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RESEARCH ARTICLE

Quantitative targets for leopard conservation in sub-Saharan Africa

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Abstract

1. Large carnivores continue to decline across Africa, yet effective conservation planning for the leopard (*Panthera pardus*) is constrained by the lack of empirical, range-wide population data needed to support robust assessments and evidence-based management. Leopards have disappeared from approximately 41% of their historical African range, underscoring the need for continent-scale evaluation of their remaining population and recovery potential.
2. We compiled published leopard density estimates, developed a predictive model for sub-Saharan Africa and integrated predicted density with an independent habitat suitability model to estimate population size under current and historical conditions.
3. Leopard density was negatively associated with livestock (sheep and goats) density, proximity to human settlements and the proportion of agricultural and forest land cover, while positively associated with the species richness of wild bovids and suids.
4. The integrated model predicted a contemporary leopard population of approximately 44,800–142,600 individuals across sub-Saharan Africa, substantially lower than previous estimates, with only 2800–8700 adult males occurring in non-protected areas of countries where trophy hunting is permitted.
5. These findings have direct management implications. Current CITES leopard hunting quotas exceed the recommended offtake threshold of 10% of the adult male population in more than half of the assessed trophy-hunting countries, indicating that quota revision is urgently needed in several jurisdictions. In addition, the species' potential population under present ecological conditions within its historical range is estimated at 55,200–175,600 individuals. These estimates provide spatially explicit recovery targets to guide the prioritisation of habitat protection, prey restoration and population recovery efforts.
6. *Synthesis and applications*: By integrating density modelling with habitat suitability, we provide a decision-support framework for leopard conservation across sub-Saharan Africa. The results identify where conservation investments are most likely to yield demographic gains, support the re-evaluation of national

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hunting quotas against sustainable offtake thresholds and offer an evidence base for targeting recovery actions across protected and non-protected landscapes within the species' remaining range.

KEYWORDS
CITES, density-habitat relationship, habitat suitability modelling, *Panthera pardus*, trophy hunting

1 | INTRODUCTION

Large carnivore populations are notoriously difficult to monitor due to wide-ranging movements, naturally low densities and the cryptic nature of most species (Linnell et al., 1998; Fattebert et al., 2016; Stein et al., 2011). There remains a dearth of comprehensive, range-wide, reliable leopard (*Panthera pardus*) population estimates (Stein & Hayssen, 2013), despite advancements in understanding distribution patterns and monitoring key populations (Balme et al., 2014; Jacobson et al., 2016). This gap compels researchers to rely on assumptions and expert opinions for IUCN assessments (Stein et al., 2024), hindering the identification of high conservation concern areas and effective management decisions (Chapman & Balme, 2010).

Leopards inhabit diverse ecosystems and are the most widespread felid in both Asia and Africa (Jacobson et al., 2016). Leopards have been considered adaptable to anthropogenic pressures due to their extensive dietary range and behavioural flexibility (Hayward et al., 2006). However, despite this resilience, global leopard populations have declined due to mounting human pressures (Ripple et al., 2014; Balme et al., 2014; Jacobson et al., 2016). Key factors contributing to this decline include habitat loss, fragmentation, depleted prey base, direct persecution through poaching, indiscriminate retaliatory killings and poorly managed trophy hunting (Balme et al., 2014; Jacobson et al., 2016).

In Africa, leopards have disappeared from 41% of their historic range (IUCN, 2024). The only continental-scale leopard population estimate from the CITES 1988 assessment (Martin & De Meulenaer, 1988) used a simple relationship to rainfall and is now considered a gross overestimate (Loveridge et al., 2022). Given the strong spatial variation in leopard density, threats and survey effort across Africa, obtaining an accurate continent-wide abundance estimate remains difficult with current data, especially because published density estimates are sparse and often biased towards well-protected areas (Havmøller et al., 2019; Pitman et al., 2015; Searle et al., 2026). Nevertheless, continent-wide assessments remain valuable for delineating current distribution, identifying strongholds and data-deficient regions, and setting broad conservation priorities. By contrast, hunting quotas should be based on robust monitoring at national or subnational scales, where local population trends and offtake can be evaluated more reliably.

To address this gap, we developed a predictive model to estimate leopard abundance across sub-Saharan Africa. This model examines the relationship between published density estimates and environmental and anthropogenic variables affecting leopard density, that is integrated with species habitat suitability. It highlights key drivers of population density distribution, predicts local leopard abundance and identifies regions of potentially high conservation importance. Additionally, it helps identify areas for future studies by predicting population density in under-researched regions, provides conservation targets for restoring leopard populations across their historical range and sets quantitative baselines for revising hunting quotas.

2 | METHODS

2.1 | Data search and screening

We conducted a literature review and used the PRISMA statement to guide the reporting of our search and selection process (Page et al., 2021). Through this review, we identified and extracted spatially explicit leopard density estimates and collated associated environmental and anthropogenic factors influencing leopard density across sub-Saharan Africa (Figure S1). We performed a scientific literature search on 20 May 2023 using Clarivate's Web of Science (Clarivate, 2019) and Elsevier's Scopus (Ballew, 2009) databases, with the search query defined in Table S1. We retrieved 819 scientific records from the search. We then filtered and sorted these records systematically as outlined in Figure S1.

In the next stage, the second author evaluated 5% of randomly selected abstracts for relevance using the same selection criteria. Inter-rater reliability was checked by calculating Cohen's K (Cohen 1960) in R (R Core Team, 2023) using the *irr* package (Gamer et al., 2010). The interpretation of the values followed McHugh's guidelines (2012). There was strong and statistically significant agreement between the two authors (Kappa = 0.614, $p < 0.05$).

The rest of the systematic literature review was performed by the first author. The data were extracted and assigned to the following variables ‘title’, ‘location’, ‘land use’, ‘duration’, ‘survey method’, ‘sample area’, ‘leopards detected’, ‘estimation method’, ‘inside/outside PA’, ‘density/population estimate’, ‘density’, ‘confidence interval’ and ‘potential variables’ (Table 1). Additionally, we complemented the extracted density estimates with spatially explicit estimates obtained from the TetraDENSITY database (Santini et al., 2018) and spatially explicit capture–recapture (SECR) estimates published between 20 May 2023 and 1 July 2025.

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TABLE 1 Summary of variables extracted from full-text analysis during literature review to guide model and database construction for predicting leopard population density in Sub-Saharan Africa.

Variable	Description
Title	Defines the title of the literature
Location	Defines the location/geographic area of the study
Duration	Defines the duration of the study in months
Survey method	Defines the ecological survey method used for the study. For example, spoor survey, camera trapping, line transects, etc.
Sample area	Defines the effective sample area within the study area in km^2 as defined by the authors in each study
Leopards detected	Defines the total number of individual leopards detected in the study
Estimation method	Defines the population/density estimation method used for the survey
Inside/outside PA	Defines whether the study was conducted inside or outside a protected area
Density/population estimate	Defines whether the study's aim is obtaining a population estimate or a density estimate
Density	Defines the density of the leopards per $100\,km^2$ in available habitat present in the state space
Confidence interval	Defines the confidence interval of the density estimate
Potential Variables	Outlines the environmental and anthropogenic variables that affect density variability and guided covariate selection for model development

2.2 | Density data acquisition and preparation

Following the screening phase, we retained and extracted density data from studies that incorporated spatial components, specifically camera trap-based SECR, due to their demonstrated robustness and narrower confidence intervals compared to non-spatial methods (Sutherland et al., 2019). Most studies estimated density across all habitats or available habitats within a defined survey state space, but some studies constrained activity centres to suitable habitats using habitat masks (Table S4). We extracted the density estimate along with the coordinates of the study area. The published papers did not always use the same definition for the sampling area. Hence, we interpolated the centroid of the area either from the map, if provided (which was most of the studies), or we took the centroid of the study area extent that was provided. The density values were then log-transformed for further analysis.

2.3 | Environmental variable preparation

All raster layers were obtained at $1\,km \times 1\,km$ resolution and standardised to common coordinate system (WGS84) prior to analysis (Table S5).

2.3.1 | Anthropogenic variables

To represent human infrastructure, we converted the World Settlement Footprint raster (Marconcini et al., 2020) to a binary layer (settlement = 1, non-settlement = 0) and calculated Euclidean distance from each cell centroid to the nearest settlement. Livestock density surfaces for goats and sheep (Gilbert et al., 2018) were summed to create a composite small livestock 'shoat' density layer. Larger-sized cattle density (Gilbert et al., 2018) was retained as a separate predictor for species distribution modelling. Human population density was extracted from the Gridded Population of the World dataset (CIESIN, 2018). The Human Footprint Index (HFP; Venter et al., 2016) was used as an integrated measure of anthropogenic pressure. Road density was calculated from (Meijer et al., 2018) vector data by computing total length in a pixel per unit area.

2.3.2 | Land cover variables

The Copernicus Global Land Cover layer (Buchhorn et al., 2020) was reclassified into five functional categories: (1) cropland—rainfed cropland, mosaic cropland and mosaic vegetation with 20–50% cropland; (2) woodland—closed to open forest (>15% cover), forest regularly flooded and tree cover >5 m in height; (3) shrubland—closed to open shrubland (<5 m woody vegetation) and mosaic forest/shrubland/grassland; (4) grassland—closed to open grassland; and (5) bare/sparse vegetation. For each $1\,km^2$ cell, we calculated the proportional cover of each land cover class within circular buffers at multiple spatial scales (see Scale optimisation below).

2.3.3 | Topographic and vegetation variables

Elevation data were obtained from the SRTM digital elevation model (Farr et al., 2007). Topographic roughness was calculated as the local

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elevation range (maximum minus minimum) within a 3×3 moving window. The 20-year average Normalised Difference Vegetation Index (NDVI) was derived from the MOD13Q1 product (Didan, 2015). Canopy cover was extracted from the Vegetation Continuous Fields (VCF) product (Sexton et al., 2013).

2.3.4 | Hydrological variables

Perennial and seasonal river densities were calculated from the HydroSHEDS database (Lehner & Grill, 2013) by generating line density surfaces (km river per km^2) in each pixel.

2.3.5 | Prey richness variables

Wild prey species richness was sourced from (IUCN, 2024). We generated binary presence/absence layers for each species and summed them to create richness surfaces for: (1) bovid richness, (2) suid richness and (3) combined wild prey richness (bovids + suids + equids).

2.3.6 | Scale optimisation

For each continuous environmental variable, we generated circular buffers at multiple radii (1, 5, 10, 30, 50 km) and extracted the mean value within each buffer for all study area centroids. We then fitted univariate models relating log-transformed leopard density to each variable at each scale and selected the scale with the lowest Akaike Information Criterion (AIC) value for inclusion in subsequent analyses (following Fattebert et al., 2018; Pitman et al., 2017). The optimal scales for each retained variable are reported in Table S2. Following scale optimisation, all raster layers were aggregated to 10 km × 10 km resolution (by averaging constituent 1 km^2 cells) to match the grain size appropriate for continental-scale leopard population estimation and to reduce computational burden.

2.4 | Modelling

2.4.1 | Model structure and selection

We modelled the relationship between the density estimates and the associated predictive variables. We first explored the dataset for non-linearity and positive skewness of the data. We then checked for collinearities among explanatory variables using the variance inflation factors (VIF) and discarded any variable with a VIF > 3. Following this, we modelled the relationship between log-transformed leopard density estimates and environmental and anthropogenic variables using a generalised linear mixed model (GLM) with a Gaussian identity link function. Each study was incorporated as a random effect to account for spatial autocorrelation and to account for the variability associated with different methodologies used (Bayesian/maximum likelihood) to estimate African leopard population density in each study. We then performed forward selection (Blanchet et al., 2008) and compared the forward-selected model with the null model and the full model to obtain the most parsimonious model with the best predictive power.

The model used can be mathematically represented as follows:

$$log_{Density_i} \sim N(\mu_i, \sigma^2)$$

$$E(log(Density_i)) = \mu_i, and\ var(log(Density_i)) = \sigma^2$$

$$\mu_i = \eta_i$$

$$\eta_i = \beta_0 + \beta_1 x_i + \ \dots \ + \beta_k x_{ki} + \upsilon_j$$

where log($Density_i$) is the recorded log-transformed density using the spatial covariate of $study\ area_i$, assuming a Gaussian distribution with mean μ_i and variance σ^2. $\mathbf{\upsilon}_j$ is the random effect that accounts for variability among study statistical approaches employed.

2.4.2 | Modelling uncertainty and model projection

To predict the lower (2.5th percentile) and upper (97.5th percentile) confidence intervals of the predicted leopard population, we employed a bootstrapping technique. We created 1000 bootstrap samples and fit the most parsimonious model to each bootstrapped sample. We then used the model coefficients for each of the bootstrapped samples to predict African leopard population density using the *predict()* function from the raster package (Hijmans et al., 2022). From these 1000 bootstrap predictions, the first, median and third quartile were computed to obtain the 2.5th, 50th and 97.5th percentiles. These values were then used to spatially project the density of leopards across sub-Saharan Africa. These projections were then masked to represent the 'Broad current range' which encompassed the regions where leopards are extant and possibly extant, and the 'current range' where leopards which encompassed the only regions where leopards are extant as classified by IUCN (IUCN, 2024).

2.4.3 | Habitat suitability modelling

To predict densities at the continental scale, we combined our density model above with a habitat suitability index (HSI) model trained in a latent selection difference framework (Erickson et al., 2014; Northrup et al., 2022). This framework was designed to model environmental suitability by contrasting conditions in areas of persistent leopard occupation against those in areas where the species has been extirpated. We sampled the species' current range, classified as 'extant' by the IUCN, to generate pseudo-presence points. Comparatively, we sampled the historically occupied but now 'extinct' portion of the range (as defined by the IUCN) to generate pseudo-absence points, ensuring no spatial overlap between these sample sets. This design allows us to

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identify environmental factors associated with long-term persistence versus extirpation; a different objective from conventional species distribution modelling, which typically predicts occurrence probability across continuous space. We did not sample the 'possibly extant' and 'possibly extinct' range categories to limit uncertainties regarding species' status.

We extracted the values of the environmental variables to the above pseudo-presence–absence data. We retained closed to open grassland as a single category. We log-transformed human, shoat (sheep and goat) and cattle densities. We combined wild bovid, suid and equid richness into a single wild prey species richness. We derived a topographic roughness variable from the DEM using a 3×3 moving window. For each focal cell, roughness was calculated as the local elevation range, defined as the maximum minus the minimum elevation value among the focal cell and its eight surrounding cells. We used the 20-year average NDVI, the canopy cover component of the vegetation continuous field (VCF), human footprint index (HFP) and computed road density, perennial river density and seasonal river density.

We fitted a binomial generalised linear mixed model (GLMM) with a logit link function (logistic regression) using country as a random intercept to account for unmeasured differences in governance and wildlife management regimes. All variables were standardised to a mean of 0 and a standard deviation of 1 to facilitate model convergence. We first reduced the set of variables using the VIF criterion to keep variables with VIF < 10. We then further reduced the model using a manual backward stepwise variable selection approach, removing variables with the highest p-value until all variables remaining in the model were statistically significant at $p < 0.05$ (Model-Building Strategies and Methods for Logistic Regression, 2013). We stretched the final, reduced model spatial projection to the entire IUCN historical range between 0 and 1 as follows:

$$w(x) = (x - min) / (max - min)$$

To define a dichotomic habitat/non-habitat landscape, we extracted the habitat suitability index to out-of-sample GBIF leopard occurrence data (GBIF, 2024) and used the HSI value that encompassed 95% of these data as a threshold to define habitat (Fattebert et al., 2018; Holbrook et al., 2017).

2.4.4 | Model combination/weighting and validation

In suitable habitat defined above, we multiplied the spatial projections of density in each pixel by the value of the HSI to get a suitability-weighted prediction of leopard density at a 10 × 10 km resolution.

First, we validated the best model before projecting density predictions over the entire leopard range. We evaluated residual variance homogeneity, model adequacy, assessment of residual normality and identification of influential variables as outlined by Zuur et al. (2010). We further performed a K-fold validation on 80% of all the fitted models to assess their predictive power.

Second, after projecting the predictions spatially based on the continental 10 × 10 km resolution map layers of the covariates, we validated the model externally by assessing its predictive power using leopard occurrence data from the Global Biodiversity Information Facility database (GBIF, 2024). We kept the occurrence and human observation data with geographic coordinates from the year 2000 onwards ($n = 3152$ records). We took an approach similar to validating resource selection function models (Boyce et al., 2002; Fattebert et al., 2015) by classifying predicted densities within the current range of the species into 10 equal-area bins and correlating the frequency of occurrence with the bin values. Assuming a positive relationship between density and occurrence records, we expected the least occurrence data to fall within the lowest density bins and most occurrences to fall within the higher density bins.

2.4.5 | Adult leopard population estimate in protected and unprotected areas

The spatial projections were then used to estimate leopard populations across sub-Saharan Africa. We masked our projections according to the IUCN range map available for leopards within both the 'broad current range' ('possibly extant' and 'extant'; Jacobson et al., 2016) and 'current range' ('extant' only; Jacobson et al., 2016).

To assess the abundance of leopard populations across sub-Saharan Africa, we used the projected density layers representing current leopard populations at different confidence intervals (lower, median and higher estimates) and the country boundaries.

We multiplied the current leopard population density predictions by 100 to estimate abundance in each pixel, and we masked the layers by the boundaries of each country. We then summed the abundance values to get national estimates.

We then estimated adult male abundance outside protected areas by cropping the national male estimate outside protected areas (UNEP-WCMC and IUCN, 2024). To account for uncertainty of the population structure, the number of adult male leopards was estimated by weighting the population estimate in each pixel by a random draw of the adult male proportion around a mean of 20% (Balme et al., 2019) with a standard deviation of 5, 10,000 times. We have then computed the mean, lowest and highest adult male estimate in each country practising legal trophy hunting. The resulting numbers indicated the total number of adult male leopards available for offtake in each country, provided trophy hunting is legal.

All statistical and geospatial analyses were conducted in R software (R Core Team 4.3.1, 2023). The cartographic representation of the population distribution raster developed in R was subsequently refined using Quantum GIS 3.36 (Flenniken et al., 2020).

3 | RESULTS

3.1 | Scale selection and model selection

The results of the scale optimisation analysis (Figure S2) are reported in Table S2. Following this, our most parsimonious model

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TABLE 2 Coefficients and associated 95% confidence interval of the final averaged model for predicting leopard density in Sub-Saharan Africa.

	Estimate	95% confidence interval Lower	Higher
(Intercept)	**1.185**	**0.919**	**1.452**
scale(shoat_density_5km)	**−0.265**	**−0.422**	**−0.116**
scale(agriculture_50km)	−0.094	−0.239	0.049
scale(suid_richness_50km)	0.124	−0.071	0.319
scale(forest_30km)	−0.126	−0.273	0.021
scale(bovid_richness_50km)	0.103	−0.088	0.295
scale(distance_to_settlement_30km)	**−0.215**	**−0.364**	**−0.065**

TABLE 3 Leopard abundance in sub-Saharan Africa based on the projected estimates of the final averaged model within the IUCN leopard present range (extant) and historical range (possibly extant + extinct and possibly extinct).

	Martin and De Meulenaer (1988) Population estimates	Current study: Present range (% of Martin & De Meulenaer estimates)	Current study: Historical range (% of Martin & De Meulenaer estimates)
Lower 95% CI estimate	600,000	44,800 (7.46%)	55,165 (9.19%)
Central estimate	**700,000**	**80,276 (11.46%)**	**98,433 (14.06%)**
Upper 95% estimate	900,000	142,604 (15.84%)	175,620 (19.51%)

(Table 2) with the best predictive power highlighted a negative relationship with shoat density ($b = -0.268$; 95% CI: −0.405 to −0.099) and with distance to human settlements ($b = -0.214$; 95% CI: −0.353 to −0.058) as statistically significant predictors of leopard population density in sub-Saharan Africa (Table 3).

Additionally for the HSI, following variable selection, our reduced model indicated that suitable habitat at the continental scale is predicted by terrain ruggedness (b = 0.199, 95% CI: 0.194 to 0.204), human footprint index ($b = -0.951$, 95% CI: −0.958 to −0.944), NDVI ($b = 0.310$, 95% CI: 0.310 to 0.319), wild prey species richness ($b = 1.542$, 95% CI: 1.532 to 1.551), proportion of cropland ($b = -0.111$, 95% CI: −0.119 to −0.104), woodland ($b = 0.379$, 95% CI: 0.373 to 0.385) and grassland ($b = -0.324$, 95% CI: −0.331 to −0.316). Country fitted as a random intercept accounted for 15.95 ± 3.99 (SD) % of the variance (Table 4).

TABLE 4 Fixed-effect scaled coefficients and associated 95% confidence intervals (CI) of environmental variables predicting suitable habitat for the leopard in sub-Saharan Africa.

Variable	Coefficient	Lower 95% CI	Upper 95% CI
Roughness	0.199	0.194	0.204
HFP	−0.951	−0.958	−0.944
NDVI	0.310	0.301	0.319
Prey richness	1.542	1.532	1.551
% Cropland	−0.111	−0.119	−0.104
% Woodland	0.379	0.373	0.385
% Grassland	−0.324	−0.331	−0.316

3.2 | Model validation

Following model validation, we projected the final model across the current range of leopards in Sub-Saharan Africa. External validation with GBIF records indicated strong predictive performance within the species' contemporary range (rho = 0.878, $p = 0.002$; Figure S3), supporting interpolation within the environmental domain represented by extant populations. We then projected the model across the historical range to explore the spatial distribution of potential leopard densities under the fitted contemporary species-environment relationships (Figure 1); however, this extrapolation should be interpreted cautiously because predictive performance within the current range does not necessarily imply equivalent predictive accuracy in historically occupied but now extirpated areas.

3.3 | Projected leopard densities and predicted abundance

Within the current range of the species, we estimated a total population of 80,276 (95% CI: 44,800–142,604) leopards in Sub-Saharan Africa (Table 5). The predicted densities yield a potential total leopard abundance across the historical range of 98,433 (95% CI: 55,165–175,620) individuals in sub-Saharan Africa under the current environmental conditions. We report the number of leopards estimated to occur in each country in Table S3.

The total number of predicted adult male leopards in sub-Saharan Africa was 16,055 (CI: 8960–28,520). The number of adult

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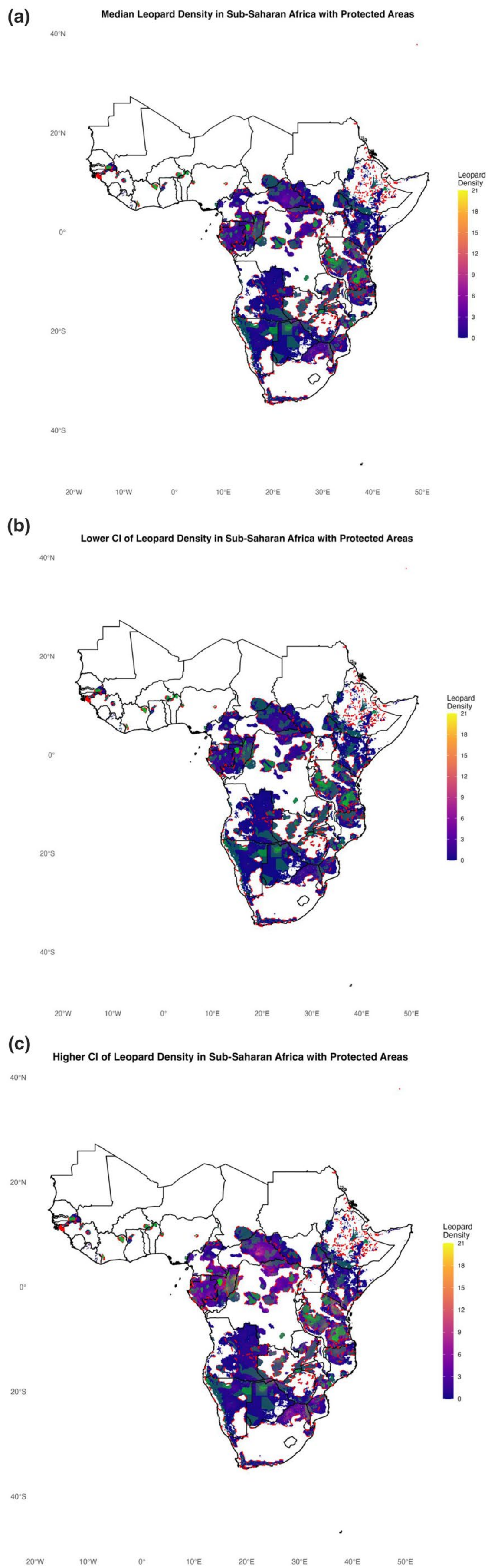

FIGURE 1 Projected leopard density across the historical range in sub-Saharan Africa. Density estimates were generated using the most parsimonious model and are expressed as leopards per 100 km^2. (a) Central density estimates derived from a Gaussian regression fitted to central estimates from published field-based spatially explicit capture–recapture studies. Predicted density quartiles for the historical range were Q1 = 2.32, Q2 = 2.93 and Q3 = 4.04 leopards/100 km^2. (b) Lower confidence-limit estimates derived from gamma regression of the lower 95% confidence limits from the same SECR studies, using the same model structure. Predicted density quartiles were Q1 = 1.28, Q2 = 1.73 and Q3 = 2.41 leopards/100 km^2. (c) Upper confidence-limit estimates derived from gamma regression of the upper 95% confidence limits from the same SECR studies, using the same model structure. Predicted density quartiles were Q1 = 2.97, Q2 = 3.96 and Q3 = 5.58 leopards/100 km^2. Within the historical range, more than 1.7 million km^2 occurs inside protected areas and more than 14 million km^2 occurs outside protected areas. Q1, first quartile; Q2, median; Q3, third quartile; SECR, spatially explicit capture–recapture.

male leopards present in non-protected areas where trophy hunting is legal was estimated as 5038 (CI: 2834–8662). Details of estimated adult male leopards outside protected areas where legal hunting is practiced, along with the predicted offtake percentage of the population if CITES quotas are fulfilled, are reported in Table 5.

4 | DISCUSSION

Our model for African leopard density predicted lower densities in areas with higher goat and sheep density, a high proportion of agricultural and forest cover and in areas closer to human settlements. Conversely, leopard densities were higher in regions with a greater variety of prey species. Based on spatial model projections, we estimated the current population of leopards in their extant range in sub-Saharan Africa to be approximately 44,800–142,600 individuals. Given the current conditions in the range of the species where there is uncertainty of extinction as classified by the IUCN (IUCN 2024), the Sub-Saharan leopard population could potentially reach approximately c. 55,200–175,600 individuals, given that adequate conservation measures are taken. In countries where trophy hunting is legal, we estimated the current population of adult male leopards between c. 2800 and 8700 outside protected areas where they could be legally harvested. We also found that the CITES quotas for leopard harvest in all trophy-hunting countries, except for the Central African Republic, exceed the recommended offtake limit of 10% of the adult male population (Braczkowski et al., 2015).

Our estimates challenge the previous continental estimate by Martin and De Meulenaer (1988), which suggested 600,000–900,000 individuals occur in Africa. Criticism of the Martin and De Meulenaer (1988) assessment is not novel, as it has been considered seriously flawed since its initial publication (Norton, 1990). However, this assessment is still used as the basis for informing national trophy-hunting quotas in most countries (Loveridge et al., 2022; Trouwborst

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TABLE 5 Overview of adult male leopard population estimates, hunting quotas and offtake rates if quotas are fulfilled across African countries where trophy hunting is legal.

	Number of adult males					Quota % ad. Males	
Country	Mean	Min	Max	Quota	Mean	Min	Max
Botswana	468	282	838	130	0.278	0.155	0.461
Central African Republic	1513	747	2824	40	0.026	0.014	0.054
Mozambique	864	515	1393	120	0.139	0.086	0.233
Namibia	469	263	927	250	0.533	0.270	0.951
South Africa	1084	639	1773	150	0.138	0.085	0.235
Uganda	14	7	35	28	2.000	0.800	4.000
Tanzania	1540	754	2809	500	0.325	0.178	0.663
Zambia	282	151	472	300	1.064	0.636	1.987
Zimbabwe	184	121	269	300	1.630	1.115	2.479
TOTAL	6418	3479	11,340	1818	0.283	0.160	0.523

et al., 2019). A key discrepancy arises from their sole use of rainfall as a proxy for prey availability to predict leopard abundance. Furthermore, their predictions are based on the historical range of leopards rather than the current range, despite evidence that leopards no longer occupy more than 41% of their historic range in sub-Saharan Africa (IUCN, 2024). When we attempted to replicate this approach, the model predicting leopard density based solely on precipitation exhibited a relatively poor fit compared to our other candidate models. Moreover, it did not reveal a statistical relationship between rainfall and leopard density, suggesting that higher rainfall does not necessarily correspond to greater leopard carrying capacity. This outcome aligns with previous, more local findings, including Loveridge et al. (2022) and supports the broader understanding that animal behaviour and population dynamics are shaped by different environmental variables depending on the spatial scale of analysis (van Moorter et al., 2013).

Our habitat suitability modelling approach differs from conventional species distribution modelling protocols (e.g. Iturbide et al., 2015). Rather than predicting occurrence probability using presence records and background pseudo-absences, we employed a latent selection difference framework contrasting IUCN-classified 'extant' (pseudo-presence) versus 'extinct' (pseudo-absence) portions of the historical range. This design explicitly identifies environmental factors associated with persistence versus extirpation, directly addressing our conservation objective of estimating recovery potential across the historical range under current conditions.

4.1 | Prey species richness, agricultural land cover and tree cover

While the relationship was not statistically significant, we observed a positive trend between leopard population and prey species (bovid and suid) richness, which is consistent with prior studies reporting strong positive associations between leopards and mammalian species richness (Tshabalala et al., 2021). Additionally, increased prey species richness expands the dietary breadth and prey biomass available to leopards, reducing interspecific competition and kleptoparasitism (Ferretti et al., 2020). Consequently, regions with high prey species richness may support greater leopard populations due to enhanced coexistence of predator species (Ferretti et al., 2020).

Prey species richness can also indicate anthropogenic influence, as variations in prey communities often result from human-driven factors such as poaching, intensive hunting and habitat degradation (Creel et al., 2018; Ferretti et al., 2020). Although not statistically significant, our model suggested a negative association between leopard density and agricultural land cover, similar to findings by Fattebert et al. (2015) and Ramesh et al. (2017). This pattern may reflect prey population declines in the region and habitat conversion associated with agricultural expansion. Furthermore, higher human density and modified landscapes might make leopards more vulnerable to human persecution, decreasing leopard numbers (Inskip & Zimmermann, 2009; Manral et al., 2016).

Although many regional studies report a positive association between leopard occurrence and forest cover, our continental-scale model indicated that leopard density declined with increasing tree cover across sub-Saharan Africa. This may partly reflect lower carrying capacity in intact rainforest systems, where prey available to leopards may be less abundant or less accessible than in savanna habitats (Bailey, 1993; Jenny, 1996; Henschel et al., 2011). However, this ecological pattern should be distinguished from the disappearance of leopards from parts of the West and Central African forest belt, which is more likely driven by anthropogenic pressures, particularly prey depletion, bushmeat hunting, habitat disturbance and increasing human access (Henschel et al., 2011; Jacobson et al., 2016). For example, leopard signs were detected in only 2 of 47 forest patches in southeastern Nigeria (Angelici et al., 1998), and local extirpations have been reported from parts of southern Cameroon (Henschel, 2010). Similarly, in South Africa's Maputaland Conservation Unit, leopard densities were significantly lower in plantation areas than in native forests. Furthermore, intermediate

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vegetation types may enhance hunting success by providing sufficient cover for effective ambush without impeding movement, potentially explaining the negative association between leopard density and forest cover at the landscape scale (Balme et al., 2007). In contrast, at regional scales, forest cover has been linked to higher leopard densities (Kittle et al., 2018; Mondal et al., 2013).

4.2 | Livestock density and distance to settlements

Our analysis indicates that the relationship between leopard density and domestic sheep and goat (shoat) density is non-linear (Figure 2), that is leopard density increases with low to moderate shoat densities, but declines as shoat density becomes high, suggesting that leopards may tolerate or even benefit from moderate livestock presence as a substitute for wild prey, while high livestock densities likely lead to negative impacts such as habitat degradation or increased human–wildlife conflict (Devlin et al., 2023; Khan et al., 2020; Khorozyan et al., 2015), which then negatively affects leopard population. Moreover, this pattern suggests that high livestock density does not necessarily translate into higher leopard density. Although livestock may represent a substantial prey resource, areas with high livestock densities are also often associated with reduced wild prey availability, greater human disturbance and altered predator–prey relationships, which together may have a net negative effect on leopard populations (Devlin et al., 2023; Khan et al., 2020; Khorozyan et al., 2015; Kuiper et al., 2024).

Our models also indicate that leopard density is higher in areas near human settlements. This might reflect a trade-off, as leopards exploit areas where livestock is more accessible, despite increased risk of detection and retaliation (Kuiper et al., 2024). Although not a causal relationship, this pattern may be related to the observed correlation between leopard density and shoat density. Additionally, supporting this, previous studies and our correlation plots show that as shoat density increases in a region, wild bovid and suid richness declines (Roberts et al., 2021; Sharma et al., 2024), suggesting that some seemingly suitable regions that are a result of ecological niche models might be functionally unsuitable due to depleted prey bases (Hinde et al., 2023).

4.3 | Continental leopard population estimates

Leveraging reserved occurrence datasets, we empirically validated the resilience of our predictive models for leopard population density, affirming the accuracy of model projections within the calibration domain. We then used the validated model to estimate potential leopard density across their historical distribution under extant habitat conditions. Based on the density-habitat relationship, we estimated a current leopard population of approximately 44,800–142,600 individuals in sub-Saharan Africa. However, it needs to be noted that these predictions are based on data from camera trap studies that estimate the density of nutritionally independent

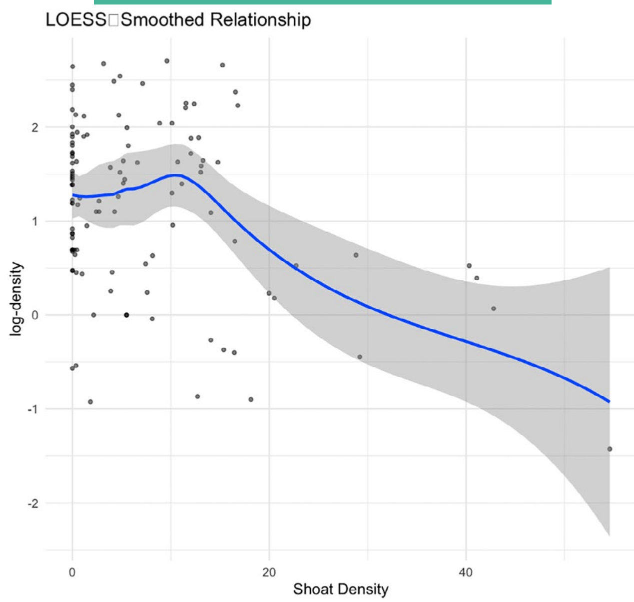

FIGURE 2 LOESS-smoothed relationship between shoat density (5 km buffer) and predicted leopard density (on the original scale) based on a generalised linear mixed-effects model. Outliers in both response (log-transformed density) and focal predictor (shoat density) were removed using the IQR method prior to model fitting. The fitted model accounts for the effects of additional anthropogenic and ecological covariates while including random intercepts by data source. The LOESS curve illustrates a non-linear trend, indicating how varying shoat densities may influence carnivore density after adjusting for other factors.

leopards, including breeding adults >3 years old and non-breeding sub-adults typically 1.5–3 years old, old enough to leave their natal range (Fattebert et al., 2015). The proportion of breeding individuals is lower. In stable, unexploited populations, leopard populations typically comprise approximately 40% adult females, 20% adult males and 40% sub-adults (Balme et al., 2019). Conservatively, we estimate 17,900–57,000 adult female and 9000–28,500 adult male leopards currently occur in sub-Saharan Africa. It is worth noting that these estimates should be interpreted cautiously as most leopard populations experience varying levels of human disturbance (Balme et al., 2010; Rogan et al., 2022) which can significantly influence their demographic composition.

4.4 | Conservation implications

Our population predictions across the continent should be interpreted not as potential population estimates but as potential carrying capacity of leopards across its IUCN defined extant and possibly extant range. Additionally, using these numbers and other predicted leopard population numbers (Pranzini et al., 2023; Slovikosky et al., 2025), as potential population estimates might result in erroneous management decisions. This is because most camera trapping data and SECR studies have been conducted in protected areas and wildlife management areas (Briers-Louw et al., 2024), which might

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bias the estimates. This bias is particularly relevant for regions outside protected areas, where depleted prey bases and human–wildlife conflict, especially regarding livestock depredation, can result in lower leopard densities than predicted (Balme et al., 2009; Balme et al., 2010; Hayward et al., 2007). Based on current habitat conditions as per available data, our predicted abundance, both within and outside protected areas, and across the extant and potential range, should serve as a benchmark for recovery efforts and a guide for targeted conservation actions.

These numbers can help define the carrying capacity of regions, which can then be used to construct spatially explicit population viability models (e.g. Bauduin et al., 2025), to estimate viable leopard populations across their range. Furthermore, where observed leopard abundance is substantially lower than the density predicted from extant habitat conditions across the historical range, this may indicate the influence of additional limiting factors such as prey depletion, habitat degradation, persecution, conflict or unsustainable offtake. In such areas, management should focus on restoring prey and habitat, reducing conflict and persecution and ensuring that any legal hunting does not impede recovery, while recognising that recovery targets should be locally realistic and aligned with broader metapopulation viability rather than a uniform expectation that all populations attain habitat-based potential density. In the part of the range where leopard extinction is uncertain, our map identified areas which could potentially harbour leopards, and thus we recommend prioritising increased opportunistic camera trapping to verify the presence of leopards, prey base restoration, cost benefit analyses for increasing leopard numbers and possible reintroduction of the species according the reintroduction guidelines defined by the IUCN (Zlatanova, 2016) to facilitate dispersal and potential natural recolonisation (Fattebert et al., 2013; Fattebert et al., 2015).

The sustainability of leopard hunting quotas in many African countries is insufficient (Balme et al., 2009). Quotas have remained unchanged since 2004 and, in some cases, since 1987 (Trouwborst et al., 2019) and are based on inflated estimates (Loveridge et al., 2022). We found significantly lower leopard populations in all the trophy-hunting countries compared to the 1988 CITES estimates (Table S3). Based on population structure (Braczkowski et al., 2015), we estimate 2800–8700 adult male leopards outside protected areas in countries with legal trophy-hunting. It is imperative to reevaluate hunting quotas numerically and spatially (Balme et al., 2010; Pitman et al., 2015), as poorly planned quotas and unmanaged harvesting could further decline leopard populations, exacerbated by unregulated, illegal killings. In 4 out of 9 of these countries (Table 5), the predicted annual offtake percentage if quotas are fulfilled exceeds the recommended 10% threshold (Braczkowski et al., 2015) (Figure 3), necessitating a reassessment of hunting quotas. Our study also highlights the non-applicability of the 1988 CITES model for leopard population estimation, as we found this model's predictive performance is significantly poorer compared to our best model. Therefore, our model is currently a better attempt at providing biologically credible estimates of leopard population on a continental scale that can be used to inform conservation management and set trophy-hunting quotas. Additionally, regular ground surveys in trophy-hunting countries are essential for accurate

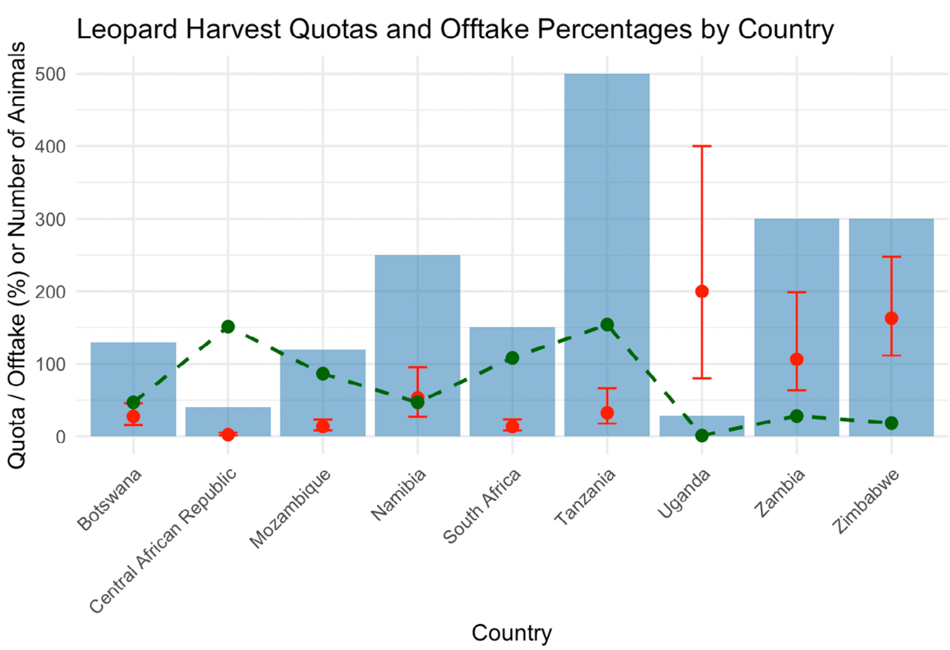

FIGURE 3 Quota (blue bars) is plotted on the left axis as the *number of* adult male leopards predicted by our model. Annual offtake percentages if quotas are fulfilled (red points with 95% confidence intervals) for adult male leopards in non-protected areas across nine African trophy-hunting countries. Offtake percentage represents the proportion of estimated adult male leopard populations harvested relative to population estimates. The dashed green line indicates a 10% offtake threshold for reference.

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population assessments and adaptive management to ensure sustainable harvests.

4.5 | Limitations and recommendations

While our study offers valuable insights into leopard conservation priorities and distribution across Africa, it is important to acknowledge key limitations that highlight the need for future research. First, most published density estimates are derived from protected areas (Briers-Louw et al., 2024) (Figure S5), which may skew the observed relationships with prey availability and human presence, potentially leading to overestimates in unprotected areas. Second, there is a geographic bias in study locations (Figure S5), with the majority of data coming from Southern and Eastern Africa. This underrepresentation of West and Central Africa may influence the density-habitat relationship, reflecting patterns specific to more studied regions rather than the continent as a whole. Conducting additional surveys in underrepresented areas, including various biomes and regions outside protected areas, is crucial for accurately estimating range-wide leopard densities and abundance (Sharma et al., 2020).

While we recognise that an adaptive management system based on annual leopard population assessment is ideal for informing trophy-hunting practices (Trouwborst et al., 2019), its implementation is context-dependent. Such an approach might be feasible in politically stable and well-resourced countries like South Africa, but it remains impractical in nations facing resource constraints or those experiencing political instability. Consequently, when regular assessment of population status with scientifically robust methodologies is not feasible, results from spatially explicit population viability analyses should be used to inform trophy-hunting quotas. This represents the most feasible strategy under current conditions.

5 | CONCLUSION

Our study addresses a critical knowledge gap by providing the continent-wide assessment of leopard populations and guiding future research and conservation priorities across sub-Saharan Africa. We present a comprehensive and robust modelling approach that links published density estimates with environmental predictors to estimate leopard abundance across the region. By projecting this model spatially, we identify areas where no empirical data exist and estimate potential population estimates based on current vegetation, protection status, human pressures and prey availability.

Our approach offers dynamic methodologies for evaluating recovery potential and conservation success across diverse ecosystems to initiatives such as the Green Status Assessment (2023), rather than merely documenting threat levels. It can also serve as a baseline for determining harvesting quotas nationally based on the population estimates that are constructed using the results of this study as carrying capacity. Importantly, our results suggest that leopard numbers within their extant range are significantly lower than previously estimated. In countries where leopard trophy hunting is permitted, this raises concerns about the sustainability of existing quotas. Our findings underscore the urgent need for quota re-evaluation and provide critical evidence to inform CITES deliberations, promoting more sustainable and science-based trophy-hunting practices.

AUTHOR CONTRIBUTIONS

Kalpapran Patowary and Julien Fattebert conceived the ideas and designed the methodology; Kalpapran Patowary collected the data; Kalpapran Patowary and Julien Fattebert analysed the data; Kalpapran Patowary led the writing of the manuscript; Antonio Uzal reviewed the manuscript and provided writing guidance, direction and thoughts for the conservation implications of the study. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.41qh7 (Patowary et al., 2026).

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SUPPORTING INFORMATION

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

Table S1. Search query used for literature review to retrieve relevant records of published leopard density estimates in sub-Saharan Africa.

Figure S1. Schematic representation of the Systematic Literature Review workflow for retrieving relevant records of published leopard density estimates in sub-Saharan Africa.

Figure S2. Schematic representation of scale analysis workflow conducted in R Environment. For each variable, the scale with the lowest AIC value obtained from the computed test statistics was used for further modelling purposes.

Figure S3. Frequency of external leopard occurrence data ($n = 2295$) (GBIF, 2024), in each equal-area bin of the spatial projection of the leopard density model in the current range in Sub-Saharan Africa. The horizontal dashed red line depicts the expected proportion of occurrence data at random. A positive correlation (rho = 0.878, $p = 0.002$) between the frequency of occurrence and density bins indicates that the weighted model has a good predictive power.

Figure S4. Schematic representation of the workflow for estimating leopard population density across sub-Saharan Africa.

Figure S5. The figure presents centroids of the study areas from various leopard population estimation studies (concentric circles). These centroids serve as reference points from where spatially explicit density estimates were extracted for constructing the mechanistic population model.

Table S2. Results of scale optimisation analysis. The variables along with their corresponding scale at which the AIC value was found to be the lowest is reported below.

Table S3. Country estimates of leopard population in sub-Saharan Africa. Estimates are presented based on our leopard density model

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within the present range of the species and the potential population within the historical range given current conditions. Estimates by Martin and De Meulenaer (1988) informing CITES are presented for comparison, along with current CITES leopard hunting quotas.

Table S4. Mean African leopard density estimates and reported uncertainty intervals across published studies. The data represent a range of study periods, locations and analytical approaches, highlighting variation in leopard densities across habitats and regions. Habitat basis indicates whether density was estimated across all habitats, available habitats or suitable habitats defined by a habitat mask. NR: not reported.

Table S5. Candidate environmental variables used in training gamma regression for predicting leopard population density in Sub-Saharan Africa.

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