, there is a risk that leopard populations could be silently lost.

In this study, we provide the first spatially explicit estimates of leopard population density in one of Africa's largest wilderness areas using data from seven camera trap surveys. Our results provide some of the first landscape-scale insights into this leopard stronghold, and should be used as a baseline for future monitoring and evidence-based management. We finish by placing our findings in the context of priorities for range-wide leopard monitoring.

## 2 | MATERIALS AND METHODS

This research was carried out under permits 2020-159-NA-1997-20, 2020-160-NA-1997-20, 2021-173-NA-2021-42, 2021-174-NA-2021-42, 2022-526-NA-2021-042 and 2022-527-NA-2021-042, granted by the Tanzania Commission for Science and Technology (COSTECH) and Tanzania Wildlife Research Institute (TAWIRI).

### 2.1 | Study area

The Selous–Nyerere ecosystem is one of Tanzania's largest contiguous protected area complexes, spanning approximately 80,000 km<sup>2</sup> in the south of the country. The ecosystem encompasses a number of protected areas, including Nyerere, Mikumi, & Udzungwa Mountains National Parks; Selous & Kilombero

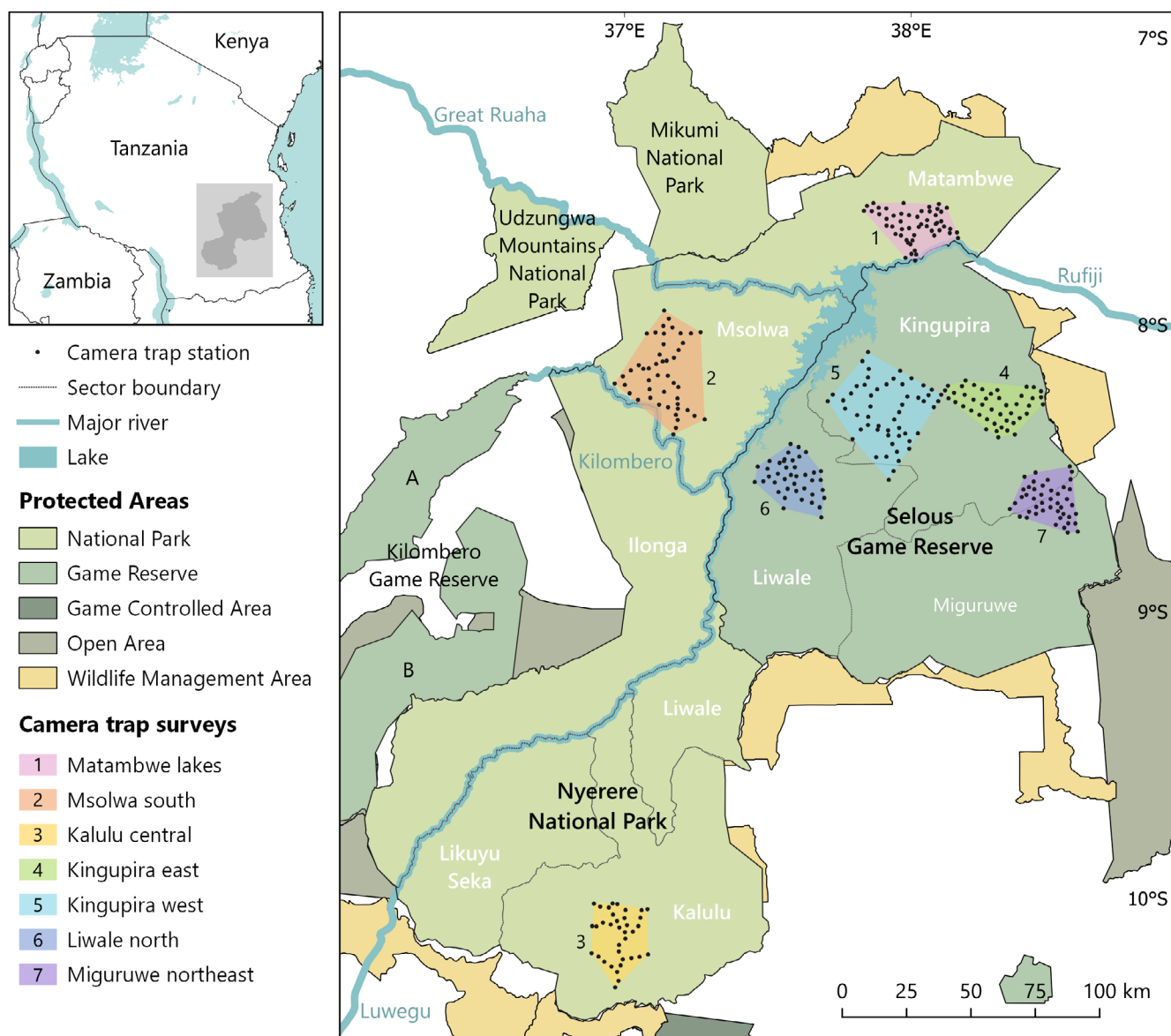
Game Reserves; and a number of Game Controlled Areas, Open Areas, Wildlife Management Areas and Forest Reserves. The ecosystem is connected to northern Mozambique as part of the Niassa-Selous Transfrontier Conservation Area, which is one of the largest TFCAs in Africa (South African Development Community, 2024).

Selous Game Reserve (GR; 18,020km<sup>2</sup>) and Nyerere National Park (NP; 30,893km<sup>2</sup>) are each the largest protected area of their kind in Tanzania and are divided into sectors for management purposes. The main source of revenue in Selous GR is trophy hunting, including of leopard, while revenue in Nyerere NP is generated via photographic tourism and sport fishing. Selous-Nyerere is recognised as a UNESCO World Heritage Site due to its importance for biodiversity (UNESCO, 2024). Most of the landscape is dominated by miombo woodlands (Olson et al., 2001) and a number of major

rivers pass through the complex, including the Kilombero, Luwegu, Great Ruaha and Rufiji Rivers.

## 2.2 | Camera trap surveys

We deployed semi-regular camera trap grids at three sites in Nyerere NP and four sites in Selous GR (Figure 1) during the dry seasons of 2020, 2021 and 2022; see Table 1 for summary information on each survey. Survey sites were selected based on accessibility and their representativeness of the wider protected areas—including different habitat types, areas used for photographic tourism and those used for trophy hunting, areas of varying distance to boundaries, and trophy hunting areas with and without investors. Six of the seven surveys were conducted in areas dominated by miombo woodland;



**FIGURE 1** Left: Selous-Nyerere landscape within southern Tanzania; Right: Detail of the study landscape, including the seven camera trap surveys (each point represents one paired station).

TABLE 1 Details on each of the seven camera trap surveys in Selous–Nyerere.

	Nyerere NP			Selous GR				All surveys combined
	Matambwe lakes	Msolwa south	Kalulu central	Kingupira east	Kingupira west	Liwale north	Miguruwe northeast	
Survey period	Sep–Dec 2020	Aug–Nov 2022	Aug–Dec 2022	Jul–Nov 2021	Nov 2021–Feb 2022	Jul–Oct 2021	Aug–Nov 2021	–
Survey duration (nights) <sup>a</sup>	90	90	90	90	90	90	90	–
Camera trap stations	53	47	36	44	53	41	45	319
Trap nights	4319	4076	3191	3936	4696	3690	3854	27,762
Mean spacing between stations (km)	2.23	3.35	2.78	3.01	3.24	3.12	2.71	–
Sampled area (km <sup>2</sup> ) <sup>b</sup>	527	1045	537	525	1124	507	409	4674
Flank used for analysis	Left	Left	Left	Right	Right	Left	Right	–
Proportion of photographs identifiable (%) <sup>c</sup>	99	99	98	99	96	99	99	99
Independent capture events <sup>d</sup>	110	292	219	383	233	238	152	1225
Adult & subadult individuals	40	65	38	57	66	49	44	254
Male	19	19	12	26	27	15	12	92
Female	7	29	10	26	23	20	20	99
Unknown sex	14	17	16	5	16	14	12	63
Mean capture events per individual	2.75	4.49	5.76	6.72	3.53	4.86	3.45	4.53
Mean stations per individual	1.65	1.86	2.50	2.74	1.76	2.20	2.05	2.09
Proportion of individuals captured at more than one station (%)	45	55	53	67	39	65	45	53

<sup>a</sup>All surveys were trimmed to 90 days for analysis.

<sup>b</sup>Calculated by applying a convex hull around all stations in each grid.

<sup>c</sup>Based on photographs of adult and subadult leopards depicting the flank with most captures for that grid.

<sup>d</sup>Based on flank used for analysis only; includes only identifiable captures.

the one exception was the Matambwe sector in Nyerere NP, which is characterised by ox-bow lakes surrounded by a mosaic of grass plains, wooded savanna and miombo woodlands in the area surveyed (Creel & Creel, 2002).

Each grid consisted of 36 to 53 paired stations of white-flash cameras (Cuddeback Professional Color Model 1347, Non Typical Inc., Wisconsin, USA). All grids followed a survey design appropriate to estimate population density of leopard, lion (*Panthera leo*) and spotted hyaena (*Crocuta crocuta*). With respect to leopard, the total area covered by each grid was large enough to account for the species' ranging patterns (>400 km<sup>2</sup> based on a convex hull around all stations), while stations were close enough together for individuals to have a non-zero probability of capture (2–5 km).

Prior to deployment, camera trap station locations were planned along roads in the target areas in line with the above area and spacing requirements, using a shapefile of roads hand-digitised from satellite

imagery. Satellite imagery was also used to fine-tune planned locations, targeting areas close to water sources and in thicker vegetation or near river crossings, where animals are more likely to be channelled onto roads.

During deployment, field teams travelled to the planned station points and selected the best possible location for each station, taking into account features likely to maximise carnivore captures, such as water points or game trails joining the road (Searle et al., 2021; Tobler & Powell, 2013). Cameras were mounted onto trees at least 1.5 m from the nearest edge and 3–5 m from the centre of the road. The paired cameras were placed on either side of the road to photograph both flanks as animals passed through, and faced the road at a perpendicular angle to optimise detection and framing of captures (Johansson et al., 2020). All cameras were secured in metal cases to protect them from damage and interference by animals or humans.

The seven grids were each active for 93–121 days, but data were restricted to 90 days for density analysis for each grid to adhere with recommended best practice for meeting the population closure assumption for large carnivores (Tobler & Powell, 2013).

## 2.3 | Individual identification

After data collection, species classification was carried out manually in the program ExifPro (Kowalski & Kowalski, 2010), by applying tags corresponding to the species photographed and any other noteworthy information to the metadata of each image. These tags were then used to extract all photographs of leopards.

Individual leopards were identified based on their unique spot patterns and sex was determined where possible based on visible external genitalia. Photographs in which individuals could not be confidently identified were excluded from analysis, and individuals for which sex could not be confidently determined were coded as being of unknown sex.

Analysis was based on the flank with the greatest number of captures for each grid. Individuals estimated to be less than 1 year old were excluded from the analysis due to the higher mortality prior to this age threshold, in line with recommended best practice for population monitoring (IUCN Standards and Permissions Committee, 2022).

Following individual identification, a capture history was prepared for each grid detailing the individual, sampling occasion (24 h period, from midday to midday), detector (camera trap station) and sex for all independent capture events. A trap layout was also prepared for each grid, detailing the location of each detector (camera trap station) and whether it was active or inactive on each sampling occasion (see dataset Searle et al., 2025 for all input files; Efford, 2024b).

## 2.4 | Density estimation

We modelled leopard population density for each grid via maximum-likelihood-based SECR analysis using package *secr* version 4.6.0 (Efford, 2024a) in R version 4.3.3 (R Core Team, 2024).

We applied a habitat mask (state-space) with a 30 km buffer to the Matambwe and Msolwa grids to classify the area of large-scale agriculture west of Msolwa and the Kilombero & Rufiji Rivers (which lie at the southern edge of the surveyed areas in Msolwa and Matambwe, respectively) to be impassable boundaries for leopards at a population level. We made this decision on the basis that, while individual leopards may venture into or across these features on occasion, we do not consider them to represent generally usable habitat for the leopard populations in the surveyed areas. For all other grids, we selected an initial buffer width using the functions *suggest.buffer* and *esa.plot* (Efford, 2024a) and increased the buffer width by 1 km increments until the density estimate stabilised to ensure there was no truncation bias.

We classified detectors as 'proximity'; used a half-normal function to model detection (as this typically fits camera trap data well; Efford, 2024a; Green et al., 2020) and fitted a Bernoulli or binomial encounter model (Efford, 2024b; Strampelli, Searle, et al., 2022).

As leopard movement patterns differ based on sex (Searle et al., 2021), we included sex as a covariate affecting capture probability ( $g_0$ ), the movement parameter ( $\sigma$ ), or both by fitting hybrid mixture models, which apply a random effect to individuals of unknown sex (Efford, 2024b). We also fitted models with a behavioural trap response (trap-happiness or trap-shyness) on  $g_0$ . As a result, we fitted eight candidate models for each grid (where  $s$  is sex and  $b$  is behavioural response:  $g_0 \sim 0$ ,  $\sigma \sim 0$ ;  $g_0 \sim s$ ,  $\sigma \sim 0$ ;  $g_0 \sim 0$ ,  $\sigma \sim s$ ;  $g_0 \sim s$ ,  $\sigma \sim s$ ;  $g_0 \sim b$ ,  $\sigma \sim 0$ ;  $g_0 \sim s + b$ ,  $\sigma \sim 0$ ;  $g_0 \sim b$ ,  $\sigma \sim s$ ;  $g_0 \sim s + b$ ,  $\sigma \sim s$ ). We did not include any environmental covariates that may affect detection as all cameras had the same flash type (white flash) and were placed on roads, and it was not possible to quantify habitat type as a covariate due to its variability.

Model ranking was carried out based on Akaike information criterion scores corrected for small sample size (AICc; Burnham & Anderson, 2004), and final density and other parameter estimates were calculated by averaging all models with strong support ( $\Delta AIC < 2$ ) for each grid. We used the predict function in *secr* to establish whether learned responses reflected trap-happiness or trap-shyness. Buffer width was validated by re-fitting the top-ranked model for each grid with a buffer of increasing width until the density estimate stabilised (Searle et al., 2021).

For each density estimate, we calculated the half relative confidence interval width (HRCIW) using the formula  $HRCIW = \frac{0.5 \times (UCL - LCL)}{Density} \times 100$  (UCL and LCL = the upper and lower 95% confidence limits), to measure the level of population change that would be able to be detected for each estimate (Dröge et al., 2020).

## 2.5 | Relative abundance of preferred prey

We could not directly test the effect of prey availability on leopard population density as we could not extrapolate prey relative abundance index (RAI) beyond our station locations (Efford, 2025). We therefore instead explored the relationship between leopard density and prey availability by testing the level of correlation between leopard density and prey RAI for each site. We acknowledge that this can only provide limited insights due to the small number of data points and inability to incorporate the error in our density estimates.

We calculated the RAI of preferred prey for leopard for each survey site from the camera trap dataset, to provide a measure of prey availability. Seven mammal species were classified as preferred prey based on the species' known dietary preferences (Hayward et al., 2006): bushpig (*Potamochoerus larvatus*), bushbuck (*Tragelaphus scriptus*), common duiker (*Sylvicapra grimmia*), common warthog (*Phacochoerus africanus*), impala (*Aepyceros melampus*), Natal red duiker (*Cephalophus natalensis*) and Sharpe's grysbok (*Raphicerus sharpei*; see Appendix S2 for further details).

We calculated RAI for each species at each site by dividing the number of independent captures of that species by the number of trap nights for that survey and multiplying by 100 (Rovero & Zimmermann, 2016). Subsequent captures were considered independent if they took place more than 30 min after the last capture of the same species at the same station. An overall relative abundance of preferred prey was then calculated for each survey by summing the RAI of the seven prey species for that site.

## 2.6 | Survey coverage

The amount of leopard range within different countries and ecoregions was calculated by transforming the latest IUCN Red List range map for the species (Stein et al., 2024) and the WWF Ecoregions of the World (Olson et al., 2001) into the Albers equal area conic projection for Africa in QGIS version 3.28.3 (QGIS, 2022).

## 3 | RESULTS

### 3.1 | Survey effort and leopard captures

Using the 90-day period for each survey, a combined 27,762 camera trap nights across 319 stations yielded 3563 photographs of leopards. Reducing the dataset to only the flank with the most captures for each grid resulted in 1785 leopard images, 98% of which were identifiable (Table 1).

A total of 359 individual leopards were identified (130 male, 135 female, 95 of unknown sex), including one female leopard with strawberry colouration in Selous GR (Searle, Strampelli, Parsais, et al., 2024). Cubs were photographed in four of the seven survey sites.

Excluding captures of the same individual at the same location on the same sampling occasion resulted in 1627 independent capture events. For all grids combined, the mean number of capture events per individual was 4.53, with males (mean=6.18, range: 1–30) captured more times than females (mean=4.61, range: 1–21). The mean number of stations at which individuals were captured was 2.09, with males (mean=2.76, range: 1–12) captured at a larger number of stations on average than females (mean=1.95, range: 1–7). The proportion of individuals captured at more than one station was 53% for all individuals combined; 69% for males, 57% for females and 24% for individuals of unknown sex (Table 1).

### 3.2 | Population density

All grids had multiple models with strong support ( $\Delta AIC < 2$ ), and all strongly supported model sets featured both sex and behavioural response as covariates (see Table 2; results of model ranking can be

found in Appendix S3). Sex had a significant impact on movement ( $\sigma$ ) in all sites and on capture probability ( $g_0$ ) in all sites except western Kingupira. We found evidence of trap-shyness ( $g_0$  higher for naïve individuals than previously captured individuals) in four sites (Nyerere NP Kalulu, Msolwa and Matambwe; Selous GR Miguruwe) and trap-happiness ( $g_0$  higher for previously captured individuals than naïve individuals) in three sites (Selous GR eastern Kingupira, western Kingupira and Liwale; see Appendix S3).

Based on model averaging of all models with strong support, we estimated the highest leopard population density in the lakes area of Nyerere NP's Matambwe sector ( $8.08 \pm SE 1.54$  adult and subadult leopards per  $100 \text{ km}^2$ , 95% confidence interval: 5.57–11.71) and the second highest density in the northeast of Selous GR's Miguruwe sector ( $7.38 \pm 1.26$  per  $100 \text{ km}^2$ , 95% CI: 5.30–10.29). We estimated intermediate densities in Nyerere NP's Msolwa sector ( $6.05 \pm 0.78$  per  $100 \text{ km}^2$ , 95% CI: 4.71–7.78), followed by Selous GR's Liwale sector ( $5.93 \pm 0.88$  per  $100 \text{ km}^2$ , 95% CI: 4.42–7.92), western Kingupira sector ( $5.58 \pm 0.87$  per  $100 \text{ km}^2$ , 95% CI: 4.12–7.56) and eastern Kingupira sector ( $5.22 \pm 0.71$  per  $100 \text{ km}^2$ , 95% CI: 4.00–6.82). The lowest density was estimated in the Kalulu sector of Nyerere NP ( $3.80 \pm 0.64$  per  $100 \text{ km}^2$ , 95% CI: 2.73–5.29; Figure 2). Full outputs can be found in Appendix S3.

All seven estimates from this study were sufficiently precise to fall below the threshold HRCIW of 50% required to detect a critical population decline (range: 25%–38%; Table 2; Dröge et al., 2020).

### 3.3 | Relative abundance of preferred prey

The RAI of preferred prey species for leopard was highest in the Matambwe sector of Nyerere NP (RAI=169) and the Miguruwe sector of Selous GR (161). The lowest prey RAI was recorded in the Kalulu sector of Nyerere NP (30). Intermediate prey RAIs were estimated in the Msolwa sector in Nyerere NP (60) and the Liwale (46), eastern Kingupira (44), and western Kingupira (38) sectors in Selous GR. Full RAI estimates can be found in Appendix S2.

Leopard population density was strongly positively correlated with relative abundance of preferred prey across the seven sites ( $r(5)=0.92$ ,  $p=0.003$ ) – in contrast to lion in the same system, which showed a positive but non-significant correlation with lion preferred prey RAI ( $r(5)=0.59$ ,  $p=0.161$ ; Searle et al., 2025).

### 3.4 | Survey coverage

The seven survey grids together covered  $4674 \text{ km}^2$ , based on the summed area of convex hulls around each grid. This represents 12% of the combined area of Selous GR and Nyerere NP ( $38,913 \text{ km}^2$ ), and 1% of extant leopard range in Tanzania ( $\sim 467,800 \text{ km}^2$ ; Stein et al., 2024).

If we consider the densities estimated through these surveys to be broadly representative of leopard status across Selous GR and

TABLE 2 Population density and parameter estimates for leopard for the seven camera trap surveys in Selous–Nyerere.

	Nyerere NP			Selous GR			
	Matambwe lakes	Msolwa south	Kalulu central	Kingupira east	Kingupira west	Liwale north	Miguruwe northeast
Models with strong support ( $\Delta AIC < 2$ ) <sup>a</sup>	$g0 \sim s$	$g0 \sim s, \sigma \sim s$	$\sigma \sim s$	$\sigma \sim s$	$g0 \sim b, \sigma \sim s$	$g0 \sim s, \sigma \sim s$	$\sigma \sim s$
	$g0 \sim s + b$	$g0 \sim s + b, \sigma \sim s$	$g0 \sim b, \sigma \sim s$	$g0 \sim s, \sigma \sim s$	$g0 \sim s + b, \sigma \sim s$	$g0 \sim s + b, \sigma \sim s$	$g0 \sim b, \sigma \sim s$
	$g0 \sim s, \sigma \sim s$		$g0 \sim s, \sigma \sim s$	$g0 \sim b, \sigma \sim s$	$\sigma \sim s$		$g0 \sim s, \sigma \sim s$
Population density <sup>b</sup>	8.08	6.05	3.80	5.22	5.58	5.93	7.38
(Standard error)	(1.54)	(0.78)	(0.64)	(0.71)	(0.87)	(0.88)	(1.26)
95% confidence interval	5.57–11.71	4.71–7.78	2.73–5.29	4.00–6.82	4.12–7.56	4.44–7.92	5.30–10.29
Capture probability <sup>c</sup>							
$g0_{\text{FEMALE}}$	0.0082	0.0791	0.0719	0.0414	0.0264	0.0507	0.0216
(Standard error)	(0.0033)	(0.0145)	(0.0207)	(0.0055)	(0.0070)	(0.0097)	(0.0044)
$g0_{\text{MALE}}$	0.0266	0.0365	0.0761	0.0402	0.0271	0.0177	0.0212
(Standard error)	(0.0062)	(0.0063)	(0.0172)	(0.0049)	(0.0068)	(0.0035)	(0.0042)
Movement parameter <sup>d</sup>							
$\sigma_{\text{FEMALE}}$	1656	1526	1927	2228	1597	1854	1441
(Standard error)	(176)	(87)	(120)	(109)	(115)	(105)	(123)
$\sigma_{\text{MALE}}$	1666	2781	2992	3509	2862	3097	3665
(Standard error)	(118)	(161)	(147)	(162)	(147)	(219)	(297)
HRCIW (%) <sup>e</sup>	38	25	34	27	31	29	34
Preferred prey RAI <sup>f</sup>	169	60	30	44	37	46	161

<sup>a</sup>Based on model ranking ( $\Delta AIC < 2$ ); final parameter estimates for each site were derived by averaging all models with strong support; s = sex, b = behavioural trap response.

<sup>b</sup>Number of adult and subadult leopards per 100 km<sup>2</sup>.

<sup>c</sup> $g0$  = capture probability at home range centre.

<sup>d</sup> $\sigma$  = distance parameter related to home range size.

<sup>e</sup>HRCIW = half relative confidence interval width; a measure of the magnitude of population change that could be confidently detected.

<sup>f</sup>RAI = relative abundance index.

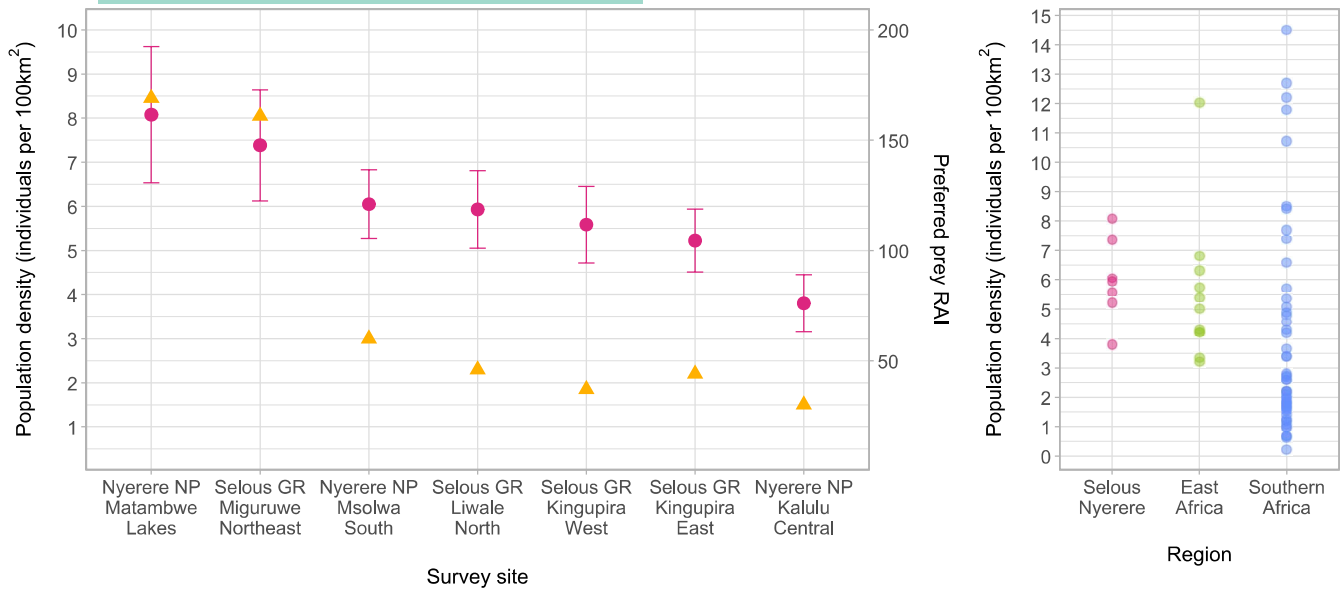
Nyerere NP, the proportion of Tanzanian extant leopard range effectively encompassed by this study increases to 10%. However, it is important to note that leopard range in Tanzania varies considerably in terms of habitat, protection status and anthropogenic impacts, and these surveys should not be considered representative of this wider national range.

## 4 | DISCUSSION

Our findings show that Selous–Nyerere is home to a relatively high-density leopard population, with densities ranging from  $3.80 \pm 0.64$  (95% CIs: 2.73–5.29) to  $8.08 \pm 1.54$  (95% CIs: 5.57–11.71) in the surveyed sites. Given the size and relative intactness of Selous–Nyerere and surrounding protected areas, our findings therefore suggest that the ecosystem is an important stronghold for leopard in Africa, in addition to being a stronghold for lion (Riggio et al., 2013; Searle et al., 2025) and African wild dog (*Lycaon pictus*; Creel et al., 2004; Parsais et al., 2025).

Our estimates for the Matambwe sector of Nyerere NP ( $8.08 \pm 1.54$  per 100 km<sup>2</sup>, 95% CI: 5.57–11.71) and the Miguruwe sector of Selous GR ( $7.38 \pm 1.26$  per 100 km<sup>2</sup>, 95% CI: 5.30–10.29) are the highest spatially explicit leopard densities estimated to date in Tanzania, including compared with the main tourist area of Ruaha NP ( $6.81 \pm 1.24$  per 100 km<sup>2</sup>, 95% CI: 4.78–9.70; Searle et al., 2021), and four of our seven estimates are higher than leopard density estimated in the dry season in Serengeti NP (5.41 per 100 km<sup>2</sup>, 95% CI: 2.23–9.26; Allen et al., 2020). The range of densities estimated in Selous–Nyerere is comparable to the neighbouring Udzungwa Mountains, where densities ranged from 2 to 8 per 100 km<sup>2</sup> (average 4.22 per 100 km<sup>2</sup>, 85% CI: 3.33–5.35; Havmøller et al., 2019).

Compared with SECR-based leopard density estimates elsewhere in Africa (see Appendix S1), the densities estimated in Selous–Nyerere are higher than estimates from Malawi (Davis et al., 2020) and Mozambique (Briers-Louw et al., 2024; Strampelli et al., 2018), and a number of estimates from Zimbabwe (Loveridge et al., 2022) and South Africa (e.g. Devens et al., 2020), while comparable densities have been estimated in Uganda (Braczkowski, Gopalaswamy,



**FIGURE 2** Left: Leopard population density (number of adult and subadult leopards per 100km<sup>2</sup>) with standard error bars (left axis) and combined relative abundance index (RAI) of preferred prey species (right axis) in the seven survey sites. Right: Comparison of the Selous-Nyerere estimates to SECR-based leopard density estimates in East and Southern Africa (see [Appendix S1](#)).

et al., 2022; Braczkowski, Schenk, et al., 2022), Zambia (Rosenblatt et al., 2016) and parts of South Africa (Morris et al., 2022; Ramesh et al., 2017; Swanepoel et al., 2015) and Zimbabwe (du Preez et al., 2014; Loveridge et al., 2022). Higher leopard densities have been estimated in a handful of sites with particularly strong protection and/or high abundances of prey, including Namibia's Okonjima NR (Noack et al., 2019), Botswana's Central Tuli GR (Vissia et al., 2022), Zimbabwe's Matusadona NP (Loveridge et al., 2022), Kenya's Mpala Ranch (O'Brien & Kinnaird, 2011) and South Africa's Sabi Sands GR (Balme et al., 2019) and Soutpansberg Mountains (Chase Grey et al., 2013).

This study makes an important contribution to the small but growing literature on large carnivore ecology in miombo woodland habitats (Davis et al., 2020; Jorge, 2012; Searle et al., 2021, 2025; Strampelli, Searle, et al., 2022). For leopard, this habitat represents a major component of the species' remaining African range (18% of extant range), and more than half of its extant range in Tanzania (56%; Olson et al., 2001; Stein et al., 2024). The densities estimated in this study are the highest densities yet documented for leopard in miombo, which include estimates from Tanzania's Ruaha NP ( $3.23 \pm 1.25$  per 100km<sup>2</sup>, 95% CI: 1.55–6.73) and Rungwa GR ( $3.36 \pm 1.09$  per 100km<sup>2</sup>, 95% CI: 1.82–6.23; Searle et al., 2021), Mozambique's Niassa National Reserve (2.18–4.31 per 100km<sup>2</sup>; Jorge, 2012) and Malawi's Kasungu NP ( $1.9 \pm 0.19$  per 100km<sup>2</sup>; Davis et al., 2020).

Although we were limited by the small number of data points, our finding that leopard densities were closely correlated with the relative abundance of preferred prey adds to the evidence base that prey availability is an important driver of leopard density (Searle et al., 2021; Stein et al., 2024). Aerial surveys suggest that warthog and common duiker – two important leopard prey species

– have increased in Selous-Nyerere over recent decades, which should benefit the landscape's leopard population, but this positive trend is likely to have been offset by the substantial habitat loss that has occurred in the landscape's edges during the same period (TAWIRI, 2023).

Interestingly, lion densities estimated from the same dataset were not significantly correlated with the relative abundance of their own preferred prey (Searle et al., 2025). There was a particularly strong contrast between leopard and lion densities in north-eastern Miguruwe, at the eastern boundary of Selous GR: despite this area having a high relative abundance of prey for both species and the second highest leopard density in this study, it had the lowest lion density of the surveyed sites (Searle et al., 2025). This suggests that there may be top-down pressures being felt by lions in this area that aren't affecting leopards in the same way. One possible candidate for this is poisoning, which is known to be a growing threat in the area (TAWA, pers. comm.). Although leopards are vulnerable to poisoning (Ogada, 2014), competition with the lions, spotted hyaena and packs of wild dogs that also inhabit this area may reduce their ability to feed on poisoned carcasses. The lower density of lions in this area may also in turn help bolster leopard densities through reduced competition, as suggested in Uganda's Lake Mburo NP (Braczkowski, Schenk, et al., 2022) and Botswana's Central Tuli GR (Vissia et al., 2022). While large carnivore densities are often positively correlated due to different species responding to similar environmental and anthropogenic drivers (Loveridge et al., 2022; Searle, Strampelli, Smit, et al., 2024), our findings therefore highlight that these species are not always uniformly affected by anthropogenic threats. Nevertheless, in Selous-Nyerere, efforts should be made to better understand the extent to which poisoning is affecting different species and continue developing mitigation strategies, such as

the poisoning prevention trainings which have been introduced by NGOs Lion Landscapes and North Carolina Zoo.

Although this study provides evidence of a large leopard population persisting at relatively high densities, the population is subject to a number of growing threats. The rate of settlement around the boundaries of Selous GR and Nyerere NP, which was previously very low (Creel & Creel, 2002), has increased rapidly in recent years (TAWIRI, 2023). As a result, human pressures in parts of the landscape are on the rise, and aerial surveys have shown increasing evidence of livestock presence, conversion of natural habitat to agriculture and tree-felling (TAWIRI, 2023). Large carnivore mortalities have been documented due to both targeted poisoning events and by-catch in bushmeat snares, particularly in boundary and unprotected areas (TAWA & TANAPA, pers. comm.). Although the core of the complex remains relatively protected from edge effects, they are likely to continue to rise as these buffer zones degrade (TAWIRI, 2022; TAWA & TANAPA, pers. comm.; Lion Landscapes, unpublished data).

One shift that may have particularly strong consequences for leopard is the changing nature of bushmeat poaching. The last 5–10 years have seen a shift from firearms-based bushmeat poaching to the use of wire snares (TAWA pers. comm.), particularly around eastern Selous GR – an unintended consequence of a crackdown on poaching with firearms. The increased use of snares can have a direct impact on leopards that become caught in them (Becker et al., 2024), but may also affect the relative impact of poaching on different prey species. In our north-eastern Miguruwe survey site, warthog and bushpig comprised a uniquely large proportion of the leopard prey base versus the other survey sites, and are therefore likely to be an important component of the species' diet in this area. It is possible that these species have been able to thrive in this area in part because they were not preferred targets for bushmeat poaching due to the area's predominantly Muslim population. Now that poaching has shifted from targeted methods towards indiscriminate wire snares, these species may experience declines which could have a knock-on effect on the area's leopards. In light of this, we recommend increased efforts to discourage bushmeat poaching and remove wire snares, particularly in the eastern boundary areas of Selous–Nyerere.

While our study included sites in both photographic tourism and trophy hunting areas, the landscape's recent history of land use changes makes it difficult to draw inferences from our results about possible impacts of hunting pressure. For example, the Msolwa sector of Nyerere NP – which had a very similar density to the Liwale sector of Selous GR, an area with active hunting investment at the time of the survey – was hunted up until its conversion to National Park status in 2019, 3 years prior to the 2022 survey (TAWA, pers. comm.), while the Miguruwe sector of Selous GR – where we estimated the second highest density – was the one site within Selous GR that did not have active hunting investment when surveyed, and in fact had not been hunted for 5 years at the time of the 2021 survey (not hunted since 2016; TAWA, pers. comm.). Nevertheless, we encourage policymakers to use our results to inform sustainable offtake quotas for leopard in Selous GR.

## 4.1 | Monitoring leopards in focus and at scale

This study contributes to a growing body of work from the last 5 years that has sought to address knowledge gaps on the status of leopard in Tanzania (Allen et al., 2020; Havmøller et al., 2019; Searle et al., 2021), which is thought to contain 8% of the species' remaining continental range (Stein et al., 2024). We recommend further efforts to assess and monitor leopard populations in the country, particularly in western Tanzania and areas that are unprotected or of lower protection status.

Remarkably little is still understood about how most leopard populations are faring in Africa, despite the species having repeatedly been shown to be a favourite among tourists (Albert et al., 2018; Di Minin et al., 2013; Lindsey et al., 2007) on a continent where protected areas generate \$48 billion in direct in-country expenditure (Space for Giants, 2019). What's more, the information we do have is highly clustered (Strampelli, Campbell, et al., 2022): more than half of the published studies on leopard density via SECR modelling are from South Africa (53%; see Appendix S1), a country which contains only 6% of the species' extant continental range (Stein et al., 2024). While these studies of course make an important contribution to our knowledge of the species' status, including in areas strongly affected by human impacts (e.g. McKaughan et al., 2024), efforts should continue to be made to understand how leopard populations are faring elsewhere in their range. With this said, assessments in unsurveyed areas should not happen at the expense of monitoring populations in key sites that have already been surveyed, given the importance of reliable long-term monitoring for evidence-based conservation management.

In some areas, the lack of information on leopard can be partly attributed to the prioritisation of more threatened carnivores (such as cheetah, *Acinonyx jubatus* and lion; Wolf & Ripple, 2017), but in many cases, it is primarily due to insufficient capacity and funding to carry out reliable monitoring (Schmeller et al., 2017). Given how well-established methods for monitoring leopard populations now are, we encourage individuals and institutions with knowledge of how to carry out such assessments to share this knowledge with researchers and conservation practitioners in range states where these skills are not yet developed. In all cases, leopard monitoring efforts should be closely tied to management and protection activities to ensure that investments in research are investments in conservation (Balme et al., 2014).

Nevertheless, even with increased knowledge sharing and financial means, surveys to estimate population density across the entirety of the leopard's African range would not be feasible. Deploying camera traps across the species' remaining extant range in Africa at regular 5 × 5 km spacing (which is likely to in fact be too wide in some parts of the species' range) would require approximately 237,000 stations; adding possibly extant range to this would require another ~91,000 stations. In light of this, there is an unavoidable need for flexibility in how best to obtain the evidence base for effective conservation of Africa's leopard populations.

In this context, we encourage continued efforts to apply modelling approaches that integrate different types of data to monitor leopard populations at larger scales (Pranzini et al., 2023) – particularly those combining capture–recapture and presence-absence data (Linden et al., 2017), as the latter can be collected across large areas relatively quickly and cost-effectively (Strampelli, Henschel, et al., 2022). At the same time, researchers and practitioners should think about how best to prioritise sites for SECR assessments and monitoring within their study system. While estimates from core populations are an important reference point for wider systems, in isolation they risk suggesting that populations are faring better than they actually are (Suryawanshi et al., 2019). Where possible, landscape-level monitoring should also incorporate estimates from areas where the species is thought to be doing better and those where they are likely to be doing less well, such as areas close to or outside protected area boundaries where they are more vulnerable to edge effects, like our north-eastern Miguruwe site.

For hunted species like leopard, trophy hunting areas also represent important sites for monitoring. Past leopard population assessments in Tanzania's trophy hunting areas (Searle et al., 2021) have been outnumbered by those in areas without hunting tourism (Allen et al., 2020; Havmøller et al., 2019; Searle et al., 2021), despite more than half of the country's protected land being used for trophy hunting (TAWA, 2024). This aligns with a broader bias among African large carnivore population assessments towards photographic tourism areas (Strampelli, Campbell, et al., 2022). Addressing this mismatch should be treated as a priority for leopard, given the importance of reliable population density estimates for setting sustainable offtake quotas (Balme et al., 2009; Pitman et al., 2015).

#### AUTHOR CONTRIBUTIONS

Charlotte E. Searle, Paolo Strampelli and Amy J. Dickman conceived the ideas and designed methodology. Charlotte E. Searle, Paolo Strampelli, Singira N. Parsais, Leonard Haule, Kandey Olesyapa, Nasri D. Salum, Samuel Mtoka, Germanus Hape, Daniel Mathayo and Manase Elisa collected the data. Charlotte E. Searle, Paolo Strampelli, Singira N. Parsais, Leonard Haule, Kandey Olesyapa, Nasri D. Salum, Daniel Mathayo and Manase Elisa analysed the data and drafted the content of the discussion. Charlotte E. Searle and Paolo Strampelli led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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#### CONFLICT OF INTEREST STATEMENT

None of the authors have any conflicts of interest to declare.

#### PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.70159>.

#### DATA AVAILABILITY STATEMENT

All data used in this manuscript are archived on Dryad at DOI <https://doi.org/10.5061/dryad.2jm63xt3j>.

#### STATEMENT OF INCLUSION

Our study brings together authors from different countries, the majority of whom are researchers and conservation practitioners from the study country. These authors were strongly engaged in data collection, which was carried out as part of a wider capacity-building programme. Data analysis was carried out collaboratively with a number of these authors as part of a training workshop, which was also used as an opportunity to discuss and interpret the results, taking into account these authors' personal experiences in the study ecosystem. Recommendations arising from this research have been shared with key stakeholders, including protected area management authorities (TAWA, TANAPA) and the national wildlife research institute (TAWIRI).

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## SUPPORTING INFORMATION

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

**Appendix S1.** SECR-based African leopard population density estimates.

**Appendix S2.** Preferred prey relative abundance indices (RAI).

**Appendix S3.** Model ranking and outputs.

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