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ORIGINAL RESEARCH

Spatially explicit estimates of global population potential for leopard (*Panthera pardus*)

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Abstract

Many studies have assessed local densities of threatened carnivore species, but few have synthesized existing data into range-wide estimates based on habitat potential. Identifying where observed densities differ from expected values may help focus conservation attention. Herein, we related published leopard density estimates and a random selection of 0 values from across their extirpated range ($N=209$) to environmental and anthropogenic drivers. We then produced a spatially explicit estimate of expected density throughout the contemporary range of this species. We compared 16 candidate models that weighed density estimates by the inverse of their standard error, controlled for study design effects, and included spatial covariates at their optimal scale as determined by Akaike's Information Criterion. Expected leopard density ranged from 0 to 8 individuals/100 km^2 and was positively and strongly related to the proportion of protected area at the 5-km scale, less so to the proportion of developed land cover (5-km), and negatively associated with human density (1-km), temperature (20-km), and longitude. Prediction error ranged from 0 to 12 leopards/100 km^2, being greatest in India and its bordering countries. Overall, our model produced an expected value of 131,300 (42,692–428,498 95% CI) leopards globally. We predicted high expected densities in southern and eastern Africa where many published studies originate. Central and West Africa also hold high potential but lack estimates. Fine-scale variables and legacies of armed conflict that have depleted biodiversity should be considered when evaluating contemporary species status, and our predictions may highlight areas where conservation action could be most effective.

Keywords Expected density · Leopard · Prediction uncertainty · Range-wide · Scale

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Introduction

Species around the world are threatened with extinction from a variety of factors, including habitat loss, overexploitation, and invasive species (McNeely 2001; Mantyka-Pringle et al. 2013; Darimont et al. 2015; Tilman et al. 2017). Data on species status informs conservation action (Nichols and Williams 2006) and involves two related but distinct aspects. First, patterns of species occurrence or site occupancy define species distributions. Monitoring changes in the geographic range of a species, especially contractions in range, is fundamental to inferring species vulnerability to extinction and focusing conservation effort (Mace et al. 2010; Jacobson et al. 2016). Yet occurrence patterns alone are insufficient to ensure species persistence as the probability of site occupancy may remain constant despite an order of magnitude decline in overall species abundance (Ellis et al. 2014). Thus, the second important piece of information on species status is population density. Although generally positive (Holt et al. 2002), the relationship between site occupancy and species density is not always linear or clear (Gaston et al. 2000; Ellis et al. 2014). Hence, for rare and at-risk species, abundance estimates become critically important for monitoring conservation status (Gaston and Fuller 2009; Jones 2011). They can also be used to establish target recovery goals (Johnston et al. 2015; Loveridge et al. 2022a) by assessing where discrepancies between published and expected densities are greatest.

Globally, large mammals, and especially large carnivores, have suffered large-scale contractions of geographic range in addition to reductions in local abundance (Woodroffe 2000; Wolf and Ripple 2017). Considerable conservation and research effort has been focused on large carnivores, yielding a large number of published occupancy and abundance studies relative to smaller mammals (Srivathsa et al. 2022). The majority of studies have been conducted at the scale of individual protected areas, provinces, or countries to inform relatively fine-scale management for park or regional wildlife authorities (Hebblewhite et al. 2011; Ellis et al. 2014; Wang et al. 2018; Havmøller et al. 2019; Gebretensae and Kebede 2022). Taken collectively, these disparate studies may provide a means of evaluating range-wide habitat drivers of species abundance. For example, Jędrzejewski et al. (2018) used estimates of site occupancy and local density of jaguar (*Panthera onca*) from 117 published studies to model range-wide jaguar distribution and density. Pranzini et al. (2023) likewise used local density estimates of leopards (*Panthera pardus*) and tigers (*Panthera tigris*) to model range-wide density of these species. Such estimates may be useful for establishing baseline values against which future increases or declines can be compared, as well as prioritizing geographic regions in which conservation efforts may be most needed (Durant et al. 2007; Jacobson et al. 2016; Loveridge et al. 2022a; Clavero et al. 2023).

Large carnivores are sensitive to human persecution (Darimont et al. 2015; Oriol-Cotterill et al. 2015), yet live within increasingly human-dominated landscapes (Fahrig 2007; Kowalczyk et al. 2015). Armed conflict and anthropogenic exploitation can lead to low densities even in good habitat, leading to “empty forests and savannas” (Redford 1992; Lindsey et al. 2013; Petracca et al. 2020). Although animals may be able to spatially avoid conflict within landscapes providing refuges (Selwood and Zimmer 2020), or where the overall imprint of human activities is low or moderate (Basille et al. 2013), human modification of the landscape will eventually lead to habitat loss, higher levels of human-carnivore conflict, and ultimately population extirpation (Nyhus 2016; Slovikosky et al. 2024; Li et al. 2025). Thus, large discrepancies between high predictions and low estimates can help clarify where management action could be most effective. However, single studies in a local geographic region fail to capture variation in broad-scale context over which a species' resource selection patterns are driven and thus can lead to confusion over globally relevant drivers of habitat quality for a species. Moreover, political boundaries will drive variation in human-exploitation patterns that may muddy the relationship between apparent habitat quality and animal abundance (Weber and Rabinowitz 1996; Nyhus 2016). As such, comprehensive modeling of expected species density across their range must focus on the most fundamental and globally relevant variables (e.g., relating to vegetation cover, prey base), consider that habitat relationships are likely to vary with scale of observation (Mayor et al. 2009) and, for widely distributed species, consider variation due to changes in ecological and political domains (Nyhus 2016). Moreover, any such attempt must effectively account for potential biases in the available data, since certain geographic regions have more resources with which to conduct formal density estimation.

Following the approach used to model range-wide density for jaguars (Jędrzejewski et al. 2018), we modelled the expected density of leopards across their range. By some estimates, leopard range has been reduced up to 75% since the mid-18th century, and the species currently exists in fragmented and vulnerable populations throughout much of its range (Jacobson et al. 2016; Swanepoel et al. 2016; Stein et al. 2020). Like jaguars, leopards exhibit a solitary and territorial nature that should facilitate expected density predictions (Jędrzejewski et al. 2018). Yet, leopards are perhaps the most ecologically plastic species within the genus *Panthera* as they have the largest distribution of all wild cats, ranging from the Russian Far East to sub-Saharan Africa (Swanepoel et al. 2016; Stein et al. 2020). As such, geographic context may drive patterns of leopard abundance beyond what we can account for with specific ecological covariates. Fortunately, the published literature on density estimates for leopards is large and geographically widespread (Balme et al. 2014; Jacobson et al. 2016), and can be used to infer expected leopard abundance in unsampled areas (Stein et al. 2020). Discrepancies between published and modeled densities can highlight areas for conservation attention (e.g., see Pranzini et al. (2023). Moreover, alternative modeling approaches and inclusion of different sets or scales of variables can help inform how robust overall predictions of key drivers of expected density are across a species' range. Thus, the results of this work will help (1) determine the covariates and appropriate scales for modeling expected leopard population densities range-wide, and (2) better define areas of conservation need given high expected but unrealized densities of leopards, and thus help refine conservation targets for the species across its range.

Materials and methods

We searched for published estimates of leopard density through May 2021 in Web of Science, Google Scholar, and the IUCN Cat Specialist Group database using the following searches: (1) leopard AND (densit* OR number*), and (2) *Panthera pardus* AND (densit* OR number*) (Online Resource 1). We excluded studies that did not include density estimates in addition to those reports focusing solely on species other than the common leopard (ex. clouded leopard *Neofelis spp.* or leopard cat *Prionailurus bengalensis*). We recorded point estimates for density, the standard error of these estimates, and type of capture-recapture analysis employed (non-spatial versus spatial capture-recapture). Non-spatial analyses usually add a buffer around the trap array, equivalent to the mean or half of mean maximum distance moved to account for effective area sampled (Karanth and Nichols 1998). This approach derives density from abundance estimates rather than estimating density explicitly, as spatial approaches do (Borchers 2012), and is known to generally overestimate density (Sharma et al. 2010; Noss et al. 2012). For this reason, we only included spatial capture-mark-recapture estimates of leopard density. Further, for those studies reporting both Bayesian and maximum likelihood approaches, we retained the more conservative estimate of the two (mean observed difference in density $=0.01 \pm 0.68$ SE, $N=21$). For studies that reported density estimates for multiple years, we retained the most recent estimate only. Lastly, we randomly sampled points from the “Extinct” category of the IUCN Red List distribution map for leopards (Stein et al. 2020), subsequently assigning these a density value of “0” and appending them to our dataset. The number of points generated was equivalent to the number of published estimates.

We built a spatial database within a Geographic Information System (ESRI 2025) of leopard densities based on latitude and longitude coordinates of the center of each study location, either as directly provided in the paper or deduced from study area description. At each location we extracted environmental and anthropogenic covariates presumed to influence leopard densities. Covariates included human population density per square kilometer (Woodroffe 2000), Human Footprint Index (Sanderson et al. 2002), proportion of protected area (PA; Rogan et al. 2022), Terrain Ruggedness Index (TRI; Riley et al. 1999; Rather et al. 2021), proportion of developed land cover (Rather et al. 2021; Loveridge et al. 2022b), mean forest canopy cover, the Normalized Difference Water Index (NDWI), and mean annual temperature and precipitation. We also included several indices of productivity that might affect prey biomass, specifically the Enhanced and Normalized Difference Vegetation Indices (EVI and NDVI; Sims et al. 2006; Pettorelli et al. 2011; Searle et al. 2021), and gross and net primary productivities (GPP and NPP). We further included latitude and longitude (Woodroffe 2000; Jacobson et al. 2016) to account for broad geographic trends. With respect to land cover, we reclassified the original eight classes (see Online Resource 2 for variable descriptions) into two categories based on whether they included human disturbance (developed) or lack thereof (undeveloped). The protected area layer was rasterized and classified into two categories based on whether the center of the cell was within a PA (1) or otherwise (0). Mean annual temperature and precipitation, human density, and human footprint were directly downloaded from the web (Online Resource 3). Terrain ruggedness, forest canopy cover, NDWI, temperature, precipitation, EVI, NDVI, GPP, and NPP were obtained via Google Earth Engine (Gorelick et al. 2017; Online Resource 3). Temporal periods of data extraction corresponded to mean values across the range of years represented (1998–2019), whereas the most common occurring value was used for land cover class. The shapefile of protected areas was obtained from the World Database on Protected Areas (UNEP-WCMC and IUCN 2018). Raster layers were converted to the WGS 1984 World Mercator projection at a 1 km^2 resolution. At each record of leopard density continuous covariates were extracted as the average value, and PA and land cover classes as proportions, within five different buffer sizes: 1-, 5-, 10-, 15-, and 20-km radii (McGarigal et al. 2016; Loveridge et al. 2022b). Leopards move an average distance of 1-km in six hours (McManus et al. 2021), and a 5-km buffer loosely corresponds to the minimum radius of a leopard’s home range (Simcharoen et al. 2008; Stein et al. 2011). The 10- and 15-km buffers therefore fall within expected home range diameter depending on the sex of the animal

(Simcharoen et al. 2008). The 20-km buffer captures broad-scale habitat selection behavior (Rather et al. 2020). We then screened for correlations among variables at the 1-km scale, with strong correlations being defined as pairs where Pearson's r was equal to or greater than 0.70 (Dormann et al. 2013). We removed the less informative of each pair based on R^2 values from univariate models.

Our models included covariates to control for four aspects of study design known to influence density estimates. First, following Mandal et al. (2017), we included the area sampled (km^2) as the minimum convex polygon as reported in the study. Second, following Noor et al. (2020), we included survey length as the number of study days (i.e., the maximum length of time during which any part of the trapping array was sampled given that splitting study areas into sections and rotating cameras throughout is a common practice). Third, following Rather et al. (2021), we included the number of camera trap sites (i.e., the number of stations as opposed to the number of individual cameras). Lastly, following Vinks et al. (2022), we included the number of trap nights as the number of individual cameras multiplied by the number of nights those cameras were operating. For our randomly generated points, we assigned a constant value for these four variables based on the mean value from the published estimates. There were no strong correlations (Pearson's $r < 0.70$) among these four design effects.

In contrast to Pranzini et al. (2023), who fitted all covariates simultaneously within a Bayesian framework, we opted for maximum likelihood estimation and model selection using Akaike's Information Criterion (AIC) to identify the most influential variables (Akaike 1987). Prior to fitting models, we centered and scaled all continuous covariates. Also in contrast to Pranzini et al. (2023), we determined the optimal scale for each predictor variable prior to their inclusion in final models (McGarigal et al. 2016; Loveridge et al. 2022b). To do so, we regressed density against a given covariate expressed at each of the five scales while controlling for all other covariates (each included at the 10-km scale), compared the five resulting models using AIC, and identified the optimal scale from the model yielding the lowest AIC value. Next, we used AIC to test for non-linearity in all continuous covariates by comparing models including linear terms to models containing quadratic terms. For all variables, models with and without the quadratic term were within two AIC units, and we therefore used the simpler linear form for all continuous covariates. Including quadratic terms also introduced strong multicollinearity as evidenced in a variance inflation factor (VIF) greater than 10. We then compared plausible candidate models using AIC (Online Resource 4). Candidate models included a null model (containing the four design-based covariates only) and null + subsets of covariates specific to human impacts and environmental conditions. Covariates specific to human impacts were protected area, human density, human footprint, and land cover, whereas covariates specific to environmental impacts were temperature, NDWI, TRI, and NPP (Online Resource 4). The inverse of the standard error was included as a weight in all candidate models to mitigate potential bias caused by uncertainty in estimated leopard densities. For the randomly generated points, we assigned a constant weight corresponding to the mean standard error of published estimates. We then examined the VIF to test for multicollinearity in the top models ($\Delta AIC < 2.0$), further removing any variables where the VIF was greater than 5 (James et al. 2013). We used the adjusted R^2 value and residual plots to evaluate model fit.

From our best supported model, expected density was predicted within the "Extant" category of the IUCN Red List distribution map for leopards (Stein et al. 2020). Prior to this extrapolation, data values within raster layers were scaled and truncated to match the range of values used during model fitting. To map expected density predictions, we first used the focal statistics tool in ArcGIS Pro to create a raster layer summarizing each variable at the optimal scale as previously identified (ESRI 2025). Each map of 1-km^2 cells was then imported to R. We applied the selected model to the data frame to predict expected density and calculated 95% confidence intervals as the estimate ± (1.96 * standard error). This approach resulted in three new data frames (mean expected density, lower 95% confidence interval, and upper 95% confidence interval) per model. Following Jędrzejewski et al. (2018), we resampled the landscape to a 100 km^2 resolution by averaging values across 1-km^2 cells. The predictions and confidence intervals were truncated to the maximum and minimum values observed within our empirical data and converted to raster layers. We summed cell values to estimate country- and range-wide expected population sizes, and represented prediction uncertainty based on the standard errors. Finally, we symbolized discrepancies between predicted and published values based on the absolute value of residuals. All analyses were conducted within program R 4.5.0 (R Core Team 2025) and ArcGIS Pro 3.5 (ESRI 2025).

Results

Of the 464 estimates of leopard density that we extracted from published and grey literature, we retained 108. These datapoints were all spatial estimates and represented the most recent estimates for papers reporting multiple densities in the same study site. Seventy-seven (71%) of these came from Africa, with South Africa represented most ($N=63$, 82% of the African observations). There were roughly equal numbers of maximum likelihood ($N=59$) and Bayesian ($N=49$) estimates. We subsequently generated an equivalent number of random points with density value “0,” although given several NAs in the explanatory variables due to missing raster data, ultimately fit our models to 209 data points (Online Resource 5). These represented 105 published estimates and 104 random values.

After testing correlated pairs of variables using univariate models, we excluded mean forest canopy cover, NDVI, EVI, GPP, and precipitation from further consideration. The remaining variables were not strongly correlated. There was a single top model (Table 1), which included all remaining covariates. After testing for multicollinearity, we further excluded NDWI, NPP, and latitude, which brought the VIF for all variables in the model below 5. Hence, our final model explaining expected leopard density included TRI (1-km), land cover (5-km), protected area (5-km), human density (1-km), human footprint (20-km), temperature (20-km), and longitude in addition to the four control variables (Table 2).

Most estimated coefficients were significant at $a=0.05$ (Table 2). Expected leopard density decreased with temperature ($\beta = -0.87$, SE$=0.25$, $p<0.001$), longitude ($\beta = -0.92$, SE$=0.24$, $p<0.001$), and human density ($\beta = -0.39$, SE$=0.15$, $p<0.01$). Thus, a 10% increase in each of these variables would lead to a decrease in expected leopard density by 12.27% (temperature), 5.34% (longitude), and 0.64% (human density) (Online Resource 6). By contrast, expected density increased with protected area ($\beta=2.11$, SE$=0.12$, $p<0.001$) and proportion of developed land cover ($\beta=0.62$, SE$=0.30$, $p<0.05$). Hence, expected leopard density would increase by 7.93% (protected area) and 1.08% (land cover) for a 10% increase in these variables. For design effects, area sampled had a negative effect

Table 1 AIC support for candidate models predicting number of leopards/100 km^2. "Human impact" refers to human density, human footprint, protected area, and land cover class. "Environmental" refers to temperature, NDWI, NPP, and TRI

Model Variable(s)	Number	K	LL	ΔAIC	AIC Weight
All	1	16	−499	0.0	0.97
All (without Latitude/Longitude)	2	14	−505	6.9	0.03
Human Impact	3	12	−540	71.2	0
Human Impact (without Latitude/Longitude)	4	10	−544	75.4	0
Protected Area	5	7	−558	97.6	0
Environmental	6	12	−554	99.2	0
Environmental (without Latitude/Longitude)	7	10	−562	112.4	0
NPP	8	7	−566	112.5	0
Latitude + Longitude	9	8	−658	298.8	0
Human Footprint	10	7	−659	299.4	0
Human Density	11	7	−662	305.8	0
NDWI	12	7	−664	308.6	0
Land Cover	13	7	−669	318.6	0
Null	14	6	−671	320.5	0
TRI	15	7	−670	321.6	0
Temperature	16	7	−671	322.3	0

Shown for each model is the number of parameters estimated (K), model log-likelihood (LL), ΔAIC values, and AIC weight. Model definitions are given in Online Resource 4.

Table 2 Summary of covariate effects for the top model predicting number of leopards/100 km^2, including the estimated coefficient value (β; for centered and standardized variables), standard error (SE), and *p*-value for the *t*-test of non-zero coefficient value. A **bolded** asterisk (*) indicates statistical significance at $a = 0.05$

Variable	Scale (buffer radius)	β	SE	*p*-value
Intercept	NA	1.93	0.18	**<0.001***
Protected Area	5-km	2.11	0.12	**<0.001***
Longitude	NA	−0.92	0.24	**<0.001***
Temperature	20-km	−0.87	0.25	**<0.001***
Land Cover Developed	5-km	0.62	0.30	**<0.05***
Area Sampled	NA	−0.57	0.10	**<0.001***
Human Footprint	20-km	0.55	0.29	0.06
Human Density	1-km	−0.39	0.15	**<0.01***
Camera Sites	NA	0.30	0.13	**<0.05***
Terrain Ruggedness Index	1-km	−0.28	0.22	0.21
Trap Nights	NA	−0.09	0.14	0.54
Study Days	NA	−0.04	0.17	0.81

on expected leopard density ($\beta = -0.57$, SE = 0.10, $p < 0.001$), whereas number of camera sites had a positive effect ($\beta = 0.30$, SE = 0.13, $p < 0.05$). Expected leopard density therefore decreased by 1.46% (area sampled) and increased by 1.76% (camera sites) for a 10% increase in these variables. The adjusted R^2 value for this model was 0.76, although residuals displayed positive skew, indicating few positive values (Online Resource 7).

Predictions of expected leopard density ranged from 0 to 8 individuals/100 km^2 with the highest values in southern and eastern Africa, corresponding to regions with the most protected areas (Fig. 1A). We estimated the potential global leopard population to be 131,300 (95% CI 42,692–428,498) individuals. On a continent level we estimated Africa (107,369; 95% CI: 41,813–296,737) as having more potential for leopards than Asia (23,931; 95% CI:

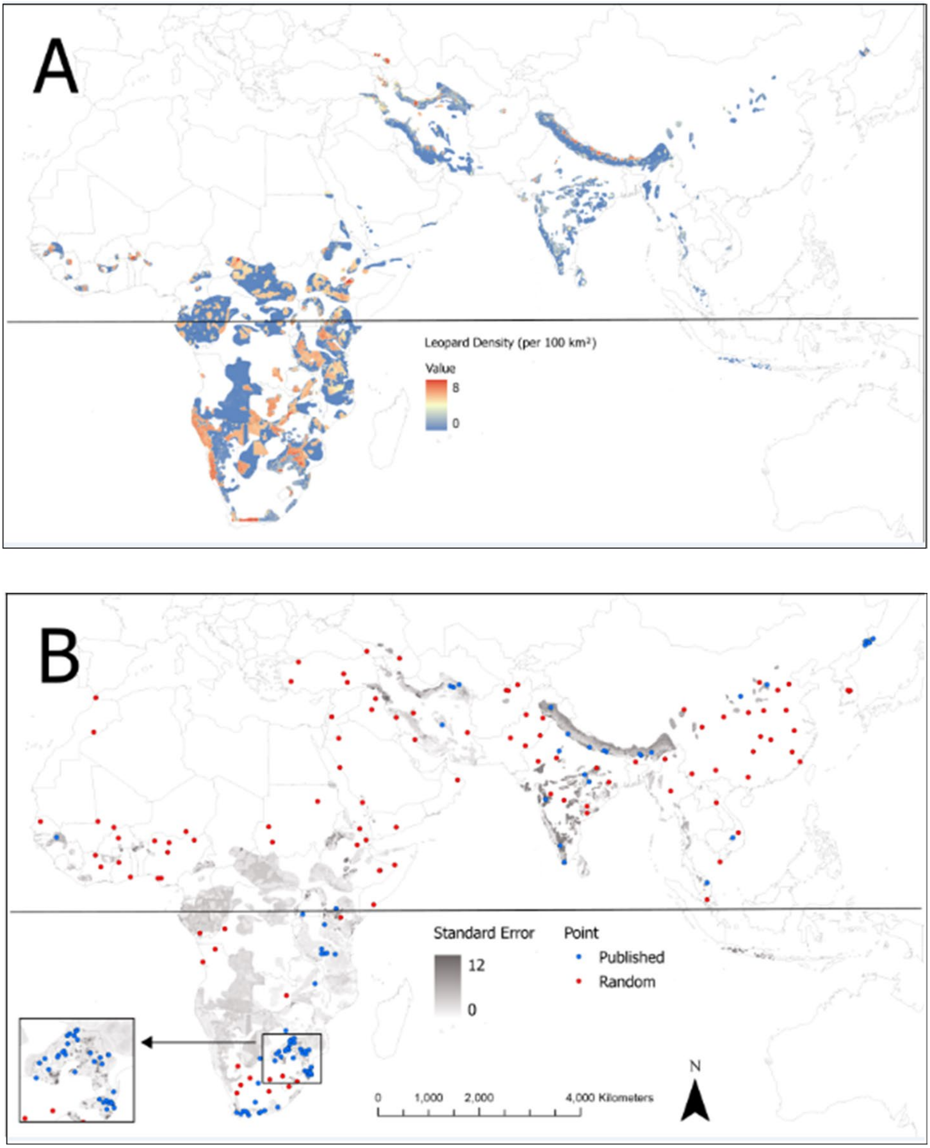

Fig. 1 Within extant leopard range as defined by the IUCN (Stein et al. 2020), shown is the expected leopard density (individuals/100 km^2) from the most supported model (**A**) with uncertainty expressed as the standard error in expected leopard density (**B**). Both panels also show the equator (horizontal line), and the data used to fit the models is shown on (**B**)

879–131,761). On a country level, Namibia had the highest potential for supporting leopards (14,543; 95% CI: 7,011–31,582) (Table 3). The standard error of predictions ranged from 0 to 12 leopards/100 km^2 and was greatest in India and its bordering countries to the northeast (Fig. 1B). When comparing published and expected values, overpredictions were more common than underpredictions (Fig. 2). The latter were not evenly distributed,

Table 3 Expected population size for leopards by country

Country	Predicted *N* (95% CI)	Country	Predicted *N* (95% CI)
Namibia	14,543 (7,011–31,582)	Malawi	343 (138–636)
Tanzania	14,087 (6,017–29,158)	Ghana	324 (95–896)
South Africa	10,192 (3,445–22,649)	Sri Lanka	307 (0–1,399)
India	8,437 (1–59,735)	Liberia	302 (83–1,206)
DRC	8,126 (3,425–25,127)	Thailand	283 (0–1,432)
Zambia	8,084 (3,990–13,378)	Pakistan	278 (0–2,151)
Iran	7,119 (602–29,723)	Afghanistan	266 (19–701)
Botswana	7,027 (2,920–18,735)	Myanmar	257 (0–2,202)
Ethiopia	6,971 (2,110–17,803)	Egypt	248 (44–473)
Zimbabwe	4,919 (2,162–9,050)	Guinea-Bissau	193 (59–451)
Mozambique	4,749 (1,625–16,442)	Armenia	191 (16–421)
Kenya	3,848 (936–12,893)	Equatorial Guinea	151 (50–529)
CAR	3,650 (1,091–15,064)	Turkey	147 (0–665)
Angola	3,444 (1,516–23,721)	Eswatini	120 (12–449)
South Sudan	2,957 (999–9,384)	Georgia	107 (11–245)
Chad	2,188 (707–4,269)	Cambodia	107 (0–461)
Congo	2,163 (740–11,612)	Malaysia	99 (0–995)
Gabon	2,020 (723–9,713)	Saudi Arabia	75 (4–308)
Nepal	1,672 (2–8,390)	Lesotho	65 (25–111)
Cameroon	1,404 (501–5,552)	Eritrea	63 (14–719)
Uganda	1,283 (309–3,383)	Oman	49 (1–273)
China	1,229 (0–10,074)	Sierra Leone	28 (7–53)
Iraq	919 (11–2,881)	Rwanda	24 (4–81)
Russia	808 (100–2,057)	Mali	20 (0–278)
Bhutan	806 (1–2,981)	Niger	16 (5–28)
Guinea	721 (231–1,832)	Indonesia	15 (0–2,107)
Côte d’Ivoire	703 (231–1,794)	Togo	8 (0–42)
Benin	635 (109–1,507)	Bangladesh	7 (0–232)
Burkina Faso	543 (166–1,213	Laos	6 (0–25)
Senegal	425 (121–1,573)	Vietnam	4 (0–24)
Nigeria	404 (148–782)	Somalia	2 (0–935)
Azerbaijan	393 (47–847)	Yemen	0 (0–266)
Sudan	371 (47–1,563)	Burundi	0 (0–7)
Turkmenistan	350 (63–1,169)	Djibouti	0 (0–62)

as underpredictions were most common in the northeastern region of South Africa and throughout India, as well as a few locations in East Africa and the Russian Far East.

Discussion

Any broad-scale extrapolation like ours to predict range-wide leopard density should be interpreted as expected abundance based on a high-level view of environmental conditions (i.e., remotely sensed ecological and anthropogenic data) and should not be interpreted as indications of present population status. Such work may be particularly useful for focusing conservation attention in areas where leopards are expected to be abundant but are not, or

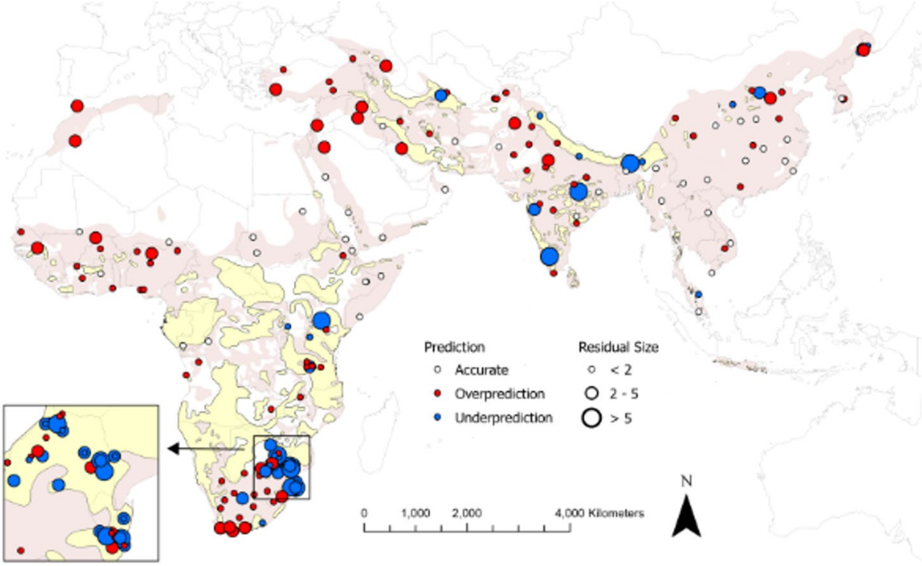

Fig. 2 Distribution of over- and underpredictions of expected leopard density (individuals/100 km^2) within historic (faded red) and extant (pale yellow) leopard range as defined by the IUCN (Stein et al. 2020). Points are symbolized by color (accurate, overprediction, underprediction) and size (absolute value of residual). For randomly generated points (density value of "0"), predicted values were frequently negative and we capped these at 0, hence classifying them as "accurate"

where data to improve the precision of predictions are needed. In short, our results demonstrate that at a coarse scale expected leopard density is driven primarily by human impact (protected areas>>proportion of developed land cover>human density), although metrics reflecting environmental conditions (e.g., temperature) can also affect expected densities. While our global estimate of 131,300 (42,692–428,498) potential leopards overlaps with Pranzini et al.'s (2023) estimate of 261,636 (146,768–461,512), our point estimate is lower by half and our confidence intervals are 22.5% wider. Hence, our efforts to eliminate methods known to bias density estimates (i.e., non-spatial estimates), identify the appropriate scale of each variable (which ranged from 1-km^2 for human density, 5-km^2 for protected areas and developed land cover, to 20-km^2 for temperature), add additional controls for potential design effects, and embrace uncertainty in the original density estimates may have resulted in a more conservative outcome.

Our model indicated eastern and southern Africa as having a high potential for leopard abundance, areas where published survey data on leopard populations are generally abundant and known density estimates are among the highest documented globally (O'Brien and Kinnaird 2011; Rogan et al. 2019). This expectation is due to the prevalence of protected areas, many of which are fenced, which was the most significant factor influencing expected leopard density in our model. Protected areas are important in explaining variation in large mammal abundances, including those with less strict measures of protection according to IUCN classification (Balme et al. 2010; Leroux et al. 2010; Clements et al. 2019; Pacifici et al. 2020; Rogan et al. 2022). Temperature was the only variable in our model reflecting environmental conditions regardless of human impact. Its negative coefficient was unexpected because carnivore densities generally increase with measures of productivity such as temperature, GPP, or precipitation due to a higher abundance of prey (Woodroffe 2000; Carbone and Gittleman 2002; Ugbaje et al. 2017; Jędrzejewski et al. 2018; Pranzini et al. 2023). However, warmer areas, especially near the Equator, coincide with depleted mammal populations due to civil unrest, poverty, lower institutional capacity, bushmeat poaching, and war. These human factors can deplete forests of biodiversity and their prey base and result in “empty forests and savannas” (Redford 1992; Dudley et al. 2002; Lindsey et al. 2013; Petracca et al. 2020). Indeed, we detected a negative effect of human density on expected leopard population size, which could be associated with habitat loss or persecution of large carnivores (Constant et al. 2015; Mukeka et al. 2019). Current efforts to control human-leopard conflict (Balme et al. 2009) will be important in determining contemporary leopard status and could potentially cause major discrepancies between expected density and how many leopards actually occur in a region. Rogan et al. (2022) also found a negative association between human footprint and leopard density, whereas Loveridge et al. (2022b) documented a similar relationship with regard to snaring hotspots and risk of trophy hunting. We found a positive relationship between the proportion of land cover developed and expected leopard density, which was unanticipated but could simply reflect that leopards are highly adaptable to human-dominated landscapes (Athreya et al. 2013; Chase Grey et al. 2013; Gubbi et al. 2020; Wang et al. 2024). It might also reflect habitat selection in areas with higher livestock densities (Athreya et al. 2016), or the development of communities at protected area edges for tourism revenue and resource extraction. We categorized land types that included cropland as “developed,” although leopards often persist in comparatively high densities in forest-cropland mosaics (Gubbi et al. 2020; Webb et al. 2020). There was also a negative relationship between longitude and expected density, reflecting that the expected size of leopard populations is lower in the eastern part of their range. This association could reflect higher human densities (e.g., India), more fragmented habitat, and the endangered status of several subspecies (Jacobson et al. 2016; Stein et al. 2020).

On a country level, we predicted Namibia, Tanzania, and South Africa to have the highest potential to support large leopard populations, followed by India on the Asian continent. The high expected density in Namibia (7,011–31,582) is due to the large network of protected areas along the western coast, and hence conservation action in this region could be fruitful (Marker and Dickman 2005; Noack et al. 2019; Portas et al. 2022). Tanzania had the second highest estimate (6,017–29,158), in line with prior work indicating ≥ 5–6 leopards/100 km^2 in the best protected areas in this country (Allen et al. 2020; Searle et al. 2021). Estimates in South Africa consistently rank among the highest globally (Chase Grey et al. 2013; Rogan et al. 2019), so our prediction of 3,445–22,649 individuals there was unsurprising. However, we consistently underpredicted density in the northeastern corner of South Africa by more than 5 individuals while overpredicting by 2–5 in the Western Cape, mirroring the fact that these two regions contain among the highest (Chase Grey et al. 2013; Rogan et al. 2019) and lowest (Devens et al. 2018; Müller et al. 2022) leopard densities in the country, respectively. Within India, our high expected density estimate was consistent with previous work (Harihar et al. 2011; Kalle et al. 2011), however, we also observed the highest prediction uncertainty in India and its bordering countries to the northeast despite the prevalence of protected areas in this region. This result was likely caused by sparser data availability, especially when compared to South Africa which likewise has many protected areas but more data. India also contained the highest leopard densities documented in Asia (Kalle et al. 2011; Mandal et al. 2017), resulting in underpredictions from our model of over 5 individuals and contributing to large standard errors. Nevertheless, our predictions reflected Jacobson et al. (2016) who reported that three leopard subspecies comprise 97% of extant leopard range, including the African (*P. p. pardus*) and Indian (*P. p. fusca*) subspecies. By contrast, within the Middle East and the Russian Far East, low density estimates were likely caused by small, isolated populations and lack of transboundary conservation initiatives (Vitkalova et al. 2018; Zafar-ul Islam et al. 2018; Farhadinia et al. 2021; Pranzini et al. 2023).

We predicted high expected densities in several countries that lack published estimates, notably in Central Africa (Democratic Republic of Congo, Central African Republic, Angola) and West Africa (Benin, Guinea, Senegal, Côte d'Ivoire). Several countries in the southern part of Africa, such as Namibia, Botswana, and Zambia, also lack published data yet were predicted to have high expected densities. Indeed, these southern African countries, in addition to the Central African Republic, rank in the top 10 countries that provide the most contributions to megafauna conservation as measured in ecological, protected area, and financial metrics (Lindsey et al. 2017a). The smaller countries in West Africa likewise consistently rank above average on the Megafauna Conservation Index (Lindsey et al. 2017a). Thus, ongoing governance and international investment in protected areas throughout these regions hold significant potential to increase the leopard population to sustainable numbers. In the Middle East, by contrast, Iran has high expected densities and few published estimates, yet ranks below average in contributions to megafauna conservation (Lindsey et al. 2017a). Increasing leopard populations in this region to expected numbers will therefore be more challenging.

Leopards are one of the most broad-ranging and ecologically adaptable carnivore species. They tolerate extreme variation across their range in terms of habitat and environmental conditions, rendering efforts to predict their expected density range-wide challenging. Our model explained 76% of variance based on the adjusted R^2, a figure we consider to be informative given the broad ecological conditions they inhabit (from snowy northern regions to deserts). In contrast, Jędrzejewski et al. (2018) reported 45% of variation explained when predicting jaguar density across that species' considerably more narrow ecological range. Pranzini et al. (2023) reported that their model explained 56% of variation for leopards. However, that does leave a large amount of unexplained variation to consider when interpreting the utility of predictions for conservation purposes. We believe that by embracing uncertainty in our data and predictions, we have contributed to a stronger foundation upon which to direct conservation action for leopards. A more accurate picture of actual global abundance will depend on finer-scale drivers of leopard abundance unavailable to this current modeling effort. Important local predictors likely include human activities (i.e., bushmeat poaching, trophy hunting, armed conflict; Dudley et al. 2002; Packer et al. 2011; Rosenblatt et al. 2016; Lindsey et al. 2017b), non-consumptive effects of human presence (Creel 2018), leopard-livestock conflict (Inskip and Zimmermann 2009), interference competition with large predators (i.e., tigers and lions; Steinmetz et al. 2013; du Preez et al. 2015; Loveridge et al. 2022b), habitat fragmentation (Crooks 2002; Swanepoel et al. 2013), spatial distribution of prey in response to seasonal shifts (Mduma et al. 1999; Allen et al. 2020), and management to restrict human activities or improve habitat quality (Rosenblatt et al. 2016; Havmøller et al. 2019; Searle et al. 2021). Although it was not possible to include all these covariates in a range-wide comparison like this, our analysis uncovered human and environmental features that are broadly relevant to leopards and identified regions of prediction uncertainty where additional on-the-ground surveys are warranted. We note that lack of data availability for the covariates we included, specifically area sampled and number of camera trap sites, led to the exclusion of ~20% of the data available for model fitting and future culminations of published accounts would benefit from the inclusion of such information. We emphasize the need to control for potential data biases and embrace uncertainty in any efforts for broad-scale predictions such as undertaken herein.

A few limitations of our study bear further consideration. First, over half our data points originated from South Africa, so we lacked balanced representation of leopard populations and ecological conditions across their extant range. Much of the published data also occurred within protected areas (Balme et al. 2014). Leopards, however, are highly adaptable predators that can maintain sustainable populations both within game reserves and in lands interspersed with farming areas and high levels of harvest, particularly in South Africa and India (Athreya et al. 2013; Chase Grey et al. 2013; Swanepoel et al. 2015). As a result, our estimates outside of protected areas may be biased low. Second, we pooled all leopard subspecies into a single analysis, although given their generalist nature, leopards might be differentially influenced by various habitat types depending on the continent on which they are found. For instance, in Thailand, leopards prefer mixed deciduous and dry evergreen forests (Simcharoen et al. 2008), whereas in South Africa, leopards principally hunt in open bush savanna (Balme et al. 2007). Stark differences may further exist within a country or among similar habitat types. For example, in Tanzania, published leopard densities differed by >2 individuals/100 km^2 within the same mixed-use landscape based on differences in woodland habitat and levels of protection (Searle et al. 2021). Given the uneven distribution of data geographically, we lacked sufficient data across subspecies for finer regional analysis, indicating a data gap for future research to fill. Moreover, the IUCN Red List distribution map is likely to exhibit inaccuracies, which would manifest in the analysis. Lastly, the 10+year timespan of our data is worth noting (2007–2019), during which time human density and human-dominated habitat have certainly changed and so some prediction error may be associated with mismatches between experienced conditions (by the leopards) and predictions (based on remotely-sensed data). Again, we emphasize that our predictions represent expected abundances based on observed conditions rather than contemporary population status.

Conclusion

Leopards select for landscapes at broad scales based on environmental conditions that reflect ideal habitat and abundant prey (Rather et al. 2020) while avoiding human activity (Odden et al. 2014), patterns consistent with our analysis and other similar broad-scale modeling efforts (Pranzini et al. 2023). Gaining insights into the specific covariates predicting expected leopard density requires consideration of potential sources of bias in data sources, as well as including uncertainty in the original density estimates and model predictions. By embracing uncertainty, our study provides a strategic, landscape-scale perspective for leopard conservation while recognizing that finer-scale insights will be needed for effective on-the-ground management. Ultimately, our study provides baseline values of expected abundance to guide management and target recovery goals. Regions where we predicted relatively high leopard density, notably in Central and West Africa that lack contemporary estimates, highlight where research and conservation attention may be particularly fruitful. Moreover, large mismatches in expected and observed densities highlight the need for better control of poaching and illegal trade, with transboundary cooperation, habitat connectivity, and an increase in wild prey likely necessary to secure leopard populations.

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